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RESEARCH ARTICLE

Predicting dispersal and conflict risk for wolf recolonization in Colorado

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Abstract

1. The colonization of suitable yet unoccupied habitat due to natural dispersal or human introduction can benefit recovery of threatened species. Predicting habitat suitability and conflict potential of colonization areas can facilitate conservation planning.
2. Planning for reintroduction of gray wolves (*Canis lupus*) to the US state of Colorado is underway. Assessing which occupancy sites minimize the likelihood of human–wolf conflict during dispersal events and seasonal movements is critical to the success of this initiative.
3. We used a spatial absorbing Markov chain (SAMC) framework, which extends random walk theory and probabilistically accounts for both movement behaviour and mortality risk, to compare the viability of potential occupancy sites (public lands >500 km^2 to minimally meet wolf pack range area). The SAMC framework produced spatially explicit predictions of wolf dispersal, philopatry and conflict risk ahead of recolonization prior to reintroduction efforts. Our SAMC model included: (1) movement resistance based on terrain, roads and housing density; (2) mortality risk and potential conflict (absorption) based on livestock presence, social tolerance, land ownership and state boundaries; and (3) site fidelity based on habitat quality. Using this model, we compared 21 public land units by deriving predictions of: (A) relative survival time outside each site, (B) intensity of use and retention time within each site and (C) the probability of use on adjacent public lands. We also predicted and mapped potential conflict hotspots associated with each site.
4. Among the units assessed, a complex of USFS Wilderness areas near Aspen, chiefly the Hunter-Fryingpan and Collegiate Peaks Wilderness areas, had the best overall rankings when comparing predictions of each metric. The area balances high-quality, well-connected habitat with relatively low livestock density and high social tolerance.

5. *Synthesis and applications*. Our findings highlight the utility of the SAMC framework for assessing colonization areas and the capacity to identify locations for effective proactive management, especially of conflict prone species. The flexibility of the SAMC framework enables predicting likely areas of philopatry and human–wildlife conflict using spatially explicit metrics which can improve the success of conservation translocations and management of species with changing geographic extents.

KEYWORDS

conservation translocation, dispersal, human–wildlife conflict, movement ecology, species colonization, wolf reintroduction

1 | INTRODUCTION

The colonization of suitable yet unoccupied habitat can benefit recovery of threatened species (Camaclang et al., 2015). Efforts to buffer vulnerable species from extinction threats such as climate change, habitat loss, invasive species and direct human conflict often focus on increasing connectivity among remaining populations (Peck et al., 2017; Ripple et al., 2022; Thatte et al., 2018). In situations where populations cannot be connected or face barriers that inhibit natural colonization of remaining suitable habitat, conservation translocations (e.g. reintroductions, assisted colonization) have become common practice (Seddon et al., 2005). For example, within the United States, conservation translocations have aided, or are planned as part of recovery efforts, for approximately 70% of species listed as 'vulnerable' or 'endangered' under the US Endangered Species Act (Novak et al., 2021).

Conservation translocations are also often components of proposals to restore or 'rewild' landscapes (Svenning et al., 2016). A growing number of efforts have focused on restoration of native carnivores within historic ranges (Carver et al., 2021; Ripple et al., 2022; Wolf & Ripple, 2018). Apex carnivores can enhance ecosystem function, acting as keystone species and generating trophic cascades with myriad direct and indirect effects on herbivores, mesopredators and plant communities (Estes et al., 2011; Peterson et al., 2014). Large carnivores are also routinely translocated away from areas of high human conflict (Linnell et al., 1997) or to enhance ecotourism (Banasiak et al., 2021). Regardless of the rationale for carnivore translocations, carnivores are typically highly vagile, often require large home ranges, and can travel long distances to successfully hunt and reproduce, requiring them to navigate unsuitable (i.e. 'matrix') habitat and exposing them to potential conflict risks with humans (Woodroffe & Ginsberg, 1998). The two largest problems cited for failure in carnivore translocation efforts have been related to direct anthropogenic mortality at the reintroduction area and dispersal from preferred relocation areas into places with elevated conflict or mortality risk (Stepkovitch et al., 2022). Human-caused mortality is estimated to be the cause of death in >50% of fatalities in translocated carnivores (Jule et al., 2008). As such, functional connectivity for translocated individuals is key to establishing a viable population (Richardson et al., 2015), not only to overcome short-term threats, but also to ensure long-term gene flow (Linnell et al., 2009) and adaptive movements due to climate and environmental changes (Schwartz & Martin, 2013).

Approaches that quantify connectivity based on landscape resistance have advanced and been used for numerous conservation and land use planning purposes (Zeller et al., 2012). However, many approaches fail to fully integrate factors that limit dispersal or functional connectivity through the non-habitat matrix or cannot discern landscape resistance (i.e. reduced movement) from risk of mortality (i.e. termination of movement; Yamaura et al., 2022). Determining potential occupancy areas that not only optimize habitat quality, but also account for future movement, connectivity and dispersal success as it relates to potential conflict and mortality risks, can improve translocation success by guiding development of proactive management plans (Seddon et al., 2007). The spatial absorbing Markov chain (SAMC) framework is well-suited to assessing these critical components of translocation success by determining how movement behaviour and spatially explicit mortality, or conflict risk, can influence connectivity, survival and space use (Fletcher et al., 2019). For example, Vasudev et al. (2023) used a SAMC framework to assess habitat connectivity and inform management of likely conflict prone areas for Asian elephants (*Elephas maximus*). Like other connectivity modelling approaches, the SAMC framework incorporates landscape resistance and biased random walks into predictions of animal movement and dispersal, but it additionally allows for the distinction between factors that impact movement paths, such as landscape permeability, and those that terminate movement, such as mortality. Isolating these factors allows incorporation of mortality rates quantified from other studies and provides predictions of life expectancy and dispersal success. These, along with other metrics calculated with the SAMC framework, such as estimated space use and philopatry within an area, offer a means of comparing the suitability of potential occupancy sites and predicting likely conflict hotspots if individuals disperse or expand their distribution.

Here we use the SAMC framework to predict connectivity and potential conflict hotspots for wolves (*Canis lupus*) prior to reintroduction efforts in the state of Colorado, USA. Wolves were extirpated from Colorado during the 1940s, but the state has been identified as containing some of the best unoccupied wolf habitat in the Western US (Carroll et al., 2003, 2006), including areas of both ecological suitability and social tolerance (Ditmer, Wittemyer, et al., 2022), two elements necessary for wolf population viability (Mech, 2017). Following a highly competitive and politicized statewide wolf restoration ballot initiative (Niemiec et al., 2022), state wildlife officials are required to start reintroducing wolves prior to the end of 2023. Wolf reintroduction, and wolves in general, stir high levels of passion among people (Bangs et al., 1998) that often reflects larger societal conflicts beyond the species itself (Nie, 2001). Consequently, minimizing human–wolf conflict is key for maintaining tolerance and long-term coexistence (Lute et al., 2018).

Once restored to Colorado, wolves are likely to disperse into and colonize other areas in the state, particularly public lands with sufficient prey and less potential for conflict with humans (Carroll et al., 2003; Ditmer, Wittemyer, et al., 2022). Our goal was to assess landscape connectivity among large public land units that wolves may occupy in Colorado and to determine likely areas of conflict outside of these focal sites. We targeted large public lands because wolf survival is higher in areas with greater land protection and less conflict with humans (Smith et al., 2010; Barber-Meyer et al., 2021). The SAMC framework was used to determine conflict risk during seasonal movements and dispersal events, to evaluate connectivity among public land units, and to estimate the intensity of use or length of occupancy within each unit. We assumed that short-term restoration success will be determined in part by the duration of wolf occupancy within large public lands prior to seasonal movements or dispersal (Richardson et al., 2015). Specifically, we contrast public land units based on SAMC-derived metrics of: (1) residency time in each unit; (2) time to predicted conflict for each unit; and (3) probability that dispersal or seasonal migration will remain on public lands (assuming higher conflict risk on private land). We provide the predictions of conflict risk, connectivity and philopatry metrics for numerous public land units to assist proactive management ahead of any geographic expansion of wolves.

2 | MATERIALS AND METHODS

The SAMC framework decomposes the roles of landscape resistance and the termination of movement (absorption) on movement behaviour using random walk theory while accounting for mortality risk (Fletcher et al., 2019). Here we assumed that human–wolf conflict risk is the same as mortality risk. Due to the controversial nature of wolves and the reintroduction process, we assumed that areas of high human–wolf conflict potential would eventually result in mortality, as conflict that does not directly result in wolf mortality may result in subsequent lethal management actions, retaliatory killing or reduced human tolerance. Importantly, the SAMC framework enabled us to assign spatially explicit probabilities of conflict risk based on mortality rates published in the literature for wolves within human-dominated landscapes. Based on a review of dispersing wolves in the Northern Rocky Mountains by Jimenez et al. (2017), we made the following assumptions: (1) wolf dispersal would occur during the winter season, (2) other wolves on the landscape do not significantly influence dispersal or movement behaviour, (3) dispersal occurrence is not biased in any direction and (4) the maximum dispersal distance is 100 km. Much longer wolf dispersal distances have been recorded, but we considered the typical dispersal distances and conditions for most individuals, excluding the outliers. Although a small group of wolves recently colonized northern Colorado via natural dispersal from the Greater Yellowstone Ecosystem, we assumed that one peripheral pack would not influence the movements of reintroduced individuals throughout the expansive West Slope of Colorado. Additionally, predicting how territories of potential future packs may influence the dispersal routes and conflict areas within our modelling context would be difficult at this stage when the vast majority of Colorado remains unoccupied.

2.1 | Model inputs

The SAMC framework is flexible in the kinds of inputs that can be used and their interpretation. Here we focus on four key elements: occupancy of large public land units; site fidelity that can reflect habitat quality and will influence the rate of movement through landscapes; landscape resistance that alters movement paths; and absorption that reflects the termination of movement due to conflict.

2.1.1 | Occupancy

We chose public land units within Colorado by selecting United States Forest Service (USFS) Wilderness Areas, Bureau of Land Management (BLM) properties and National Park Service (NPS) lands that were at least 500 km^2. We used a 500 km^2 threshold to ensure occupancy sites were minimally large enough to match the territory sizes of wolf packs in other areas of the northern Rocky Mountains (Rich et al., 2012). We analysed 21 public land units that fit our criteria (17 USFS wilderness, three NPS including two wilderness, one BLM wilderness). The names of all public land units can be found in figure legends and Supplemental Results. We note that the initial release sites for wolves in Colorado will have a variety of additional constraints (e.g. west of the Continental Divide as stipulated in the ballot initiative) and are still being determined. However, our goal was to use the SAMC framework to quantify and compare areas of potential future occupancy. The 500 km^2 threshold limited the occupancy sites to the western half of Colorado because no large areas of public land are found in the eastern half of the state. In addition, the eastern half of Colorado contains few areas of suitable habitat for wolves (Ditmer, Wittemyer, et al., 2022).

For each public land unit, we determined the sites' centroid location and buffered it by 100 km based on a review of wolf dispersal by Jimenez et al. (2017). The buffer created a 40,000 km^2 area, encompassing and extending well beyond the boundaries of each unit. For comparison purposes we wanted to ensure all units were considered using the same area for analysis. If the 40,000 km^2 area extended beyond the Colorado state border when buffering any unit, we added an area equal to the portion that extended beyond in the opposite cardinal direction of the state border. Within each public land unit, we designated locations of occupancy along the unit boundary, as we were interested in the movement of wolves outside of our focal public land units rather than internal dynamics and movement within units. See Supplemental Methods for more details.

2.1.2 | Site fidelity

In combination with landscape resistance (see below), site fidelity influences the probability of movement in our SAMC framework. Site fidelity reflects the probability of staying in each location, or specifically, a given raster cell. We assumed site fidelity increased with habitat quality and that higher prey densities provided wolves with greater habitat quality, while ignoring anthropogenic influences and prey accessibility which are both reflected in the landscape resistance layer. We quantified prey densities and distribution throughout Colorado following the approach of Ditmer, Wittemyer, et al. (2022). We used Colorado Parks and Wildlife's (CPW) annual prey abundance estimates and winter seasonal distribution maps for the primary prey species of wolves in the Northern Rockies: deer (both mule [*Odocoileus hemionus*] and white-tailed [*O. virginianus*]) and elk (*Cervus canadensis*). See Supplemental Methods for more details. Values for the resulting fidelity layer, reflecting total winter prey densities across species, were rescaled to a range of 0–0.99 (least to most site fidelity probability) across the entire study region of Western Colorado (Figure 1a).

2.1.3 | Landscape resistance

The landscape resistance layer combined equal weights for terrain and anthropogenic factors (Figure 1b). Because wolves are coursing predators, wolf hunting success is negatively correlated with steep slopes (Paquet et al., 1996). To create the terrain resistance component, we used a digital elevation model (DEM) with a spatial resolution of 30 m to calculate slope in degrees. We created a combined anthropogenic layer by including the maximum value for each cell using estimates of housing and road density layers. Wolves tend to avoid areas near buildings even at low densities (Malcolm et al., 2020), and especially locations with high housing densities (Carricondo-Sanchez et al., 2020; Zimmermann et al., 2014). Areas with higher road densities reduce the probability of wolves establishing packs (Houts, 2000; Mladenoff et al., 1995) and roads with higher traffic volumes tend to be avoided more strongly relative to lower traffic volume roads (Oakleaf et al., 2006). Because low volume roads can be used as conduits for movement by wolves (Dickie et al., 2017; Whittington et al., 2005), we did not include them in the resistance layer. The anthropogenic layer was then added to the slope layer. The combined resistance layer was rescaled so values ranged from 0 to 1. See Supplemental Methods for more details.

2.1.4 | Absorption—conflict risks

We defined the absorption input for our SAMC framework—representing the probability of the termination of movement—within areas containing higher probability for wolf–human conflict. We developed estimates of potential wolf–human conflict based on four components: (1) winter livestock availability on public lands based on density estimates of number of livestock on public land grazing allotments managed by the US Forest Service (USFS) and the Bureau of Land Management (BLM) and on private land using areas of remotely sensed crops used in livestock production, (2) land ownership maps, (3) social tolerance for wolves based on precinct-level voting proportions for the wolf restoration ballot initiative and (4) Colorado state borders (Figure 1c). Components 1–3 were previously used by Ditmer, Wittemyer, et al. (2022) to develop a wolf conflict layer. We assumed that tolerance is a critical determinant of the ability of carnivores to persist in human-dominated systems (Carter et al., 2020), and that areas with higher voting percentages in favour of wolf restoration generally tolerate sharing the landscape with wolves relative to areas with less support. Here, we included state borders into our conflict layer because wolves leaving the state of Colorado do not contribute towards a viable state population, nor are they protected in Wyoming or Utah. Additionally, southward movements into New Mexico are considered problematic due to potential interbreeding with Mexican gray wolves (*Canis lupus baileyi*; Odell et al., 2018) and would likely result in management intervention. The Supplemental Methods provides further details on these layers, methods for combining components, and the studies providing mortality rates in conflict prone areas used to scale the absorption values.

We considered a second set of models whereby we altered the absorption layer to reflect only livestock within our study area, including estimates of both winter public and private land livestock availability (Figure 1d). To provide conservative estimates of conflict risk we did not smooth the livestock layer, but rather only the exact locations of potential livestock were mapped. We created these second set of models because: (1) conflict with livestock producers can quickly reduce tolerance for wolves in general (Mech, 2017), (2) livestock depredation is considered by many in Colorado to be the most likely negative consequence of wolf reintroduction (Niemiec et al., 2020) and (3) a variety of management options exist to reduce the likelihood of livestock depredation and to mitigate its impact (e.g. Lance et al., 2010).

In the livestock models we again included state boundaries as an area of high mortality risk, whereby all state boundaries were also assigned the maximum value of the livestock layer prior to all values being rescaled to the annual survival range of 0.6–0.99. All other model inputs and analyses were conducted in the same manner as

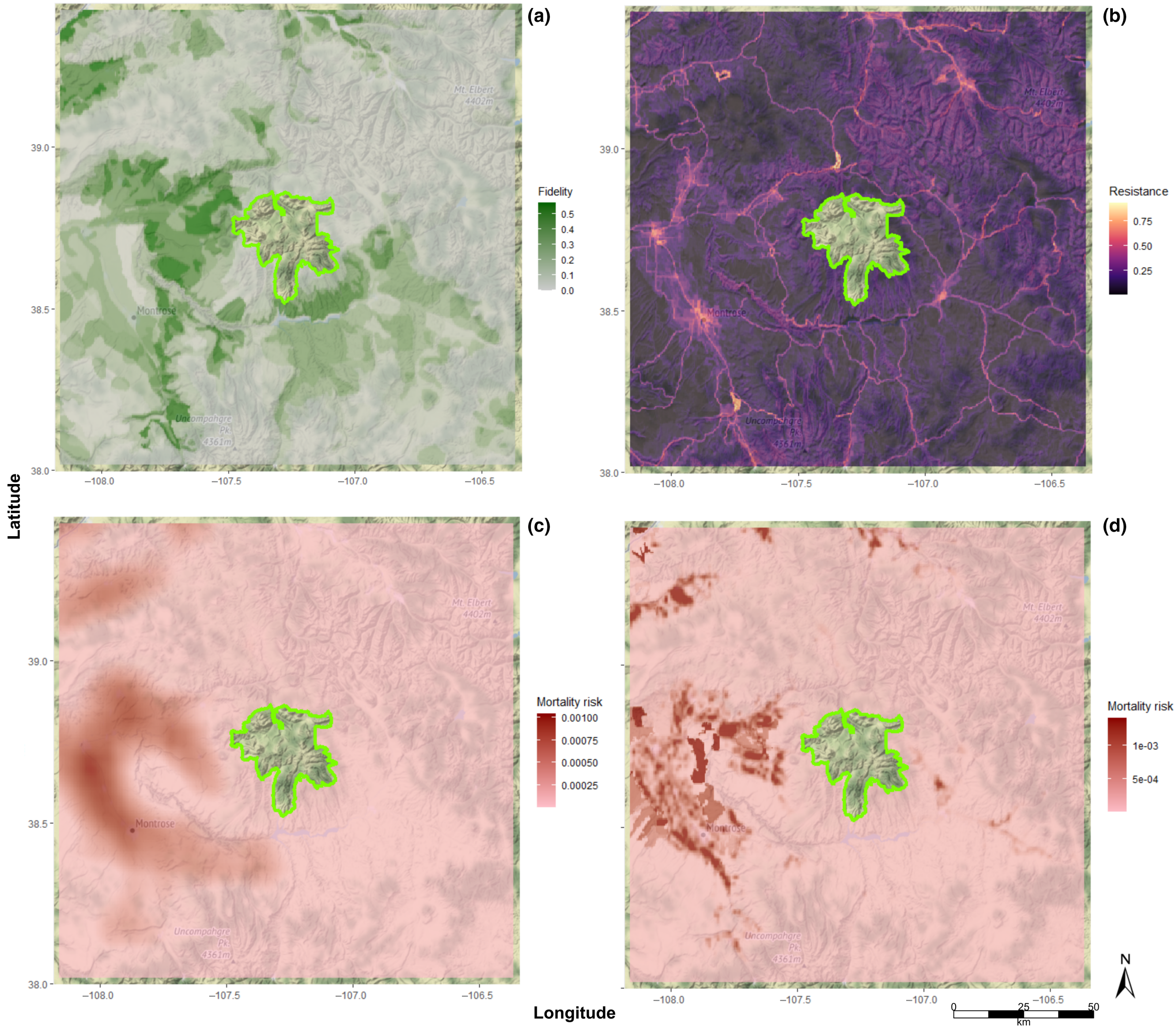

FIGURE 1 Model inputs into our spatial absorbing Markov chain (SAMC) framework for assessing wolf conflict, survival, connectivity and dispersal in Colorado, USA using the USFS's West Elk Wilderness as an example. The SAMC framework incorporated (a) site fidelity; (b) landscape resistance to movement; (c) mortality risk in the form of human–wolf conflict defined by livestock, land ownership, social tolerance and state borders (values represent the probability of conflict at a location for each movement step); and another scenario, (d) that considered only livestock and state borders as sources of conflict. Values for each metric within the West Elk Wilderness were removed in these maps because our focus was on estimated dispersal metrics (time to potential conflict, dispersal to other public lands) from the West Elk Wilderness boundary.

the multi-source absorption models. All layer preparations and operations were done within program R (R Core Team, 2020) and all layers were resampled to a resolution of 500m^2 using the bilinear method. We used 500 m^2 because we felt it captured a fine-enough resolution for our model input layers and was not overly burdensome for computational efficiency given the number of model runs. Additionally, because we were interested in only comparing relative time values of our SAMC metrics (based on the number of time steps), we did not need to approximate an average wolf movement distance (e.g. hourly, daily), which can be difficult especially during dispersal events.

2.2 | SAMC framework and outputs

We implemented a SAMC framework for the selected public land units using the package ‘samc’ (Marx et al., 2020) in program R (R Core Team, 2020). We created a samc object for each unit consisting of the previously described inputs, used an eight-neighbour rule for transitions, and a transition function that used the mean of all surrounding cell values between pairs of cells. We then used the functions for estimating long-term dynamics for visitation, survival, mortality and dispersal.

The 'visitation' function in the samc package provided estimates of long-term visitation rates calculated as the expected number of times an individual, starting at a given location, uses a location before it is expected to be absorbed into areas of high conflict (i.e. absorption layer). Unlike the other samc functions, which can use the occupancy layer to represent an initial starting area, visitation uses a specific starting location. As such, we ran the visitation function 50 times for each public land unit, randomly selecting a different starting location within the unit for each iteration. The initial location was determined by a random location placed within the unit based on values from the fidelity layer that fell within the top 80th quantile of fidelity values inside the unit, assuming initial colonization would occur in high resource areas. We view visitation outputs as philopatry in potentially future occupied units. We used the 50 visitation output layers and calculated the mean visitation within the unit to represent the average intensity of use within the unit (i.e. an indicator of habitat quality while also accounting for landscape resistance). We also summed the mean pixel values across each unit to provide an estimate of the total intensity of use within each unit. The summed value represents relative length of time remaining within the unit (i.e. a measure of unit area, predicted movement and habitat quality).

We used the 'mortality' function within the samc package to provide estimates of the unconditional probability of absorption, or in our analysis, direct conflict. The outputs provide spatially explicit locations of elevated conflict risk surrounding each public land unit given the initial wolf distribution represented by the unit's initial occupancy within 1 km of the unit boundary. The resulting probability layer provides a map of the areas outside of the focal unit where direct human–wolf conflict is likely to occur. We calculated the predicted life expectancy, or in our example, expected time until direct conflict, using the 'survival' function, which also included the occupancy layer as the initial distribution. We compared the survival times among public land units to assess the relative length of time that a wolf is expected to avoid direct conflict once moving or dispersing from a unit.

We predicted and mapped the probability of movement between the initial occupied cells within a public land unit and the surrounding landscape using the 'dispersal' function in the samc package. The long-term predictions of movement provide the probability that all 500 m^2 cells are ever visited by wolves leaving a unit. We then overlaid our map of land ownership on the resulting dispersal maps to quantify the average dispersal into other surrounding public lands and the ratio of mean public to private land use.

We summarized the SAMC framework outputs by calculating the mean rank for each unit across all metrics. We then assigned an overall rank to each unit based on the average rank. Finally, to better assess the magnitude of differences among all units, we plotted the scaled values for average survival time (all components and livestock + state borders only predictions), average philopatry (total and mean values of visitation within each unit) and connectivity to other public lands (dispersal into public land average).

3 | RESULTS

The Weminuche Wilderness (USFS) of southern Colorado was predicted to have over 14.5X the amount of total expected visitation within the unit before dispersal (i.e. philopatry) relative to the area with the least visitation, the Black Ridge Canyons Wilderness (BLM; see units 16 and 21, Figure 2a; Figure S1). Although the Weminuche Wilderness, the largest public land unit considered (~2023 km^2), had the highest total expected visitation, the much smaller Hunter-Fryingpan Wilderness (~332 km^2), near Aspen in central Colorado, had the largest mean visitation value per 500 m^2 pixel (see units 16 and 9, Figure 2b; Figure S1), a potentially more meaningful metric than total visitation. The Mount Zirkel Wilderness had the least mean expected total visits and mean visitation by wolves prior to movements outside of the unit (Figure S1).

Our SAMC models predicted that wolves occupying the Hunter-Fryingpan Wilderness, situated among a complex of USFS Wilderness areas (Holy Cross, Maroon Bells-Snowmass, and Collegiate Peaks), would be expected to use the surrounding landscape outside the unit the longest prior to conflict (see units 7, 9–11, Figure 2c; Table S2). The low conflict potential surrounding these wilderness units resulted in all units in the complex being ranked in the top 5 for time until potential conflict (Figures 2c and 3a–c). The most likely area of conflict risk was predicted to the southeast of the Hunter-Fryingpan Wilderness (Figure 3a). In contrast, the BLM property Black Ridge Canyons Wilderness, located on the Colorado–Utah border, ranked last when considering time until potential conflict, with an estimated time to conflict that was over 68× shorter than that of the Hunter-Fryingpan Wilderness (see units 9 and 21, Figures 2c and 3e; Table S2). Generally, focal units located on or near the state border had shorter time-to-conflict predictions because of the high value of conflict potential placed on the border areas themselves (Figures 2c and 3d–f).

When livestock and state borders were the only source of conflict considered in our absorption layer, several of the top-ranked units from the multi-source absorption SAMC model did not rank as high (Figure 2d; Table S2). For example, the Hunter-Fryingpan and Collegiate Peaks Wilderness areas that ranked first and second, respectively, in the multi-source model for time to potential conflict, ranked 7th and 6th respectively, due to the highly weighted areas of private land livestock production near the borders of both units. Units with less livestock closer to the densely populated Front Range, such as the Mount Evans Wilderness and Lost Creek Wilderness, received the longest time to potential conflict under the livestock + state borders only model (see units 6 and 8, Figure 2d; Table S2).

The group of wilderness areas around Aspen that had the highest ranks for several metrics in the multi-source absorption models also ranked the highest in our predictions of mean dispersal probability into other public lands (Figure 4a; Table S3). These top-ranked wilderness areas are spatially aggregated and are located within the expansive White River, Pike and San Isabel National Forests (see units 7, 9–11 in Figure 2). The Black Ridge Canyons Wilderness

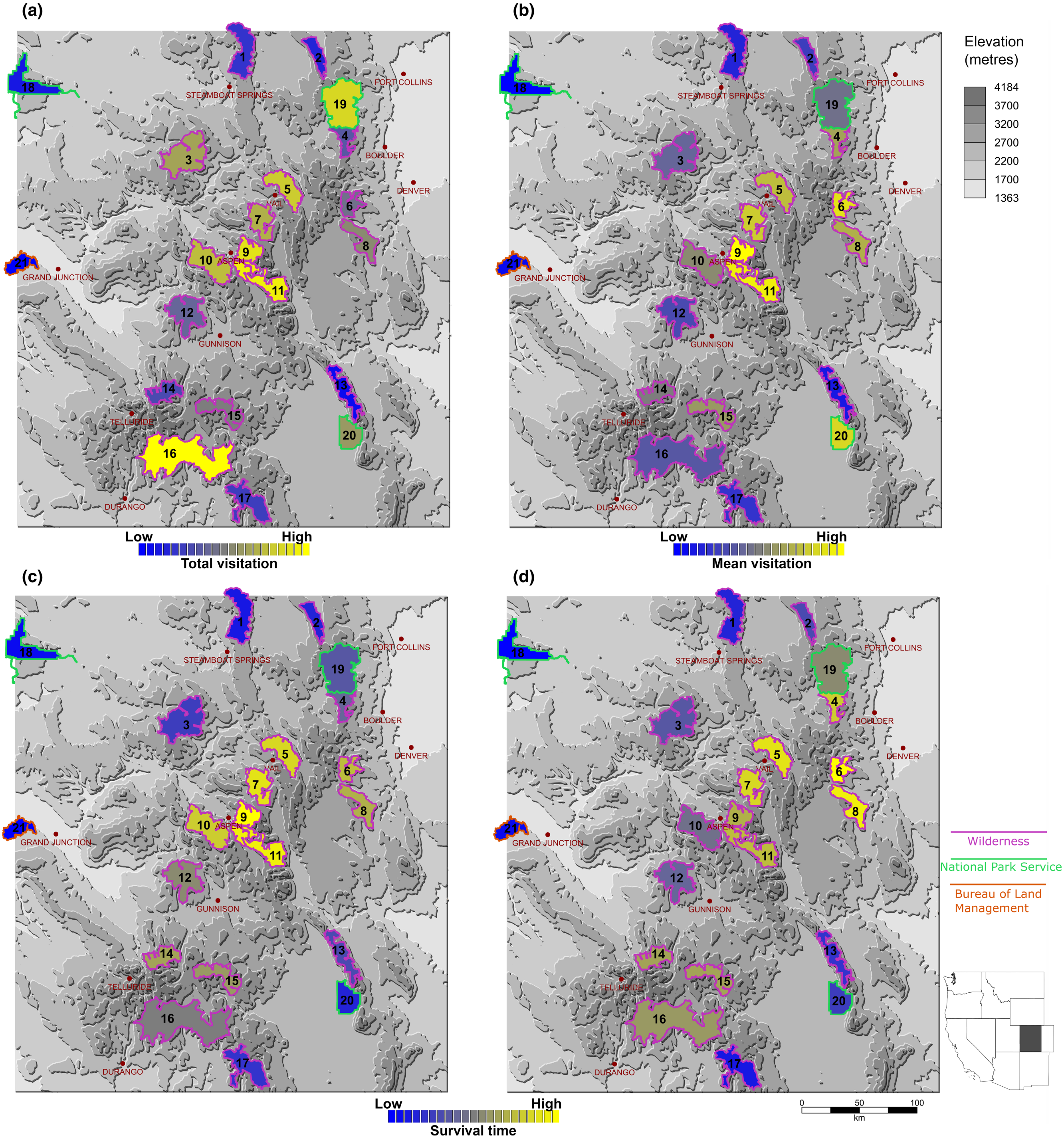

FIGURE 2 All focal public land units considered in our analysis of wolf conflict, survival, connectivity and dispersal in Colorado, USA ranked by (a) philopatry inside the unit measured as total number of visitations within the focal unit, (b) the mean value of visits per raster cell, and relative survival time (i.e. time to first human conflict) in the (c) all conflict source scenario, and the (d) livestock and state borders only scenario. USFS Wilderness Areas: 1. Mount Zirkel, 2. Rawah, 3. Flat Tops, 4. Indian Peaks, 5. Eagles Nest, 6. Mount Evans, 7. Holy Cross, 8. Lost Creek, 9. Hunter-Fryingpan, 10. Maroon Bells-Snowmass, 11. Collegiate Peaks, 12. West Elk, 13. Sangre de Cristo, 14. Uncompahgre, 15. La Garita, 16. Weminuche, 17. South San Juan; National Park Service Lands: 18. Dinosaur National Monument, 19. Rocky Mountain National Park, 20. Great Sand Dunes National Park; BLM Lands: 21. Black Ridge Canyons. For predicted visitation metrics of all focal public land units, see Table S1.

had the lowest mean dispersal value into public lands, 27% lower than the Hunter-Fryingpan Wilderness. Contrastingly, if the restoration goal is not to maximize the likelihood of geographic expansion across public lands, but instead to minimize the likelihood of dispersal through private lands, the ratio of mean public to private land use ranked several units at the top that were not included in the

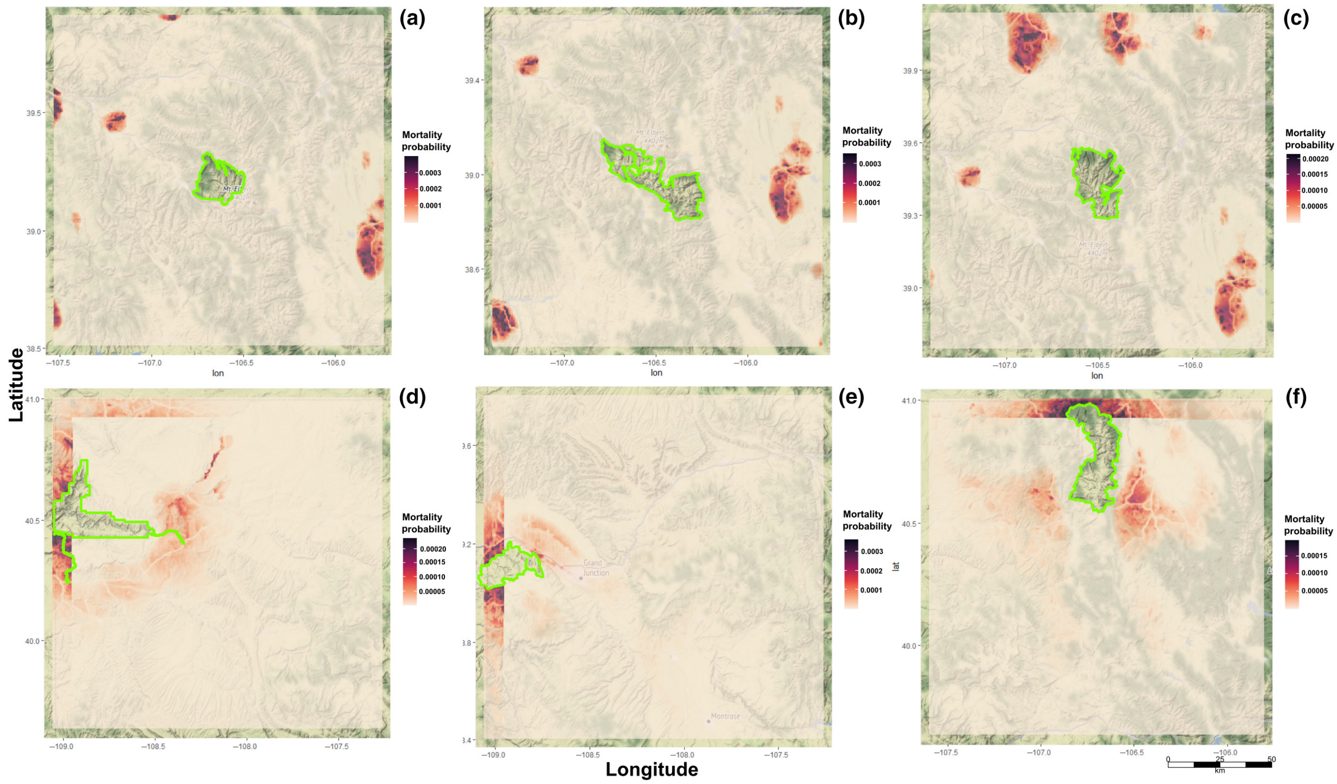

FIGURE 3 Predicted estimates of long-term average mortality probability for the focal public land units with the (a–c) longest average survival time (i.e. time to first human conflict) and the (d–f) shortest survival times when considering all sources of potential conflict. (a = Hunter-Fryingpan Wilderness; b = Collegiate Peaks Wilderness; c = Holy Cross Wilderness; d = Dinosaur National Monument; e = Black Ridge Canyons; f = Mount Zirkel Wilderness). For predicted survival times of all focal public land units, see Table S2.

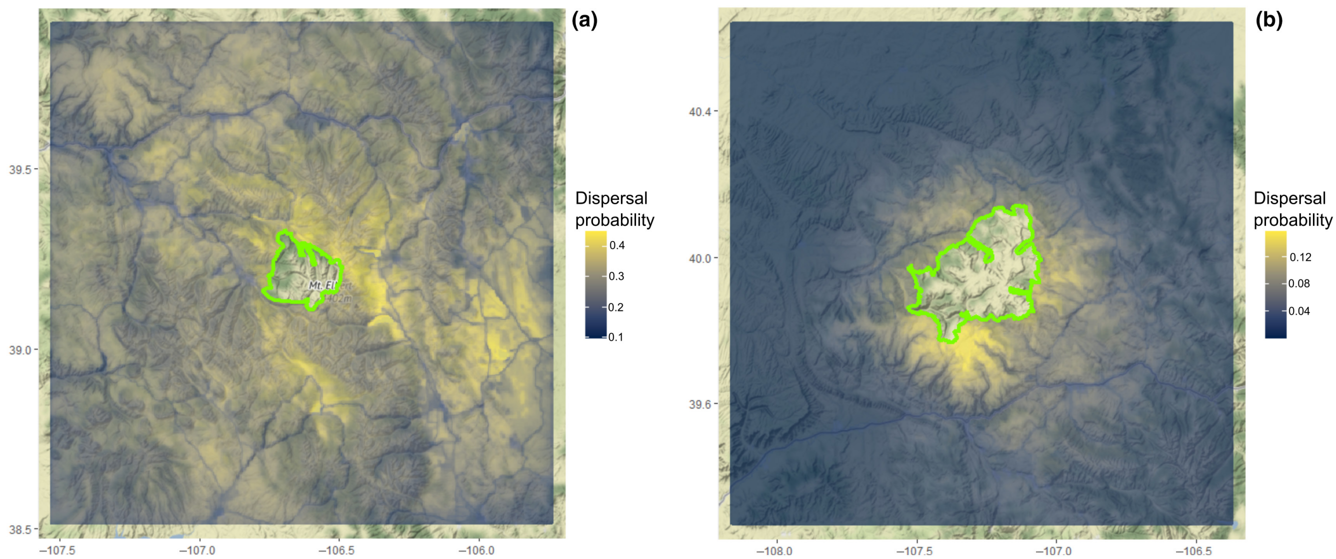

FIGURE 4 Examples of predicted dispersal probability of wolves from select focal public land units: (a) Hunter-Fryingpan Wilderness and (b) the Flat Tops Wilderness. The Hunter-Fryingpan Wilderness had the highest predicted average dispersal onto other public lands. In contrast, the Flat Tops Wilderness had more limited dispersal probability, but the predicted dispersal was primarily all on public rather than private lands. For predicted dispersal metrics of all focal public land units, please see Table S3.

mean public probability ranking. For instance, dispersal from the Flat Tops Wilderness was predicted to be particularly limited due to potential conflict on public and private land associated with areas of livestock production and low social tolerance. However, the Flat Tops Wilderness had a high public to private ratio ranking because predicted dispersal was primarily all on public lands (i.e. an adjacent section of the White River National Forest) rather than private lands (see unit 3 in Figures 2 and 4B; Table S3).

Overall, the Hunter-Fryingpan Wilderness, along with several other USFS Wilderness units around Aspen, ranked the highest using the simple average of ranks across SAMC output metrics (Figure 5; Table S4). The visualization of scaled average scores for survival time, philopatry and connectivity to other lands clearly showed that both the Hunter-Fryingpan Wilderness and the Collegiate Peaks Wilderness far outperformed the other focal units along all three axes (see units 9 and11 in Figures 2 and 5B).

4 | DISCUSSION

The colonization of unoccupied habitat through conservation translocations or natural dispersal can benefit threatened populations (Camaclang et al., 2015; Novak et al., 2021; Seddon et al., 2005). For large and highly mobile carnivores, especially species prone to human conflict, balancing potential conflict and functional connectivity is difficult but critical for establishing viable populations and maintaining public support for conservation efforts (Ghoddousi et al., 2021). Our study demonstrated the capabilities of the SAMC framework for developing quantified comparisons and predictions of wolf space use among multiple large public land areas within the state of Colorado in anticipation of future occupancy and geographic expansion. The SAMC framework integrated estimates of habitat quality, conflict probability, specific management and policy implications (e.g. conflict risk beyond state borders), and landscape resistance to create spatially explicit predictions of likely dispersal routes, space use and conflict hotspots. Colorado contains over >9.7 million hectares of public land, with numerous potential habitable areas (Carroll et al., 2003, 2006; Ditmer, Wittemyer, et al., 2022). However, our metrics and spatially explicit predictions demonstrated that different public land units provided drastically varying levels of conflict potential, connectivity to other public lands and relative predicted survival time. In general, successful planning and implementation of wildlife translocations cannot rely exclusively on biological and ecological information within colonization areas. A metanalysis by Serota et al. (2023) found that out of the 305 conservation translocations of vertebrates considered, those projects that also incorporated human dimension objectives (i.e. social, political, psychological, economic and cultural components of conservation) were significantly more likely to have positive outcomes. Critically, by accounting for movement behaviour and conflict risks separately, the SAMC framework provided fine-scale predictions of potential future conflict sites to help guide proactive management strategies.

Restoring large carnivores can enhance ecological integrity (Wolf & Ripple, 2018), yet it is often a logistically and financially difficult effort for practitioners (Miller et al., 1999) and can encompass a wider set of political (Ditmer, Niemiec, et al., 2022) and social (Clemm von Hohenberg & Hager, 2022; Nie, 2001) debates. Without properly considering and alleviating human–wildlife conflict, carnivore recolonization can

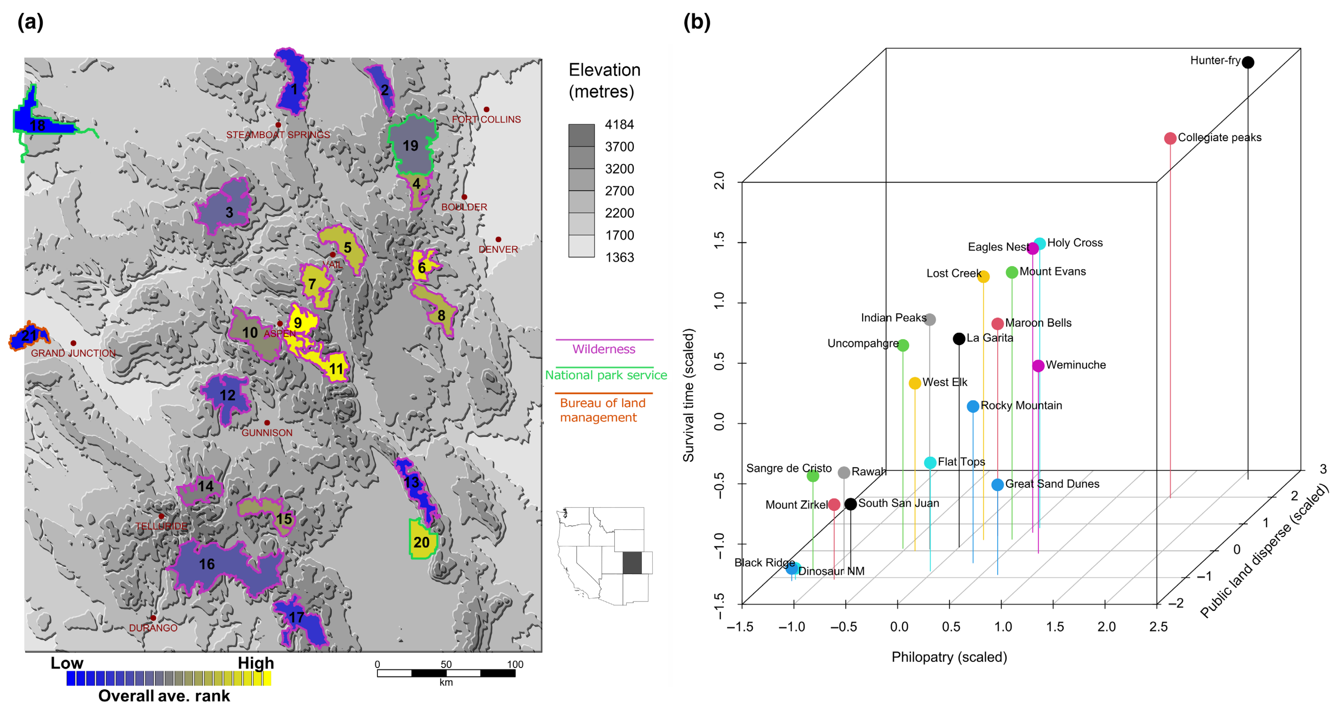

FIGURE 5 (a) Map depicting the overall ranking of all focal public land units considered in our analysis of wolf conflict, survival, connectivity and dispersal in Colorado, USA. A 3D plot of (b) scaled average metric values for predicted survival time (average for all conflict aspects and just livestock and state borders), philopatry (visitation metrics) and metrics for dispersal into public land. For a complete overall ranking of all focal public land units, please see Table S4. USFS Wilderness Areas: 1. Mount Zirkel, 2. Rawah, 3. Flat Tops, 4. Indian Peaks, 5. Eagles Nest, 6. Mount Evans, 7. Holy Cross, 8. Lost Creek, 9. Hunter-Fryingpan, 10. Maroon Bells-Snowmass, 11. Collegiate Peaks, 12. West Elk, 13. Sangre de Cristo, 14. Uncompahgre, 15. La Garita, 16. Weminuche, 17. South San Juan; National Park Service Lands: 18. Dinosaur National Monument, 19. Rocky Mountain National Park, 20. Great Sand Dunes National Park; BLM Lands: 21. Black Ridge Canyons.

result in poaching or retaliatory killing (Liberg et al., 2012), failure of entire restoration efforts (Linnell et al., 1997) and reductions in tolerance for other species and conservation efforts (Mateo-Tomás et al., 2012). Reviews of carnivore conservation translocations indicate many end in failure (Bubac et al., 2019; Fischer & Lindenmayer, 2000; Stepkovitch et al., 2022). Linnell et al. (1997) suggested targeting extremely large areas without potential conflict or expending management resources to reduce conflict. However, management resources are often limited, and few places remain where suitable habitat does not overlap with the expanding human footprint (Carter & Linnell, 2016). Surprisingly, one of the relatively smaller USFS Wilderness Units—the 33.2k acre Hunter-Fryingpan Wilderness northeast of Aspen—ranked highest across several metrics we considered. This site is adjacent to a complex of several other wilderness units (Holy Cross, Maroon Bells-Snowmass and Collegiate Peaks) that offer high habitat connectivity combined with predicted high survival/low conflict as the area has a relatively low density of livestock and relatively high social tolerance for wolves.

Although the best survival rates for wolves are within wilderness areas (Barber-Meyer et al., 2021), wolves do not necessarily require wilderness but do require an adequate prey base and tolerance from humans (Mech, 2017). Carroll et al. (2006) examined potential suitable habitat through the Western United States and found Colorado to contain some of the best remaining wolf habitat that could support long-term viable populations despite the rapid human population growth in the state. Ditmer, Wittemyer, et al. (2022) examined the juxtaposition of ecological and social suitability for wolves in Colorado at a broad spatial scale and found extensive areas of high socio-ecological suitability in the summer months, but these areas were diminished during winter as prey species moved to lower elevations closer to human populations, private land and livestock operations. Here, the SAMC framework goes further by taking a movement ecology approach to predict dispersal and functional connectivity routes and areas of high conflict potential for 21 of the state's largest public land units.

Our findings not only demonstrated the importance of the spatial configuration of low conflict wilderness areas for wolves, but also the importance of integrating social tolerance estimates. For instance, the Hunter-Fryingpan Wilderness ranked highest for several of our SAMC framework outputs when considering social tolerance via the voting data as an index of social acceptance of wolves. Yet, it ranked 7th in the models that included only livestock and state borders. The area around the Hunter-Fryingpan Wilderness contains some livestock holdings, but the largest nearby town, Aspen, largely supported the wolf reintroduction measure (Ditmer, Niemiec, et al., 2022). The region's combination of high-quality habitat and connectivity and general human tolerance may benefit not only wolves, but also potentially the local economy through ecotourism (Duffield et al., 2006). Similarly, Behr et al. (2017) used social surveys to predict wolf acceptance in Switzerland, but due to the effort to survey landowners in a large landscape, tolerance predictions had to be greatly extrapolated from models. The near population-level survey (>72% of eligible voters cast ballots on the ballot initiative) of wolf tolerance within the state, delineated within political precincts, offered a novel way to incorporate this critical component of wolf population viability across the entire state (Ditmer, Wittemyer, et al., 2022). Importantly, the Hunter-Fryingpan Wilderness, along with other top-rated areas for wolves, are located within the interior of Colorado, away from state borders with their associated conflict risks due to current policies in other states and a loss of individuals towards the goal of establishing a viable population in Colorado.

Our predictions of future wolf movement and conflict risk within the SAMC framework are an initial assessment without the benefit of empirical data on wolf movement in the state. Data collected from the small number of wolves that have naturally migrated and are currently present in Colorado, as well as wolves to be reintroduced in the future, would further inform our models. Our assessment only considered large, federally managed land parcels, but did not assess other potentially viable areas managed by state or local governments or privately owned. As such, our model does not assess all possible locations of either initial reintroduction and/or subsequent geographic expansion. Additionally, some inputs within our models required assumptions taken from other studies in the northern Rocky Mountains that may not hold true within the southern Rocky Mountains of Colorado. For instance, we scaled our site fidelity values to the range of prey density estimates within Colorado. Colorado contains some of the most abundant populations of elk and mule deer in the United States (Bergman et al., 2015; Colorado Parks and Wildlife, 2020), thus making our fidelity estimates conservative, resulting in less use within starting focal areas and potentially inflating estimates of encounters with high conflict areas. In addition, wolf dispersal events, while typically occurring during winter months (Jimenez et al., 2017), as we have assumed here, can occur throughout the year. Wolf summer dispersal is less likely to result in immediate potential human conflict because prey are more widely distributed across high-elevation summer habitats with lower human presence. However, wolves could encounter livestock which are also widely distributed during summer throughout USFS and BLM grazing allotments (Ditmer, Wittemyer, et al., 2022).

Regardless of the areas occupied by wolves, the SAMC framework can be updated and expanded (e.g. to include gene flow; Fletcher et al., 2022) to better model wolf recovery as restoration progresses, more empirical data become available, and more specific management goals are developed or policies change (e.g. protection status of wolves federally or in surrounding states). The SAMC framework can be used to ask specific questions about connectivity between multiple occupied areas, or an occupied area and places of interest on the landscape. For instance, mapping corridors and considering directionality in movement among the wilderness areas around Aspen might be of interest. The capacity to change propagule pressure, representing population abundance among different occupied units, may better reflect wolf demographics and result in more accurate model predictions. Colorado-specific wolf survival rates, once estimated, can be used in updated models with the option to consider multiple absorbing states. For example, some types of roadways may act as barriers to movement within the resistance layer, while some may cause mortality. Roadways associated with wolf–vehicle strikes could be included as their own absorbing state with a probability of mortality separate from other conflict risks. As telemetry data from wolves or prey species in the region become available, they can be used to both evaluate the accuracy of these models and to develop new more refined predictions of habitat selection that can further improve SAMC model inputs by informing the fidelity and resistance layers.

Our findings provide several quantified estimates of important aspects for carnivore conservation translocations that can be compared among potential reintroduction or colonization areas by managers for any species. Previously, Fletcher et al. (2022) demonstrated the effectiveness of the SAMC framework to predict population structure better than more traditional methods of connectivity analysis, such as least-cost and circuit theory, because of its ability to consider directional movement resistance. Vasudev et al. (2023) were able to test SAMC model predictions using conflict data for Asian elephant (*Elephas maximus*) in a shared landscape and found that accounting for animal movement improved their predictive ability of conflict hotspots, which could then be integrated into the conservation management planning process. As efforts to restore ecological integrity of ecosystems via conservation translocations of carnivores increases globally (e.g. Eurasian lynx [*Lynx lynx*], Ovenden et al., 2019; cheetah [*Acinonyx jubatus*] Walker et al., 2022), tools such as a the SAMC framework can help to increase the probability of successful conservation translocations and predict places to focus management efforts and resources more efficiently and proactively. Importantly, the flexibility of the SAMC framework can be tailored to the specifics of any locale and species and can be designed to test model assumptions and assess a wide variety of possible scenarios.

AUTHOR CONTRIBUTIONS

Mark A. Ditmer, George Wittemyer, Robert J. Fletcher Jr., and Katherine A. Zeller conceived the ideas and designed the methodology. Mark A. Ditmer led the writing of the manuscript. George Wittemyer, Katherine A. Zeller, Kevin R. Crooks, Stewart W. Breck and Robert J. Fletcher Jr. provided support and insights into the modelling process and development of the analysis. All authors contributed critically to the writing of each draft and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

No conflicts to declare.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.5qfttdzc6 (Ditmer et al., 2023).

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SUPPORTING INFORMATION

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

Figure S1. Mapped output of the mean visitation prior to movements outside of the unit within starting public land units for wolves in Colorado, USA.

Table S1. Predictions of total visitation within each focal public land unit prior to dispersal (left half) and mean visitation per pixel within the unit prior to dispersal for wolves in Colorado, USA.

Table S2. Predictions of survival time (defined here as time until likely human-wolf conflict) outside of each focal public land unit when considering all sources of conflict (left half) and when only considering livestock and state borders as drivers of conflict potential (right half) for wolves in Colorado, USA.

Table S3. Predicted probability of dispersal to other surrounding public lands (left) and the ratio of mean public to mean private lands dispersal (right) from each focal public land unit for wolves in Colorado, USA.

Table S4. Overall rankings for the primary metrics listed in Supplemental Tables S1–S3 and an overall rank based on a basic average of all rankings for each focal public land unit for wolves in Colorado, USA.

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