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RESEARCH ARTICLE

How sampling design of GPS collar deployment influences consistency of mapped migration corridors over time

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Abstract

Federal and state agencies within the United States have recently issued directives prioritizing the conservation of ungulate migration corridors and winter ranges. The ability to identify and delineate the spatial distribution of seasonal ranges underpins these policies. While such delineations are often derived from global positioning system (GPS) collar data collected for a few years on a focal population, they are being used in long-term conservation planning. Our objectives were to quantify consistency in migration corridors from year to year and cumulatively across multiple years and identify which aspects of the sampling design of GPS collar deployment will delineate a consistent and relatively complete migration corridor. We used data from 6 sub-herds of mule deer (*Odocoileus hemionus*), a species known to have high migratory fidelity, located in Wyoming and northern New Mexico, USA, monitored for 5–7 years (510 unique individuals). We calculated 2 types of migration corridors over time: cumulative corridors where each new year of data was added to all previous years and yearly corridors where each year was based only on data collected in that year. We then calculated the year-to-year consistency in the 2 types of migration corridors by calculating the percent overlap between corridors calculated in sequential years.

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We found that collaring a higher proportion of a sub-herd increased the consistency in migration corridors, whereas collaring new individuals via redeployments in a subsequent year of monitoring caused corridors to shift. To obtain a corridor with ≥90% consistency (i.e., approaching the complete area used by a population in our data), our results suggest that biologists should strive to collar ≥6% of a sub-herd for a minimum of 2 years. However, if ≥6% of a sub-herd cannot be collared, monitoring for longer (3–4 years) will provide roughly 90% consistency in a migration corridor estimate for mule deer. Furthermore, adding 16–25% new individuals each year will help capture variation among individuals while maintaining corridor consistency of ≥90%, leading to a more accurate delineation of the corridor. Our results provide managers with a logistical framework for collaring projects aimed at delineating migration corridors that are durable into the future.

KEYWORDS

habitat conservation, logistical framework, migration corridor, movement ecology, mule deer, *Odocoileus hemionus*, sampling design

Migration, the seasonal and reoccurring movement of individuals from one spatially distinct area to another (Berger 2004, Kauffman et al. 2021*a*), is found across many taxa (Loredo et al. 1996, Egevang et al. 2010, Abrahms et al. 2018). For ungulates, migration allows individuals to increase access to high quality and beneficial resources while also allowing animals to avoid natural threats (e.g., harsh weather conditions or predators; Fryxell et al. 1988, Kauffman et al. 2021*a*). Despite the benefits of migration, ungulate migrations are declining worldwide because of human disturbance, overharvest, disease, and climate change (Bolger et al. 2008, Harris et al. 2009, Sawyer et al. 2017, Kauffman et al. 2021*a*). In the western United States, migratory mule deer (*Odocoileus hemionus*) have experienced broad declines in numbers in the last decade (Wyoming Game and Fish Department Mule Deer Working Group 2015, Cooley et al. 2020). Likewise, the migratory segments of some elk (*Cervus canadensis*) populations are also in decline (Cole et al. 2015). In response, state and federal agencies in the western United States have recently issued directives to conserve migratory ungulates and habitat within their migration corridors (Kauffman et al. 2020, 2021*a*, *b*; Middleton et al. 2020, Sawyer et al. 2020). For example, the United States Department of the Interior released a Secretarial Order (Zinke 2018) in February 2018, mandating that their agencies work with state wildlife management agencies to improve habitat quality on western big game winter ranges and migration corridors. In 2019, the governor of the state of Colorado issued an Executive Order (Polis 2019) outlining expectations for the state's agencies (e.g., Colorado Parks and Wildlife, Colorado Department of Transportation, Department of Natural Resources) to work in concert to conserve big game migrations, winter ranges, and general habitat. Today, California, Colorado, Nevada, New Mexico, Oregon, and Wyoming all have policies that facilitate the conservation of ungulate migrations.

Conserving ungulate migration requires identifying the spatial location of current migration corridors, which is a complex, multi-step process. First, a potential population (i.e., herd) or segment of a population (i.e., sub-herd) that is suspected to migrate is identified, and global positioning system (GPS) tracking collars are affixed to a sample of individuals in that sub-herd. Collars are typically programmed to collect fine scale (8–24 locations per day) movement data for as long as the collar battery can last or until the death of the animal (deployments typically last

1–3 years; Ortega et al. 2023, Poulin et al. 2023, Verzuh et al. 2023). Once data are collected, migration start and end dates and the associated sequences are identified using a variety of methods including plotting points in a geographic information system (GIS), using automated methods (e.g., MigrateR; Spitz et al. 2017), or plotting displacement from winter range over time (Bunnefeld et al. 2011, Aikens et al. 2017, Merkle et al. 2022). Then, individual migratory routes can be delineated using a movement analysis, such as a Brownian bridge movement model (BBMM; Horne et al. 2007, Sawyer et al. 2009) or a line buffer method (Merkle et al. 2023). Finally, spatial aggregating techniques are used to meld the spatial distribution of each individual into a sub-herd-level migration corridor (i.e., where most of a sub-herd migrates). Spatially explicit products—such as migration corridors—identify the habitat most important to a sub-herd's migration and thus can be used in conservation planning (Middleton et al. 2020, Merkle et al. 2022).

While migration corridors are often based on data collected for only 2–3 years because of financial and logistical constraints, they can be used in relatively long-term conservation planning, policy, or actions. For example, when the State of Wyoming designates a migration corridor, it is integrated into the state's critical habitat repository. These designations do not expire, though they may be updated through a formal biological evaluation and public-input process. For years into the future, identified and designated corridors can then inform housing or energy development plans (Wyoming Game and Fish Department 2017) and conservation actions, such as where to place over- or under-passes across roads (Coe et al. 2015) or remove or modify fencing (Middleton et al. 2020). All these actions have long-lasting implications for the conservation of migratory ungulates. Thus, it is important for policy makers and wildlife management agencies to be confident that a sub-herd's migration corridor has been accurately identified and will correctly demarcate the corridor into the future. Ultimately, efforts to delineate a migration corridor must balance the need to identify a sub-herd's migration corridor as accurately as possible with the practicalities of large sample sizes or repeated data collection over many years due to constraints in funding and field personnel. Optimizing this trade-off requires an understanding of the consistency of migration corridors through time, and how altering different aspects of the sampling design of GPS collar deployment affects the delineation of corridors.

Migration corridors might shift over time because animal behavioral decisions can vary annually, often in response to annual variation in resource availability or human development (Xu et al. 2021). In the case of migratory animals, these changes in spatial behavior are known as migratory plasticity. Migratory plasticity can involve individuals switching between a migratory strategy and a resident strategy (Eggeman et al. 2016) or choosing a different migration route from one year to the next (Sawyer et al. 2019*b*). For instance, mule deer in western Wyoming reduced their use of migratory routes when surface disturbance by energy development in those routes surpassed 3% (Lambert et al. 2022). Further, elk can switch from being a resident to a migrant multiple times throughout their lifetime (Eggeman et al. 2016). Elk can also alter their migration routes in response to human pressures such as hunting (Boyce 1991). Migratory plasticity presents a potential challenge to long-term conservation of migration corridors. To account for and conserve such movements, static protected areas must be relatively large (Taillon et al. 2012, Nandintsetseg et al. 2019). Determining the ideal scope of such protected areas requires, in part, properly delineating the sub-herd's migration corridor, which must encompass the areas a sub-herd uses across multiple years. For example, when there is relatively high variation in individual behavior from year to year, delineating a migration corridor may require collaring more individuals over a longer period of time. Biologists can alter different aspects of the sampling design of GPS collar deployment that may influence the estimated footprint of migratory corridors: the number of individuals to collar in the first and subsequent years of a study, coverage of the landscape (i.e., spatial distribution of collared animals), and duration of the study. Quantifying the overall consistency of migration corridors and how corridor consistency is affected by sampling decisions will allow biologists to use a data-driven approach in designing future studies.

Mule deer have been the focus of much ungulate conservation work in the western United States (Middleton et al. 2020; Sawyer et al. 2006, 2020), as many of their populations have been declining (Wyoming Game and Fish Department Mule Deer Working Group 2015, Cooley et al. 2020), likely owing to a number of threats (Johnson et al. 2017, Sawyer et al. 2017). Mule deer exhibit a high degree of fidelity, meaning they use similar migration routes year after year (Sawyer et al. 2019*b*). For instance, in a meta-analysis of 9 sub-herds, Sawyer et al. (2019*b*) found that on average mule deer use 81% of their first year's spring migration route (i.e., individual fidelity). However, Sawyer et al. (2019*b*) also demonstrated a wide range of individual fidelity from 0% (changing a route completely) to 100% (using the exact same route each year). Further, van de Kerk et al. (2021) demonstrated plasticity in mule deer migration in Utah, with 51% of mule deer monitored for 2 or more years switching their migratory trajectory (e.g., dual-range migrants, multi-range migrants, gradual movers; i.e., individual fidelity). These studies indicate that while mule deer have strong individual fidelity, small variations in individual behavior could possibly scale up to changes in the migration corridor at the sub-herd level over time.

Using long-term datasets from 6 unique partially migratory sub-herds of mule deer that were captured in the same winter range areas over time, our objectives were to quantify 1) the consistency in migration corridors from year to year and cumulatively across years, and 2) test the influence of different aspects of the sampling design of GPS collar deployment—the proportion of a sub-herd collared and the proportion of newly collared individuals each year—on the consistency of migration corridor estimates over time. Because mule deer display some amount of migratory plasticity (Sawyer et al. 2019*b*) and collaring designs (number of animals collared) often vary from year to year, we expected some small level of variation in migration corridors from year to year. However, because mule deer have overall strong fidelity, we expected that over time and as data accumulated, migration corridors would become relatively consistent compared to annual fluctuations. Furthermore, we expected that the more individuals collared within a sub-herd, the more consistent the migration corridor would be, but that this consistency should asymptote because the estimate will eventually approach the complete migration corridor, which is unknown. We then created a logistical framework to design sampling protocols that will accurately delineate migration corridors through time.

STUDY AREA

We used data from GPS-collared female mule deer from 6 partially migratory sub-herds located in the western United States (Figure 1A). Sub-herds located in western Wyoming included the Mesa, Red Desert, Wyoming Range North, and Wyoming Range South sub-herds. These sub-herds occupied winter ranges that were characterized by sagebrush (*Artemisia* spp.) communities at elevations of roughly 1,300–2,200 m (Merkle et al. 2016; Sawyer et al. 2006, 2017, 2019*b*). Animals in these sub-herds migrated on average 154 km up in elevation to their summer ranges (~2,400–3,100 m) into the Wyoming, Gros Ventre, and Wind River mountain ranges (Merkle et al. 2016; Sawyer et al. 2006, 2017, 2019*b*). In southern Wyoming, mule deer in the Atlantic Rim South sub-herd migrated an average of 82 km from their winter ranges (elevation = 1,920 m) just west of the Sierra Madre mountains to their summer ranges (elevation = 2,530 m) within the foothills of the Sierra Madre or into northern Colorado (Sawyer et al. 2009). Migrating Atlantic Rim South animals crossed areas that comprised primarily shrub species such as big sagebrush (*Artemisia tridentata*), black greasewood (*Sacrobatus vermiculatus*), and Utah juniper (*Juniperus osteosperma*; Sawyer et al. 2009). The San Juan sub-herd was located near the border of northern New Mexico and southern Colorado. These mule deer migrated on average 107 km from areas dominated by pinyon (*Pinus edulis*), juniper (*Juniperus scopulorum*), and sagebrush just east of Navajo Reservoir, New Mexico (winter range) to higher elevations that included montane vegetation communities in the southern San Juan Mountains of Colorado (summer range; Sawyer et al. 2019*a*, *b*).

METHODS

Mule deer captures and movement data

We captured female mule deer via helicopter net-gunning and outfitted them with a GPS store-on-board collar while on winter range (Telonics, Mesa, AZ, USA, and ATS Iridium, Isanti, MN, USA; Table 1). The median fix rate for

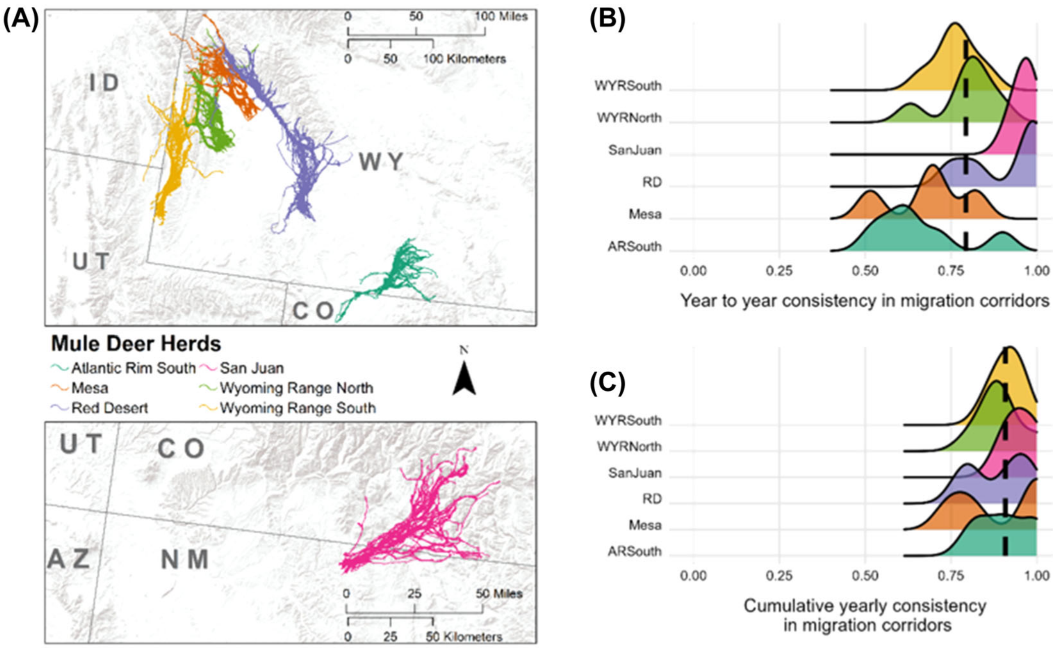

FIGURE 1 Spring migration routes of individual mule deer (A) and the densities of consistency in migration corridors from year to year (B) and cumulatively (C) for the Atlantic Rim (ARSouth; 2006–2005, 2009, 2018–2015), Mesa (2016–2012), Red Desert (RD; 2012–2011, 2019–2016), Wyoming Range North (WYRNorth; 2019–2013), and Wyoming Range South (WYRSouth; 2019–2013) sub-herds located in Wyoming, USA, and the San Juan (SanJuan; 2017–2012) sub-herd in northern New Mexico, USA.

TABLE 1 Study years, sample size (*n*; number of years), the number of spring migration sequences, and the estimated number of individuals wintering in the area that captures took place for each of the 5 sub-herds of mule deer located in Wyoming, USA, and 1 sub-herd located in northern New Mexico, USA.

Study sub-herd	Study years	*n* (number of years)	Migration sequences	Estimated number of mule deer on winter range
Atlantic Rim South	2005–2006, 2009, 2015–2018	6	141	2,500
Mesa	2012–2016	4	97	2,800
Red Desert	2011–2012, 2016–2019	5	316	3,000
San Juan	2012–2017	5	206	1,000
Wyoming Range North	2013–2019	6	194	10,000
Wyoming Range South	2013–2019	6	183	10,000

each sub-herd was 2 hours; although fix rates ranged from 1 hour to 24 hours in our dataset. Because ungulates profit (e.g., in terms of fat gain) from the consumption of high-quality forage at intermediate growth stages along their migration routes (Aikens et al. 2017, Middleton et al. 2018), we included only spring migrations in our analyses. In previous studies, springtime intra-individual variation in site fidelity was higher compared with autumn migration (Sawyer et al. 2019*b*).

We used annual plots of net-squared displacement to isolate spring migration sequences from the data (Aikens et al. 2017, Sawyer et al. 2019*b*) using a starting point within winter range (Bunnefeld et al. 2011). We kept a rather broad definition of spring migration that included movements on extended stopovers (even >1 month) until the animal settled on a summer range that was in a generally consistent area for >2 months. We defined migration routes (i.e., the general footprint delineating where individual deer migrated) by creating lines between each chronologically ordered individual-year sequence of GPS data, then buffering those lines by 382 m to accommodate GPS collar error and the habitat needs of mule deer (Merkle et al. 2023). The line buffer method ensured all corridors were contiguous and had consistent widths even though fix rates varied in our dataset, which allowed standardized inter-herd comparisons (Merkle et al. 2023).

Migration corridors and proportion collared

To create a sub-herd level migration corridor for each year, we spatially stacked individual buffered routes on top of one another and isolated where ≥10% of the sub-herd's migration routes overlapped (Sawyer et al. 2009, Merkle et al. 2022). When sample size for a given sub-herd and year was <20 individuals, we defined the sub-herd migration corridors as a minimum of 2 individuals (Kauffman et al. 2020). The 10% cut-off provides a clear-cut delineation (i.e., polygon) of a sub-herd's migration corridors including areas with relatively high use by a sub-herd. We determined the percentage of spatial overlap (consistency in a migration corridor) from one year to the next by overlapping the current year's corridor area with the previous year's corridor area and divided the area of intersection by the area of the previous year's corridor.

To assess cumulative migration corridors, we first created an initial sub-herd level corridor for the first year of data using the same methods outlined for the year-to-year migration corridors. For each additional year of data, however, we added data from new individuals to the initial year to create a cumulative migration corridor. For example, the migration corridor in the second year was inclusive of individuals monitored in the first and second year. When individuals had ≥2 spring migration sequences and thus multiple migration routes, we merged those migration routes into a single polygon representing the union of those 2 migration routes before creating the sub-herd level corridor (Merkle et al. 2022). To determine the percentage of spatial overlap (consistency in migration corridor), we intersected the current year's cumulative corridor area with the previous year's cumulative corridor area and divided the overlapping area by the area of the previous year's cumulative corridor.

To estimate the effect of sampling protocols on year-to-year and cumulative corridor estimates, we calculated 2 metrics for each year in each sub-herd. First, we estimated the proportion of individuals collared in a sub-herd by taking the number of collars and dividing it by the estimated total number of individuals wintering in the area the captures took place (Table 1). We based these estimates on local biologist and researcher expertise who knew the study areas well and counted deer annually from the air. These population estimates do not include estimates of error, nor do they vary by year, so our results should be interpreted with some caution. That said, our estimates of proportion of animals collared should provide useful guidance because they are based on typical aerial survey methods to estimate herd sizes of mule deer. Second, we calculated the proportion of collared individuals that were newly collared in a sub-herd for a given year (i.e., a proportion of newly collared individuals of 0.1 indicates that 10% of individuals collared in a given year were not collared in the previous year).

Statistical analyses

We assessed the influence of the proportion of a sub-herd collared and the proportion of newly collared individuals on 2 response variables, cumulative and year-to-year consistency in migration corridors. We examined empirical support for an interaction between the proportion newly collared and the proportion of the herd collared for each response variable. A significant interaction would suggest that the influence of the proportion of newly collared individuals on the consistency in migration corridors would vary depending on the proportion of the herd collared (or vice versa). We removed interaction terms from the model if they were not significant and did not present those results. In a univariate model, we tested how the number of cumulative collaring years influences consistency in migration corridors (cumulative). Our response variables were proportional; thus, we fit models using a generalized linear mixed effects models with a beta distribution (glmmTMB package in R; Brooks et al. 2017). Because we had multiple data points for each sub-herd (representing each year of data), we included sub-herd as a random intercept in each of the 3 models to reduce the effects of pseudoreplication. We checked for collinearity in our variables and did not find any; all variance inflation factors (VIFs) were <3 (Zuur et al. 2007). We used ArcMap 10.8 (Esri, Redlands, CA, USA) to create route and corridor distribution maps and R version 4.3.1 (R Core Team 2021) for all data importing, cleaning, statistical analyses, and additional data visualization (ggplot2 package in R, version 3.4.3; Wickham 2016).

RESULTS

We used 1,137 spring migration sequences from 510 unique individuals across 6 sub-herds located in Wyoming, Colorado, and New Mexico, USA (Figure 1A). The consistency in a migration corridor from year to year (Figure 1B; Figure 2A–C) was lower than when the data accumulated over time (Figure 1C; Figure 2D–F). The mean year-to-year consistency in a migration corridor across sub-herds and years was 79.3% (±14.3% SD) and ranged from 51.5% (Mesa) to 99.7% (Red Desert). The mean cumulative consistency in a migration corridor across sub-herds and years was 90.9% (±7.3% SD) and ranged from 74.3% (Mesa) to 100.0% (Atlantic Rim South).

From year to year, the proportion of newly collared individuals fluctuated within and among sub-herds (Figure 3). After the first year monitored, the average proportion of newly collared individuals was 0.359 (±0.259 SD). We found that the proportion of newly collared individuals influenced the year-to-year consistency in migration corridors (Figure 4A; $\beta = -0.733$, 95% CI = −1.436 to −0.031, $P = 0.041$). As the proportion of newly collared individuals increased, the consistency in migration corridors from year to year decreased. The average year-to-year proportion of individuals in a sub-herd collared was 0.012 (±0.012 SD) and ranged from 0.002 (Wyoming Range South) to 0.037 (San Juan; Figure 4B). As the proportion of marked individuals in a sub-herd collared increased, the year-to-year consistency in a migration corridor also increased (Figure 4B; $\beta = 92.780$, 95% CI = 51.188–134.371, $P < 0.001$).

Overall, there was a positive relationship between cumulative consistency in migration corridors and cumulative collaring years ($\beta = 0.407$, 95% CI = 0.255–0.559, $P < 0.001$). The more years a sub-herd was collared, the more consistent the sub-herd's migration corridor became (Figure 5A). We did not find evidence that consistency of a sub-herd's cumulative migration corridor was affected by the proportion of the sub-herd collared ($\beta = 0.623$, 95% CI = −18.112–19.359, $P = 0.948$). We found that increasing the proportion of newly collared individuals in a year reduced the consistency in the migration corridor ($\beta = -6.881$, 95% CI = −9.829 to −3.934, $P < 0.001$; Figure 5B). We also found evidence of an interaction between proportion of the sub-herd collared and the proportion of new collars on cumulative corridor consistency ($\beta = 113.497$, 95% CI = 11.693–215.301, $P = 0.029$). When a higher proportion of the entire sub-herd was collared, the proportion of new collars added in a given year had a reduced effect on overall corridor consistency (Figure 5B).

DISCUSSION

Migration corridors are often delineated with just a few years of GPS collar data, and those delineations can inform relatively long-term conservation policy. To determine the influence of sampling design on the consistency in migration corridors, we assessed the spatial stability of corridors in 6 sub-herds of mule deer monitored for

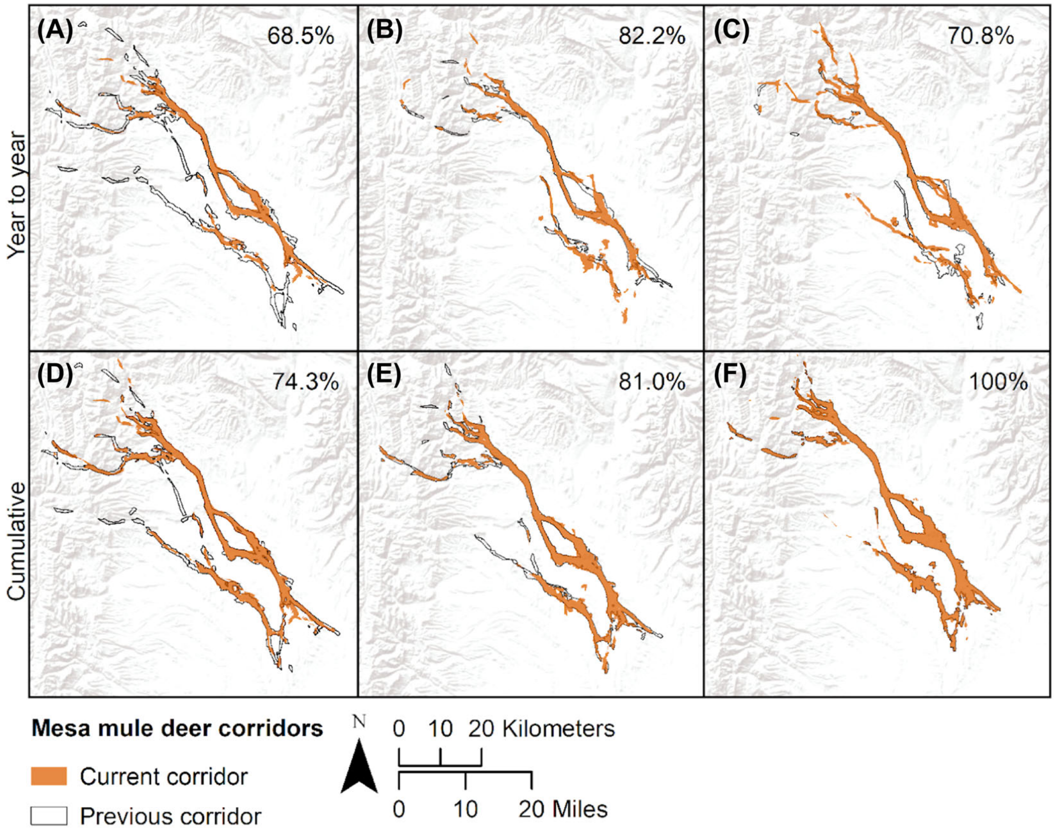

FIGURE 2 Migration corridors of the Mesa mule deer sub-herd located in Wyoming, USA, from year to year during A) 2013–2012, B) 2014–2013, and C) 2015–2014 and cumulatively during D) 2013–2012 compared to 2012 (2 years), E) 2014–2012 compared to 2013–2012 (3 years), and F) 2015–2012 compared to 2014–2012 (4 years). Percentages in the upper right corner represent the overlap of migration corridors (area of use by 10% or ≥2 of the individuals in a sub-herd).

5–7 years (totaling 510 individuals). There was moderate year-to-year variation in spring migration corridors (overall consistency was 79.3%), suggesting that both interannual variation in individual movements and the integration of newly collared individuals each year can influence the spatial delineation of a migration corridor. However, we found that monitoring a sub-herd for multiple years clearly increased the consistency of spring migration corridor estimates. Further, the consistency of spring migration corridors also depended on the proportion of the sub-herd initially collared and how many new animals are collared in each subsequent year. Our results collectively demonstrate that sampling design can play a strong role in properly delineating a migration corridor.

The presence of annual variation in spring migration corridors—even in species with known fidelity to migratory routes—can be explained in part by annual variation in habitat-based movement decisions. To maximize fitness, animals should distribute themselves across the landscape in a way that maximizes the intake of resources and subsequently minimizes costs (MacArthur and Pianka 1966, Pulliam 1974, Pyke 1984, Stephens and Krebs 1986, Brown 1999). For instance, feral horse (*Equus ferus caballus*) density on Sable Island (Canada) reflects the distribution of high-quality forage, and as horse density increases individuals tend to increase their use of areas with lower quality forage (van Beest et al. 2014). Additionally, because migratory animals use the landscape in accordance with the distribution of high-quality habitat (Monteith et al. 2018) and because availability and spatial distribution of high quality or preferred habitats may fluctuate from year to year (Aikens et al. 2020), individuals

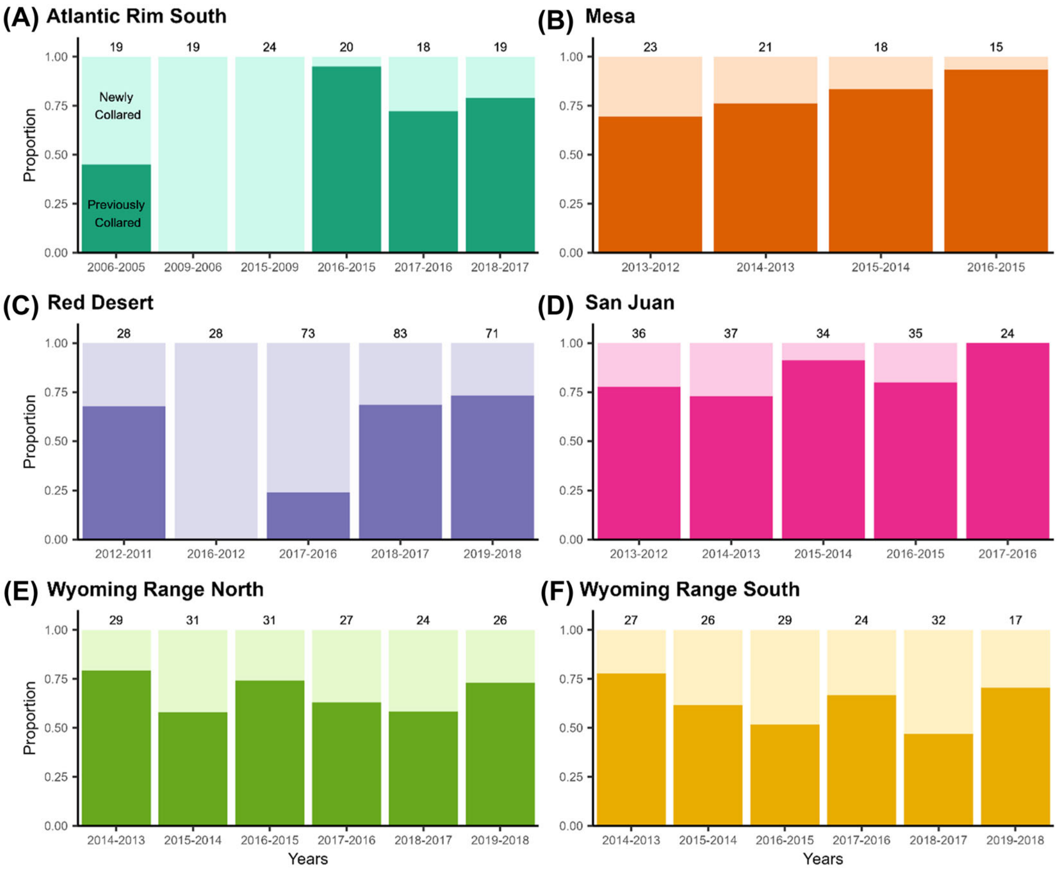

FIGURE 3 The year-to-year proportion of newly (lighter hues) and previously (darker hues) collared individuals compared to the previous year across collaring years in the A) Atlantic Rim South (2006–2005, 2009, 2018–2015), B) Mesa (2016–2012), C) Red Desert (2012–2011, 2019–2016), E) Wyoming Range North (2019–2013), and F) Wyoming Range South (2019–2013) sub-herds located in Wyoming, USA, and the D) San Juan (2017–2012) sub-herd in northern New Mexico, USA. The number of collared individuals in the current year are represented by values on top of each sub-herd's yearly bars. Approximate sub-herd sizes for each sub-herd: 2,500 (Atlantic Rim South), 2,800 (Mesa), 3,000 (Red Desert), 1,000 (San Juan), and 10,000 (Wyoming Range North and South). The first year of collaring is not represented because it was all newly collared individuals.

correspondingly alter their patterns of space use, including migration routes (Morrison et al. 2021). For example, caribou (*Rangifer tarandus*) herds in northern Québec and Labrador slightly shifted the location of their calving grounds from year to year potentially because of habitat reduction by intraspecific grazing pressure (Taillon et al. 2012). In mule deer, we found moderate year-to-year shifts in the distribution of spring migration corridors (average consistency = 79.3%), suggesting that annual variation in response to environmental changes or density (even if small; Sawyer et al. 2019*b*) in individuals' spring migration routes are manifesting into year-to-year changes in spatial distribution at the sub-herd level. We did not assess consistency in spatial distribution of stopovers (areas that are important to forage gain during migration; Sawyer and Kauffman 2011) in our study, but doing so would be useful for a more complete understanding of how sampling design influences inference on migration ecology in general. Furthermore, our analysis did not provide strong inference on how spring migration corridors were influenced by increasing overall sample size (i.e., adding additional collars to a sub-herd) over time, trade-offs in collaring new animals versus recollaring the same individuals, or the spatial distribution of the sampling design (i.e.,

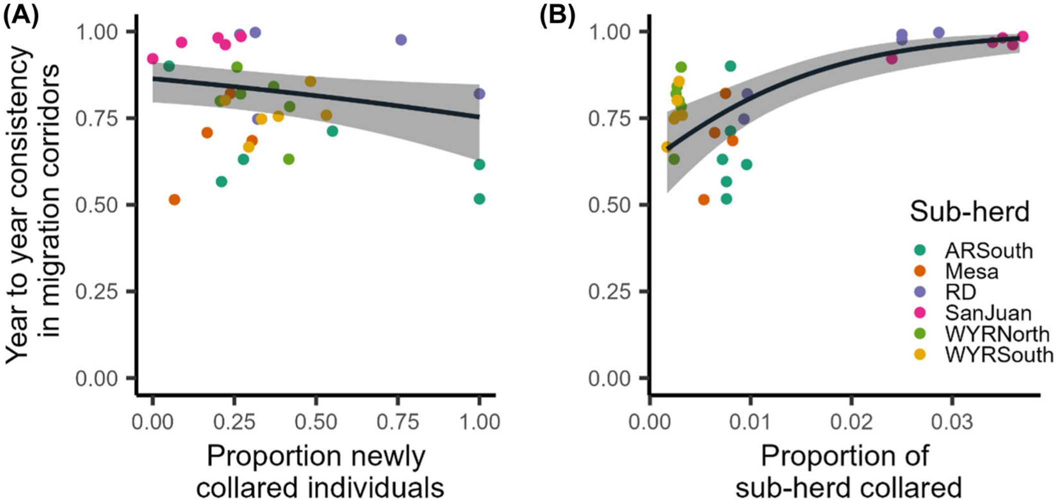

FIGURE 4 How year-to-year consistency in migration corridors is influenced by A) the proportion of newly collared individuals and B) the proportion of a sub-herd collared for the Atlantic Rim (ARSouth; 2006–2005, 2009, 2018–2015), Mesa (2016–2012), Red Desert (RD; 2012–2011, 2019–2016), Wyoming Range North (WYRNorth; 2019–2013), and Wyoming Range South (WYRSouth; 2019–2013) sub-herds located in Wyoming, USA, and the San Juan (SanJuan; 2017–2012) sub-herd in northern New Mexico, USA (*n* = 32).

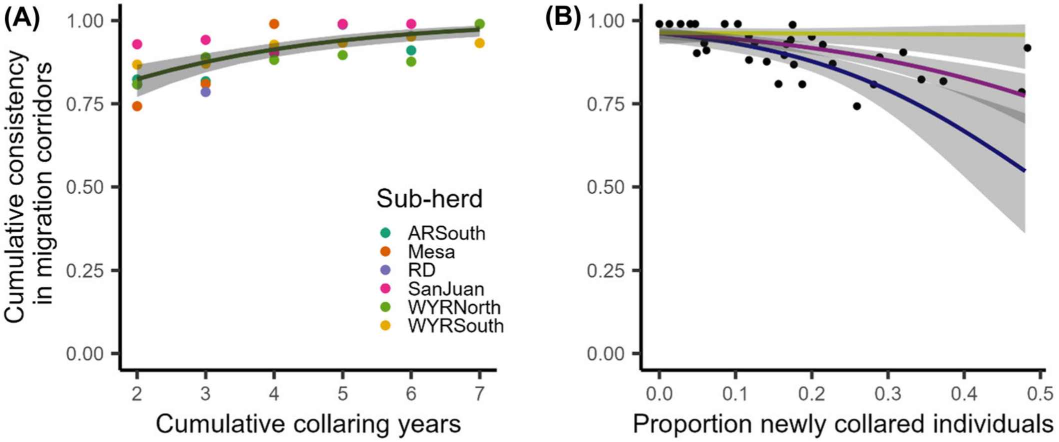

FIGURE 5 The relationship between cumulative consistency in migration corridors and A) the number of years a sub-herd is collared and B) the proportion of newly collared individuals (black points) when <1% of the sub-herd is collared (10% quantile; dark blue line), 2% of the sub-herd is collared (mean; magenta line), and 6% of the sub-herd is collared (90% quantile; yellow line) for the Atlantic Rim (ARSouth; 2018–2005), Mesa (2016–2012), Red Desert (RD; 2019–2011), Wyoming Range North (WYRNorth; 2019–2013), and Wyoming Range South (WYRSouth; 2019–2013) sub-herds located in Wyoming, USA, and the San Juan (SanJuan; 2017–2012) sub-herd in northern New Mexico, USA (*n* = 32).

concentrated deployment of collars versus interspersing collars out over a larger area). Evaluating these aspects would be a useful extension of this research in future studies.

In addition to true shifts in the space use of individuals from year to year in response to habitat heterogeneity, our results highlight how sampling design in a given year or sub-herd can lead to annual variation in the estimates of migration corridors. Collaring new individuals in a given year resulted in a change in both year-to-year and cumulative migration corridors. For instance, when new individuals are added to the collar sample, particularly when <6% of the sub-herd is collared in the first place, the cumulative spring corridors can shift each year by up to 26%. We found that when 1% of the sub-herd was collared and roughly 25% of those individuals were newly collared, the spring corridor consistency was predicted to be 84% (Figure 5B). Because each new year's and all previous year's variability in individual behavior is accounted for in the cumulative spring corridor, the variation in the consistency we observed was mainly due to variation among individuals instead of annual environmental variation along the corridor. Cumulative corridors can provide a better metric of corridor consistency over time given the positive correlation between the cumulative number of years of collaring data and spring corridor consistency (Figure 5A). Using cumulative corridors accounts for variation among individuals over time and therefore can provide managers with a robust estimation of corridor consistency over their study period.

For cumulative spring migration corridors, while our results suggest that collaring ≥6% of a sub-herd for a minimum of 2 years is the ideal standard to achieve ≥90% spring corridor consistency for mule deer, there are other pathways to delineate a relatively consistent migration corridor. If financial or other constraints preclude collaring ≥6% of a sub-herd, collaring an additional 16–25% new individuals each year for roughly 3–4 years will maintain a spring corridor consistency of ≥90%. Both of these sampling designs will allow biologists to gain more information on inter-annual variation in the corridor and inter- and intra-individual variation in spring migration routes. For example, we can consider 3 different approaches to collaring efforts between sub-herds (scenarios A, B, and C; Table 2). In scenario A, which is the ideal standard, ≥6% of a sub-herd is collared in the first year. In the second year, no new animals are collared. Based on our results, scenario A's consistency in spring migration corridor would be ≥96%. In scenario B, 2% of a sub-herd is collared in the first year. If in the second year, 2% of the sub-herd remains collared, but roughly 25% of the collars are redeployed onto new animals because of mortality or drop-off, the consistency in spring migration corridor would be approximately 90%. Finally, in scenario C, <1% of the sub-herd is collared in the first year. If in the second year, <1% of the sub-herd remains collared, but roughly 25% of the collars are redeployed onto new animals because of mortality or drop-off, the consistency in spring migration corridor would be approximately 84%. Despite the variation in corridor consistency in all 3 scenarios, and based on our results regarding cumulative collaring years (Figure 5A), monitoring into a third year would result in all consistencies increasing. Overall, adding more new collars and a higher proportion of a sub-herd collared increases our ability to capture variation in individual migration routes and delineate more representative migration corridors from year to year.

Our results inform conservation of migration corridors for mule deer, a species with relatively high migratory fidelity (Sawyer et al. 2019*b*, Morrison et al. 2021). Thus, our results likely represent conservative assessments of changes in the consistency of spring migration corridor estimates over time and the cumulative number of years required to robustly estimate a consistent migratory corridor for a given sub-herd. Elk and pronghorn (*Antilocapra americana*), for instance, have lower fidelity than mule deer (Morrison et al. 2021) and thus may require more sampling for a longer period of time to properly delineate a migration corridor. For instance, elk in the northern Rockies switch

TABLE 2 Proposed global positioning system (GPS) collar sampling design scenarios and the expected consistency of migration corridors estimated from the data for each scenario based on data collected from mule deer sub-herds in Wyoming and New Mexico, USA, in 2005–2019.

Scenario	Year 1 percent of sub-herd collared	Year 2 percent of sub-herd collared	Year 2 percent redeployed collars	Migration corridor consistency
A	6%	6%	0%	≥90%
B	2%	2%	25%	~90%
C	<1%	<1%	25%	~84%

between migration strategies at a mean rate of 15% each year (Eggeman et al. 2016), likely resulting in a more stochastic year-to-year and cumulative migration corridor. In addition, our analyses only considered shift and not directionality in the consistency in a migration corridor. We could imagine a case where year-to-year changes in the location of migration corridors could be directional (e.g., moving slowly up in elevation). For example, research on the effect of climate change on species' ranges suggests that many are shifting up in latitude (Lehikoinen et al. 2013).

MANAGEMENT IMPLICATIONS

Our work provides data-driven information for collaring projects aimed at determining spring migration corridors that are robust past the period when animals are collared. Our results clearly suggest that 1 year of collar data is not enough to delineate a robust migration corridor. The ideal standard sampling design is to collar ≥6% of the sub-herd for a minimum of 2 years. If collaring ≥6% of a sub-herd is not possible, monitoring for 3–4 years (Figure 5A) will provide roughly 90% consistency in a migration corridor. Moreover, adding 16–25% new individuals through collar redeployments each year will help capture inter- and intra-individual variation while maintaining a highly consistent corridor (≥90%), resulting in a robust corridor delineation. Careful consideration is necessary for defining sub-herds in a collaring project, but our framework can help refine and delineate accurate migration corridors for mule deer conservation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

University of Wyoming Institutional Animal Care and Use Committee permitted all capture and animal handling following the guidance and recommendations of the American Society of Mammalogists (Sikes and Gannon 2011).

DATA AVAILABILITY STATEMENT

Data used in this study is not publicly available because of sensitivities around the data itself and the ongoing nature of some of the projects, but the data owners are open to considering reasonable data sharing requests.

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