PRACTICAL TOOLS

Methods in Ecology and Evolution | BRITISH ECOLOGICAL SOCIETY

Migration Mapper: Identifying movement corridors and seasonal ranges for large mammal conservation

Jerod A. Merkle[1] | **Josh Gage**[2] | **Hall Sawyer**[3] | **Blake Lowrey**[4] |
Matthew J. Kauffman[5]

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

[2]Gage Cartographics, Bozeman, MT, USA

[3]Western Ecosystems Technology, Inc., Laramie, WY, USA

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

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

Correspondence
Jerod A. Merkle
Email: jmerkle@uwyo.edu

Funding information
Knobloch Family Foundation; U.S. Geological Survey; Western Association of Fish and Wildlife Agencies

Handling Editor: Dr. Paul Galpern

Abstract

1. Modern tracking technology has facilitated a novel understanding of terrestrial mammal movement while revealing that movements are being truncated and lost. The first step towards conserving mobile animals is identifying movement corridors and key seasonal ranges. Yet, the identification and subsequent mapping of these important areas has remained a challenge due to the analytical skills necessary to conduct such analyses.

2. Migration Mapper (MM) is a user-friendly software that provides tools to analyse global positioning system (GPS) collar data to create season-specific, population-level polygons representing areas where most of a population moves (i.e. movement corridors) and areas where most of a population spends time (e.g. high-use areas, seasonal ranges).

3. MM consists of six standalone modules including data cleaning and review, seasonal movement delineation, movement model application, calculation of population-level outputs and visualization of results.

4. Analysis of GPS data using MM can provide the spatial polygons necessary to facilitate conservation and policy planning. New initiatives at the local and global levels are already beginning to use MM to facilitate conservation of large, terrestrial mammals.

KEYWORDS
animal movement, home range, migration corridors, movement ecology, occurrence distribution, seasonal ranges, stopovers, ungulate conservation, utilization distribution

1 | INTRODUCTION

Advances in tracking technology have revolutionized the study of terrestrial animal movement, providing a new and detailed lens of where animals move every hour of their lives (Kays et al., 2015). For terrestrial large mammals in particular, global positioning system (GPS) technology has helped reveal previously unknown large-scale movements (Naidoo et al., 2016), the mechanisms driving those movements (Teitelbaum et al., 2015) and the nutritional benefits afforded to animals that move long distances (Middleton et al., 2018). Furthermore, GPS collars have helped identify the diversity of migratory behaviours within and among populations (Lowrey et al., 2020) and how migration is learned and retained (Jesmer et al., 2018; Merkle et al., 2019). Ultimately, the last decade of research based

on GPS collar data has significantly advanced our understanding of when, where, how and why animals move and consequences of movement to ecosystems (Altizer et al., 2011; Bauer & Hoye, 2014).

GPS tracking technology has also revealed that animal movements like migration are being restricted or slowed (Tucker et al., 2018) and even lost (Wilcove & Wikelski, 2008), sparking new efforts to conserve habitat that facilitates animal movement (Hardesty-Moore et al., 2018; Nandintsetseg et al., 2019). For instance, identifying and conserving migration corridors has become an important management priority for state and federal agencies in the United states (US; Middleton et al., 2020), as well as international conservation efforts such as the Kavango-Zambezi Transfrontier Conservation Area (Kauffman et al., 2021). The first step towards any place-based conservation action for mobile animals is identifying and mapping movement corridors and key seasonal ranges.

Although the GPS data, analytical methods and computing power are readily available (Nathan et al., 2022), the identification and subsequent mapping of important animal habitat has remained a challenge (Kauffman et al., 2021). Behind every polished map of movement corridors or seasonal ranges are numerous analytical steps. Data analysts must organize and manage data and files, define the biological unit of interest (i.e. the population), choose between and conduct complex statistical analyses, synthesize analytical outputs from individuals to the population, and finally visualize results (Nathan et al., 2022). Furthermore, there is no comprehensive software to mend together these analytical steps, and the available options (Joo et al., 2020) all require proficient coding skills and must be stitched together to develop useful products from raw GPS data. Because of the many difficult steps involved in creating maps, many GPS collar datasets go underutilized, limiting their utility to inform conservation policy.

Here we present Migration Mapper (MM), a browser-based mapping software that provides a user-friendly platform and workflow to generate grids and polygons that delineate important areas for animals from GPS locations (Merkle et al., 2022). Our aim in creating MM was to provide field biologists and managers (as well as seasoned data scientists) a pre-packaged but rigorous analytical workflow that removes the need to write code. Furthermore, the ability for users to more easily implement multiple methods within MM provides a robust platform to compare and contrast different space use methods as well as different outputs across taxa and ecosystems (sensu Laver & Kelly, 2008; Lewis et al., 2018). MM consists of a frontend user interface that opens in the user's web browser, where users navigate a straightforward 'point and click' workflow that includes helpful mapping and visualization features. The backend code of MM is scripted in the open-source R program for statistical computing (R Core Team, 2021) and relies on Shiny as the user interface (Chang et al., 2021). All the features in MM are built upon efficient memory management and parallel processing workflows.

The core analytical framework of MM is based upon the methods outlined in Sawyer et al. (2009). Parts of MM were initially released in 2017, and our team provided multiple workshops on how to use MM for biologists, managers and researchers in the western US over subsequent years. Today, MM is being used by numerous biologists, managers and researchers, and has proven to be an important tool to delineate movement corridors and seasonal ranges of ungulates in the western US using a consistent and repeatable framework (Kauffman et al., 2020, 2022).

2 | OVERVIEW OF THE WORKFLOW

MM provides the tools to work from nearly raw GPS collar data to create season-specific, population-level (i.e. merged across individuals) grids and polygons representing areas where most of the population moves (i.e. movement corridors) and areas where most of the population spends significant time (e.g. seasonal ranges, stopover sites). MM is modular and consists of six standalone applications representing distinct steps of the workflow. Modularity clarifies the step-by step process and allows users to easily navigate between steps, fix errors in a previous step or skip steps in the workflow. The modules include (1) data import and review, (2–3) seasonal sequence delineation, (4) movement model application, (5) estimation of population use and corridors and (6) product visualization.

Prior to using MM, users must isolate individuals that form a relatively distinct population (e.g. shared seasonal range). Delineating a distinct population could involve expert opinion, a plotting exercise in a GIS, a spatial clustering analysis (Legendre & Fortin, 1989) or adherence to a policy-based management unit. This step is important because the outputs of MM are strongly dependent on the sample size of a single population and may not be interpretable if two distinct groups of individuals are combined in an analysis (See more details in Appendix S1). Once a distinct population has been identified, users must generate a GPS dataset in ESRI Shapefile format (in any georeferenced coordinate system) that includes a column denoting unique animal ID and the date and time of each GPS location.

To effectively operate MM, users should have an adequate Internet connection (>1 mb/s) to download dependencies and load base maps used in the mapping components. MM requires a host of associated R packages and other dependencies (Appendix S1), which are automatically downloaded and installed when first running MM. All parameters and options in MM can be adjusted by the user.

3 | MODULES OF ANALYSIS

3.1 | Module 1: Data import and review

Once the user has imported their data, Module 1 checks for erroneous locations (e.g. where there is an unreasonable speed simultaneously approaching and leaving a location) and mortalities (i.e. by identifying strings of locations where the animal did not move a set distance for a set amount of time). MM then presents the user with a mapping tool and some basic plots of the data. For each individual animal (hereafter ID) and each year of data for each ID (hereafter ID-YR), the user can visualize the points (and

lines connecting the points) on an interactive map alongside plots of elevation, displacement from 1 January and speed over time. The user can interactively review the data and manually identify erroneous locations, mortalities or add comments to each location (Figure 1, top panel).

3.2 | Module 2: Seasonal sequence delineation

In Module 2, the user specifies the biological year start date and how many seasons they would like to potentially isolate for each ID-YR. MM then presents the user with an interactive interface for visualizing each ID-YR of data in space and time with a number of metrics (Figure 1, bottom panel) inspired by previous studies on how to isolate seasonal movements (Bunnefeld et al., 2011; Cagnacci et al., 2016; Fauchald & Tveraa, 2003; Sawyer et al., 2005; Spitz et al., 2017). Those metrics include Net or Net Squared Displacement (NSD) from the centroid of data from the first week of the biological year, NSD based on 6 months before and after the current biological year, elevation, speed, and multiple scales of first passage time. The user then manually moves sliders to identify migration periods or other seasons or events of interest (e.g. winter range, parturition period, core summer range, dispersal) for each ID-YR (Figure 1, bottom panel).

3.3 | Module 3: Generating seasonal sequences

Module 3 provides multiple options for generating the seasonal sequences (i.e. distinct strings of GPS locations) for each ID-YR. In addition to generating the sequences for the exact seasons identified in Module 2, users can use the season dates to define additional periods. For instance, if the user used Module 2 to only identify the migratory periods, they could then define the summer period using the end of spring migration and the start of fall migration. It is also possible to define seasonal periods using specified dates, for example defining winter as 1 December through 28 February for every ID-YR. We provide ample flexibility for the user to delineate any biological season of interest, even relatively specific seasonal ranges such as parturition.

3.4 | Module 4: Movement model application

For every season identified in module 3, the user can apply a movement model to create an occurrence distribution (OD) and a footprint of use (a contour around the OD; Figure 2). Outputs in module 4 are all created and saved in grid format. The user has the ability to implement any or all the following utilization distribution or OD techniques: bivariate kernel (Seaman et al., 1999), regular Brownian Bridge Movement Model (Horne et al., 2007), dynamic Brownian Bridge Movement Model (Kranstauber et al., 2012), Continuous Time Movement Model (Calabrese et al., 2016) and a line buffer method.

The line buffer method adds a user-specified spatial buffer to the strait lines between subsequent locations (Figure 2; Appendix S1).

3.5 | Module 5: Estimating population use and corridors

A number of steps are necessary to scale from individual sequences to population-level movement corridors and seasonal ranges (Sawyer et al., 2009). First, the multiple ODs of each individual animal (i.e. across years or seasons) are merged for each individual separately. This consolidation could involve taking a mean across all ODs, calculating a mean by year and then by season, or by calculating a mean by season and then by year. Once an OD is calculated for each individual, an individual-level footprint is delineated based on a user-specified contour (e.g. 99% contour around the volume of the OD). To calculate a movement corridor of the population, individual footprints are then stacked to create a grid representing the proportion of individuals in a population moving through an area. This grid can then be used to delineate the most important areas where a significant number of animals move (e.g. a contour delineating where more than 20% of a population moves). To calculate high-use areas (e.g. stopover sites, high-use winter ranges), a mean of all the individual ODs is calculated to create a population-level occurrence map (Sawyer et al., 2009). Final high-use areas are delineated by user-specified contours of the volume or area of the population OD (Figure 2).

3.6 | Module 6: Product visualization

After completing any or all of modules 2 through 5, the user can visualize results in module 6. Users can toggle through seasonal sequences (in both line and point format), population corridors and population high-use areas in a single, interactive map. There are options to change colours and obtain information (by clicking) on each of the different layers. The user can export images of the resulting maps to facilitate sharing and collaboration.

4 | DISCUSSION

By providing a user-friendly yet advanced workflow to identify and map movement corridors and important habitats, MM is already helping applied biologists keep pace with the growing volumes of movement data being collected. Contemporary conservation requires a balance between the habitat needs of wide-ranging animals with increased development demands (e.g. housing, agriculture, energy). The maps of movement corridors and important areas produced by MM (see maps in Kauffman et al., 2020) provide science products that managers can use to triage or prioritize key habitats so that impacts on animal populations are avoided or minimized. For example, managers might limit the amount of disturbance allowed
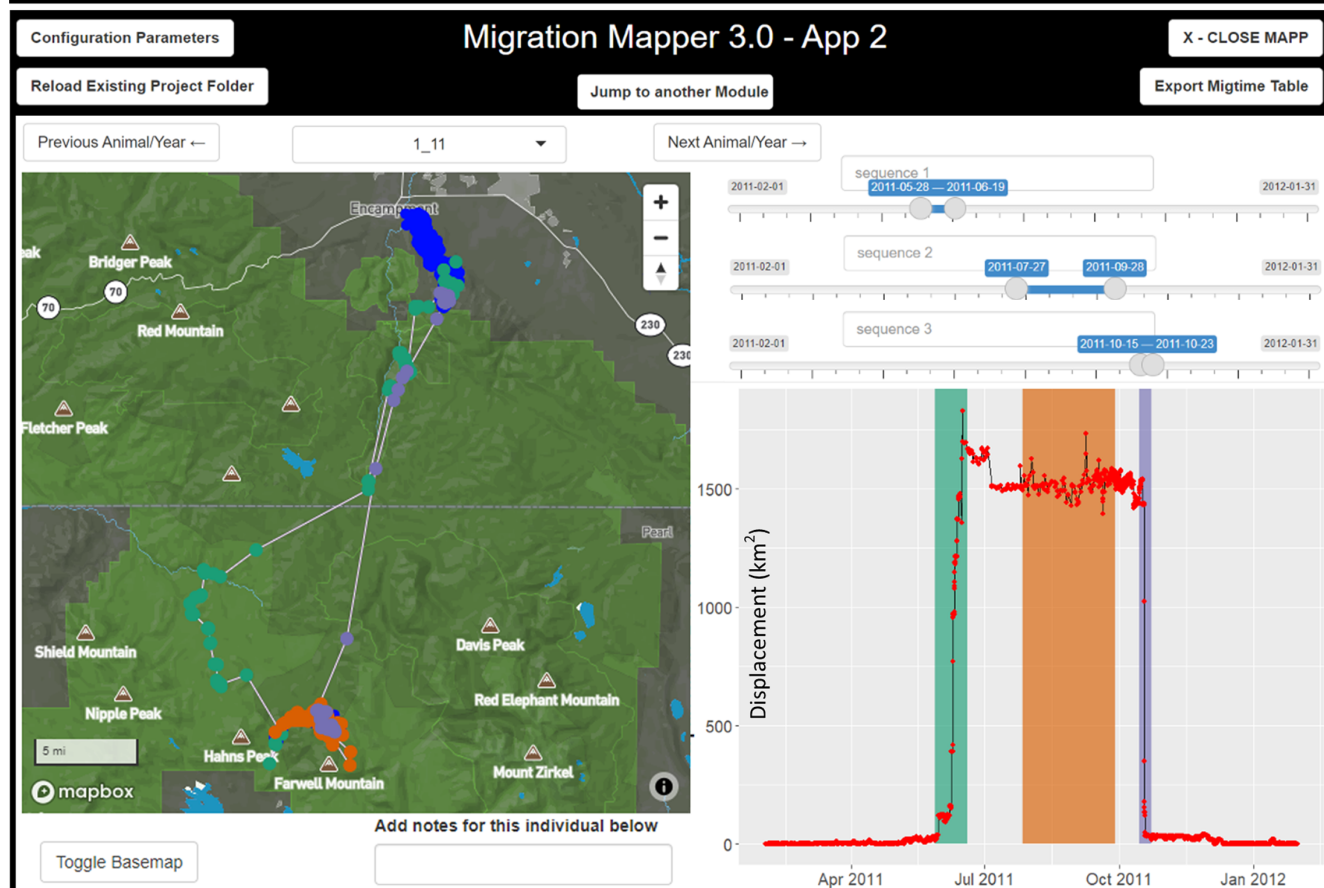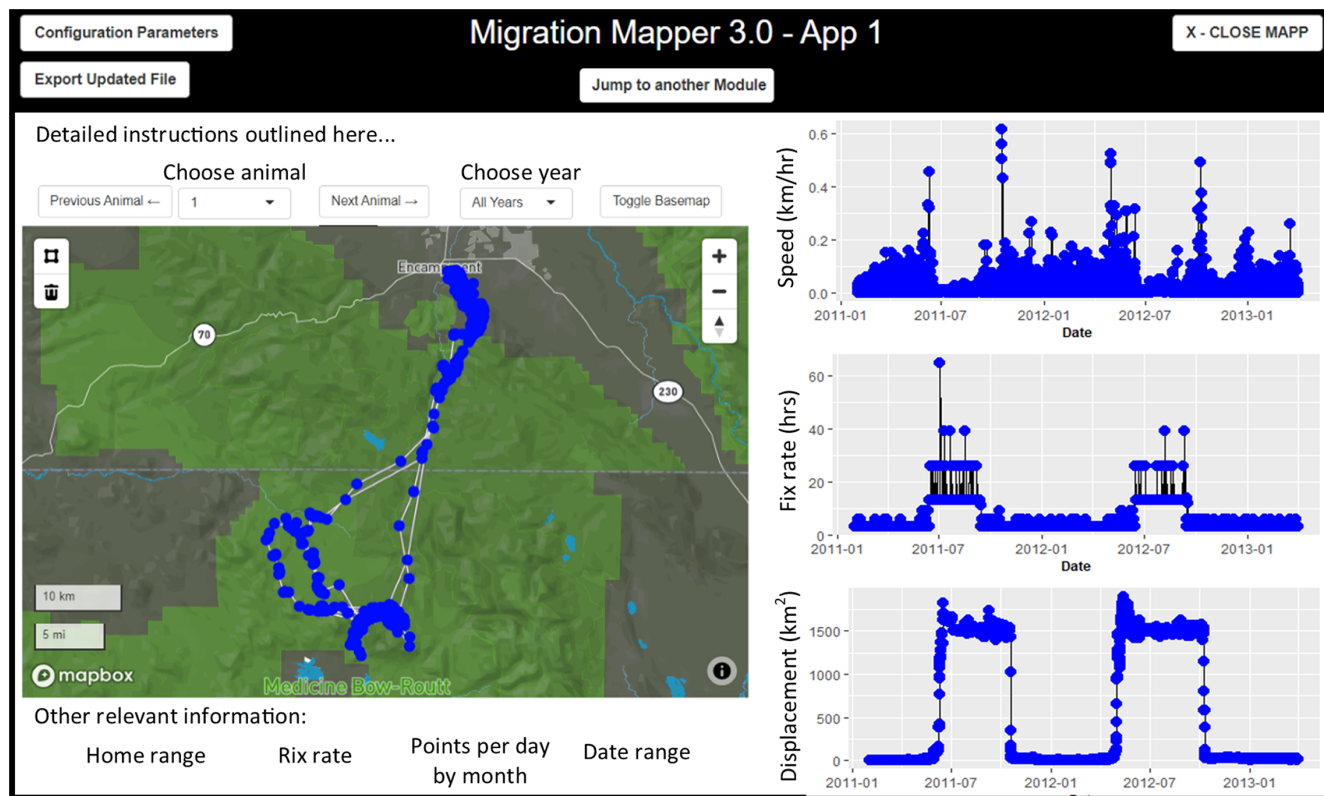
Migration Mapper 3.0 - App 1

Configuration Parameters

Export Updated File

Jump to another Module

X - CLOSE MAPP

Detailed instructions outlined here...

Choose animal

Previous Animal ← | 1 ▾ | Next Animal →

Choose year

All Years ▾ | Toggle Basemap

10 km

5 mi

mapbox

Medicine Bow-Routt

Other relevant information:

Home range   Rix rate   Points per day by month   Date range

Migration Mapper 3.0 - App 2

Configuration Parameters

Reload Existing Project Folder

Jump to another Module

X - CLOSE MAPP

Export Migtime Table

Previous Animal/Year ← | 1_11 ▾ | Next Animal/Year →

Bridger Peak

Red Mountain

Fletcher Peak

Shield Mountain

Nipple Peak

Hahns Peak

Farwell Mountain

Davis Peak

Red Elephant Mountain

Mount Zirkel

5 mi

mapbox

Add notes for this individual below

Toggle Basemap

sequence 1
2011-02-01   2011-05-28 — 2011-06-19   2012-01-31

sequence 2
2011-02-01   2011-07-27   2011-09-28   2012-01-31

sequence 3
2011-02-01   2011-10-15 — 2011-10-23   2012-01-31

FIGURE 1 Migration Mapper's user interface for reviewing and troubleshooting (module 1; top panel) and isolating seasonal sequences (module 2; bottom panel). Global positioning system (GPS) collar data from a migratory mule deer monitored for 2 years are shown as an illustration. Module 1 can be used to initially review data and identify and remove problem points or mortalities by assessing movement metrics on the right hand figures or by clicking directly on individual or groups of points. Module 2 can be used to isolate specific seasons of movement (using maps on left paired with sliders on right), including broad seasonal ranges (e.g. summer range), migration or other movement between seasonal ranges (including nomadic movements), and areas used for parturition. The user identifies how many seasons (or sliders) they want to specify, and once those sliders are moved, the point data in each season are given corresponding, unique colours. The tabs in the bottom right (not shown in figure) provide the user with plots of numerous movement derived metrics (e.g. displacement, elevation, first passage time) over time.

FIGURE 2 Outline of the steps to calculate population movement corridors and high-use areas (modules 4–5 of migration mapper) from movement sequences isolated using modules 2–3 in migration mapper. Sequences from 25 migratory mule deer monitored with global positioning system (GPS) collars for 2 years are used as an illustration. The movement sequence panel illustrates the steps to calculate occurrence distributions (ODs) and footprints from each isolated sequence of point data from modules 2 and 3. The individual panel illustrates how to merge the multiple occurrences (i.e. across multiple seasons and/or years) for each individual. The bottom two panels illustrate how the footprints or ODs of each individual are merged to create main corridors or high-use areas of the population. Orange arrows represent stages in the workflow where a decision is made or a movement analysis is employed. The workflow related to population high-use areas is relatively flexible and can be used to delineate stopovers during migration or broad seasonal ranges such as high-use winter ranges. Photo credit B. Krashaar.
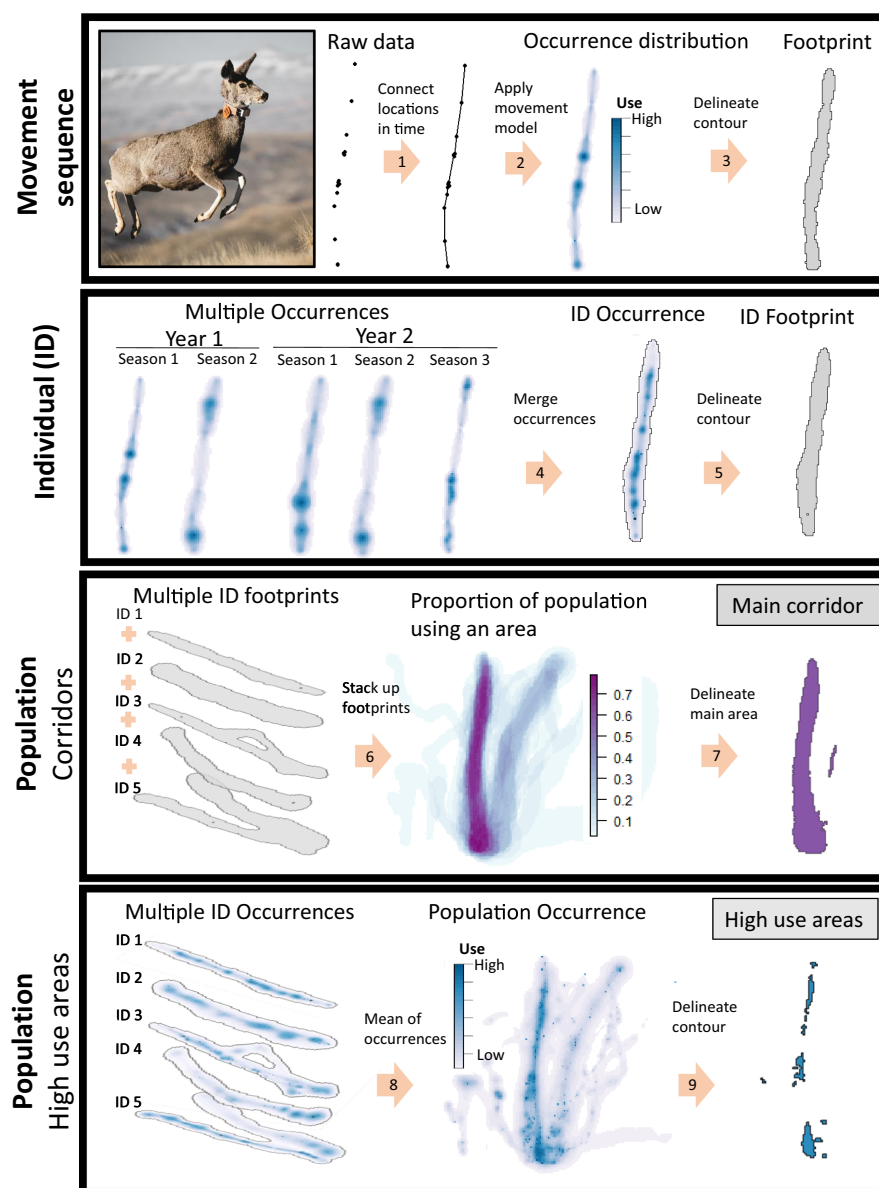
in high-use corridors or areas, target them for habitat improvement projects, or prioritize specific private parcels for land protection programmes (Tack et al., 2019).

In the United States, maps of movement corridors and high-use habitats can have immediate conservation impact with new initiatives at both state and federal levels. For example, the US Department of Interior issued Secretarial Order 3362 in 2018 to encourage federal agencies to support western states in their efforts to enhance migration and winter habitat for ungulates on federal lands (Department of the Interior, 2018). Since then, this federal directive has provided millions of dollars to western states for migration research and on-the-ground mitigation efforts. Additionally, this broader emphasis on migratory ungulates and conserving migration corridors has prompted various policy actions across a number of states. For example, the US

federal government deferred 5674 ha of oil and gas leases after the State of Wyoming designated a mule deer migration corridor to be managed for no net loss of function (Kauffman et al., 2021).

Similar mapping efforts are also informing international conservation efforts. For example, the recently formed Global Initiative on Ungulate Migration, working in partnership with the Convention on Migratory Species, aims to build a digital atlas of ungulate migrations worldwide largely using the approach made available in MM (Kauffman et al., 2021). Such mapping could guide efforts to reduce fencing in the movement corridors of many impacted populations, such as the Loita wildebeest herd in the Mara Ecosystem (Stabach et al., 2022). Detailed migration maps would also advance planning in the Kavango-Zambezi Transfrontier Conservation Area, where connectivity between protected areas is mandated by an international treaty signed by five southern African countries (Kauffman et al., 2021). Finally, development projects such as China's Belt and Road Initiative are occurring where world's migrations still exist (Laurance et al., 2014), and detailed maps can facilitate maintenance of movement corridors amid planned development.

The human footprint continues to grow at an alarming rate, adding additional impediments and challenges to mobile animals globally (Tucker et al., 2018). Within the next 25 years, for instance, humans are expected to build 25 million km of new roads worldwide (Laurance et al., 2014). Successful conservation of wide-ranging species is, in part, dependent on transforming large datasets of animal location data into meaningful polygons and maps that are used to guide planning decisions. MM provides a rigorous yet user-friendly platform to accomplish these tasks. With the data revolution upon us and the increasing size of GPS datasets, MM will help to empower a wider set of biologists to use GPS data to inform local and regional management and conservation.

AUTHOR CONTRIBUTIONS

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

Authors declare no conflict of interest.

PEER REVIEW

DATA AVAILABILITY STATEMENT

Code for Migration Mapper is archived in Zenodo (Merkle et al., 2022), and kept up to date on GitHub (https://github.com/jmerkle1/Migration-Mapper). No data were used in this research.

ORCID

Jerod A. Merkle https://orcid.org/0000-0003-0100-1833
Hall Sawyer https://orcid.org/0000-0002-3789-7558
Blake Lowrey https://orcid.org/0000-0002-4994-2117
Matthew J. Kauffman https://orcid.org/0000-0003-0127-3900

REFERENCES

Altizer, S., Bartel, R., & Han, B. A. (2011). Animal migration and infectious disease risk. *Science*, *331*, 296–302.

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, *344*, 1242552.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. *Journal of Animal Ecology*, *80*, 466–476.

Cagnacci, F., Focardi, S., Ghisla, A., Van Moorter, B., Merrill, E. H., Gurarie, E., Heurich, M., Mysterud, A., Linnell, J., & Panzacchi, M. (2016). How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. *Journal of Animal Ecology*, *85*, 54–68.

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). Ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*, 1124–1132.

Chang, W., Cheng, J., Allaire, J. J., Sievert, C., Schloerke, B., Xie, Y., Allen, J., McPherson, J., Dipert, A., & Borges, B. (2021). *Shiny: Web application framework for R*. R package version 1.7.1. https://www.CRAN.R-project.org/package=shiny

Department of the Interior. (2018). *Secretarial order 3362—Improving habitat quality in western big game winter range and migration corridors*. Department of the Interior.

Fauchald, P., & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, *84*, 282–288.

Hardesty-Moore, M., Deinet, S., Freeman, R., Titcomb, G. C., Dillon, E. M., Stears, K., Klope, M., Bui, A., Orr, D., & Young, H. S. (2018). Migration in the Anthropocene: How collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*, 20170017.

Horne, J. S., Garton, E. O., Krone, S. M., & Lewis, J. S. (2007). Analyzing animal movements using Brownian bridges. *Ecology*, *88*, 2354–2363.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H., Monteith, K. L., & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence for social learning from translocated animals. *Science*, *361*, 1023–1025.

Joo, R., Boone, M. E., Clay, T. A., Patrick, S. C., Clusella-Trullas, S., & Basille, M. (2020). Navigating through the R packages for movement. *Journal of Animal Ecology*, *89*, 248–267.

Kauffman, M., Copeland, H., Berg, J., Bergen, S., Cole, E., Cuzzocreo, M., Dewey, S., Fattebert, J., Gagnon, J., Gelzer, E., Chris, G., Graves, T., Hersey, K., Hurley, M., Kaiser, R., Meacham, J., Merkle, J.,

Middleton, A., Nuñez, T., … Thonhoff, M. (2020). *Ungulate migrations of the western United States, volume 1*. U.S. Geological Survey Scientific Investigations Report.

Kauffman, M., Lowrey, B., Beck, J., Berg, J., Bergen, S., Berger, J., Cain, J., Dewey, S., Diamond, J., Duvuvuei, O., Fattebert, J., Gagnon, J., Garcia, J., Greenspan, E., Hall, E., Harper, G., Harter, S., Hersey, K., Hnilicka, P., … Tatman, N. (2022). *Ungulate migrations of the western United States, volume 2*. U.S. Geological Survey Scientific Investigations Report.

Kauffman, M. J., Cagnacci, F., Chamaillé-Jammes, S., Hebblewhite, M., Hopcraft, J. G. C., Merkle, J. A., Mueller, T., Mysterud, A., Peters, W., Roettger, C., Steingisser, A., Meacham, J. E., Abera, K., Adamczewski, J., Aikens, E. O., Bartlam-Brooks, H., Bennitt, E., Berger, J., Boyd, C., … Zuther, S. (2021). Mapping out a future for ungulate migrations. *Science*, *372*, 566–569.

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*, aaa2478.

Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, *81*, 738–746.

Laurance, W. F., Clements, G. R., Sloan, S., O'connell, C. S., Mueller, N. D., Goosem, M., Venter, O., Edwards, D. P., Phalan, B., & Balmford, A. (2014). A global strategy for road building. *Nature*, *513*, 229–232.

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *The Journal of Wildlife Management*, *71*, 290–298.

Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, *80*, 107–138.

Lewis, K. P., Vander Wal, E., & Fifield, D. A. (2018). Wildlife biology, big data, and reproducible research. *Wildlife Society Bulletin*, *42*, 172–179.

Lowrey, B., McWhirter, D., Proffitt, K., Monteith, K., Courtemanch, A., White, P., Paterson, J., Dewey, S., & Garrott, R. (2020). Individual variation creates diverse migratory portfolios in native populations of a mountain ungulate. *Ecological Applications*, *30*, e2106.

Merkle, J., Gage, J., Sawyer, H., Lowrey, B., & Kauffman, M. (2022) Migration mapper: Identifying movement corridors and seasonal ranges for large mammal conservation (3.0). *Zenodo*, https://doi.org/10.5281/zenodo.6868175

Merkle, J. A., Sawyer, H., Monteith, K. L., Dwinnell, S. P., Fralick, G. L., & Kauffman, M. J. (2019). Spatial memory shapes migration and its benefits: Evidence from a large herbivore. *Ecology Letters*, *22*, 1797–1805.

Middleton, A. D., Merkle, J. A., McWhirter, D. E., Cook, J. G., Cook, R. C., White, P., & Kauffman, M. J. (2018). Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, *127*, 1060–1068.

Middleton, A. D., Sawyer, H., Merkle, J. A., Kauffman, M. J., Cole, E. K., Dewey, S. R., Gude, J. A., Gustine, D. D., McWhirter, D. E., & Proffitt, K. M. (2020). Conserving transboundary wildlife migrations: Recent insights from the greater Yellowstone ecosystem. *Frontiers in Ecology and the Environment*, *18*, 83–91.

Naidoo, R., Chase, M., Beytell, P., Du Preez, P., Landen, K., Stuart-Hill, G., & Taylor, R. (2016). A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. *Oryx*, *50*, 138–146.

Nandintsetseg, D., Bracis, C., Olson, K. A., Böhning-Gaese, K., Calabrese, J. M., Chimeddorj, B., Fagan, W. F., Fleming, C. H., Heiner, M., & Kaczensky, P. (2019). Challenges in the conservation of wide-ranging nomadic species. *Journal of Applied Ecology*, *56*, 1916–1926.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C. E., Bertram, M. G., & Bijleveld, A. I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, *375*, eabg1780.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org

Sawyer, H., Kauffman, M. J., Nielson, R. M., & Horne, J. S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, *19*, 2016–2025.

Sawyer, H., Lindzey, F., & McWhirter, D. (2005). Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin*, *33*, 1266–1273.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, *63*, 739–747.

Spitz, D. B., Hebblewhite, M., & Stephenson, T. R. (2017). 'MigrateR': Extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography*, *40*, 788–799.

Stabach, J. A., Hughey, L. F., Crego, R. D., Fleming, C. H., Hopcraft, J. G. C., Leimgruber, P., Morrison, T. A., Ogutu, J. O., Reid, R. S., & Worden, J. S. (2022). Increasing anthropogenic disturbance restricts wildebeest movement across east African grazing systems. *Frontiers in Ecology and Evolution*, *10*, 846171.

Tack, J. D., Jakes, A. F., Jones, P. F., Smith, J. T., Newton, R. E., Martin, B. H., Hebblewhite, M., & Naugle, D. E. (2019). Beyond protected areas: Private lands and public policy anchor intact pathways for multi-species wildlife migration. *Biological Conservation*, *234*, 18–27.

Teitelbaum, C. S., Fagan, W. F., Fleming, C. H., Dressler, G., Calabrese, J. M., Leimgruber, P., & Mueller, T. (2015). How far to go? Determinants of migration distance in land mammals. *Ecology Letters*, *18*, 545–552.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., & Avgar, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*, 466–469.

Wilcove, D. S., & Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing. *PLoS Biology*, *6*, e188.

SUPPORTING INFORMATION

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