



Federal Aid in Wildlife Restoration Grant W-176-R
Annual report, September 2023

Pronghorn Movement & Population Ecology



Jesse DeVoe, Research Biologist, Montana Fish, Wildlife & Parks, 1400 S. 19th Ave, Bozeman, MT 59715,
jesse.devoe@mt.gov

Dr. Kelly Proffitt, Research Biologist, Montana Fish, Wildlife & Parks, 1400 S. 19th Ave, Bozeman, MT 59715,
kproffitt@mt.gov

Dr. Joshua Millspaugh, Professor, University of Montana, Forestry 108, Missoula, MT 59812,
joshua.millspaugh@mso.umt.edu

Jessica Krohner, Research Assistant, University of Montana, Forestry 108, Missoula, MT 59812,
jessica.krohner@gmail.com

Dr. Chris Hansen, Post-doctoral researcher, University of Montana, Forestry 108, Missoula, MT 59812,
christopher.hansen@mso.umt.edu

Madison Crane, M.Sc. Candidate, University of Montana, Forestry 108, Missoula, MT 59812,
madison.crane@umconnect.umt.edu

Molly McDevitt, Ph.D. Candidate, University of Montana, Forestry 108, Missoula, MT 59812,
molly1.mcdevitt@umconnect.umt.edu

State: Montana
Agencies: Fish, Wildlife & Parks and University of Montana
Grant: Pronghorn Movement and Population Ecology
Grant #: W-176-R
Time Period: 01 July 2019 – 30 June 2023

Table of Contents

Executive summary	3
Project background	5
Study locations.....	8
Big Hole.....	8
Madison.....	8
Paradise	9
Musselshell	9
Fergus-Petroleum	9
South Philips.....	9
Garfield-Rosebud.....	9
Powder River-Carter	10
Capture, instrumentation, & sampling	12
Survival monitoring & analysis.....	16
Objective #1: Delineate seasonal range and migration routes of pronghorn in each study area.....	25
1.1 Seasonal ranges and migration routes.....	25
1.2 Pronghorn migratory behaviors.....	52
Objective #2: Create and distribute maps of seasonal range and movement areas for pronghorn	73
Objective #3: Use seasonal range and movement data to identify potential barriers to movements, inform management decisions, and prioritize locations for habitat improvement projects.....	74
3.1 Identification of potential barriers to movements.....	74
ArcGIS Online: Montana Fence Mapping.....	74
Fence permeability analysis & interactive maps.....	77
3.2 Evaluating the effect of varying fence types on pronghorn movements behaviors.....	87
3.3 Collaborative efforts to remediate movement barriers.....	89
Objective #4: Develop a population model to identify important vital rates affecting population growth rates and describe important demographic differences between populations that are growing or stable, versus those that are limited in their population performance	93
Background & objectives.....	93
Methods.....	94
Process model and vital rates.....	94
Observation models.....	98
Model fitting.....	107
Literature review related to pronghorn vital rates.....	108

Results.....	112
Objective #5: Evaluate the effect of vegetation and other landscape features on pronghorn resource selection	113
Objectives.....	113
Methods.....	113
Results.....	115
Discussion	124
Management Implications.....	124
Literature Cited.....	125

Executive summary

The Montana Pronghorn Movement and Population Ecology Project was initiated in 2020 to collect information on pronghorn movements, seasonal habitat use, and demographics in 7 study areas across Montana that included the Big Hole, Paradise, Musselshell, Fergus-Petroleum, South Philips, Garfield-Rosebud, and Powder River-Carter study areas. A coinciding pronghorn study in the Madison Valley that began in 2019 and collected identical information was also included in this study. The primary objectives of the project were to: 1) delineate pronghorn seasonal range and movement routes in the study areas; 2) create and distribute maps of pronghorn seasonal range and movement areas; 3) use pronghorn seasonal range and movement data to identify potential barriers to movements, inform management decisions, and prioritize locations for habitat improvement projects; 4) develop a population model to identify important vital rates affecting population growth rates and describe important demographic differences between pronghorn populations that are growing or stable, versus those that are limited in their population performance, and 5) evaluate the effect of vegetation and other landscape features on pronghorn resource selection.

During winters (January – March) 2019 – 2022, we captured and instrumented with GPS collars a total of 702 adult female pronghorn, including 40 in 2019 (Madison only), 390 in 2020, 168 in 2021, and 104 in 2022. This capture effort included a total of 54 in the Paradise, 82 in the Madison, 85 in the South Philips, 89 in the Big Hole, 91 in the Garfield-Rosebud, 93 in the Fergus-Petroleum, 103 in the Musselshell, and 105 in the Powder River-Carter. Across all study areas, a total of 64 (9%) collars malfunctioned, 373 (53%) animals died, and 265 (38%) collars remained active at the end of the study (June 30, 2023). We collected 10,946,734 locations from 702 individuals. Monthly survival probabilities in each population generally remained stable from 2020 – 2023, ranging 0.76 (95% credible interval [CRI] 0.60 – 0.89) to 0.97 (CRI 0.92 – 0.99). Annual survival probabilities ranged from 0.62 (CRI 0.50 – 0.74) in 2023 for the Powder River-Carter to 0.81 (CRI 0.71 – 0.90) in 2022 for South Philips.

Movement patterns of individuals were diverse within and across study areas with population-level seasonal ranges generally reflecting greater contraction from summer to winter in the montane-valley populations of southwest Montana as compared to the prairie populations of central and eastern Montana. On a monthly basis, we generated study area-specific summary reports of collared pronghorn movements and mortality information and distributed these reports widely to state and federal agency biologists, non-profit conservation organizations, and private landowners. We developed a web interface that allows biologists to view pronghorn movement trajectories and identify areas that may be barriers to pronghorn movements. FWP leadership will determine how additional web-based data sharing will proceed. In addition, we mapped fences across all study areas based on aerial imagery to identify potential movement barriers and evaluate the influence of fences on pronghorn movements and behaviors. We used the collar location data in combination with the fence spatial data to evaluate the influence of different fence types of pronghorn behavioral responses, which provides evidence for the prioritization of woven wire fence removal or modification to more permeable fence types. We also developed a tool to identify and quantify pronghorn behavioral responses to fences that outputs interactive maps ranking fences based on these responses, which can then be used to identify problematic barriers to pronghorn movement and prioritize remediation efforts.

We have continued development of the integrated population model (IPM) to 1) identify important vital rates affecting population growth rate, 2) contrast important vital rates among populations, and 3) develop hypotheses to explain why some pronghorn populations experience limitations on population growth rate. We developed a dataset of pronghorn population size and harvest, compiled priors and potential covariates that will be used in the IPM and have begun model development. The IPM will be finalized for the final report in March 2024.

Finally, we developed summer resource selection models to support habitat conservation and management efforts for pronghorn. The primary objectives of this analysis were to 1) evaluate pronghorn selection in relation to ground-based measurements of forage and fawn security resources, and 2) evaluate how selection behavior changes correspond with changing biological needs and spatiotemporal variations in plant communities during the summer. Based on the collar location data and vegetation and diet sampling efforts completed during summers 2021 and 2022, we developed 2 summer resource selection models describing: 1) overall selection without consideration of temporal variation and 2) time-varying selection. Our non-time-varying model indicated that pronghorn selection increased with higher emergent forage cover and was optimal at 70% bare ground cover. Our time-varying model indicated that pronghorn selection for forage cover, forb digestible energy, and shrub cover varied across the summer, with some evidence for positive selection for each variable prior to and during peak spring that marginally decreased thereafter. Shrub cover, however, slightly increased during and immediately following the fawning period. Overall, this study suggests pronghorn may be balancing predation risks through their selection of fine-scale resources (i.e., by selecting areas with only slightly less bare ground than available) and varying their selection for shrub cover during the summer to avoid shrub cover once fawns become reliant on early detection to avoid predation.

Project background

Pronghorn (*Antilocapra americana*) provide important ecosystem functions and recreational opportunities in Montana, which hosts the 2nd largest population and harvest of pronghorn across their range (Yoakum 2004a). Ecologically, pronghorn may serve as an umbrella species for conserving sagebrush-grasslands and maintaining landscape connectivity of these systems (Rowland et al. 2006, Gates et al. 2012). Because of the important ecosystem functions and recreational opportunities pronghorn provide, conserving and managing pronghorn and their habitats is a priority for Montana Fish, Wildlife & Parks (FWP), land management agencies, private landowners, non-governmental organizations (NGOs), and numerous additional stakeholders. However, there are limited data available regarding pronghorn movements and population dynamics for informing and prioritizing habitat and conservation efforts and effective management strategies throughout the state. To date, only very few pronghorn movement and demographic studies in Montana exist (e.g., Pyrah 1987, Dunn and Byers 2008, Poor et al. 2012, Jakes et al. 2018a, Jones et al. 2020), underscoring the need for more information on movements and population dynamics collected across the varying environments found throughout pronghorn range in Montana.

In addition, widespread pronghorn population declines in portions of central and eastern Montana in recent decades highlight the need for information regarding survival and demography to identify and understand potential issues limiting pronghorn population recovery. Pronghorn populations were abundant and at or above regional population objectives/long-term averages throughout their range in Montana during the mid-2000s with harvest totaling 33,500 at its peak in 2007 (Montana Fish Wildlife and Parks 2020a). Following widespread blue-tongue virus (BTV) outbreaks in the subsequent 2 years and the record cold and snow during winter 2010–2011, harvest fell to a low of 8,200 in 2013. Pronghorn populations typically rebound quickly with favorable weather conditions (O’Gara 2004a), yet numbers of pronghorn in many of Montana’s central and eastern populations are <50% of population objective despite multiple years of favorable weather and minimal harvest. Meanwhile, mule deer and elk populations are exceeding objective levels over much of the region (Montana Fish Wildlife and Parks 2020b, c).

The factors currently limiting pronghorn population recovery across central and eastern Montana are unknown. Stochastic events including severe winter weather may cause significant mortality events and lead to high variability in overwinter pronghorn survival rates (Martinka 1967, Pyrah 1987, O’Gara 2004a). Accordingly, survival of adult female pronghorn is lower or more variable than for other northern temperate ungulates, ranging from 0.29 to 0.87 in Montana (Boccardori 2002, Dunn and Byers 2008, Barnowe-Meyer et al. 2009, Jakes 2015). During winter 2010–2011, abnormally high snow depths in central and eastern Montana concentrated pronghorn on winter range, resulting in rapid exhaustion of browse, over-exposure of pronghorn to extreme conditions, and altered pronghorn distributions (Jakes et al. 2018a). In the Fort Peck Reservoir area of central Montana, flooding exacerbated the effects of the 2011 severe winters, as more than 2,000 pronghorn attempting to return north to fawning and summer ranges were stranded on the south side of the reservoir by unusually high floodwaters and were presumed to have died after exhausting nearby forage. Fences and roads may also act as barriers to movements within or between seasonal ranges, potentially affecting seasonal range selection and reducing habitat availability (Jakes et al. 2018b, Jones et al. 2019).

Pronghorn pregnancy and birth rates are generally constant and high due to substantial in utero maternal investment in offspring (O’Gara 2004, Kohlmann 2004). However, these vital rates may be affected by habitat

or weather conditions that may limit pronghorn population recovery. Dunn and Byers (2008) recorded pronghorn reproductive failures on the National Bison Range (NBR), Montana, following severe drought in 2003 and none of the marked females that weaned fawns in 2003 gave birth in 2004. During this same period, annual counts of other ungulates on the NBR did not indicate exceptionally low survival or fecundity rates, potentially because other ungulate species fall lower on the maternal energy-expenditure spectrum than pronghorn (Dunn and Byers 2008). Additionally, severe weather, such as drought or harsh winters, may have carryover effects on future reproductive success or survival (Webster et al. 2002). Although habitat or weather-related factors generally have a greater effect on pronghorn populations than predation, predation may limit recruitment and have important effects on population growth (O’Gara and Shaw 2004). Overall fawn mortality across 18 studies averaged 71%, with 76% of all mortalities being due to predation from coyotes (O’Gara and Shaw 2004). We expect that coyote predation is the main proximate cause of mortality of pronghorn fawns in central and eastern Montana, but its extent may vary due to habitat conditions (weather and land-use influences on vegetation), the abundance of alternate prey species (Hamlin and Mackie 1989, Berger and Conner 2008, Berger et al. 2008), or coyote control operations (Harrington and Conover 2007, Brown and Conover 2011). In addition, disease events like BTV or epizootic hemorrhagic disease (EHD) can also impact pronghorn populations via direct mortality or negative effects on reproduction (Thorne et al. 1988, Dubay et al. 2006, Gray 2013). In July 2007, a BTV outbreak occurred across portions of central and eastern Montana and precipitated the decade-long decline in pronghorn populations (Montana Fish Wildlife and Parks 2012).

The Montana Pronghorn Project was initiated in 2020 to address the lack of information on pronghorn movements and population dynamics and to improve our understanding of factors limiting population recovery in Montana for informing future population monitoring and management strategies. A coinciding pronghorn study in the Madison Valley that began in 2019 and collected identical information was also integrated into this project. The overall purpose of this project was to identify seasonal ranges and movement corridors and provide demographic data for pronghorn populations in 8 study areas broadly distributed across Montana (Figure 1). Our specific objectives included:

1. Delineate seasonal range and migration corridors of pronghorn in each study area.
2. Create and distribute maps of seasonal range and movements of pronghorn.
3. Use seasonal range and movement data to identify potential barriers to movements, inform management decisions, and prioritize locations for habitat improvement projects.
4. Develop a population model to identify important vital rates affecting population growth rates and describe important demographic differences between pronghorn populations that are growing or stable, versus those that are limited in their population performance.
5. Evaluate the effect of vegetation and other landscape features on pronghorn resource selection.

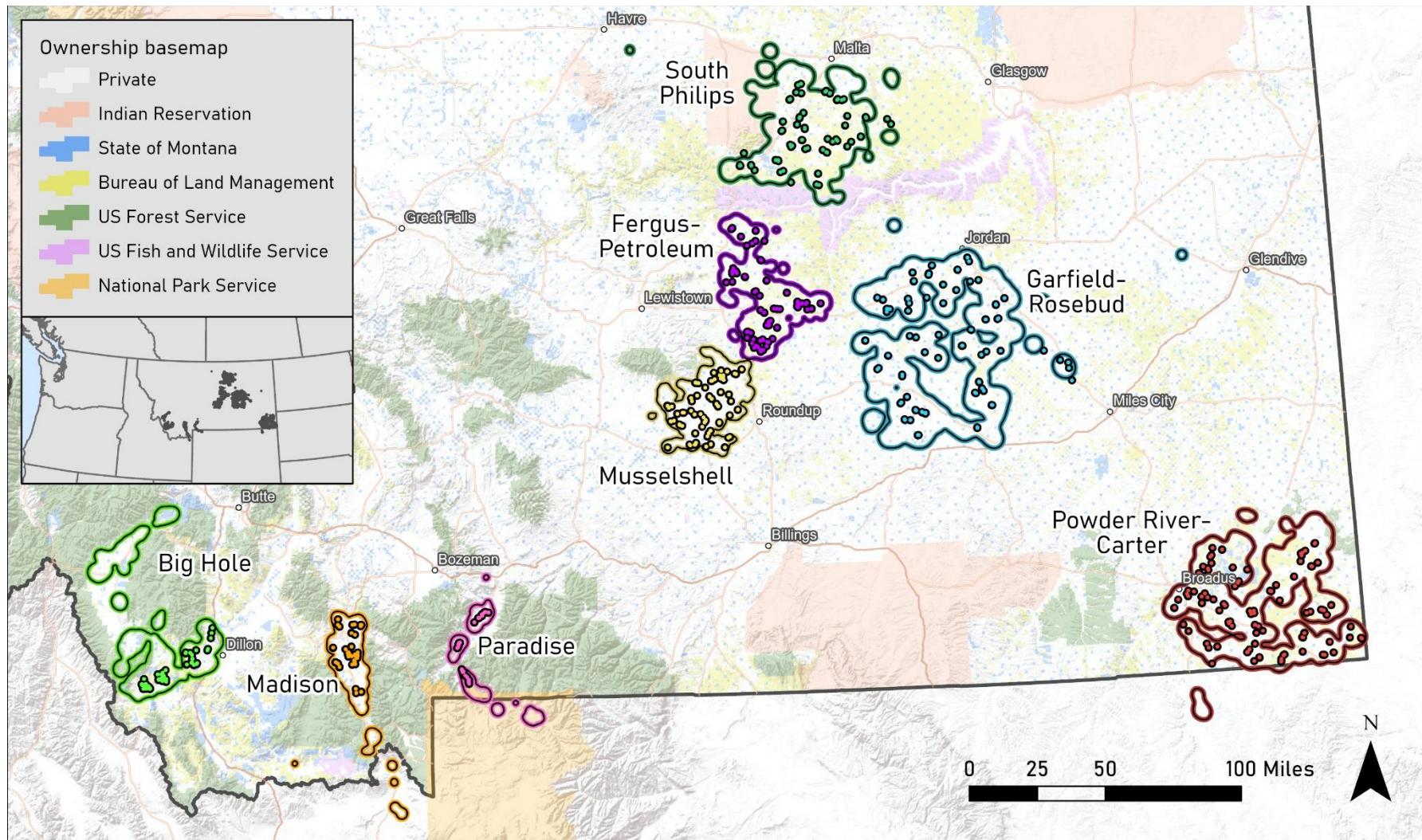


Figure 1. Locations (color-filled points) of all adult female pronghorn captured and instrumented during winters 2019 – 2021 (Madison only) and 2020–2022 (all other study areas) in the 8 study areas (polygons) for the Montana Pronghorn Movement and Population Ecology Project. Study areas are represented by annual ranges calculated from 95% kernel density estimates based on collar locations.

Study locations

The 8 study areas were located in the southwestern, central, and southeastern regions of Montana (Figure 1) and included the Big Hole, Madison, Paradise, Musselshell, Fergus-Petroleum, South Phillips, Garfield-Rosebud, and Powder River-Carter. These areas were selected based on local needs identified by FWP area biologists and where considerable community, conservation partner, and agency interest existed for understanding anthropogenic impediments, habitat, or other factors influencing pronghorn movement patterns or fitness. The study areas represent the annual ranges of pronghorn herds defined by 95% kernel density estimates of all GPS locations for each study population (see Capture, instrumentation, and sampling).

These areas typify the open and relatively flat environments occupied by pronghorn across the majority of their range. The prairie of the central and southeast study areas was dominated by sagebrush (*Artemisia* spp.) steppe and mixed grass prairie (i.e., thickspike wheatgrass [*Elymus lanceolatus*], green needlegrass [*Nassella viridula*], blue grama [*Bouteloua gracilis*], needle and thread grass [*Hesperostipa comata*]). The southwest study areas were dominated with valley grasslands (i.e., bluebunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*], western wheatgrass [*Pascopyrum smithii*]) interspersed with an understory of herbaceous forb species. Cultivated croplands also occur in each study area and consist mostly of common wheat and leguminous forbs (e.g., field peas, lentils, alfalfa). These agricultural lands comprised 7 – 22% of the study areas, with Paradise, Garfield-Rosebud, Madison, and Powder-River Carter having the least (7-10%) and Big Hole, South Phillips, Fergus-Petroleum, and Musselshell having the most (12-22%). Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus canadensis*) were sympatric with pronghorn in the study areas. Potential predators of pronghorn varied by study area and included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), gray wolf (*Canis lupis*), coyote (*C. latrans*), American black bear (*Ursus americanus*), grizzly bear (*U. arctos*), and golden eagle (*Aquila chrysaetos*).

Big Hole

The Big Hole study area (2,480 km²) is located in Beaverhead and Deer Lodge Counties and comprises hunting districts (HD) 310 and 318 in southwestern Montana. Elevation averages 1,960 m (range: 1,535 – 2,844 m), with a 30-yr mean annual precipitation of 44 cm (range: 26 – 91 cm), July temperature of 16 °C (range: 11 – 20 °C), and January temperature of -7 °C (range: -12 to -3 °C). During the study period (2020 – 2022), mean annual precipitation was 37 cm, July temperature was 17 °C, and January temperature was -6 °C (Figure 2). Ownership was dominated by private (50%), federal (38%), and state of Montana (12%). Federal lands were managed primarily by Bureau of Land Management (BLM; 20%) and United States Forest Service (USFS; 18%).

Madison

The Madison study area (1,230 km²) is located in Madison County and comprises HD 360 in southwestern Montana. Elevation averages 1,802 m (range: 1,469 – 2,793 m), with a 30-yr mean annual precipitation of 48 cm (range: 32 – 86 cm), July temperature of 17 °C (range: 12 – 21 °C), and January temperature of -6 °C (range: -10 to -2 °C). During the study period (2020 – 2022), mean annual precipitation was 48 cm, July temperature was 18 °C, and January temperature was -5 °C (Figure 2). Ownership was dominated by private (79%), federal (13%), and state of Montana (7%). Federal lands were managed primarily by USFS (9%) and BLM (4%).

Paradise

The Paradise study area (680 km²) is located in Park County and comprises HD 313 in southwestern Montana. Elevation averages 1,824 m (range: 1,468 – 2,686 m), with a 30-yr mean annual precipitation of 42 cm (range: 26 – 71 cm), July temperature of 18 °C (range: 12 – 22 °C), and January temperature of -5 °C (range: -8 to -3 °C). During the study period (2020 – 2022), mean annual precipitation was 45 cm, July temperature was 19 °C, and January temperature was -4 °C (Figure 2). Ownership was dominated by federal (53%), private (43%), and state of Montana (4%). Federal lands were managed primarily by National Park Service (41%) and USFS (11%).

Musselshell

The Musselshell study area (2,140 km²) is located in Musselshell and Golden Valley Counties and comprises HD 513 in central Montana. Elevation averages 1,203 m (range: 1,018 – 1,708 m), with a 30-yr mean annual precipitation of 38 cm (range: 36 – 53 cm), July temperature of 20 °C (range: 15 – 24 °C), and January temperature of -4 °C (range: -9 to 2 °C). During the study period (2020 – 2022), mean annual precipitation was 35 cm, July temperature was 21 °C, and January temperature was -3 °C (Figure 2). Ownership was dominated by private (85%), federal (9%), and state of Montana (6%). Federal lands were managed primarily by BLM (7%).

Fergus-Petroleum

The Fergus-Petroleum study area (2,550 km²) is located in Fergus and Petroleum Counties and comprises HD 481 and 420 in central Montana. Elevation averages 949 m (range: 753 – 1,296 m), with a 30-yr mean annual precipitation of 36 cm (range: 34 – 47 cm), July temperature of 22 °C (range: 16 – 25 °C), and January temperature of -5 °C (range: -11 to 3 °C). During the study period (2020 – 2022), mean annual precipitation was 30 cm, July temperature was 23 °C, and January temperature was -3 °C (Figure 2). Ownership was dominated by private (69%), federal (24%), and state of Montana (6%). Federal lands were managed primarily by BLM (24%).

South Philips

The South Philips study area (4,500 km²) is located in Philips County and comprises HD 620 in north-central Montana. Elevation averages 818 m (range: 684 – 1,237 m), with a 30-yr mean annual precipitation of 36 cm (range: 32 – 45 cm), July temperature of 21 °C (range: 16 – 25 °C), and January temperature of -7 °C (range: -14 to 1 °C). During the study period (2020 – 2022), mean annual precipitation was 29 cm, July temperature was 23 °C, and January temperature was -5 °C (Figure 2). Ownership was dominated by private (56%), federal (37%), and state of Montana (7%). Federal lands were managed primarily by BLM (35%).

Garfield-Rosebud

The Garfield-Rosebud study area (7,570 km²) is located primarily in Garfield and Rosebud Counties and comprises HD 701 in central Montana. Elevation averages 906 m (range: 765 – 1,131 m), with a 30-yr mean annual precipitation of 36 cm (range: 32 – 43 cm), July temperature of 22 °C (range: 17 – 26 °C), and January temperature of -6 °C (range: -12 to 2 °C). During the study period (2020 – 2022), mean annual precipitation was 32 cm, July temperature was 23 °C, and January temperature was -3 °C (Figure 2). Ownership was dominated by private (87%), state of Montana (7%), and federal (6%). Federal lands were managed primarily by BLM (6%).

Powder River-Carter

The Powder River-Carter study area (6,060 km²) is located in Powder River and Carter Counties and comprises HD 705 in southeastern Montana. Elevation averages 1,042 m (range: 853 – 1,358 m), with a 30-yr mean annual precipitation of 40 cm (range: 37 – 47 cm), July temperature of 22 °C (range: 17 – 25 °C), and January temperature of -6 °C (range: -11 to 1 °C). During the study period (2020 – 2022), mean annual precipitation was 34 cm, July temperature was 23 °C, and January temperature was -4 °C (Figure 2). Ownership was dominated by private (63%), federal (27%), and state of Montana (10%). Federal lands were managed primarily by BLM (26%).

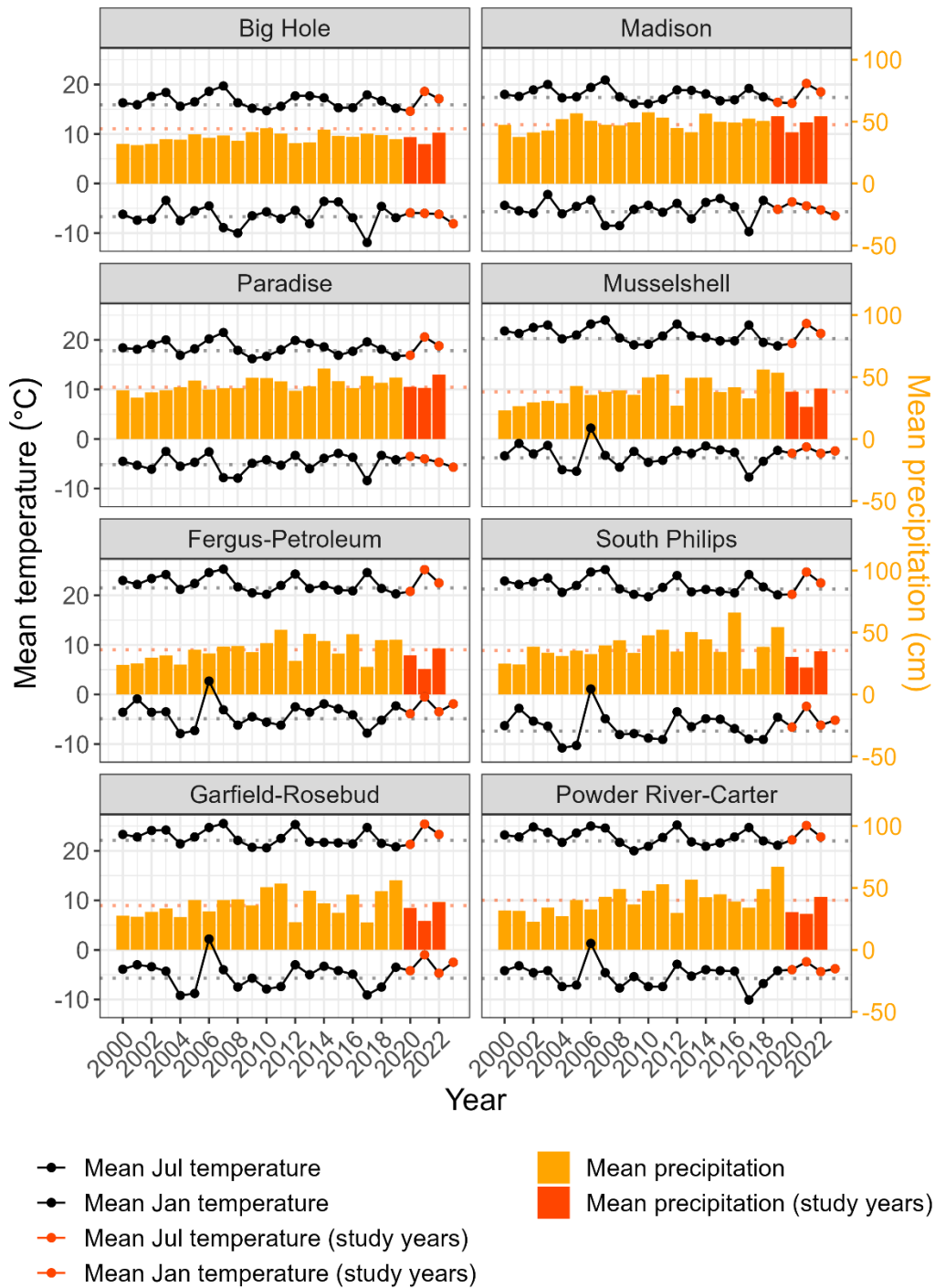


Figure 2. Climographs showing annual mean January and July temperatures (left axis) and precipitation (right axis) for each study area from 2000 – 2023 in the Montana Pronghorn Movement and Population Ecology Project. The dark orange points and bars represent values during the years of the study (2020 – 2023 for all except Madison, which additionally included 2019). Dotted lines represent respective 30-year temperature and precipitation averages. The missing precipitation and July temperature data for 2023 is due to the reporting period end date of June 30, 2023.

Capture, instrumentation, & sampling

Across all study areas during winters (January – March) 2019 to 2022, we captured and instrumented with GPS collars a total of 702 adult female pronghorn, including 40 in 2019 (Madison only), 390 in 2020, 168 in 2021, and 104 in 2022 (excluding the Madison; Table 1). From 2020 – 2022, we sought to maintain approximately 60 animals with active collars in each study area; however, accessibility and distribution of animals limited our sampling success in the Big Hole and Paradise. We outfitted each animal with a Lotek LiteTrack Iridium 420 collar programmed to collect locations every hour for 3 years, transmit a VHF signal during daylight periods, and transmit a mortality alert and signal if the device is stationary for ≥ 5 hours. These collars uploaded locations via Iridium satellites to a web platform for viewing and downloading near-real-time data. We monitored collared animals through June 30, 2023.

Table 1. Collaring accomplishments in each study area during winters of 2019 – 2021 (Madison only) and 2020 – 2022 (all remaining study areas).

	2019	2020	2021	2022	Total
Big Hole	-	46	31	12	89
Madison	40	20	22	-	82
Paradise	-	24	22	8	54
Musselshell	-	60	19	24	103
Fergus-Petroleum	-	60	18	15	93
South Philips	-	60	16	9	85
Garfield-Rosebud	-	60	18	13	91
Powder River-Carter	-	60	22	23	105
Total	40	390	168	104	702

During the 2019 (Madison only) and 2020 captures, we collected blood serum from each animal for disease screening. In 2021, we collected additional blood samples only in the Big Hole and Paradise study areas due to the prior years limited sample sizes. Blood serum samples were assayed for evidence of exposure to pathogens including *Anaplasma* bacteria, bovine herpesvirus, bovine respiratory syncytial virus, bluetongue virus, bovine viral diarrhea type 1, bovine viral diarrhea type 2, epizootic hemorrhagic disease, *Leptospira canicola*, *L. grippa*, *L. hardjo*, *L. ictero*, *L. pomona*, and parainfluenza-3. These pathogens were selected for screening because of either their known potential impact to individual or herd health (e.g., bluetongue virus and epizootic hemorrhagic disease) and/or because of their known association with livestock or wildlife health (e.g., *Leptospira* serovars, *Anaplasma*, bovine viral syncytial virus, and parainfluenza-3). All assays were conducted by the Montana Veterinary Diagnostic Laboratory (Bozeman, Montana), except for epizootic hemorrhagic disease which was conducted by the Washington Animal Disease Diagnostic Lab (Pullman, Washington). Evidence for exposure varied by pathogen and study area (Table 2). We found no serological evidence of exposure in any study area for bovine herpesvirus or *L. hardjo*. We found evidence of exposure in all study areas for *Anaplasma* (ranging from 16 – 92% seroprevalence), *L. ictero* (ranging from 1 – 20% seroprevalence), and parainfluenza-3 (ranging from 75 – 100% seroprevalence). Below, we discuss each of the pathogens identified through serology in our study areas.

Anaplasmosis, or gall sickness, is a disease of blood cells primarily affecting domestic cattle that is caused by *Anaplasma* bacteria and transmitted by ectoparasites. Pronghorn are susceptible to infection of *Anaplasma*, however, serious clinical signs have not been recorded in pronghorn and little evidence exists that pronghorn act as important carriers (Kuttler 1984, O’Gara 2004b). We found serological evidence for exposure to *Anaplasma* in all study areas with seroprevalence averaging 52% (range: 16 – 85%) with Big Hole having the lowest seroprevalence and Paradise having the highest seroprevalence. Although we found evidence of exposure across all study areas, these results are not expected to impact individual or herd health.

Bovine respiratory syncytial virus is an infection associated with respiratory disease primarily affecting domestic cattle that can cause the formation of syncytial cells – the fusion of infected cells with neighboring cells. Pronghorn are susceptible to infection by the virus, which is most likely transmitted from cattle; however, serious clinical signs have not been recorded in pronghorn (O’Gara 2004b). We found serological evidence of low levels of exposure to bovine respiratory syncytial virus in only the Big Hole (6%), Musselshell (5%), and Paradise (4%) study areas. Although evidence of exposure occurred in each of these study areas, these results are not expected to impact individual or herd health (O’Gara 2004b).

Bluetongue virus is transmitted by biting midges in the *Culicoides* genus and other arthropods and can cause acute and frequently fatal hemorrhagic disease in domestic and wild ungulates. Pronghorn are susceptible to disease caused by the bluetongue virus which can result in large, all-sex and -age die-offs that occur primarily during late summer and early autumn (Thorne et al. 1988, O’Gara 2004b). There is evidence that pronghorn can, however, be exposed to this virus without suffering high rates of mortality or showing clinical signs (O’Gara 2004b). Exposure to bluetongue virus was only detected in Garfield–Rosebud (5%). These results were not atypical of exposure rates observed in pronghorn and do not necessarily indicate pathogenicity (O’Gara 2004b, Dubay et al. 2006).

Epizootic hemorrhagic disease virus is transmitted by biting midges in the *Culicoides* genus and other arthropods and can cause acute and frequently fatal hemorrhagic disease in domestic and wild ungulates. Pronghorn are susceptible to epizootic hemorrhagic disease which can result in large, all-sex and -age die-offs that occur primarily during late summer and early autumn. There is evidence that pronghorn can, however, be exposed to this virus without suffering high rates of mortality or showing clinical signs (O’Gara 2004b, Gray 2013). Epizootic hemorrhagic disease virus exposure was detected in all study areas except Big Hole, Madison, and Paradise, with seroprevalence averaging 22% (ranging 12 – 39%) in study areas where exposure was detected. These results were not atypical of exposure rates observed in pronghorn and do not necessarily indicate pathogenicity (Barrett and Chalmers 1975, O’Gara 2004b, Gray 2013).

Bovine viral diarrhea (types 1 & 2) is a disease caused by a virus that causes diarrhea and can induce immunosuppression, which allows for development of secondary bacterial pneumonia in domestic and wild ungulates. The different types (1 & 2) reflect differences in the antigens found on the viral surface protein and do not relate to the virulence of the virus. Pronghorn are susceptible to infection of bovine viral diarrhea, however, there is little evidence of serious clinical effects or that pronghorn act as important carriers. We found a low seroprevalence of both types of bovine viral diarrhea in the majority of study areas (0 – 7%) and seroprevalence of 41% for bovine viral diarrhea type 2 in Fergus–Petroleum. These seroprevalences were similar to those found in Alberta and Saskatchewan where no clinical signs were observed (Barrett and Chalmers 1975, Kingscote and Bohac 1986).

Leptospira spp. are members of an infective serological group of bacteria that can infect nearly all mammals. Infection varies in severity from asymptomatic to fatal depending on the host and the serovar of *Leptospira*. Naturally occurring *Leptospira* infections in wildlife are usually asymptomatic, but may result in renal failure, lysis of red blood cells, fever, inappetence, hemorrhages on mucous membranes, jaundice, dehydration, infertility, abortion, stillbirths, or weakened neonates. Pronghorn are susceptible to *Leptospira* spp. infection which may cause some mortality; however, clinical disease in wildlife is rare and not likely a major limiting factor in pronghorn populations (O’Gara 2004b). We found low seroprevalence (1%) to *L. grippo* and *L. pomona* in only the Big Hole, low seroprevalence (2%) to *L. canicola* in only the Paradise, and low to moderate seroprevalence to *L. ictero* that averaged 12% (ranging 7 – 20%) in all study areas. Although few previous studies have reported exposure to these *Leptospira* serovars in pronghorn and cross-reactivity of serovars makes interpretation of seroprevalence challenging, we do not suspect our results indicate pathogenicity and are within the range of normal exposure rates to other serovars of *Leptospira* in pronghorn (O’Gara 2004b).

Parainfluenza-3 is a virus capable of causing respiratory disease in domestic ungulates. The disease is usually associated with mild to subclinical infections, but may serve an important role as an initiator under severe stress that can lead to development of secondary bacterial pneumonia. Parainfluenza-3 exposure is highly variable among pronghorn from different areas and across years; however, there is no evidence of serious disease and the virulence is unknown in pronghorn (Barrett and Chalmers 1975, O’Gara 2004b, Dubay et al. 2006). We found an average seroprevalence of 91% (ranging from 75 – 100%) to parainfluenza-3 across all populations with Big Hole having the lowest seroprevalence and Madison and Powder River-Carter having the highest seroprevalence. Although evidence of exposure occurred in each study area, these results are not expected to impact individual or herd health (Barrett and Chalmers 1975, Stauber et al. 1980, O’Gara 2004b).

Table 2. Seroprevalence for anaplasmosis (ANPLSM), bovine herpesvirus (BHV), bovine respiratory syncytial virus (BRSV), bluetongue virus (BTV), bovine viral diarrhea type 1 (BVD1), bovine viral diarrhea type 2 (BVD2), epizootic hemorrhagic disease (EHD), *Leptospira canicola* (L. CAN), *L. grippo* (L. GRI), *L. hardjo* (L. HAR), *L. ictero* (L. ICT), *L. pomona* (L. POM), and parainfluenza-3 (PI3) based on serological screening of adult female pronghorn sampled in the Madison during winter 2019, all study areas during winter 2020, and in the Big Hole and Paradise during winter 2021.

Herd	Statistic	ANPLSM	BHV	BRSV	BTV	BVD1	BVD2	EHD	L CAN	L GRI	L HAR	L ICT	L POM	PI3
Big Hole	# Sampled	76	76	76	76	76	76	75	76	76	76	76	76	76
	# Exposed	12	0	6	0	0	0	0	0	1	0	7	1	57
	% Exposed	16	0	8	0	0	0	0	0	1	0	9	1	75
Madison	# Sampled	21	21	21	21	21	21	21	21	21	21	21	21	21
	# Exposed	13	0	0	0	0	1	0	0	0	0	2	0	21
	% Exposed	62	0	0	0	0	<1	0	0	0	0	<1	0	100
Paradise	# Sampled	47	47	47	47	47	47	34	47	47	47	47	47	47
	# Exposed	40	0	4	0	0	1	0	1	0	0	8	0	42
	% Exposed	75	0	9	0	0	2	0	2	0	0	17	0	90
Musselshell	# Sampled	59	58	58	59	57	57	22	59	59	59	59	59	57
	# Exposed	33	0	3	0	0	2	3	0	0	0	4	0	48
	% Exposed	56	0	5	0	0	4	14	0	0	0	7	0	84
Fergus-Petroleum	# Sampled	61	61	61	61	61	61	58	61	61	61	61	61	61
	# Exposed	33	0	0	0	1	25	14	0	0	0	8	0	59
	% Exposed	54	0	0	0	2	41	24	0	0	0	13	0	97
South Philips	# Sampled	60	60	60	60	60	60	58	60	60	60	60	60	60
	# Exposed	32	0	0	0	1	4	7	0	0	0	7	0	58
	% Exposed	53	0	0	0	2	7	12	0	0	0	12	0	97
Garfield-Rosebud	# Sampled	61	61	61	61	61	61	49	61	61	61	61	61	61
	# Exposed	21	0	0	3	0	2	9	0	0	0	7	0	52
	% Exposed	34	0	0	5	0	3	18	0	0	0	12	0	85
Powder River-Carter	# Sampled	61	57	57	61	61	61	33	61	61	61	61	61	57
	# Exposed	36	0	0	0	2	1	13	0	0	0	12	0	56
	% Exposed	59	0	0	0	3	2	39	0	0	0	20	0	98

Survival monitoring & analysis

Of the 702 collared animals, 373 (53%) died, ranging 24 – 61 (44 – 67%) animals in each study area, and 64 (9%) collars malfunctioned, ranging 3 – 15 (3 – 22%) collars in each study area (Figure 3). Mortality investigations were completed as soon as possible after receiving the mortality alerts. We classified each mortality causation as “certain” or “probable” depending on the level of evidence available at the mortality site; however, given the challenges in determining certainty in mortality causes for pronghorn (e.g., limited ability to investigate mortalities before evidence is gone), we consider all recorded mortality causes as “probable” and report them here as such. When possible, we collected incisors from each mortality to estimate age using cementum age analysis performed by Matson’s Laboratory, Montana. Across winters 2020, 2021, and 2022, mortalities associated with capture operations (capture myopathy or injury) totaled 33, ranging 1 – 9 mortalities in each study area (Figure 4; Table 3). The remaining mortalities were classified as unknown (n = 136), predation (n = 87), natural (n = 35), legal harvest (n = 36), disease (n = 20), human-related (n = 11), injury (n = 8), starvation (n = 3) and illegal take (n = 4). We classified mortalities as natural when evidence suggested the cause was due to other mechanisms, such as birth complications, or when a carcass was found intact with little evidence to classify otherwise. Many natural mortalities included animals that were suspect of having disease but pathology results from sampled organs were negative or inconclusive. Of the predation mortalities, we classified 56 as coyote, 7 as mountain lion, 5 as bobcat, 3 as canid, and 15 as unknown. Of the disease mortalities, 13 (65%) were sampled by collecting fresh tissues from various organs and analyzed for hemorrhagic disease testing at the Southeastern Cooperative Wildlife Disease Study, Georgia. Of these samples, 6 tested positive for epizootic hemorrhagic disease (EHD) virus, 3 tested positive for blue tongue virus (BTV), 4 tested negative for both EHD and BTV, and 0 tested positive for both EHD and BTV. Fergus-Petroleum comprised 1 EHD positive, Garfield-Rosebud comprised 2 EHD positive, Powder River-Carter comprised 2 EHD and 3 BTV positive, and South Philips comprised 1 EHD positive result. Of the human-related mortalities, we classified 6 as vehicle collisions, 3 as harvest wounding loss, 1 as train collision, and 1 as snared. A total of 265 (38% of total collared) collared animals were on air at the end of the study (June 30, 2023).

We collected a total of 129 incisors for aging animals at time of mortality. The average age was 5.7 years (range: 1 – 12 years) and varied by study area (Table 4), with the oldest average ages occurring in the Big Hole (7.9 years), Paradise (6.7 years), and Madison (6.2 years), and the youngest average ages occurring in the Fergus-Petroleum (4.5 years), Garfield-Rosebud (4.8 years), and Powder River-Carter (4.9 years). The oldest individuals occurred in the Big Hole (12 years) and Paradise (12 years) study areas. Average age varied by mortality cause (Table 5), with human-related wounding loss (8 years), vehicle collision (7.5 years), and predation (6.2) comprising the oldest average age individuals and illegal take (2 years), injury (4.2 years), capture (4.9 years), and disease (4.9 years) comprising the youngest average age individuals.

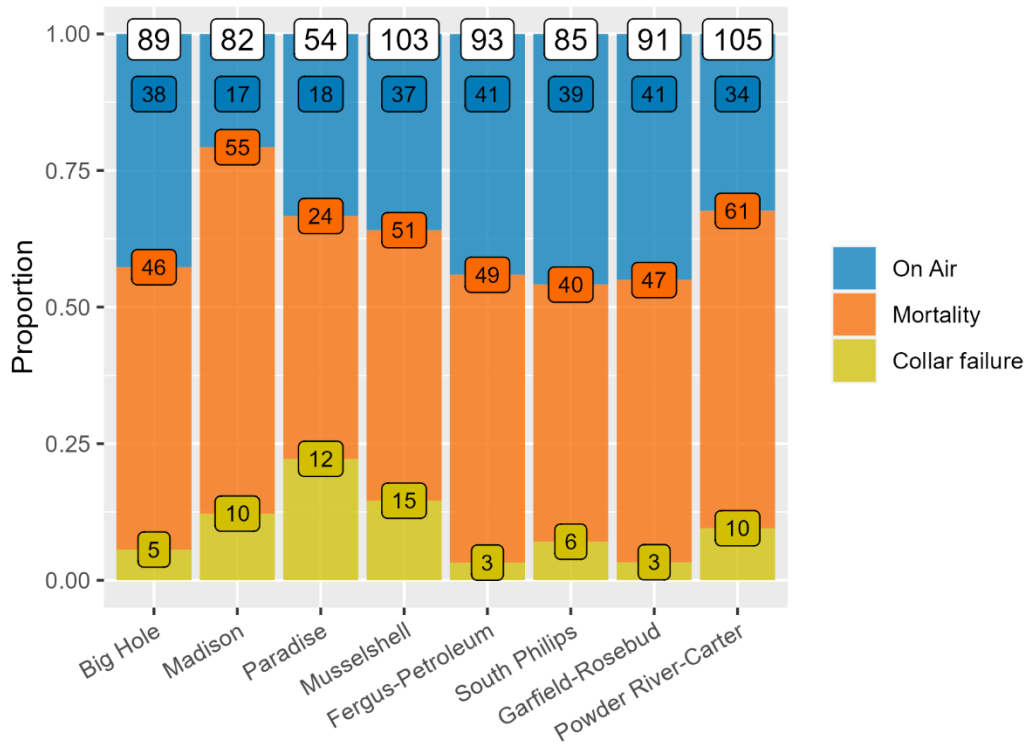


Figure 3. Number and proportion of total collared adult female pronghorn remaining on air, dead, or with a malfunctioned collar in each study area across 2019 - 2023 in the Montana Pronghorn Movement and Population Ecology Project as of June 30, 2023. The total number of collared animals in each study area is labeled at the top of each bar.

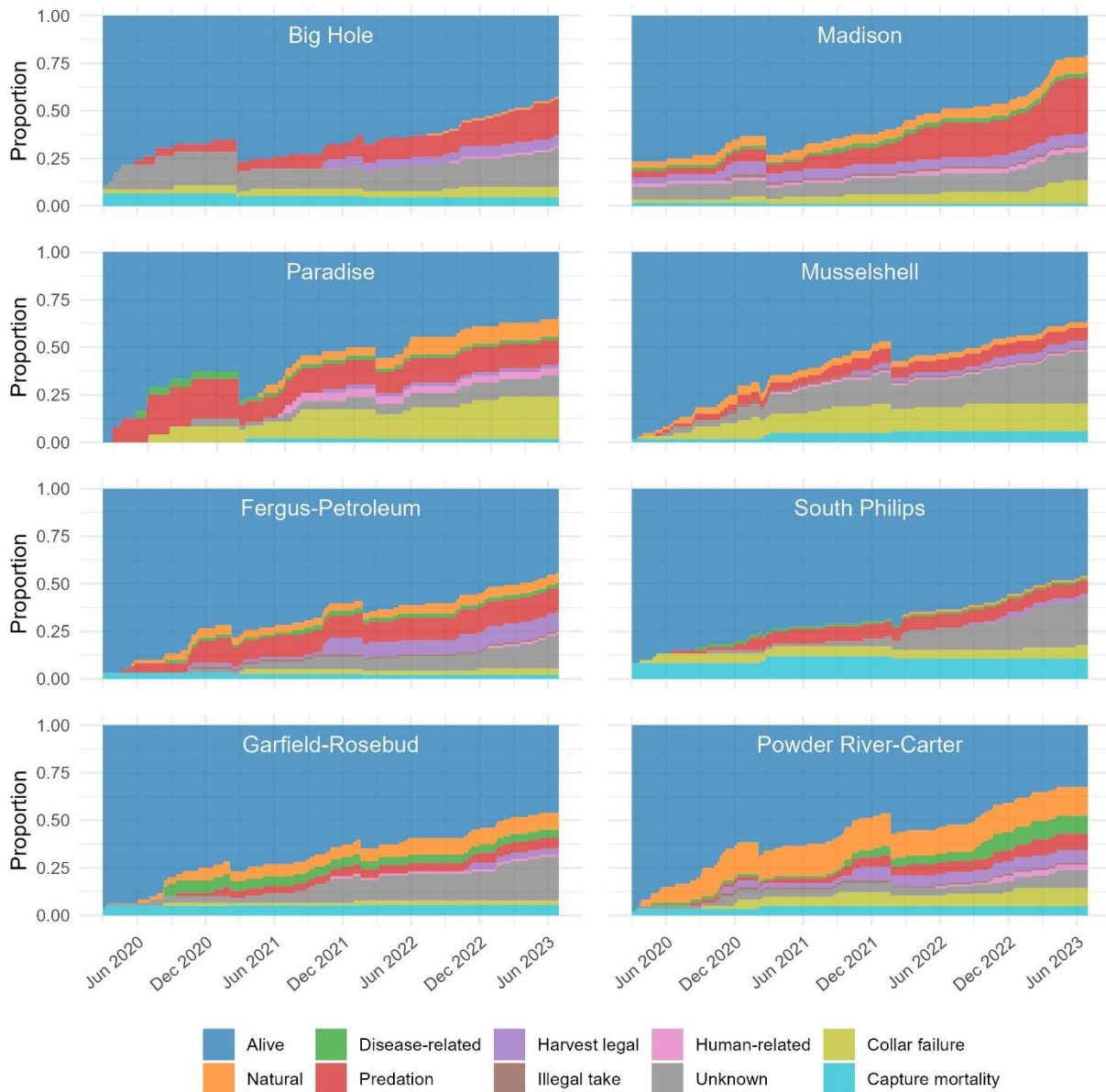


Figure 4. Proportion of the total collared adult female pronghorn alive, dead, or with a malfunctioned collar in each study area in the Montana Pronghorn Movement and Population Ecology Project spanning from January 2020 to June 2023. Cause of death was determined by field investigations. Note that this figure does not include data collected in 2019 in the Madison study area.

Table 3. Number (and proportion) of each probable mortality cause in each study area and year in the Montana Pronghorn Movement and Population Ecology Project, 2020 – 2023* (2019 – 2023* for Madison). Cause of death was determined by field investigations. *Note that 2023 only includes January – June.

Herd	Mortality Cause	2019	2020	2021	2022	2023*	Total
Big Hole	Capture	--	3 (0.21)	1 (0.11)	--	--	4
	Natural	--	--	--	1 (0.07)	--	1
	Predation - coyote	--	2 (0.14)	2 (0.22)	6 (0.43)	4	14
	Predation - unknown	--	1 (0.07)	1 (0.11)	1 (0.07)	--	3
	Harvest legal	--	--	4 (0.44)	1 (0.07)	--	5
	Human-related - vehicle collision	--	--	--	1 (0.07)	--	1
	Unknown	--	8 (0.57)	1 (0.11)	4 (0.29)	5 (0.56)	18
	Total	--	14	9	14	9	39
Madison	Capture	--	1 (0.10)	--	--	--	1
	Natural	--	--	1 (0.12)	1 (0.07)	--	2
	Injury	1 (0.10)	1 (0.10)	--	--	--	1
	Starvation	1 (0.10)	--	--	--	2 (0.15)	1
	Disease	1 (0.10)	--	1 (0.12)	--	--	2
	Predation - coyote	2 (0.20)	2 (0.20)	1 (0.12)	4 (0.29)	5 (0.38)	9
	Predation - canid	--	--	1 (0.12)	--	--	1
	Predation - lion	--	--	--	1 (0.07)	--	1
	Predation - unknown	--	--	2 (0.25)	3 (0.21)	2 (0.15)	5
	Harvest legal	2 (0.20)	2 (0.20)	--	1 (0.07)	--	5
	Illegal take	--	1 (0.10)	--	--	--	1
	Human-related - vehicle collision	--	--	--	1 (0.07)	--	1
	Human-related - train collision	--	1 (0.10)	--	--	--	1
	Unknown	3 (0.30)	2 (0.20)	2 (0.25)	3 (0.21)	3 (0.23)	11
Total	10	10	8	14	13	43	
Paradise	Capture	--	--	1 (0.11)	--	--	1
	Natural	--	--	2 (0.22)	3 (0.50)	--	5
	Disease	--	1 (0.14)	--	--	--	1
	Predation - canid	--	2 (0.29)	--	--	--	2
	Predation - lion	--	2 (0.29)	1 (0.11)	1 (0.17)	--	4
	Predation - unknown	--	1 (0.14)	--	--	--	1
	Harvest legal	--	--	1 (0.11)	--	--	1
	Human-related - vehicle collision	--	--	2 (0.22)	--	--	2
	Unknown	--	1 (0.14)	2 (0.22)	2 (0.33)	2 (1.00)	5
Total	--	7	9	6	2	22	
Musselshell	Capture	--	1 (0.08)	3 (0.17)	2 (0.15)	--	6
	Natural	--	1 (0.08)	--	--	--	1
	Injury	--	2 (0.17)	--	--	--	2
	Predation - coyote	--	3 (0.25)	1 (0.06)	1 (0.08)	--	5
	Predation - lion	--	--	2 (0.11)	--	--	2
	Harvest legal	--	--	2 (0.11)	2 (0.15)	--	4
	Illegal take	--	1 (0.08)	--	--	--	1
	Human-related - vehicle collision	--	--	1 (0.06)	--	--	1
	Unknown	--	4 (0.33)	9 (0.50)	8 (0.62)	8 (1.00)	21
	Total	--	12	18	13	8	43
Fergus-Petroleum	Capture	--	2 (0.12)	--	--	--	2
	Natural	--	2 (0.12)	--	1 (0.08)	--	3
	Injury	--	1 (0.06)	--	1 (0.08)	--	2
	Disease	--	1 (0.06)	1 (0.08)	--	--	2
	Predation - coyote	--	6 (0.35)	1 (0.08)	3 (0.23)	--	10
	Predation - unknown	--	2 (0.12)	--	--	--	2
	Harvest legal	--	1 (0.06)	6 (0.50)	2 (0.15)	--	9

Herd	Mortality Cause	2019	2020	2021	2022	2023*	Total
	Illegal take	--	1 (0.06)	--	--	--	1
	Human-related - snare	--	--	--	1 (0.08)	--	1
	Unknown	--	1 (0.06)	4 (0.33)	5 (0.38)	7 (1.00)	10
	Total	--	17	12	13	7	42
South Philips	Capture	--	5 (0.56)	4 (0.40)	--	--	9
	Natural	--	--	--	1 (0.07)	--	1
	Disease	--	1 (0.11)	--	--	--	1
	Predation - coyote	--	2 (0.22)	4 (0.40)	--	--	6
	Harvest legal	--	--	--	2 (0.13)	--	2
	Unknown	--	1 (0.11)	2 (0.20)	12	6 (1.00)	16
	Total	--	9	10	15	6	35
Garfield-Rosebud	Capture	--	3 (0.20)	1 (0.08)	1 (0.08)	--	5
	Natural	--	3 (0.20)	1 (0.08)	3 (0.25)	--	7
	Injury	--	1 (0.07)	--	--	--	1
	Disease	--	4 (0.27)	--	--	--	4
	Predation - coyote	--	2 (0.13)	2 (0.15)	1 (0.08)	--	5
	Harvest legal	--	--	--	3 (0.25)	--	3
	Human-related - wounding loss	--	--	1 (0.08)	--	--	1
	Unknown	--	2 (0.13)	8 (0.62)	4 (0.33)	7 (1.00)	17
Total	--	15	13	12	7	43	
Powder River-Carter	Capture	--	2 (0.10)	2 (0.11)	1 (0.06)	--	5
	Natural	--	10 (0.50)	4 (0.22)	1 (0.06)	--	15
	Injury	--	--	--	1 (0.06)	--	1
	Disease	--	1 (0.05)	3 (0.17)	6 (0.35)	--	10
	Predation - coyote	--	--	2 (0.11)	--	--	2
	Predation - bobcat	--	1 (0.05)	1 (0.06)	1 (0.06)	2 (0.33)	5
	Predation - unknown	--	--	1 (0.06)	1 (0.06)	--	2
	Harvest legal	--	2 (0.10)	4 (0.22)	1 (0.06)	--	7
	Illegal take	--	1 (0.05)	--	--	--	1
	Human-related - wounding loss	--	--	--	2 (0.12)	--	2
	Human-related - vehicle collision	--	--	--	1 (0.06)	--	1
	Unknown	--	3 (0.15)	1 (0.06)	2 (0.12)	4 (0.67)	6
	Total	--	20	18	17	6	57

Table 4. Summary of age at mortality for each study area in the Montana Pronghorn Movement and Population Ecology Project. Ages were estimated based on cementum analyses of incisors collected at time of death during 2020 – 2023 (2019 – 2023 for Madison).

	Total	Mean Age	SD	Min. Age	Max. Age
Big Hole	15	7.9	3.5	2	12
Madison	11	6.2	2.3	4	10
Paradise	17	6.7	3.3	1	12
Musselshell	9	6.2	2.4	3	10
Fergus-Petroleum	11	4.5	2.4	2	9
South Philips	4	5.2	2.1	3	7
Garfield-Rosebud	25	4.8	2.6	1	10
Powder River-Carter	37	4.9	2.1	2	10
Overall	129	5.7	2.8	1	12

Table 5. Summary of age at mortality for probable mortality causes for the Montana Pronghorn Movement and Population Ecology Project. Ages were estimated based on cementum analyses of incisors collected at time of death during 2020 – 2023 (2019 – 2023 for Madison).

Mortality cause	Total	Mean Age	SD	Min. Age	Max. Age
Capture	10	4.9	2.2	2	8
Disease	17	4.9	2.1	1	9
Injury	6	4.2	1.9	2	7
Natural	28	5.4	2.4	2	10
Predation	32	6.2	3.1	1	12
Harvest legal	3	6	3.6	2	9
Illegal take	1	2	--	2	2
Human-related – wounding loss	3	8	2	6	10
Human-related – vehicle collision	4	7.5	2.5	5	11
Unknown	25	5.9	3.4	1	12

Based on known fate information from the collared pronghorn, we estimated monthly survival within and across populations (Figure 5) and annual survival by population (Figure 6, Table 6) for 3 biological years spanning 01 Jun – 31 May (i.e., 2020 – 2021, 2021 – 2022, and 2022 – 2023). To do so, we used a multi-state survival model with known detection (in this case, perfect detection is assumed) in a Bayesian framework. Multi-state survival models are flexible to a range of recapture period lengths (occasion lengths) and can integrate the influence of individual animal states (i.e., alive or dead) and transition between states on survival rates. We built the model using an encounter history of length = 36 (36 months across 3 years) which includes 3 animal-years. In our analysis, we censored mortalities that occurred within 14 days of capture and estimated baseline-survival rate, which includes harvest-related mortality and illegal take (Brodie et al. 2013). The results from the model estimate survival as the probability that an animal alive at the start of one occasion (i.e., a month) will survive to the start of the next occasion (the next month). From these data, we used the survival model to first estimate mean monthly survival (Figure 5) and then estimate annual survival by taking the product of all 12 months' survival probabilities within each year and population (Figure 6, Table 6).

Monthly survival probabilities across study populations varied between 0.76 (95% credible interval [CRI] 0.60 – 0.89) and 0.97 (CRI 0.92 – 0.99), with the lowest occurring in Apr 2023 and the highest commonly occurring in several months and years (Figure 5). The lowest monthly survival estimates occurred in Apr 2023 in Madison (0.76, CRI 0.60 – 0.89), July 2020 in Paradise (0.87, CRI 0.73 – 0.96), and June 2022 in Paradise (0.87, CRI 0.74 – 0.96). There were only 10 months (4%) across the entire study duration and populations where monthly survival estimates were estimated to be less than 0.90, which occurred in Madison (Mar and Apr 2023), Paradise (Jul 2020, Nov 2020, and Jun 2022), Fergus-Petroleum (Nov 2020, Nov 2021, and Oct 2022), and Powder River-Carter (Nov 2021 and Oct 2022) study populations. The majority (55%) of months across the entire study duration and populations were estimated to have monthly survival rates of 0.95 or greater.

Annual survival estimates within populations indicated slight increases in point estimates from 2021 to 2022 in most populations (excluding Big Hole, Madison, and Paradise) and slight decreases in point estimates from 2022 to 2023 in most populations (excluding Paradise and Fergus-Petroleum). Annual survival estimates ranged from a low of 0.57 (CRI 0.43 – 0.71) in 2023 for Madison to a high of 0.81 (CRI 0.71 – 0.90) in 2022 for South Philips (Figure 6; Table 6). However, credible intervals overlapped substantially across most years within

populations and across all populations, suggesting that there was no difference in annual survival between some years for each population and across populations. The survival estimates reported here include 33 harvested individuals from all 8 of the populations. Most of the pronghorn (17 of 33) were harvested in 2021, with the majority from the Fergus-Petroleum (n = 7) and Powder River-Carter herds (n = 6).

The next steps for these analyses include adding environmental and anthropogenic covariates (drought severity, winter conditions, road, and fence densities, etc.) to gain further insight into how landscape and climatic factors influence pronghorn survival rates across populations.

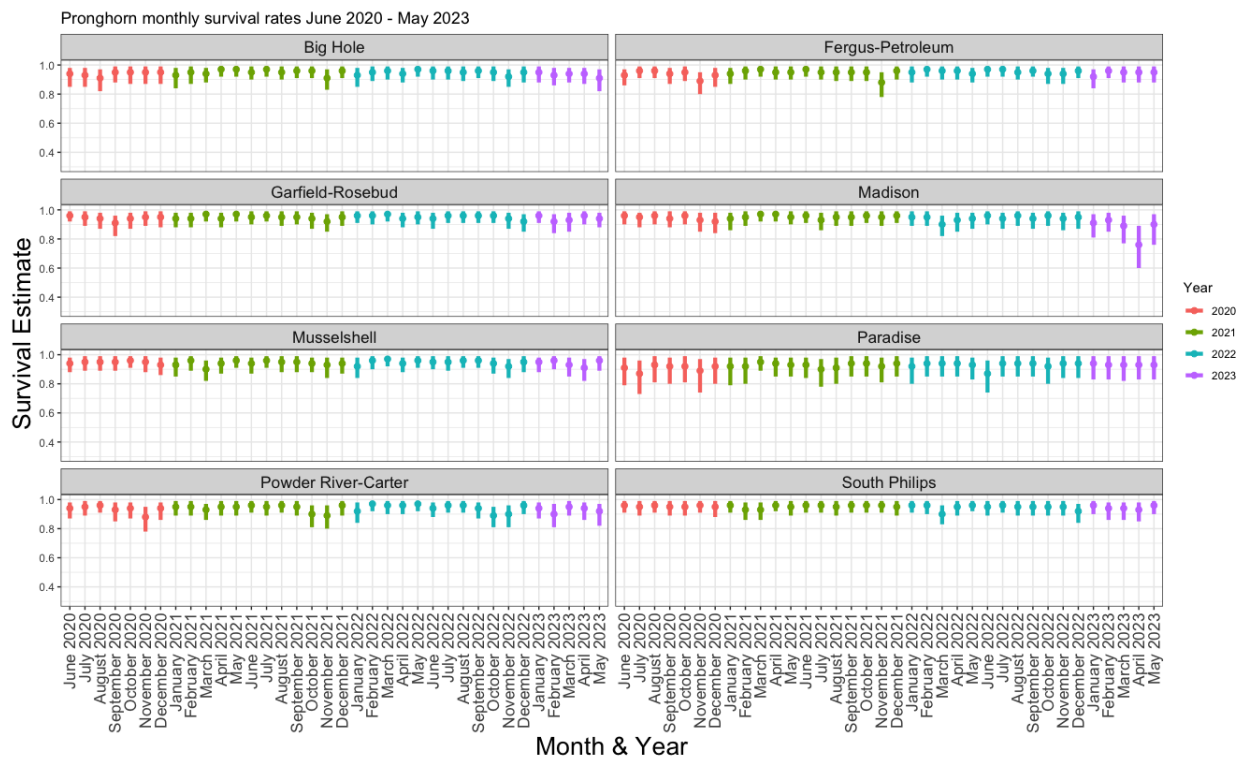


Figure 5. Mean monthly survival probabilities (and 95% credible intervals) for each study population and biological year (2021 = 01 Jun 2020 – 31 May 2021; 2022 = 01 Jun 2021 – 31 May 2022; 2023 = 01 Jun 2022 – 31 May 2023) estimated from known fate information of collared adult female pronghorn in the Montana Pronghorn Movement and Population Ecology Project. The estimated probabilities represent the probability that an animal alive in one month will survive to the next month.

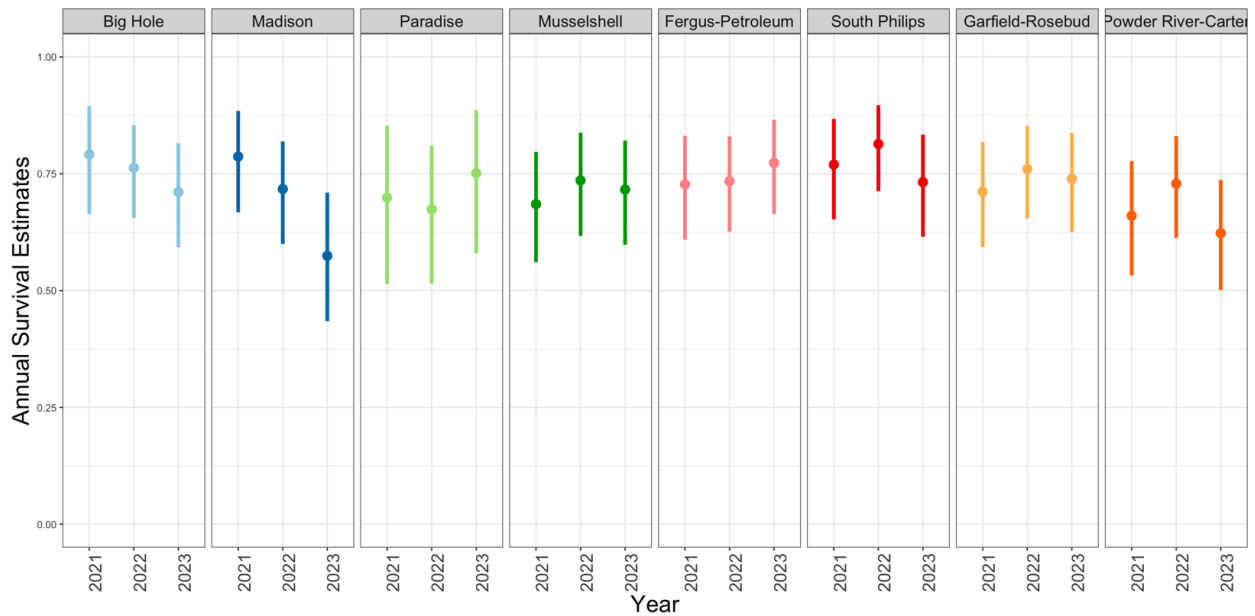


Figure 6. Annual survival probabilities (and 95% credible intervals) estimated from known fate information of collared adult female pronghorn for each study populations and biological year (2021 = 01 Jun 2020 – 31 May 2021; 2022 = 01 Jun 2021 – 31 May 2022; 2023 = 01 Jun 2022 – 31 May 2023) in the Montana Pronghorn Movement and Population Ecology Project. The estimated probabilities are the product of each respective biological years' 12 months of survival probabilities for each year and study population.

Table 6. Annual survival probabilities and 95% credible intervals estimated from known fate information of collared adult female pronghorn for each study population and for all study populations (the “Total Annual Survival” row) for each biological year (2021 = 01 June 2020 – 31 May 2021; 2022 = 01 June 2021 – 31 May 2022). The estimated probabilities are the product of each respective biological years' 12 months of survival probabilities for each study population.

Study area	n	Year	Annual survival	95% credible interval	
				2.5%	97.5%
Big Hole	61	2021	0.79	0.66	0.90
	61	2022	0.76	0.66	0.85
	47	2023	0.71	0.59	0.82
Madison	60	2021	0.79	0.67	0.88
	50	2022	0.72	0.60	0.82
	35	2023	0.57	0.43	0.71
Paradise	36	2021	0.70	0.51	0.85
	31	2022	0.67	0.52	0.81
	21	2023	0.75	0.58	0.89
Musselshell	60	2021	0.69	0.56	0.80
	60	2022	0.74	0.62	0.84
	45	2023	0.72	0.60	0.82
Fergus-Petroleum	61	2021	0.73	0.61	0.83
	61	2022	0.73	0.63	0.83
	48	2023	0.77	0.66	0.87
South Philips	62	2021	0.77	0.65	0.87
	62	2022	0.81	0.71	0.90
	47	2023	0.73	0.62	0.83

Garfield-Rosebud	61	2021	0.71	0.59	0.82
	60	2022	0.76	0.65	0.85
	49	2023	0.74	0.62	0.84
Powder River-Carter	58	2021	0.66	0.53	0.78
	60	2022	0.73	0.61	0.83
	40	2023	0.62	0.50	0.74

Objective #1: Delineate seasonal range and migration routes of pronghorn in each study area

1.1 Seasonal ranges and migration routes

We collected 10,946,734 locations from 702 individuals, averaging 15,934 (range: 7 – 38,542) locations and 1.8 (range: 0.0 – 4.4) years of locations collected per individual. This totaled 1,689 animal-years of location data. Movement patterns of individuals were diverse within and across study areas (Figure 7 – 31), with individuals that demonstrate non-migratory behaviors comprising the majority (65 – 94%) of individuals in each study area except the Big Hole (33%), and with migratory behaviors most prevalent in the Big Hole (67% of individuals), Madison (35%), and South Philips (23%) study areas relative to the other study areas (see Section 1.2 for a description of the characterization methods and summaries of migratory behaviors). Here, we present maps of each study area's individual movement trajectories and estimated population-level migration routes and seasonal ranges delineated from the collar location data. Of note in one instance in the Big Hole, a collar from an animal captured in winter 2020 that failed September 2020 was recovered spring 2022 from a private landowner in the Lemhi valley, Idaho, indicating that an unmapped movement route may exist between Montana and Idaho over Lemhi Pass (Figure 8).

To estimate migration routes (Figure 9 – 30), we first identified migration sequences for each individual-year by plotting net squared displacement (NSD; Bunnefeld et al. 2011, Merkle et al. 2022) curves and mapping movement trajectories for each animal's migratory year, which we selected to span 01 Feb – 31 Jan. We chose 01 Feb as the start of the migratory year to represent when individuals are assumed to be on their winter range for the year. We used the NSD, which uses average daily locations to measure straight-line distances from the first location to each subsequent location in the migratory year, and movement maps to assist in identifying distinct seasonal ranges, departure/arrival timings of spring/fall migrations, and migration distances. For each animal-year, we defined areas where the animal spent the majority of time between the beginning of the migratory year and a spring departure as the initial winter range and between a fall arrival and the end of the migratory year as the final winter range. We defined a spring and fall departure as a distinct, rapid change in NSD that stabilized when the animal arrived at its first summer range or final winter range, respectively. We selected departure and arrival dates based on the collar location that occurred immediately prior to the first and immediately after the last collar location of the animal's migration trajectory, respectively. We defined a summer range as an area where the animal spent >21 days and was >10 km from the winter range, or other summer ranges if the animal visited multiple summer ranges. Thus, if an animal departed from its winter range to an area that was ≤10 km away and spent >21 days, this area was considered part of its winter range. If an animal departed from its winter range to an area that was >10 km away but spent ≤21 days, the area was considered a stop-over site and not a distinct range, unless that area was also within 10 km from a subsequent area where the animal spent >21 days, in which case it was considered part of that subsequent area and, therefore, summer range. We chose the duration threshold based on other pronghorn movement studies reporting approximate average stopover durations ranging 10 – 17 days (Seidler et al. 2015, Jakes et al. 2018a). Our relatively low distance threshold of 10 km was similar to the 15 km threshold used by Kolar et al. (2011). To measure distances between ranges, we visually examined movement maps to identify the areas of the winter and summer ranges that contained the overall concentration of locations and measured the Euclidean distance between the edges of the concentrated areas, generally following the animal's spring migratory pathway to account for topographic diversions (e.g., animal pathways circuiting a mountain range separating its winter and summer ranges <10 km apart based on straight-line distance). We used the date of departure and arrival

for each spring and fall migratory period to represent migration sequences for each animal's migratory year. We identified migration sequences only for animal-years with at least 11 months of data for each migratory year.

Last, we used Brownian Bridge Movement Model (BBMM; Horne et al. 2007) methods to delineate population-level migration routes. The BBMM estimates the probability of where an animal could have traveled between two sequential GPS locations. When this process is applied to all GPS locations in a migration sequence, the BBMM provides a utilization distribution (UD) estimate of the width of the estimated movement path around the straight line between the successive locations and can be used to estimate migration routes (Sawyer et al. 2009) and stopover sites (Sawyer and Kauffman 2011). In general, we applied a 4-step process to calculate population-level migration routes which generally followed the approach outlined by Sawyer et al. (2009). We first estimated unique UD's for each migration sequence using a grid with 50-m resolution. Second, we averaged the UD's for a given individual's spring and fall migration sequences across all years to produce a single, individual level migration UD. We then rescaled this averaged UD to sum to 1. Third, we defined a migration route footprint for each individual as the 99% isopleth of the UD. Lastly, we stacked all the individual footprints for a given study area and converted the migration routes from a grid-based format to a polygon format, while removing isolated use polygons of less than 20,000 m² (i.e., less than approximately 5 acres). When converting final migration routes from grid to polygon data, all 50-m pixels were preserved in the final migration routes. Thus, the mapped migration routes represent areas used by ≥1 migrant during spring and/or fall migration periods.

To calculate seasonal ranges (Figure 10 – 31), we randomly sampled 4 locations per day per individual and estimated a 95% kernel utilization distribution (KUD) for each season and study area (i.e., population-level). The 95% KUD represents the area in which the probability of relocating an animal is equal to 0.95. We defined spring as April 1 – June 30, summer as July 1 – Aug 31, fall as September 1 – November 30, and winter as December 1 – March 31.

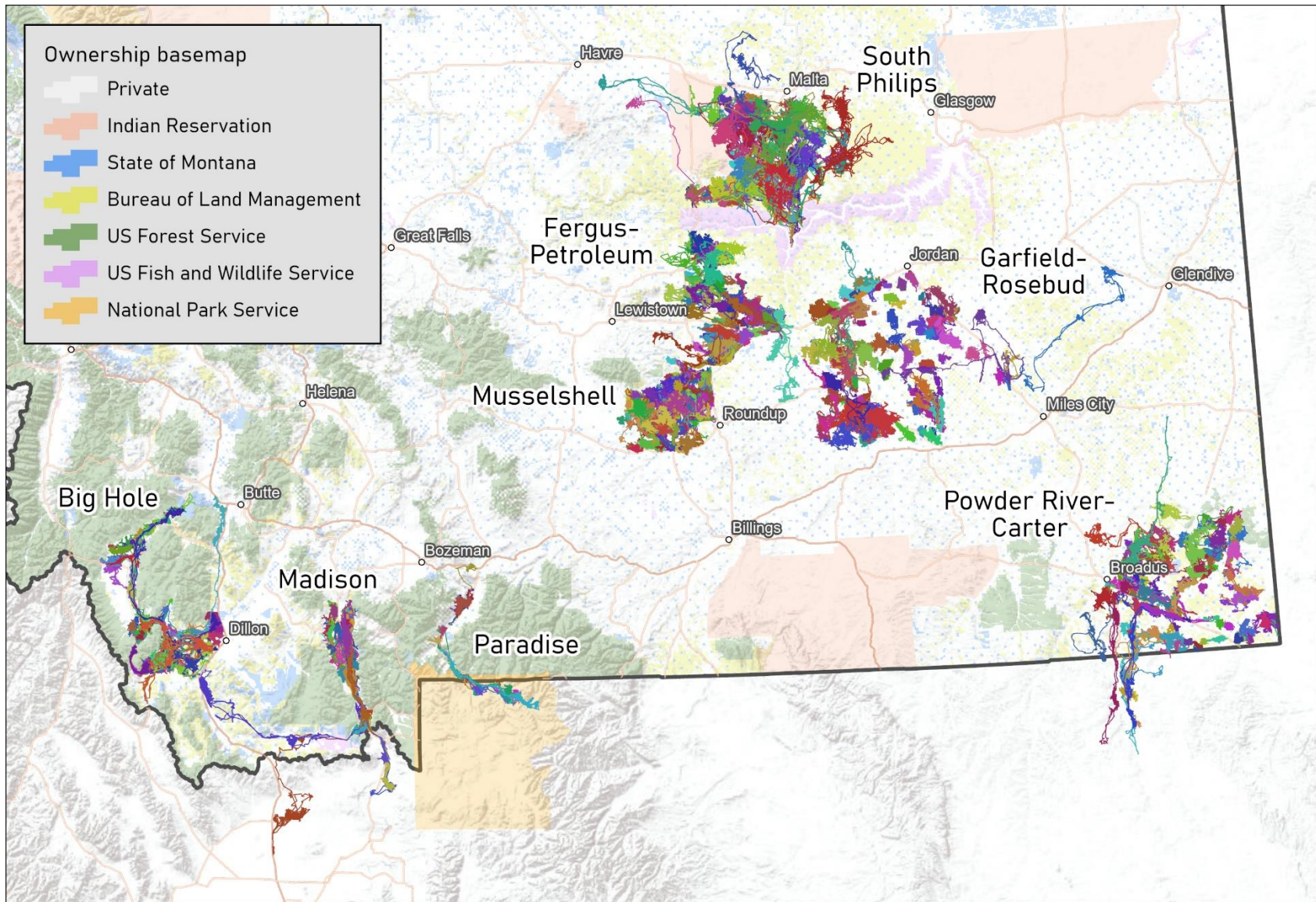


Figure 7. Movements of collared adult female pronghorn (colored by individual) in each study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 – June 2023 (January 2019 – June 2023 in Madison).

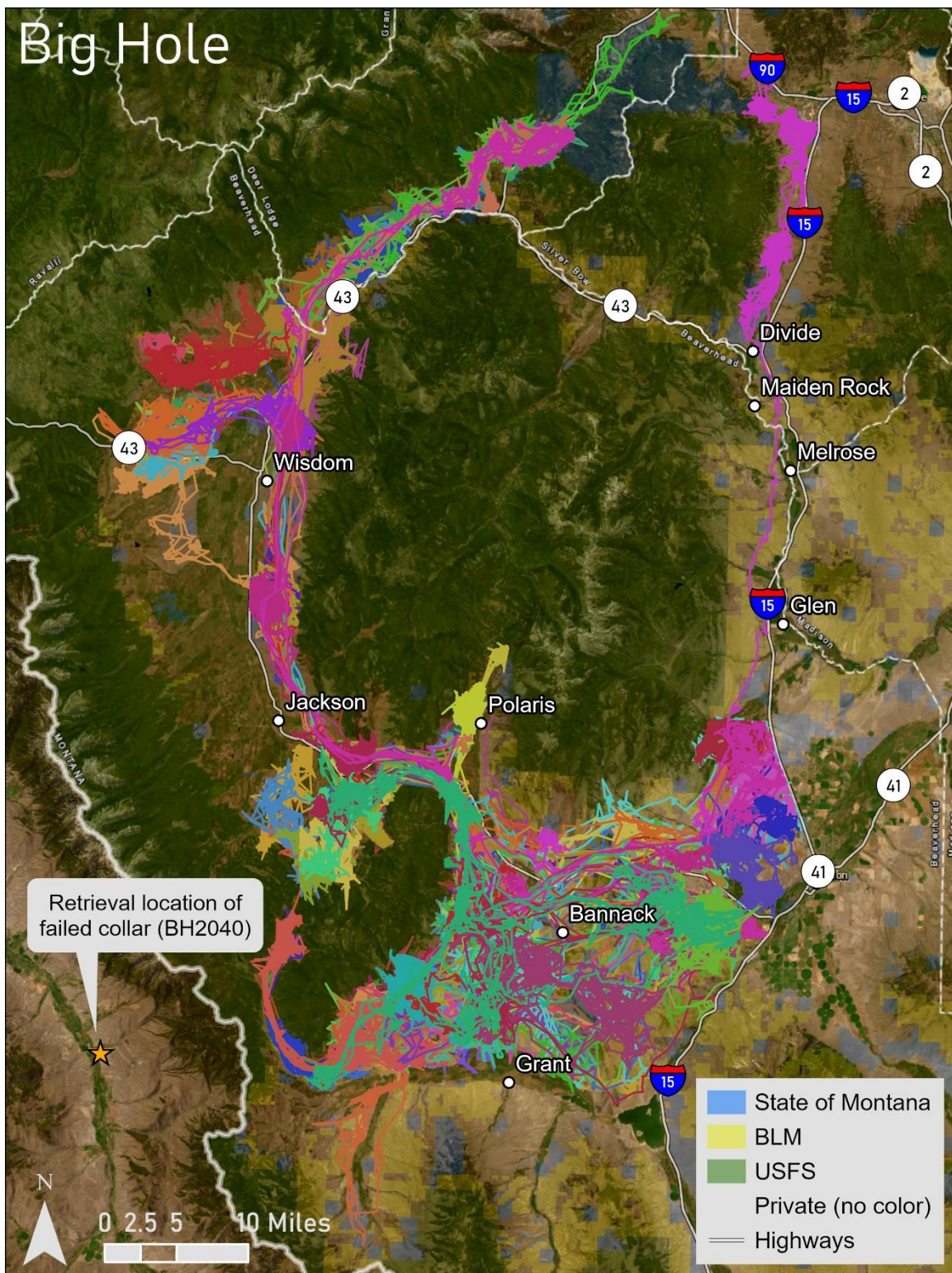


Figure 8. Movements of collared adult female pronghorn (colored by individual) in the Big Hole study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. See the text for a description related to the location of the failed collar in Idaho.

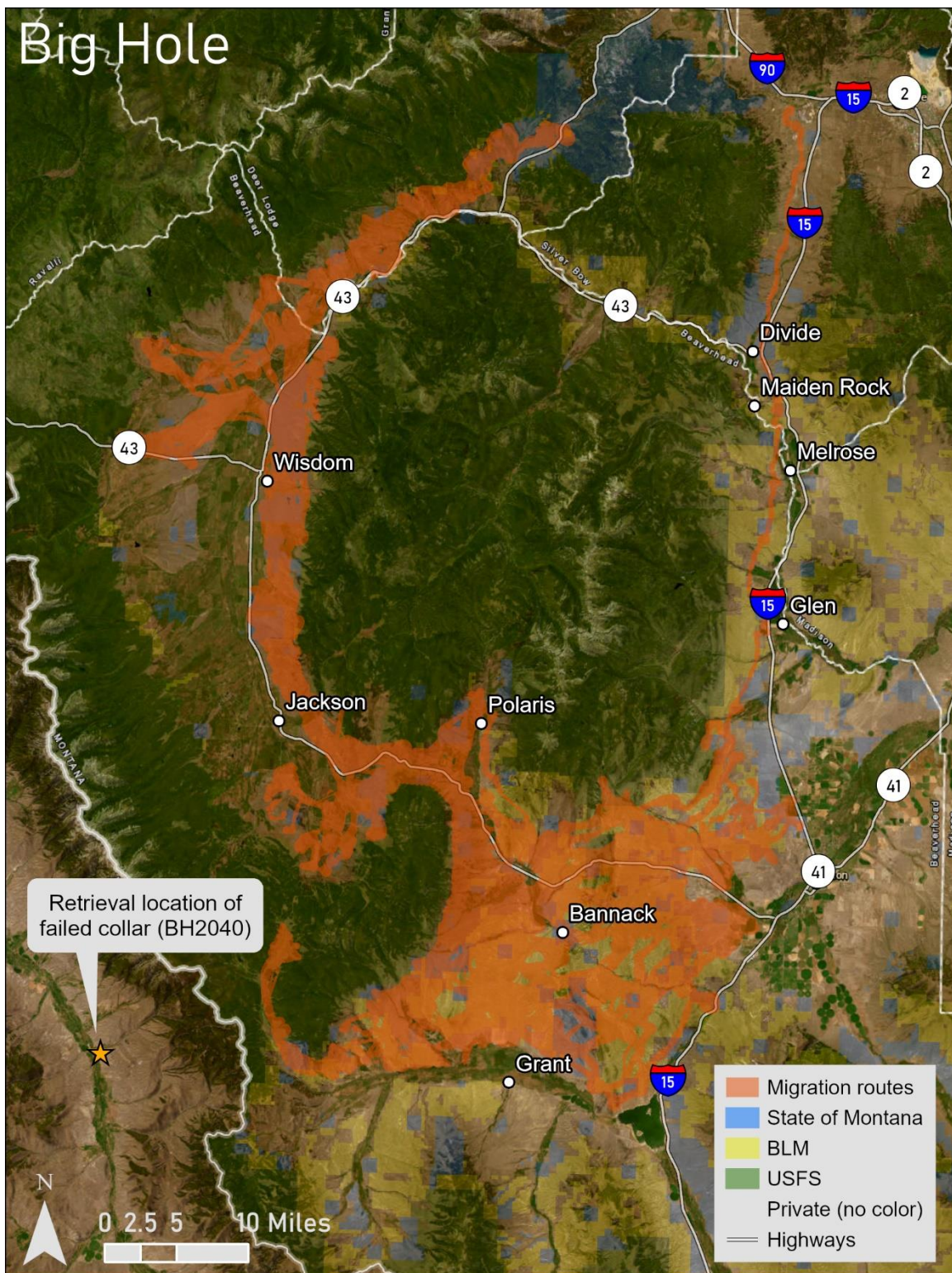


Figure 9. Estimated migration routes of migrant collared adult female pronghorn in the Big Hole study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023. See the text for a description related to the location of the failed collar in Idaho.

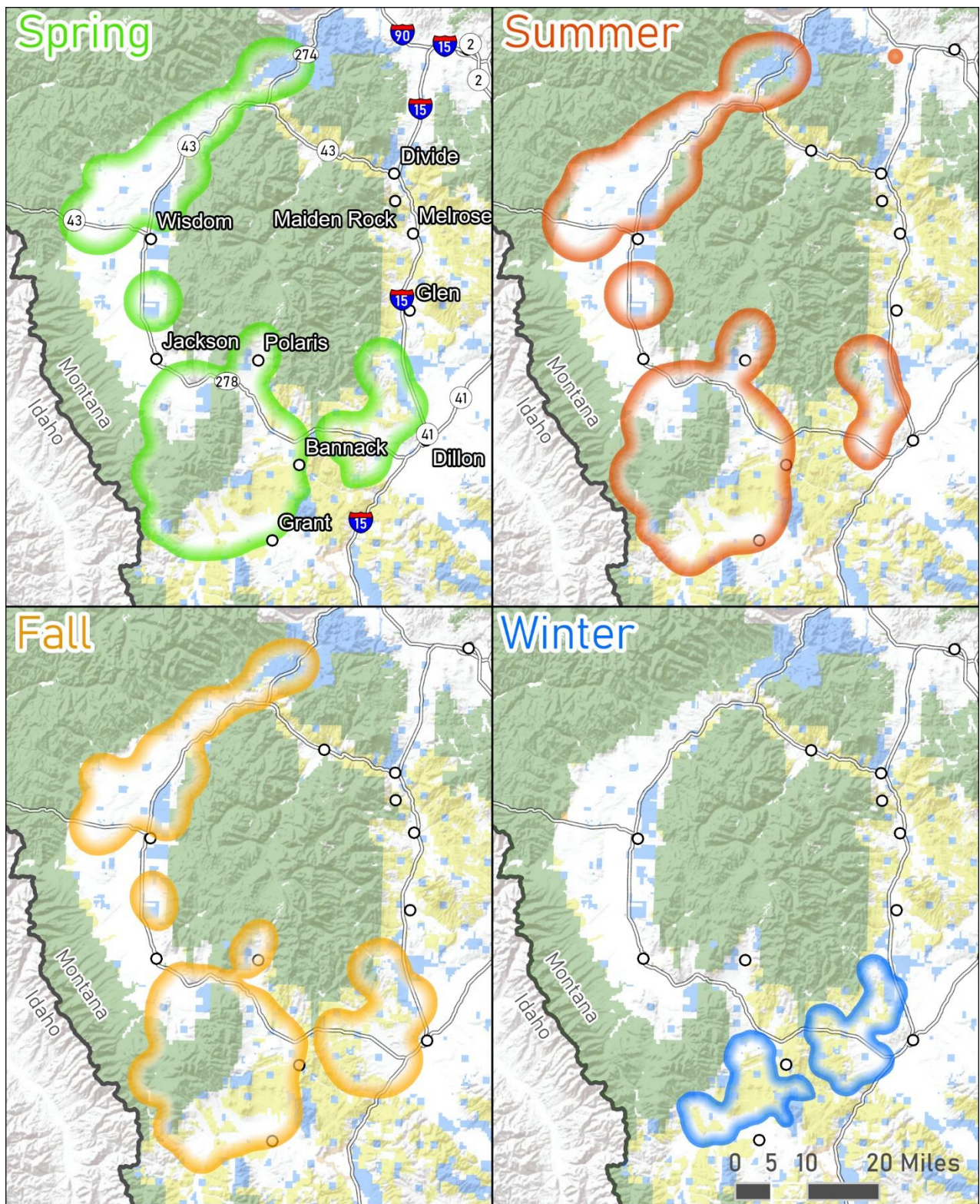


Figure 10. Seasonal ranges of collared adult female pronghorn in the Big Hole study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

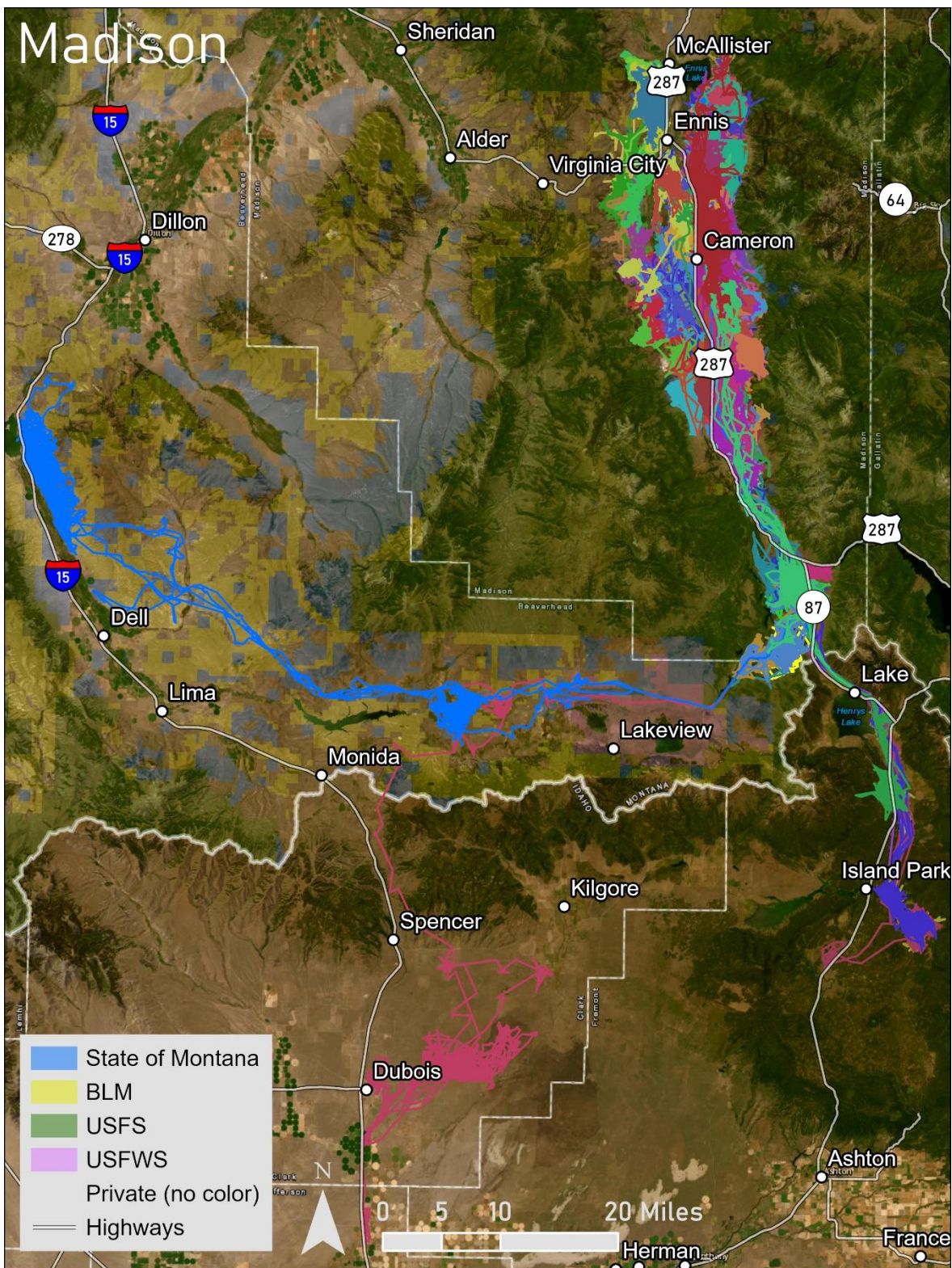


Figure 11. Movements of collared adult female pronghorn (colored by individual) in the Madison study area for the Montana Pronghorn Movement and Population Ecology Project from January 2019 to June 2023.

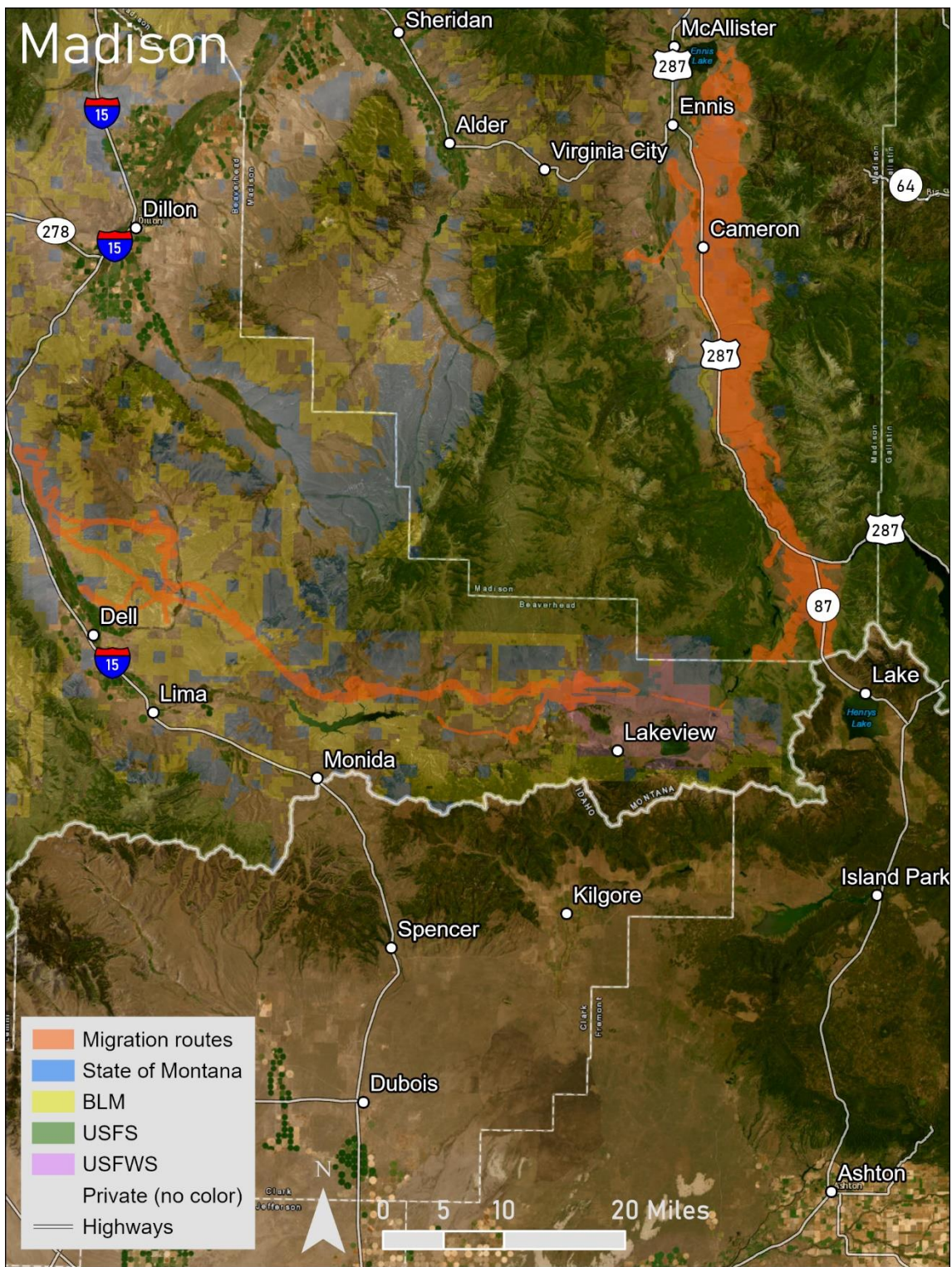


Figure 12. Estimated migration routes of migrant collared adult female pronghorn in the Madison study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2019 to June 2023 and are clipped to Montana only.

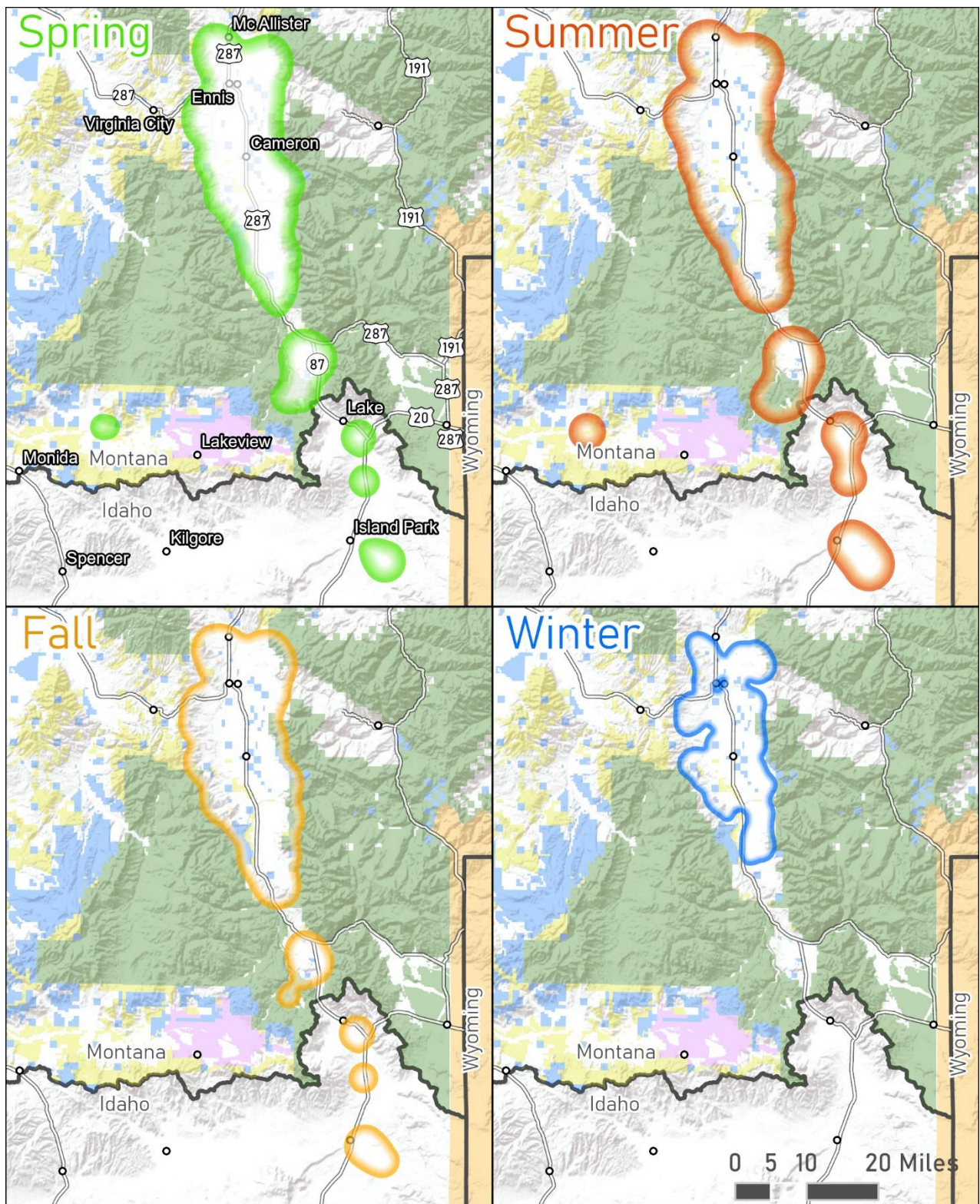


Figure 13. Seasonal ranges of collared adult female pronghorn in the Madison study area for the Montana Pronghorn Movement and Population Ecology Project from January 2019 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

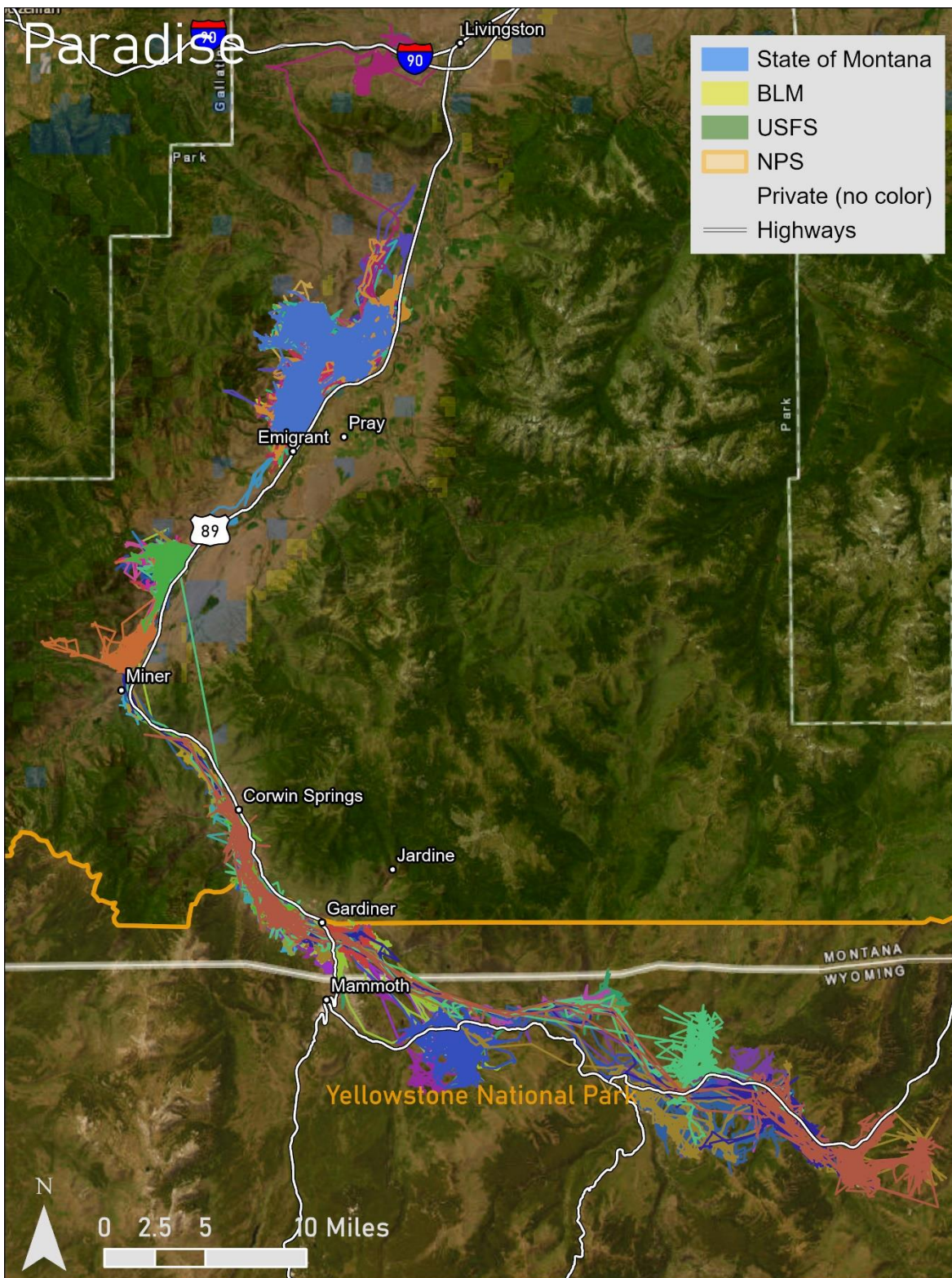


Figure 14. Movements of collared adult female pronghorn (colored by individual) in the Paradise study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023.

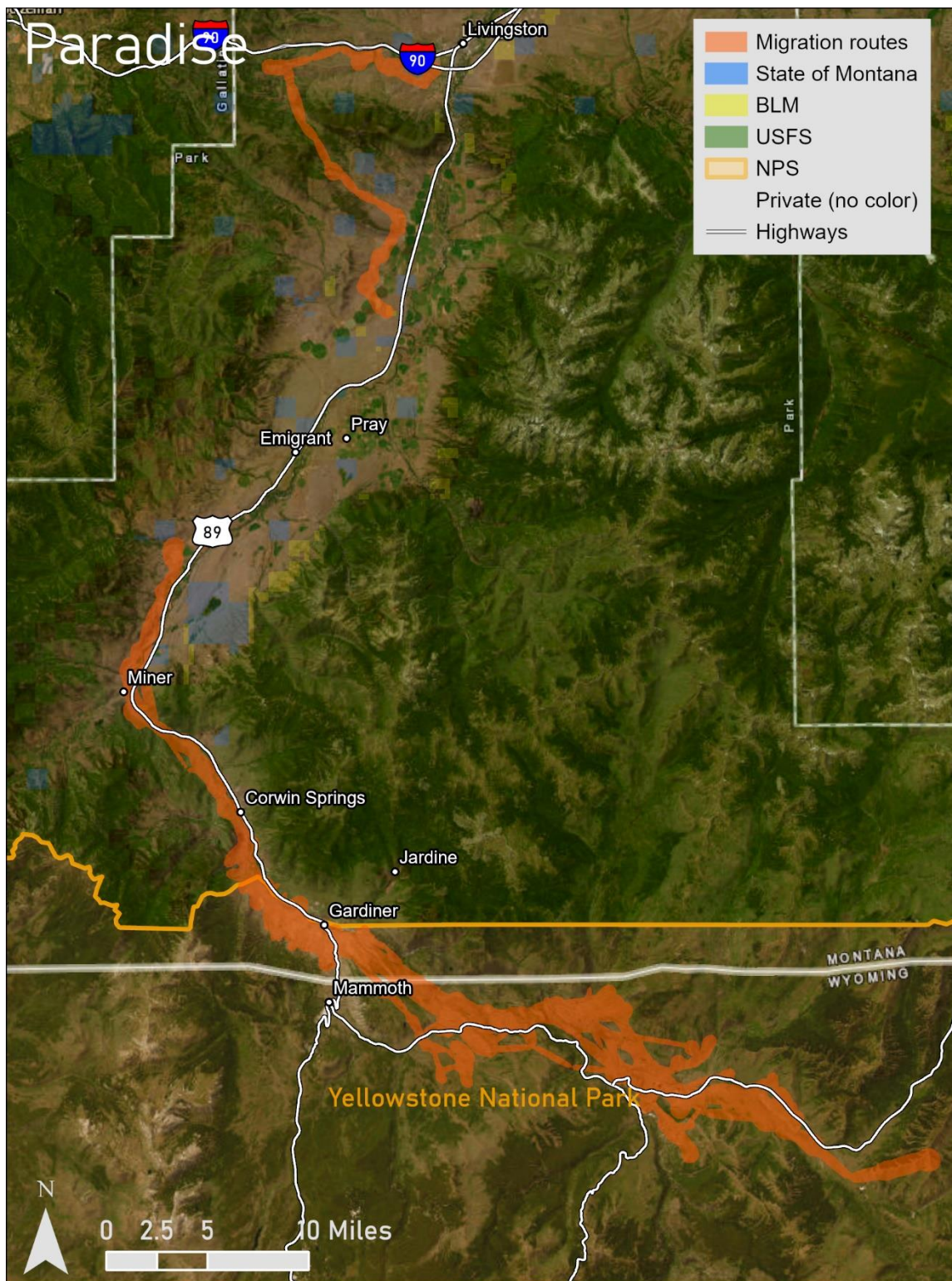


Figure 15. Estimated migration routes of migrant collared adult female pronghorn in the Paradise study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023.

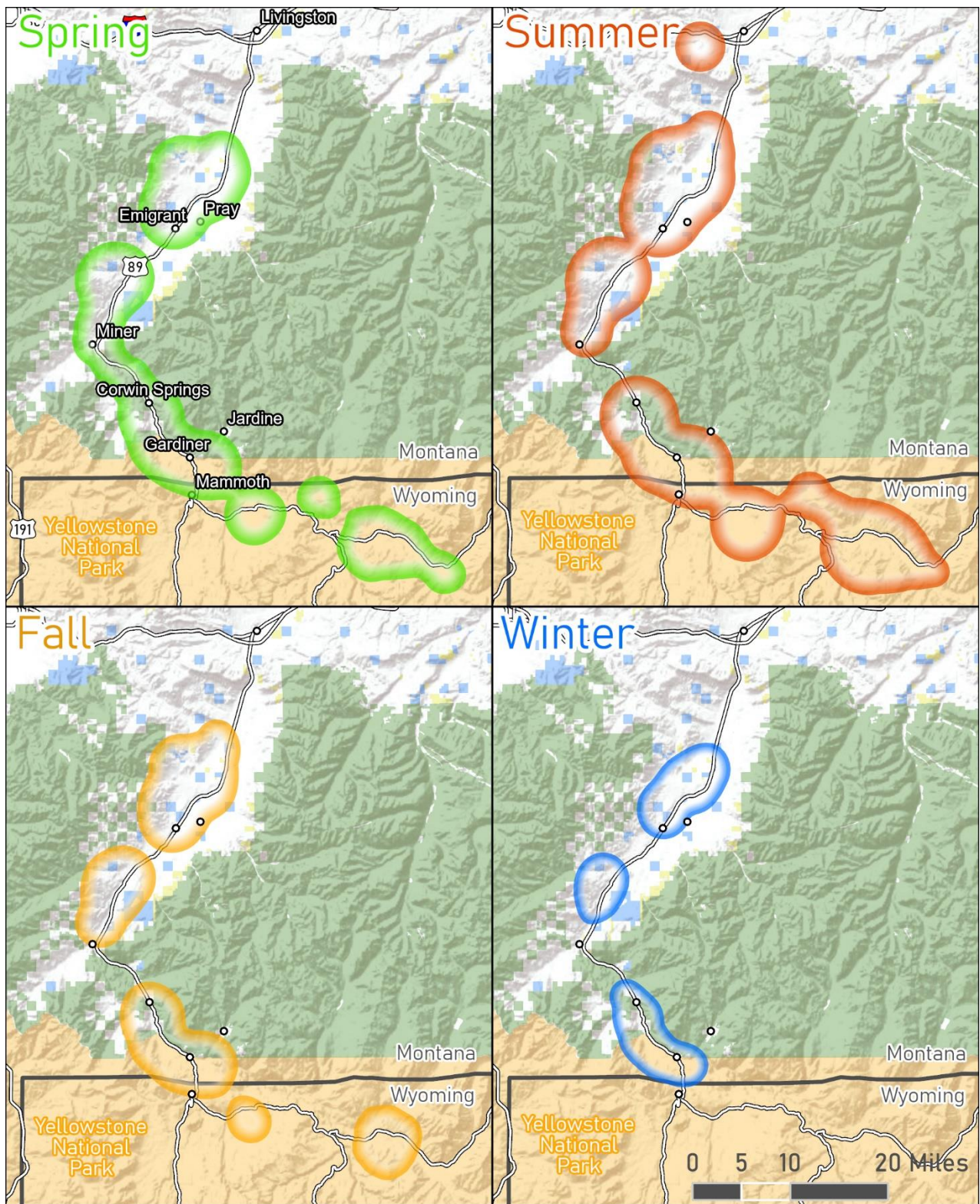


Figure 16. Seasonal ranges of collared adult female pronghorn in the Paradise study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

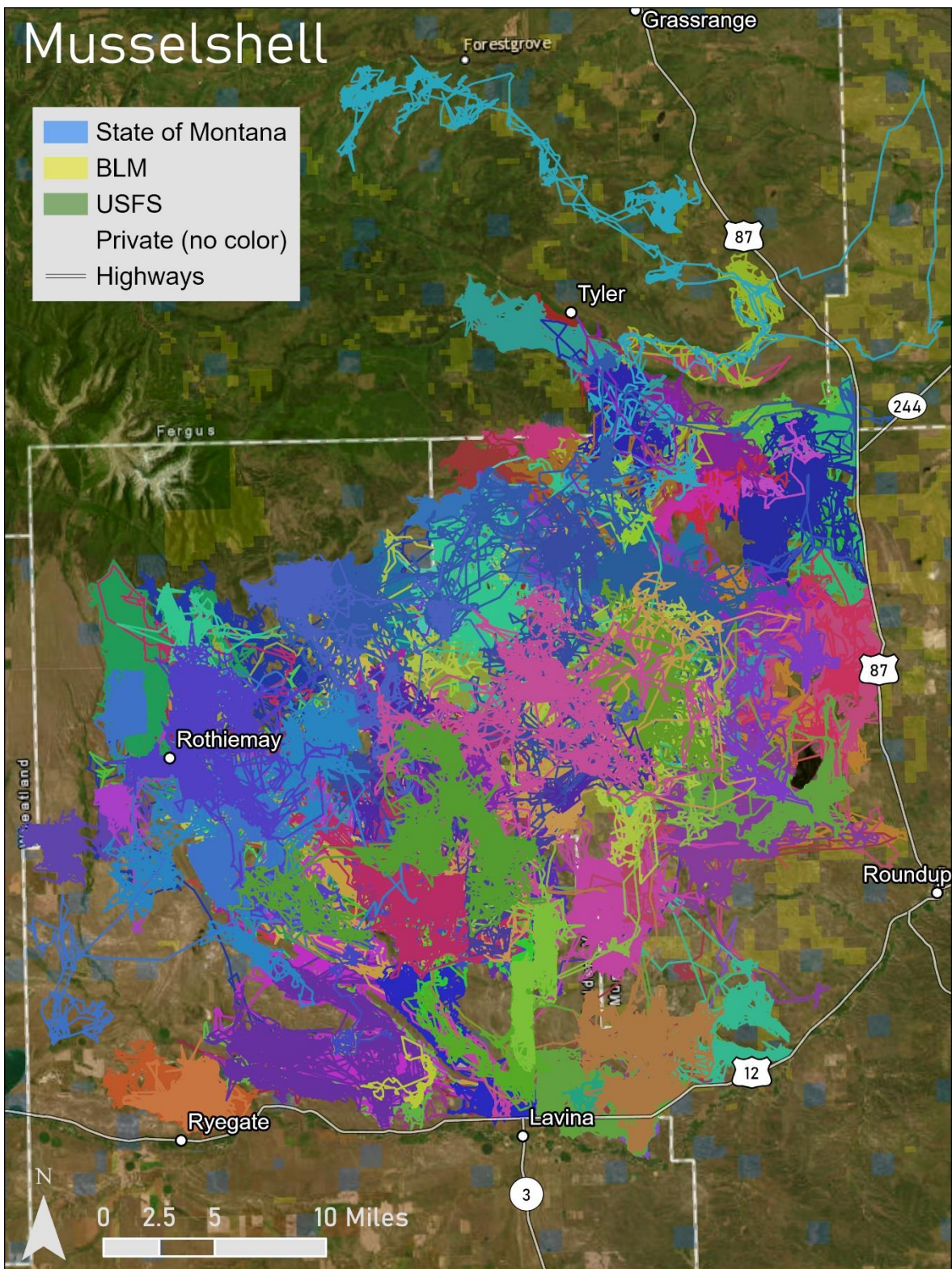


Figure 17. Movements of collared adult female pronghorn (colored by individual) in the Musselshell study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023.

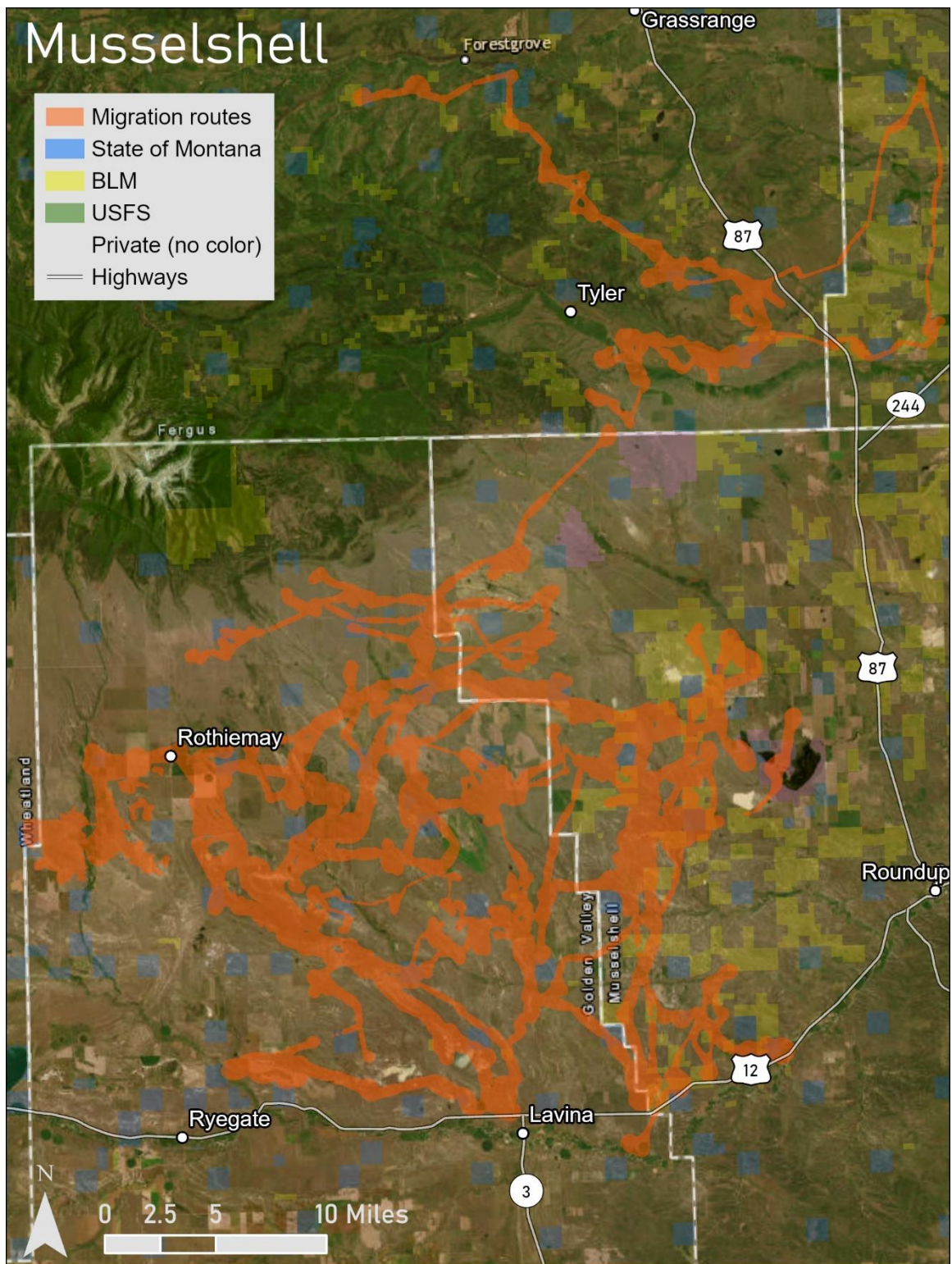


Figure 18. Estimated migration routes of migrant collared adult female pronghorn in the Musselshell study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023.

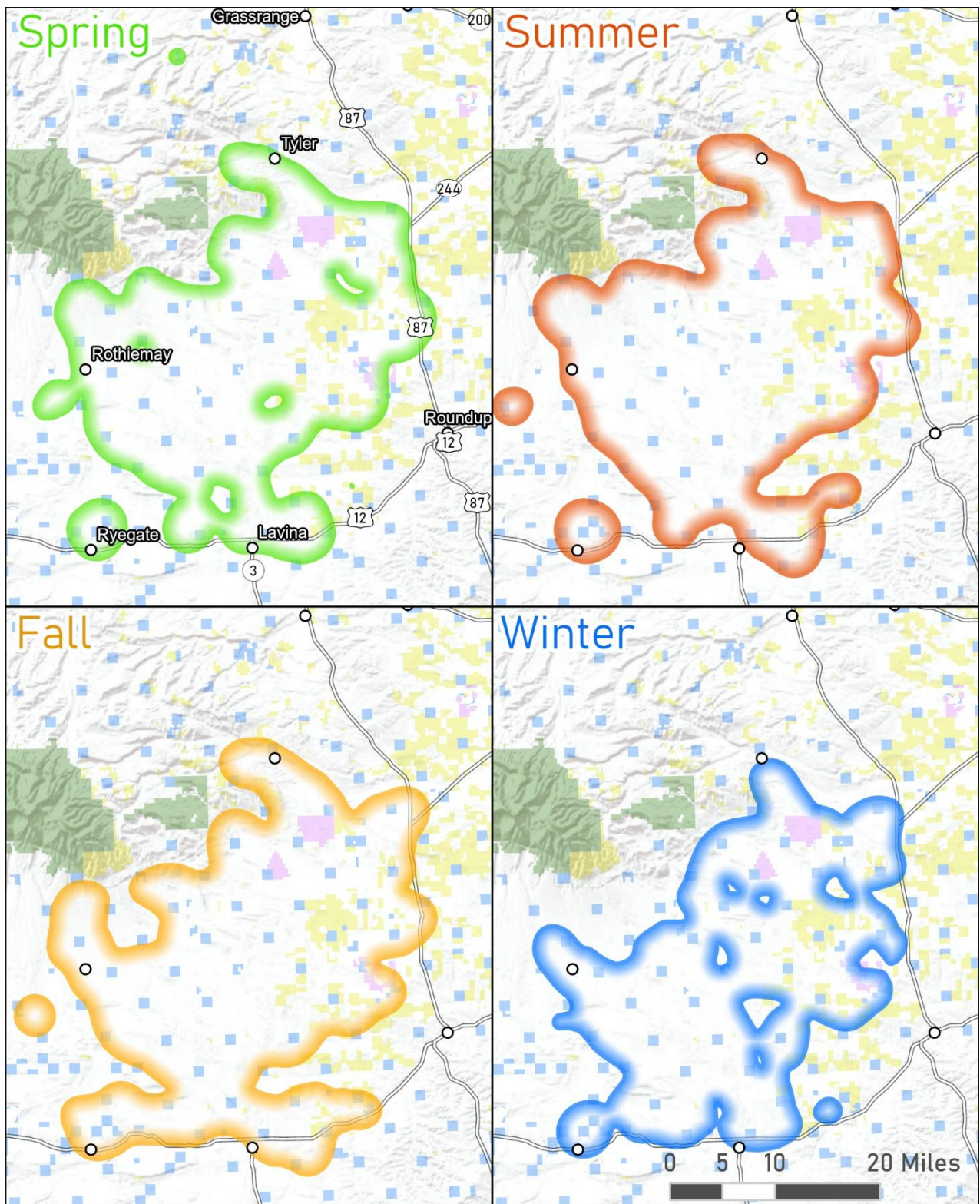


Figure 19. Seasonal ranges of collared adult female pronghorn in the Musselshell study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

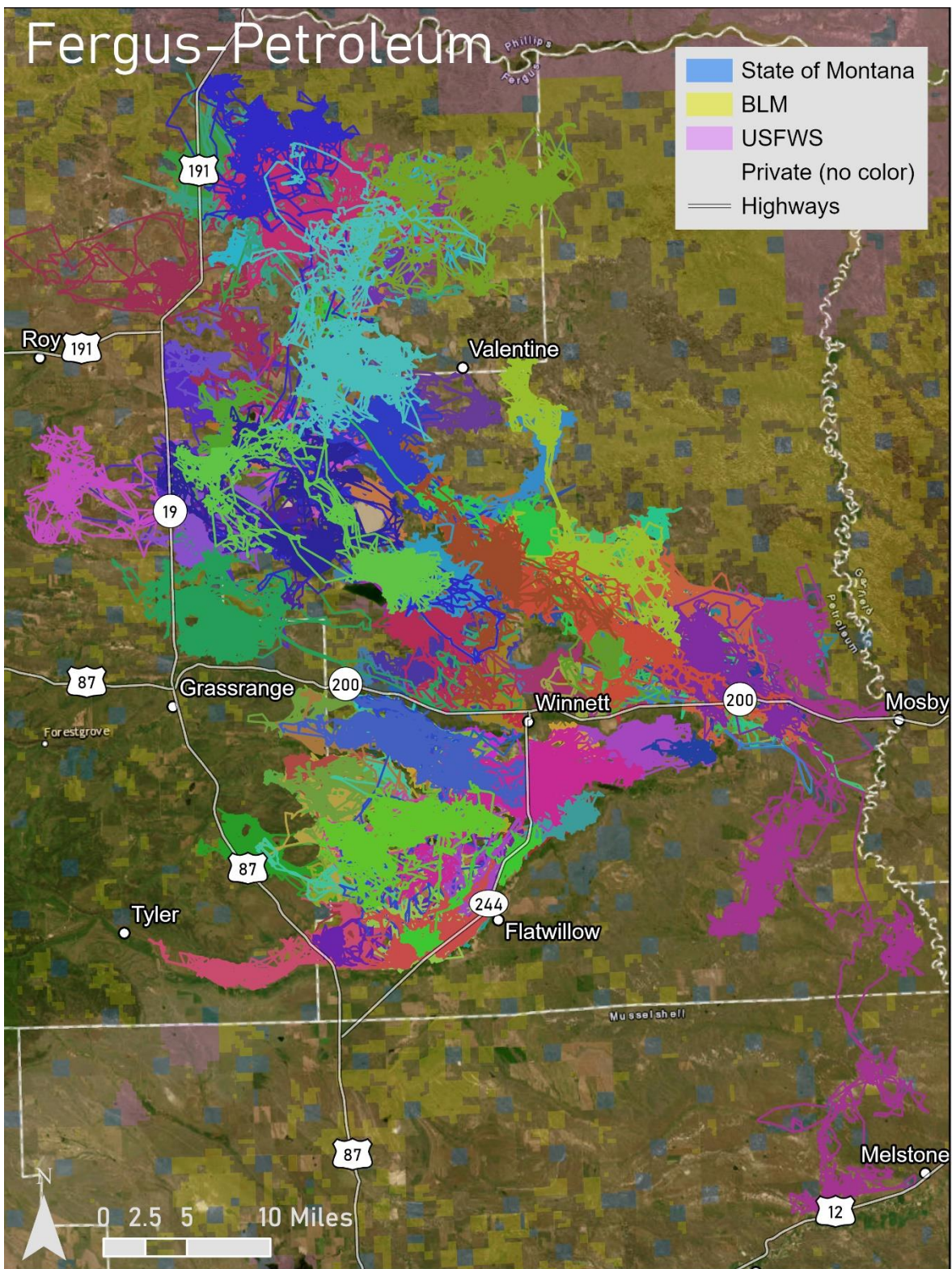


Figure 20. Movements of collared adult female pronghorn (colored by individual) in the Fergus-Petroleum study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023.

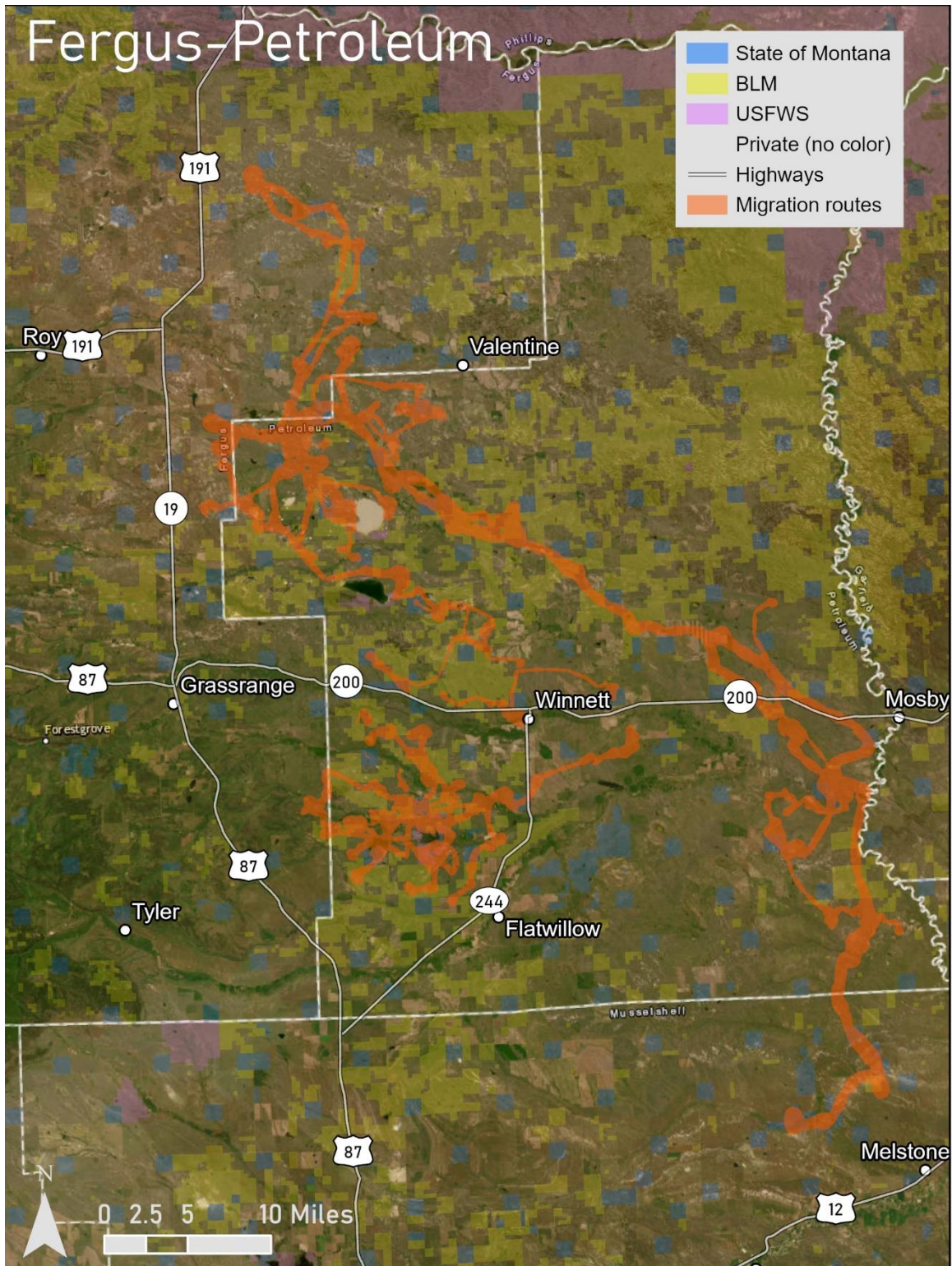


Figure 21. Estimated migration routes of migrant collared adult female pronghorn in the Fergus-Petroleum study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023.

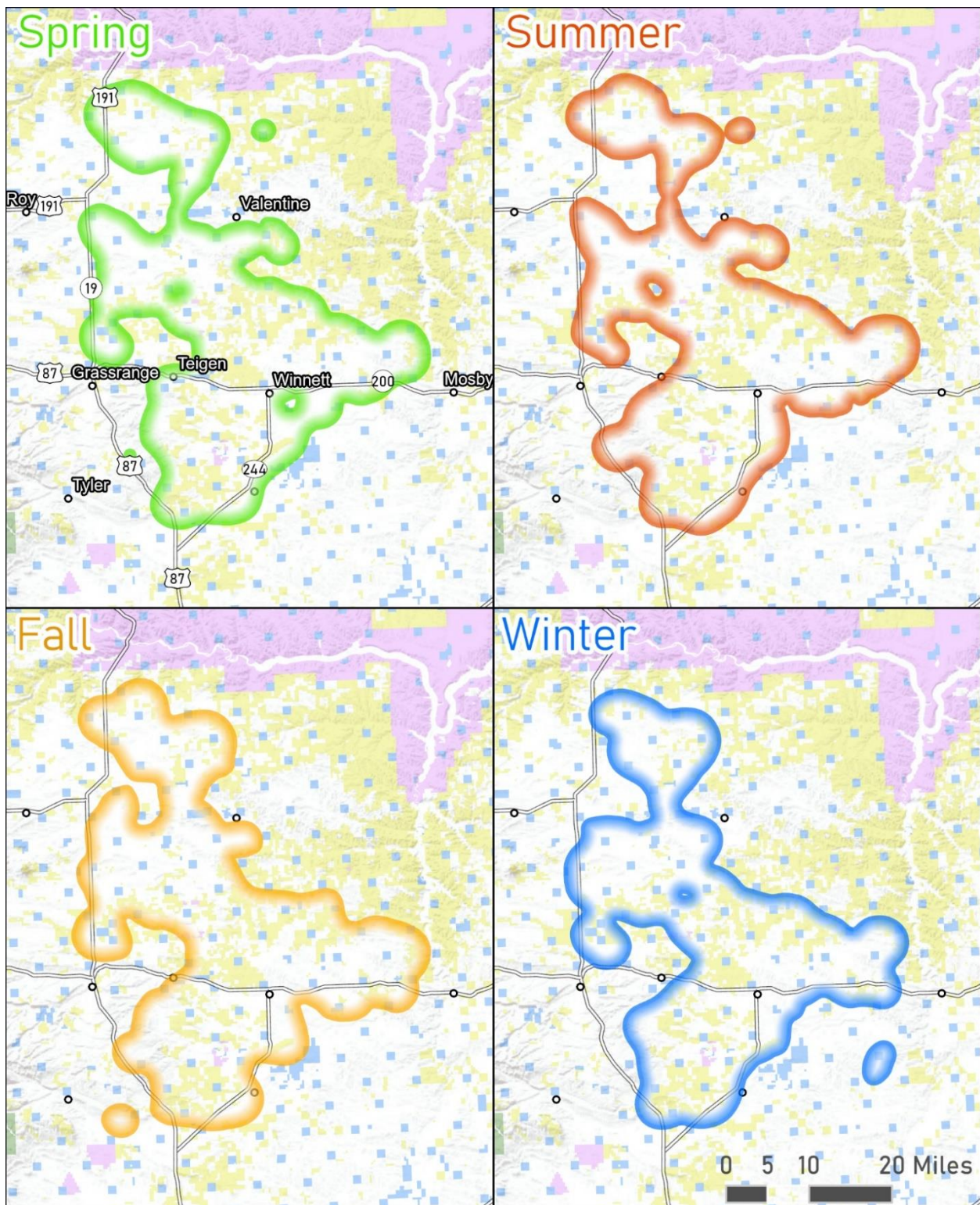


Figure 22. Seasonal ranges of collared adult female pronghorn in the Fergus-Petroleum area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

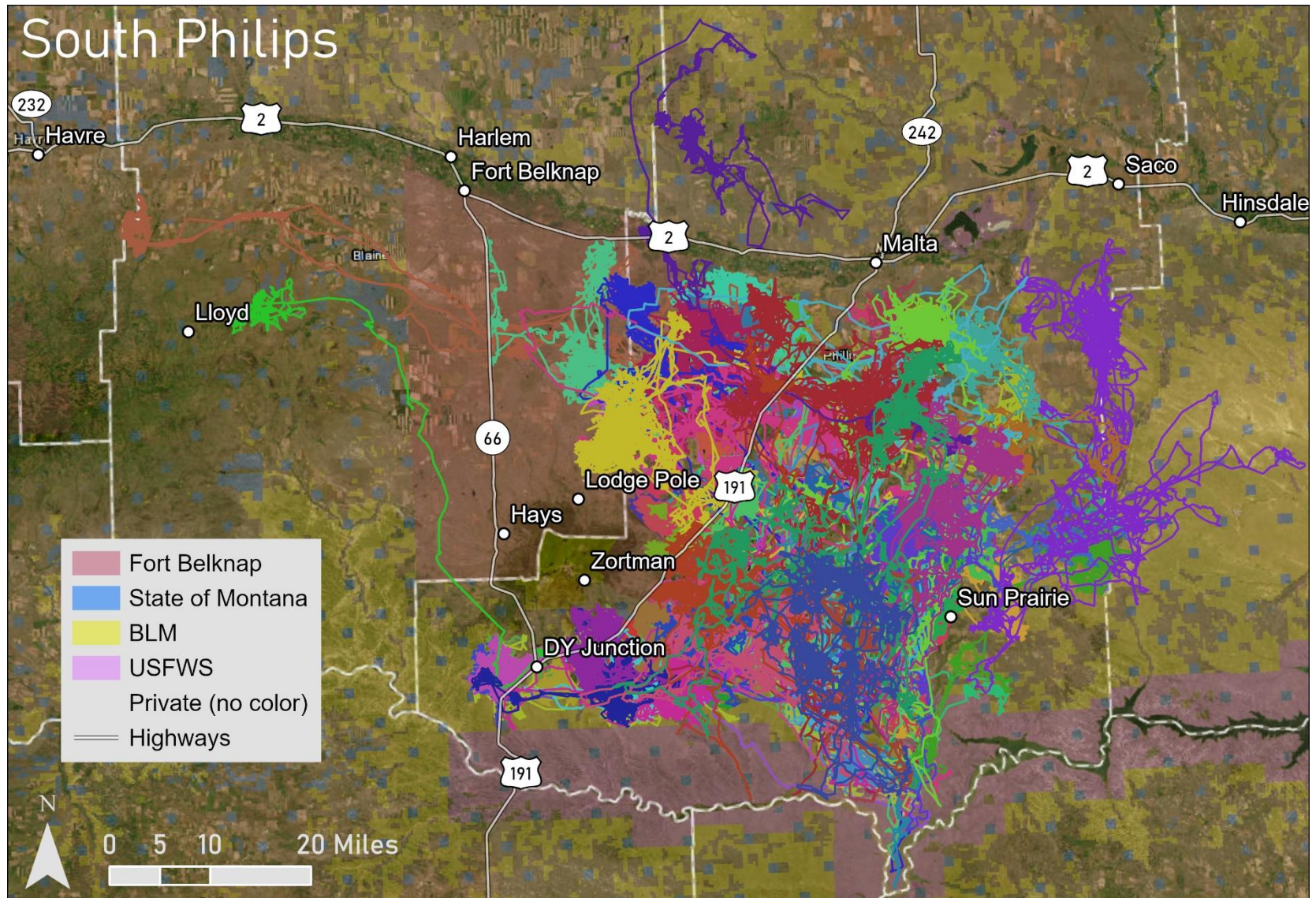


Figure 23. Movements of collared adult female pronghorn (colored by individual) in the South Philips study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023.

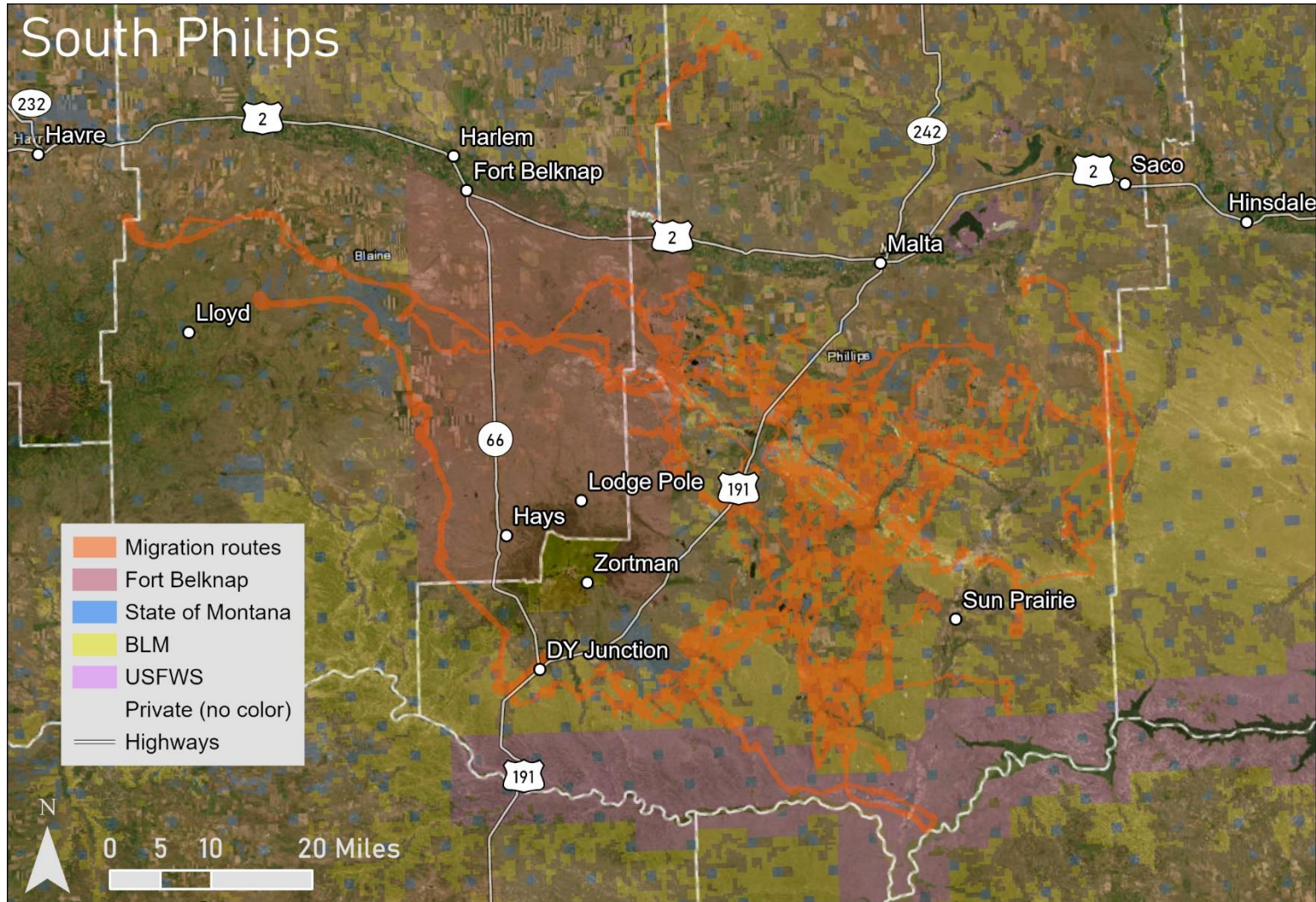


Figure 24. Estimated migration routes of migrant collared adult female pronghorn in the South Philips study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023.

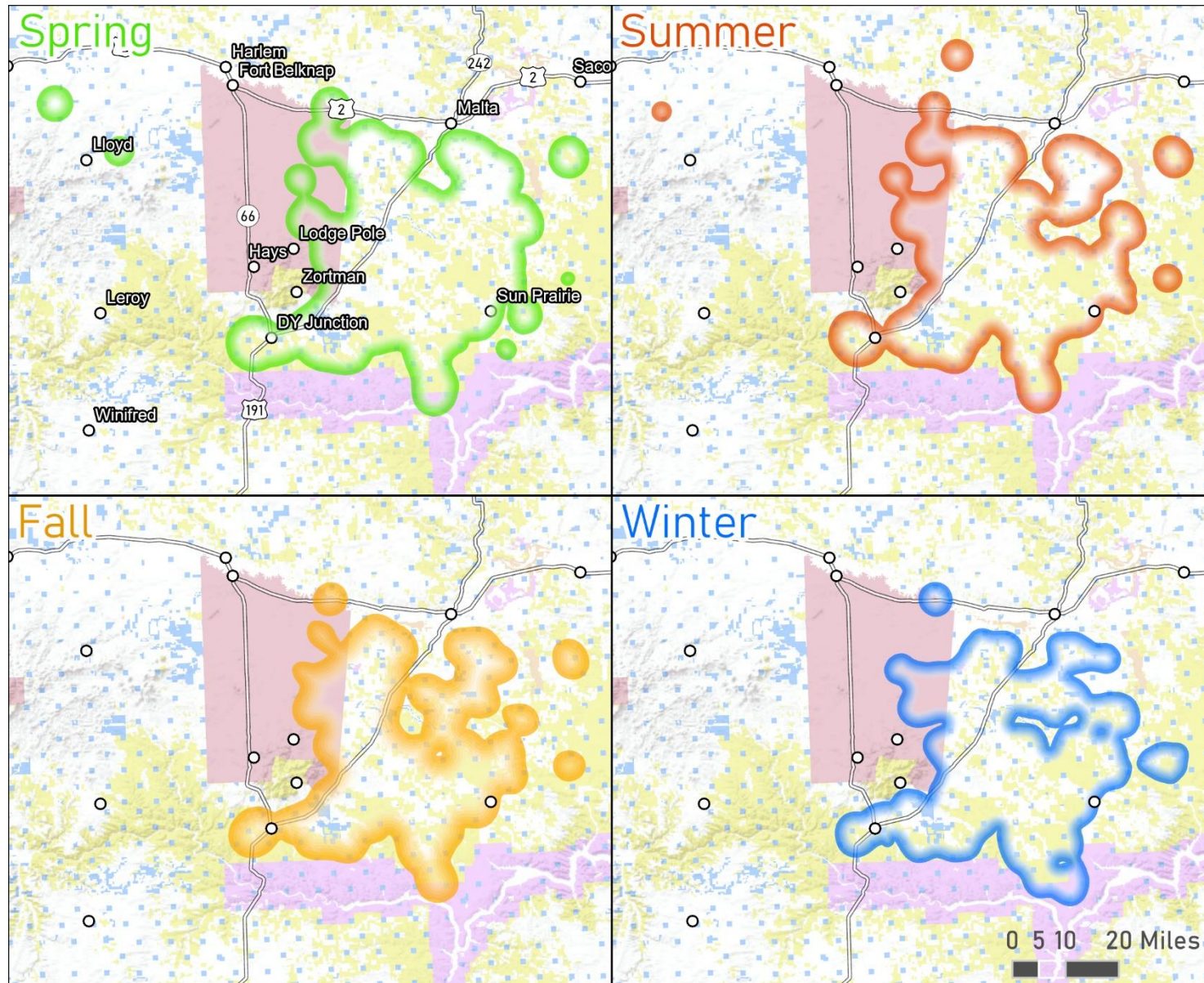


Figure 25. Seasonal ranges of collared adult female pronghorn in the South Philips area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

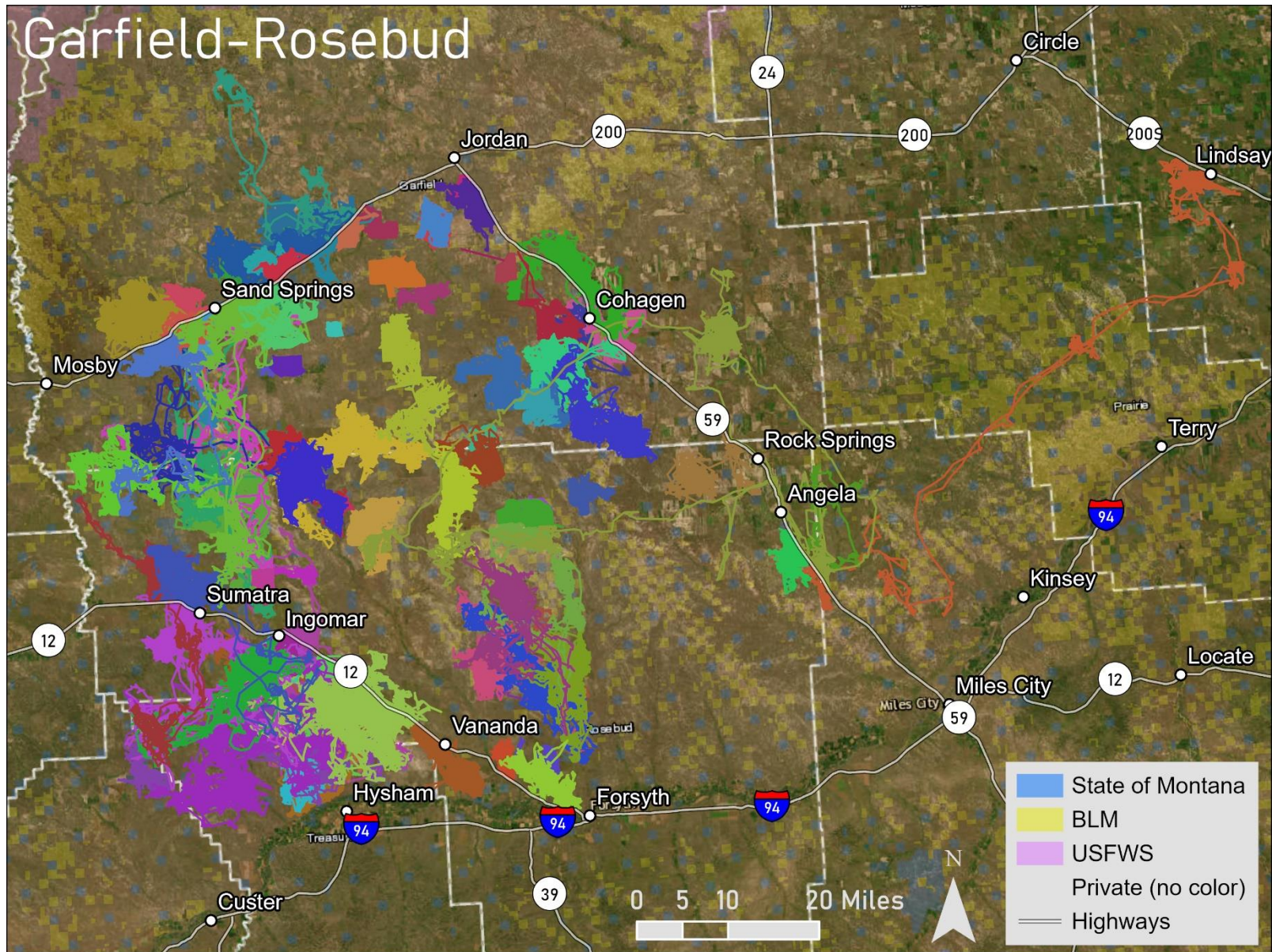


Figure 26. Movements of collared adult female pronghorn (colored by individual) in the Garfield-Rosebud study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023.

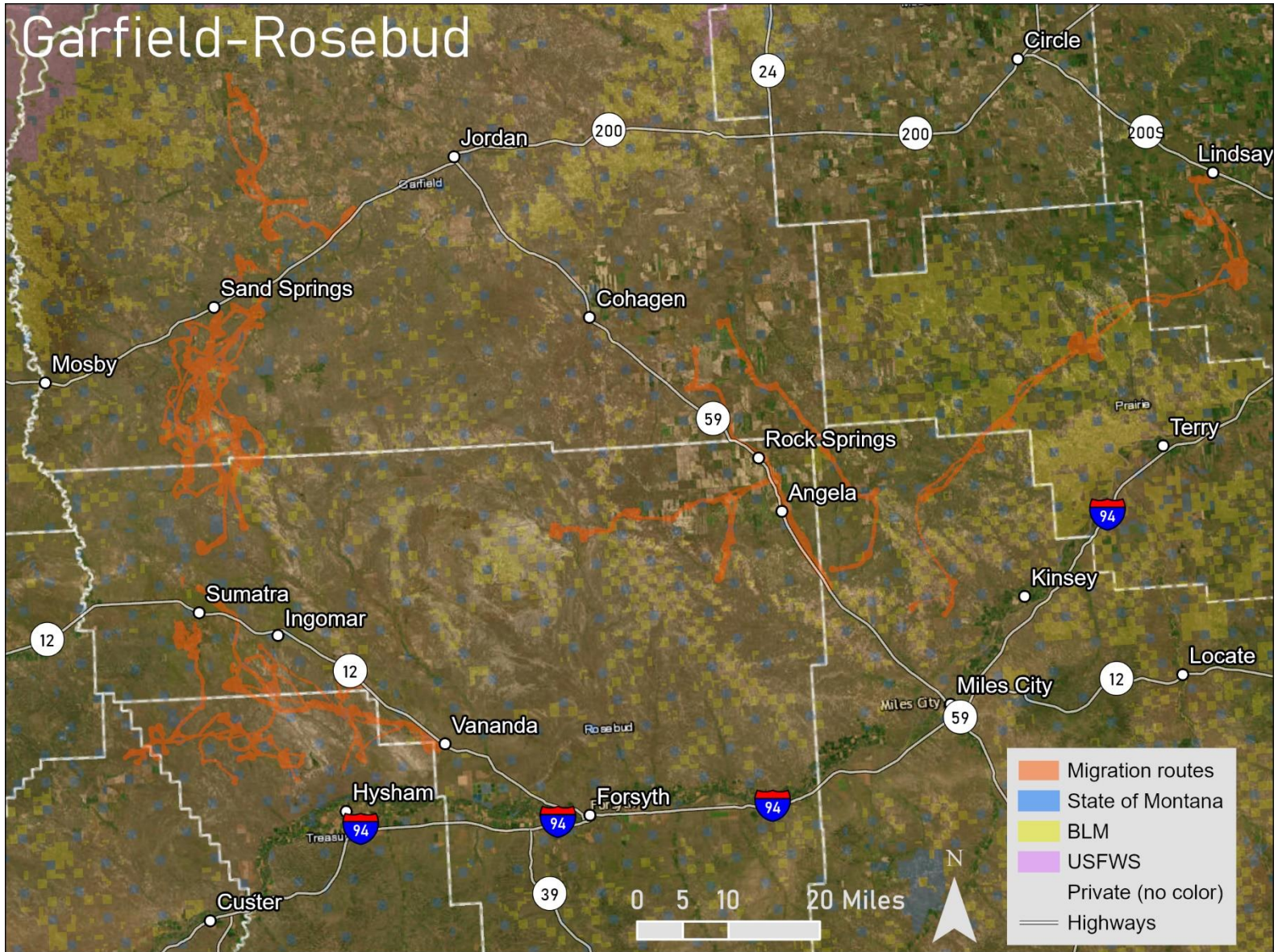


Figure 27. Estimated migration routes of migrant collared adult female pronghorn in the Garfield-Rosebud study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023.

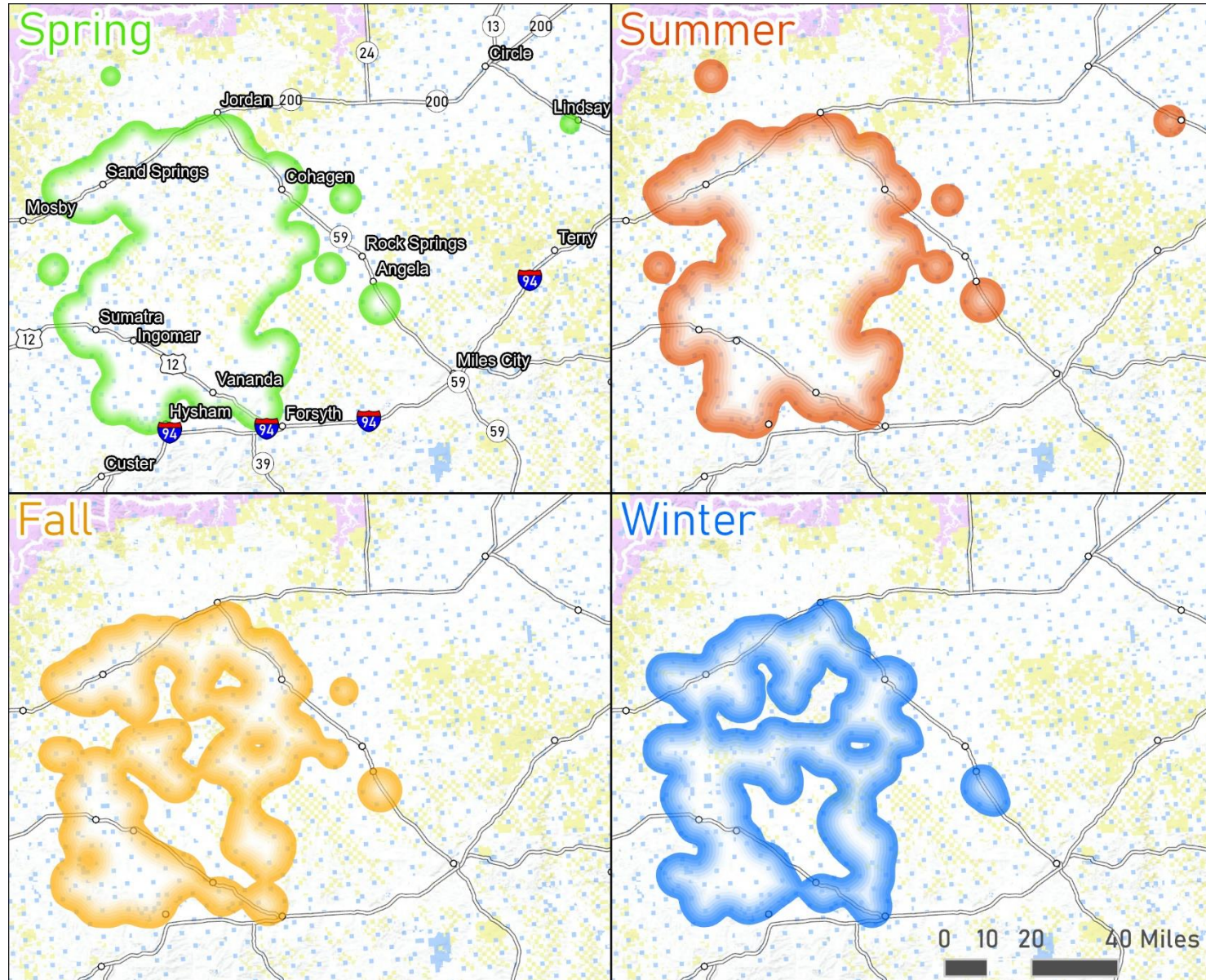


Figure 28. Seasonal ranges of collared adult female pronghorn in the Garfield-Rosebud area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

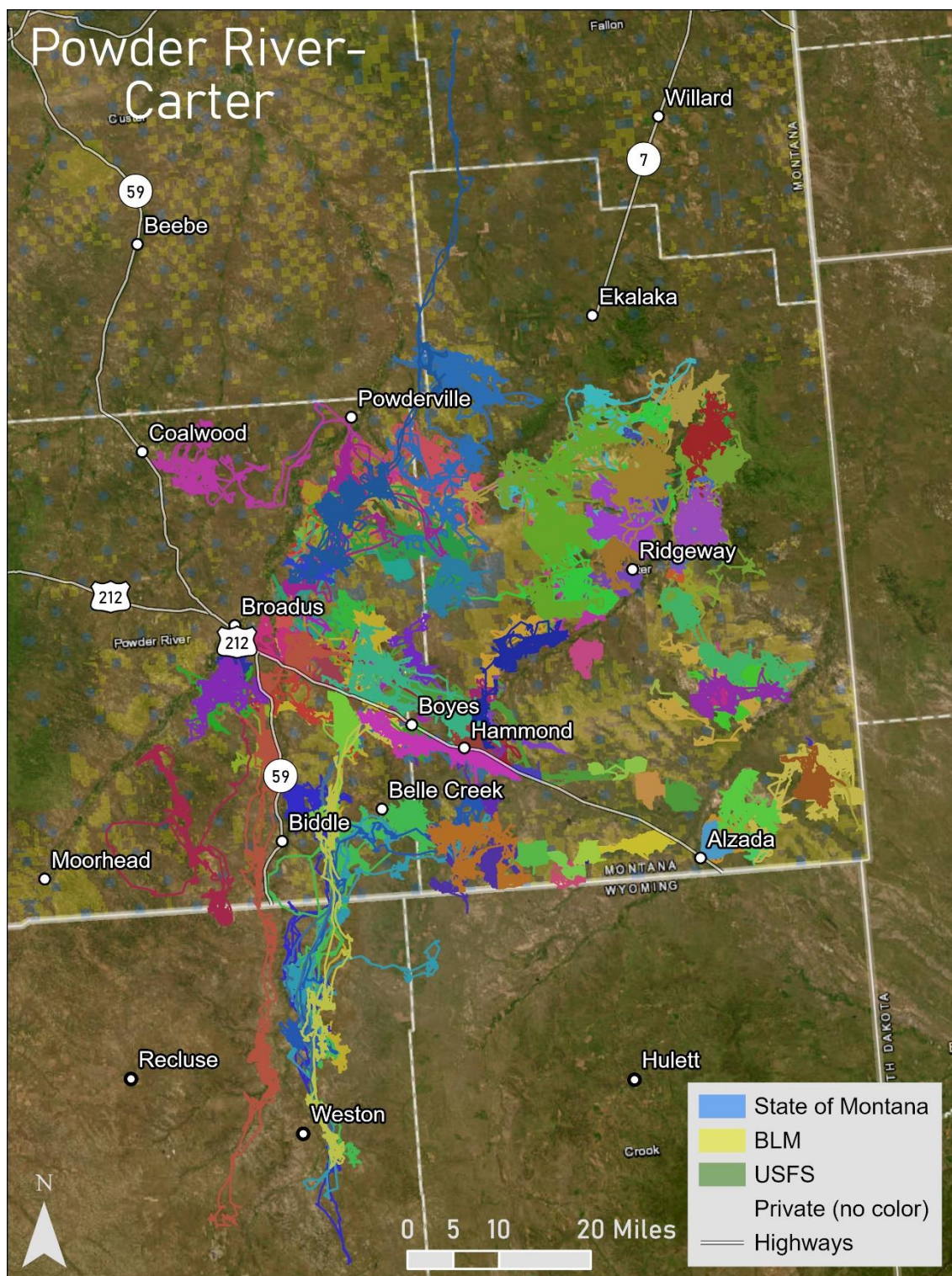


Figure 29. Movements of collared adult female pronghorn (colored by individual) in the Powder River-Carter study area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023.

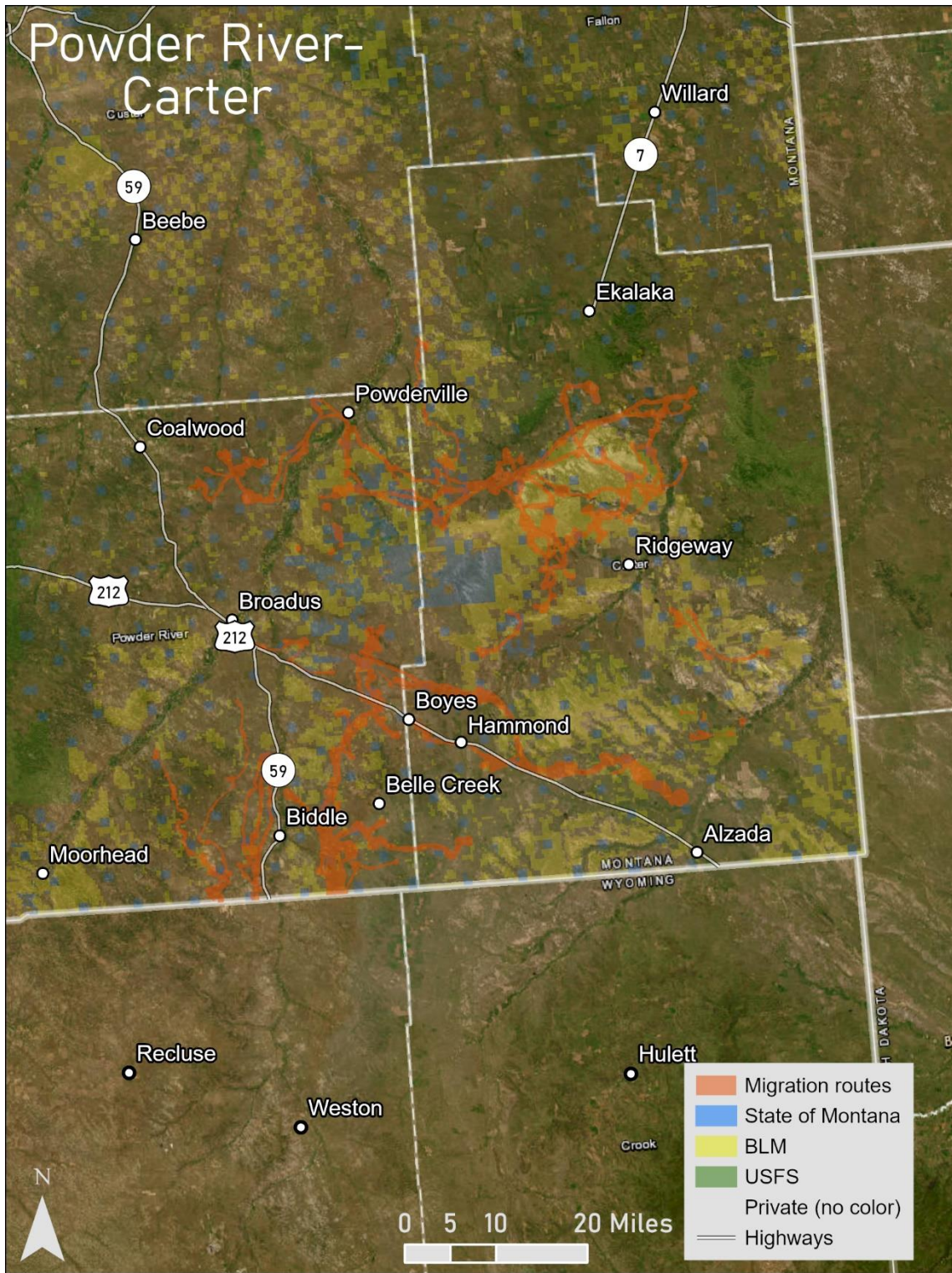


Figure 30. Estimated migration routes of migrant collared adult female pronghorn in the Powder River-Carter study area for the Montana Pronghorn Movement and Population Ecology Project. Migration routes represent areas used by ≥ 1 migrant during spring and/or fall migration periods from January 2020 to June 2023 and are clipped to Montana only.

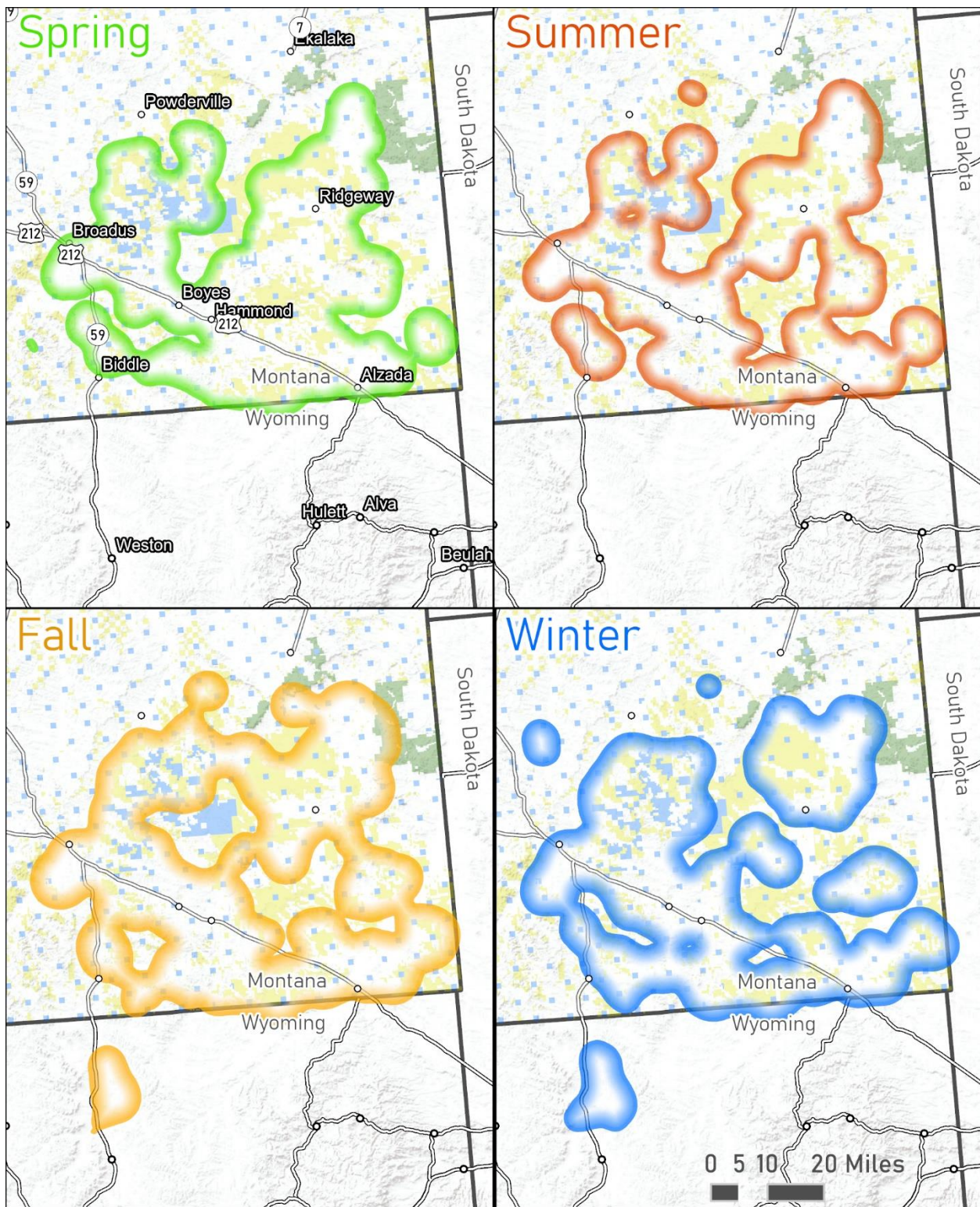


Figure 31. Seasonal ranges of collared adult female pronghorn in the Powder River-Carter area for the Montana Pronghorn Movement and Population Ecology Project from January 2020 to June 2023. Spring: Apr 1 – Jun 30; Summer: Jul 1 – Aug 31; Fall: Sep 1 – Nov 30; Winter: Dec 1 – Mar 31.

1.2 Pronghorn migratory behaviors

To better understand the diversity of individual movement patterns, we characterized migratory strategies for each animal's migratory year, which we selected to span 01 Feb – 31 Jan, with the start of the year representing when individuals are assumed to be on their winter range for that year. We used net squared displacement (NSD; Bunnefeld et al. 2011, Merkle et al. 2022) curves and maps of movement trajectories for each animal's migratory year to identify migration periods and classify individual pronghorn migratory strategies based on a combination of pre- and post-hoc rules (see Section 1.1; DeVoe et al. *in preparation*). Initial examinations of NSD curves and movement maps indicated pronghorn demonstrated a variety of migratory movement patterns that included, for example, the use of multiple summer ranges or differing year to year winter ranges. Traditionally, atypical migratory behaviors are forced into more generic categories or ignored (Cagnacci et al. 2016), even though these atypical behaviors are considered to be relatively common across ungulate species and critical for population persistence under changing environmental conditions (Cagnacci et al. 2016, van de Kerk et al. 2021, Xu et al. 2021a). We therefore adopted and expanded upon classification methods developed by van de Kerk et al. (2021) for classifying variable migratory behaviors (Figure 32 – 33).

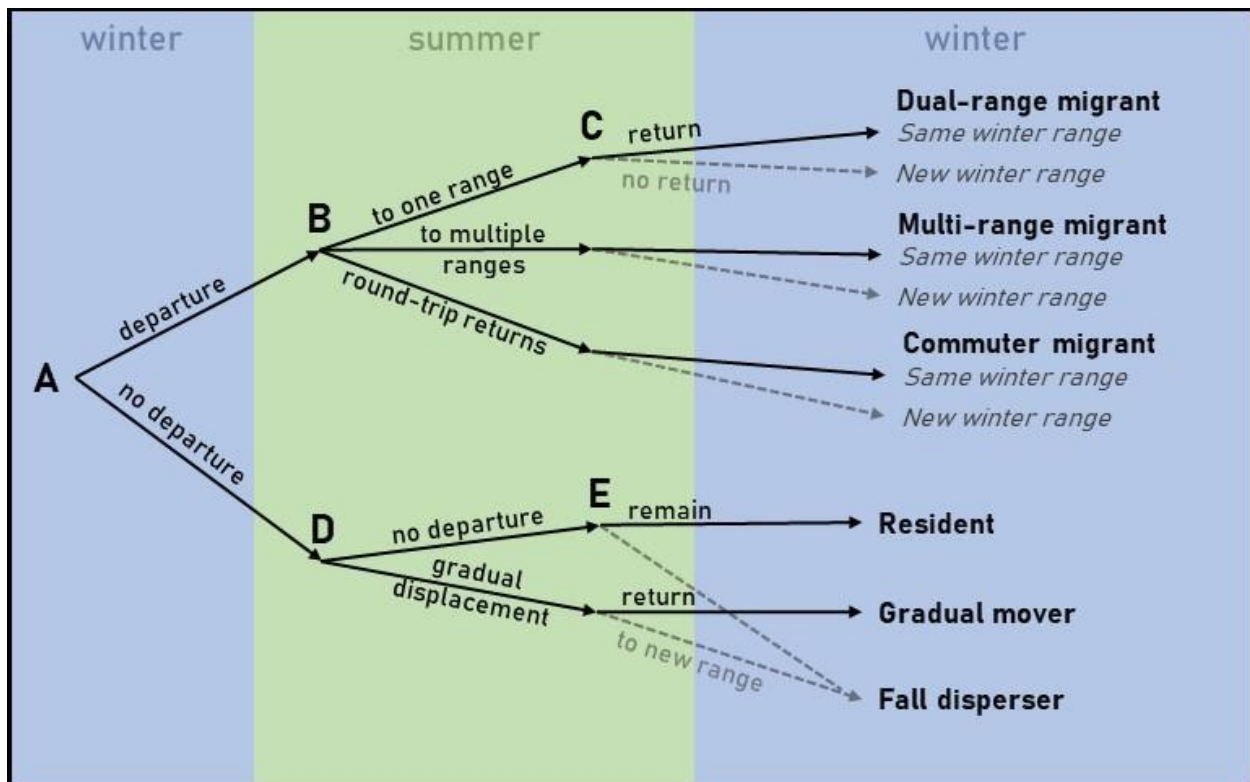


Figure 32. Decision tree adapted from van de Kerk et al. (2021) indicating how we categorized migration strategies from movement trajectories of each animal's migratory year (Feb 01 – Jan 31) for pronghorn captured between 2019 and 2023 in Montana, USA.

We classified animal-years into 6 categories to capture the highly variable migratory behaviors observed in our pronghorn, that included dual-range migrant, multi-range migrant, commuter migrant, resident, gradual mover, or fall disperser (Figure 33). We defined *dual-range migrants* as those that made only one visit to a single summer range before returning to winter range. *Multi-range migrants* visited multiple summer ranges before returning to winter range. *Commuter migrants* made multiple (≥ 2) roundtrips during the summer

between at least one summer range and their initial winter range. *Residents* did not depart their initial winter range and remained on one range the entire year, while *gradual movers* made a slow, indistinct movement outside of a typical home range, as determined by their NSDs surpassing 104 km for at least 21 days. We selected this threshold based on the median annual home range size of 104.1 km² calculated from a 95% kernel density estimate of locations for each animal-year in our study. *Fall dispersers* did not depart their initial winter range until fall, when they dispersed to a new winter range. For migrant classifications, we additionally recorded whether animals returned to their initial winter range during the fall (i.e., *same winter range*) or occupied a new final winter range (i.e., *new winter range*), which could include a non-departure from their final summer range or a range shift to an alternate winter range. For migrants with multiple years of data, we recorded whether they returned to their initial summer ranges (i.e., *same summer range*) or shifted to a different summer range in the subsequent year (i.e., *new summer range*). Last, we measured migration distances for each migrant using only the outbound spring migration trajectories (unless only a fall migration existed), visually examining movement maps to identify the areas of the winter and summer ranges that contained the overall concentration of locations, and measured the Euclidean distance between the edges of the concentrated areas, generally following the animal's spring migratory pathway to account for topographic diversions (e.g., animal pathways circuiting a mountain range separating its winter). For animals with multiple distinct summer ranges, we measured the distance to the furthest summer range.

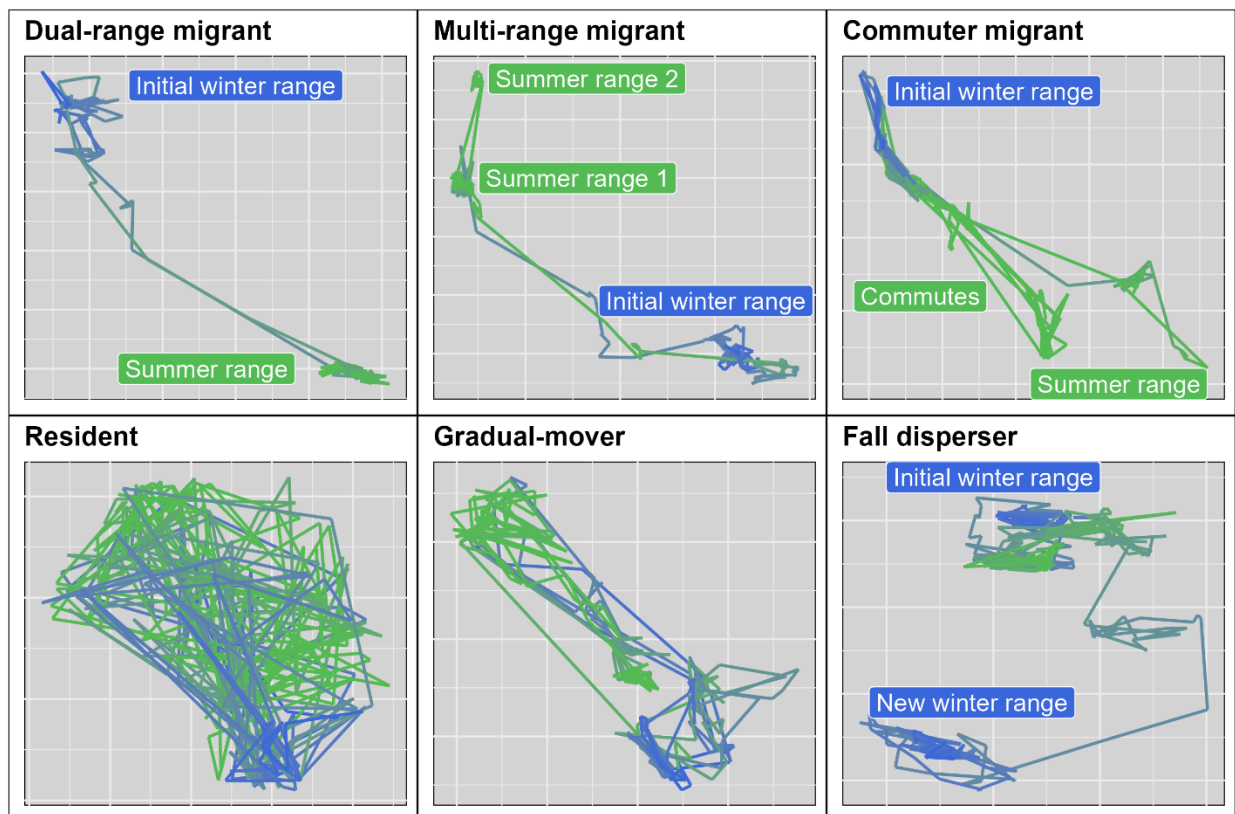


Figure 33. Examples of movement trajectories for a migratory year (Feb 01 – Jan 31) classified into 6 migration strategies based on our decision tree (Figure 32). Green colors represent summer movements and blue colors represent winter movements.

Of the 702 collared pronghorn, a total of 516 individuals and 1,011 animal-years (29, 300, 359, and 323 animal-years for 2019, 2020, 2021, and 2022, respectively) had sufficient data (i.e., >336 days or within 1 month of the

end of the migratory year on January 31) to characterize migratory strategies. Of these individuals, 198 (38%), 152 (30%), 155 (30%), and 11 (2%) had 1, 2, 3, and 4 years of data, respectively. The number of animal-years per study area averaged 126 and ranged from 60 in Paradise to 153 in Madison. Across all animal-years and study areas, departure and arrival dates of migratory individuals (i.e., those that departed their initial winter range) respectively averaged 04 Apr (range = 06 Feb – 18 Jul) and 13 Apr (range = 09 Feb – 29 Jul) for spring and 16 Oct (range = 19 Jun – 18 Dec) and 23 Oct (range = 21 Jun – 25 Dec) for fall (Figure 34). Departure and arrival dates of migratory individuals for spring and fall varied by year (Figure 35) and study area (Table 7, Figure 36 – 41). Migration distances averaged 46 km (median = 36, SD = 33.7, range = 10 – 195) across study areas and varied by study area (Figure 44).

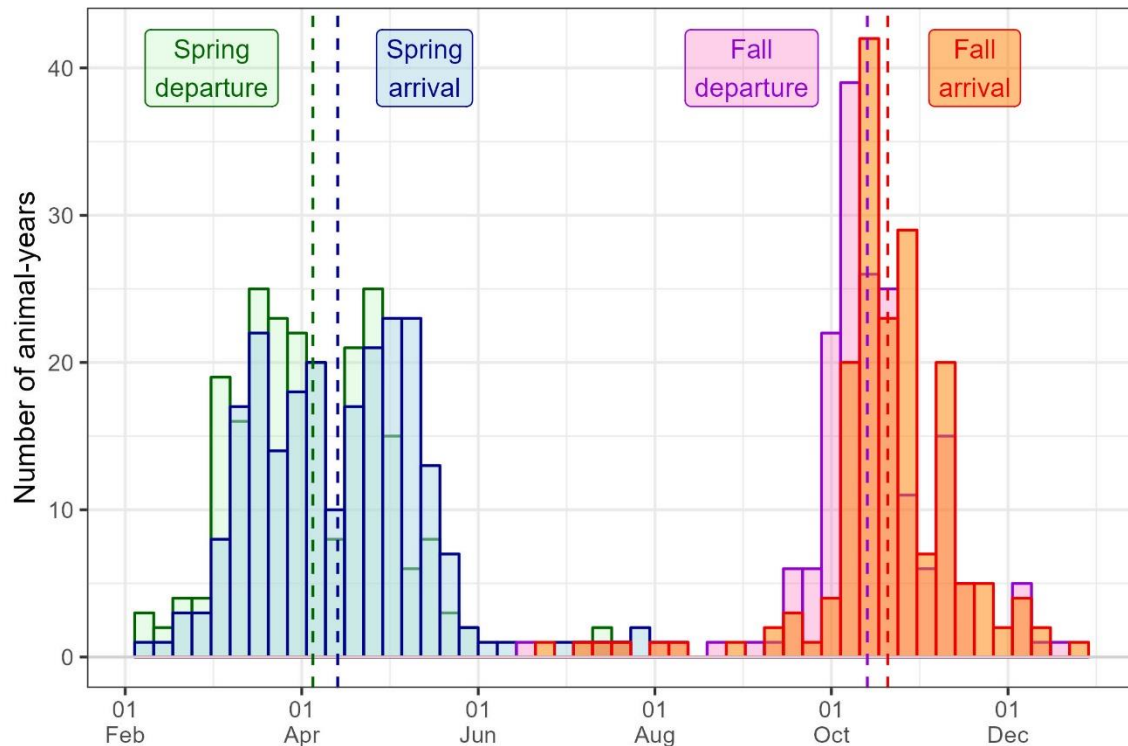


Figure 34. Distribution and average (vertical dashed lines) of migratory departure (spring \bar{x} = 04 Apr and fall \bar{x} = 16 Oct) and arrival (spring \bar{x} = 13 Apr and fall \bar{x} = 23 Oct) dates across all years (2019 – 2022) and study areas of migratory collared pronghorn in Montana, USA.

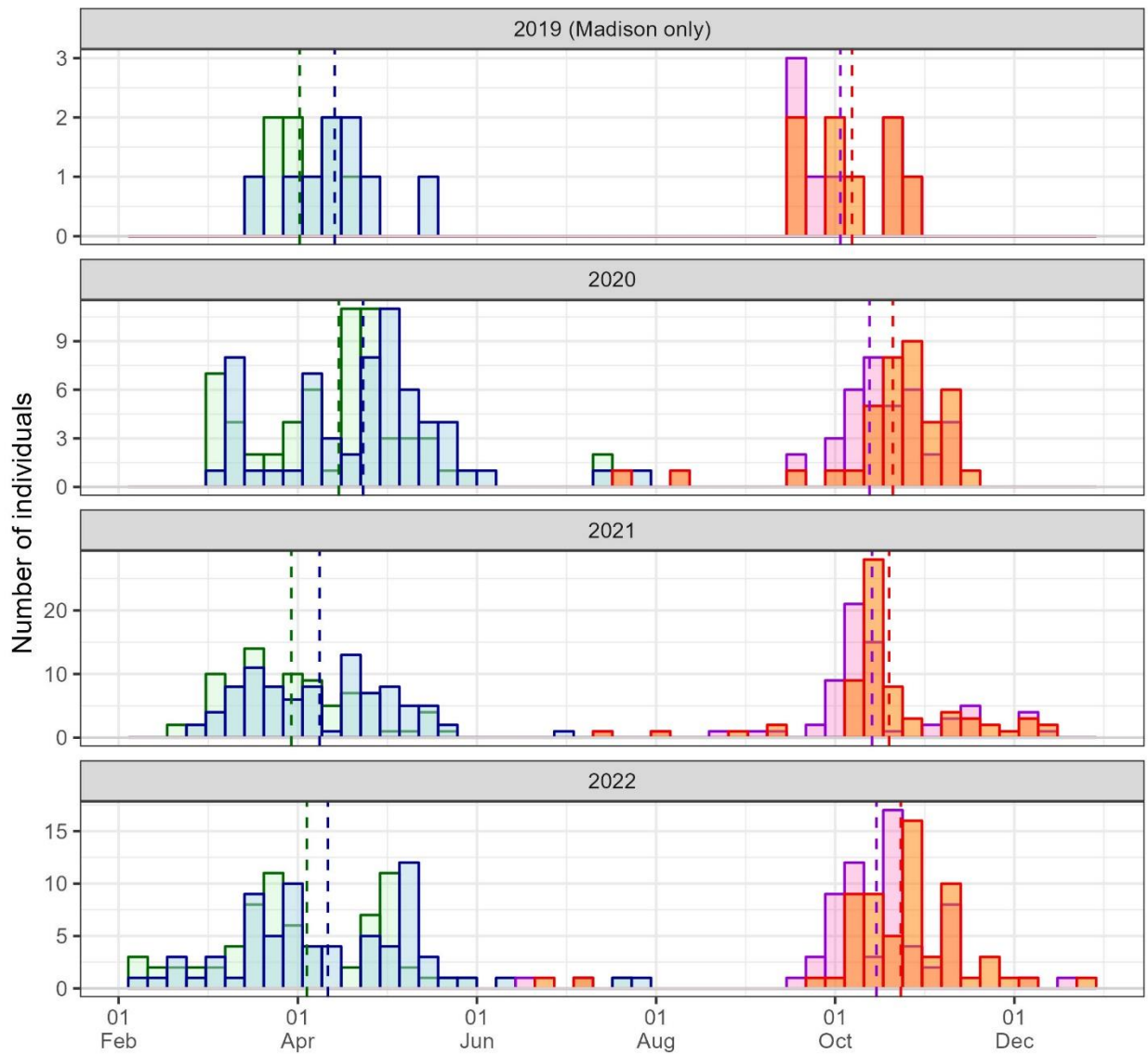


Figure 35. Distribution and average (vertical dashed lines) of dates of spring departure (green), spring arrival (blue), fall departure (purple), and fall arrival (orange) for each year across all study areas of migratory pronghorn captured between 2019 and 2023 in Montana, USA. Note differences in y-axis scales.

Table 7. Average and range of migratory departure and arrival dates for spring and fall migrations for each study area of pronghorn captured between 2019 and 2023 in Montana, USA.

Study area	Spring		Fall	
	Mean departure (range)	Mean arrival (range)	Mean departure (range)	Mean arrival (range)
Big Hole	10 Apr (12 Mar - 23 May)	20 Apr (17 Mar - 29 Jun)	15 Oct (22 Sep - 18 Nov)	22 Oct (06 Oct - 21 Nov)
Madison	05 Apr (04 Mar - 08 May)	19 Apr (08 Mar - 28 May)	07 Oct (22 Jul - 14 Dec)	14 Oct (23 Jul - 15 Dec)
Paradise	08 May (16 Mar - 13 Jul)	16 May (18 Mar - 16 Jul)	05 Oct (24 Aug - 17 Oct)	07 Oct (27 Aug - 18 Oct)
Musselshell	12 Apr (03 Mar - 28 May)	20 Apr (08 Mar - 02 Jun)	19 Oct (05 Oct - 31 Oct)	01 Nov (29 Oct - 08 Nov)
Fergus- Petroleum	31 Mar (02 Mar - 18 May)	07 Apr (08 Mar - 20 May)	15 Oct (14 Aug - 06 Dec)	20 Oct (19 Aug - 08 Dec)
South Philips	25 Mar (21 Feb - 15 Jul)	03 Apr (25 Feb - 29 Jul)	30 Oct (17 Sep - 04 Dec)	06 Nov (01 Oct - 16 Dec)
Garfield- Rosebud	31 Mar (03 Mar - 11 May)	07 Apr (06 Mar - 13 May)	25 Oct (09 Aug - 19 Dec)	04 Nov (11 Aug - 07 Jan)
Powder River-Carter	20 Mar (22 Feb - 21 Jun)	30 Mar (24 Feb - 04 Jul)	11 Oct (13 Jul - 17 Nov)	20 Oct (16 Jul - 18 Nov)

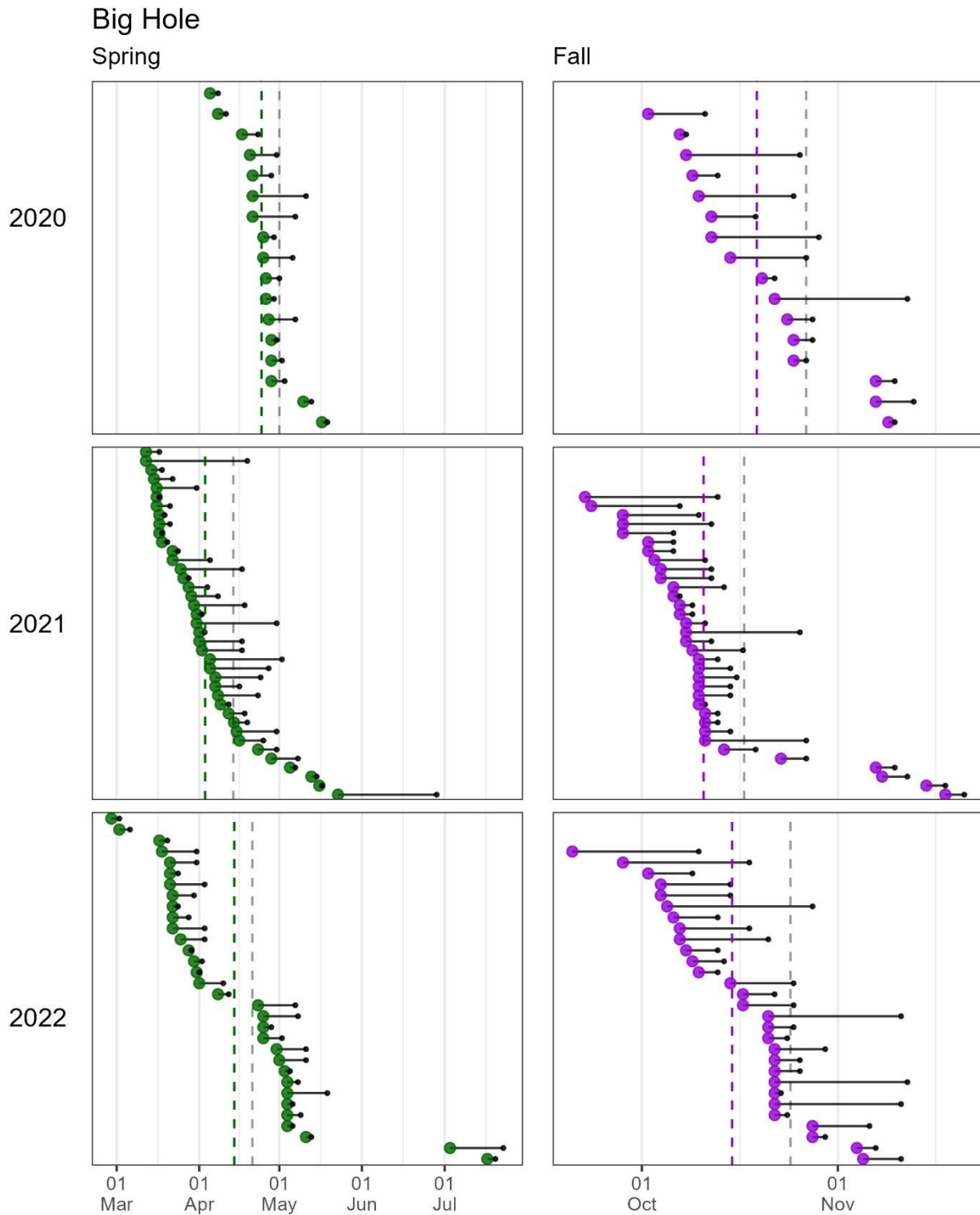


Figure 36. Timing of spring and fall migrations for individuals (y-axis) in the Big Hole study population for 2020 – 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.



Figure 37. Timing of spring and fall migrations for individuals (y-axis) in the Madison study population for 2020 – 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

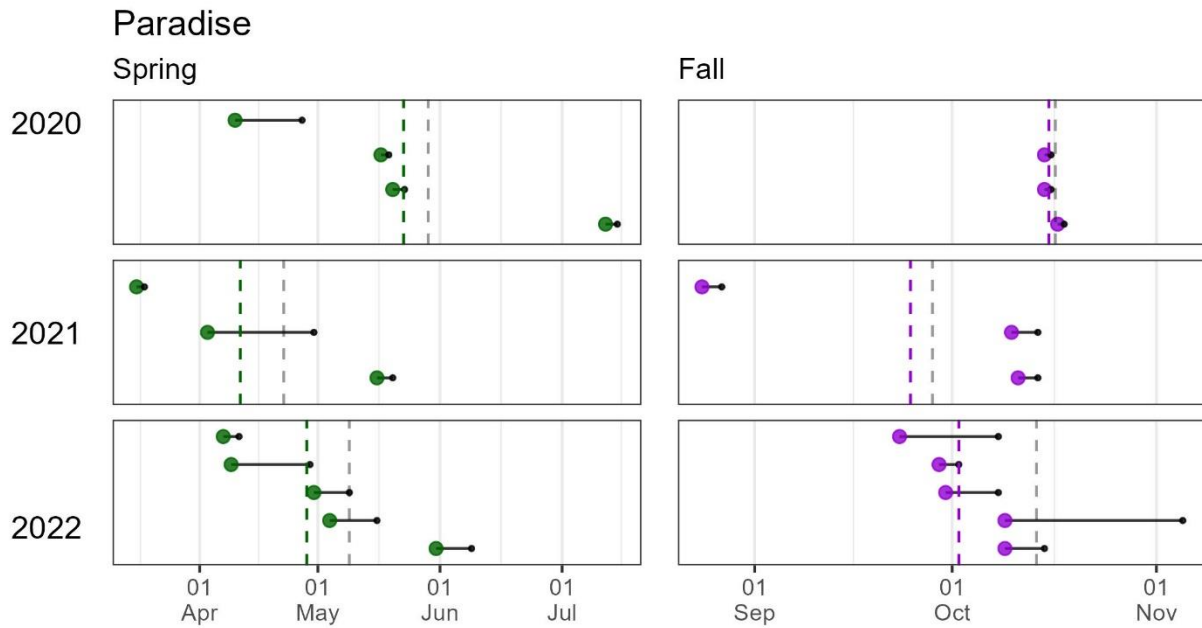


Figure 38. Timing of spring and fall migrations for individuals (y-axis) in the Paradise study population for 2020 – 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

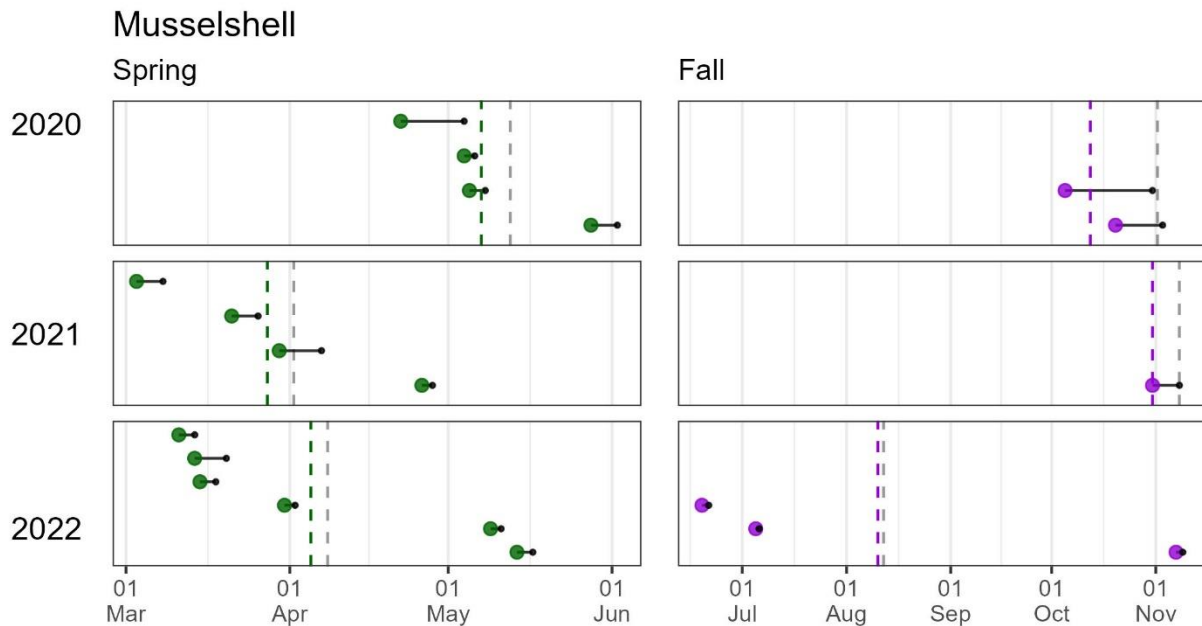


Figure 39. Timing of spring and fall migrations for individuals (y-axis) in the Musselshell study population for 2020 – 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

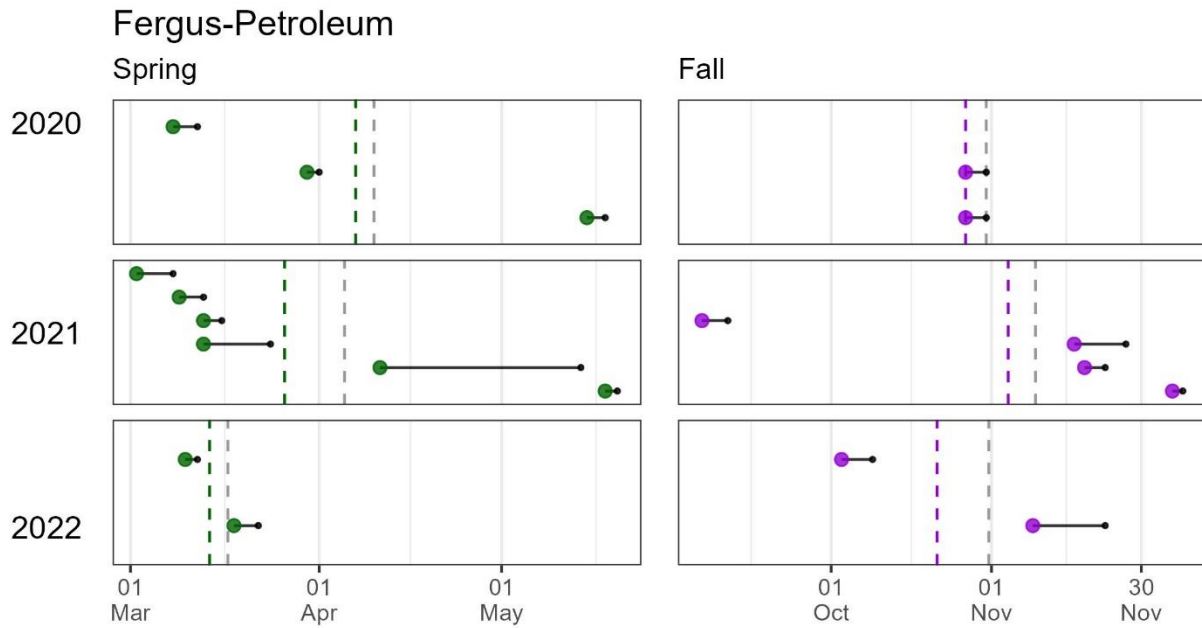


Figure 40. Timing of spring and fall migrations for individuals (y-axis) in the Fergus-Petroleum study population for 2020 - 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

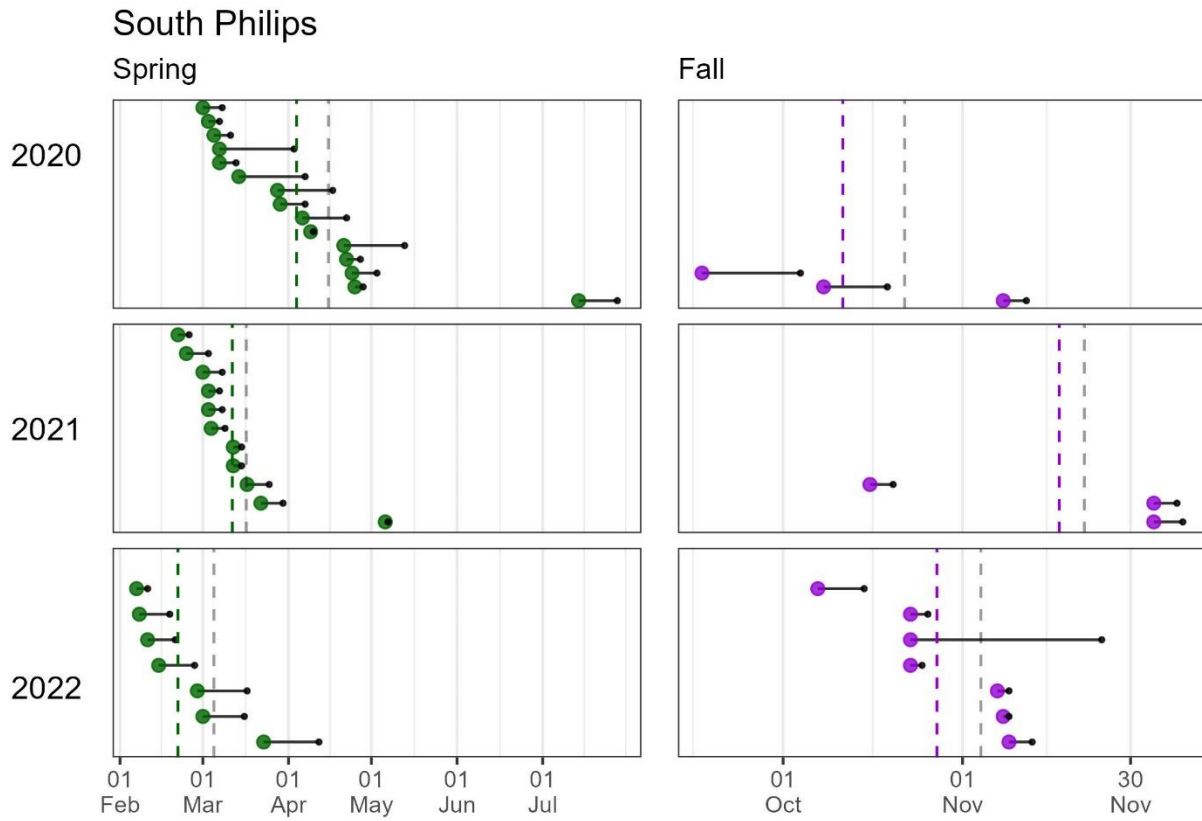


Figure 41. Timing of spring and fall migrations for individuals (y-axis) in the South Philips study population for 2020 – 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

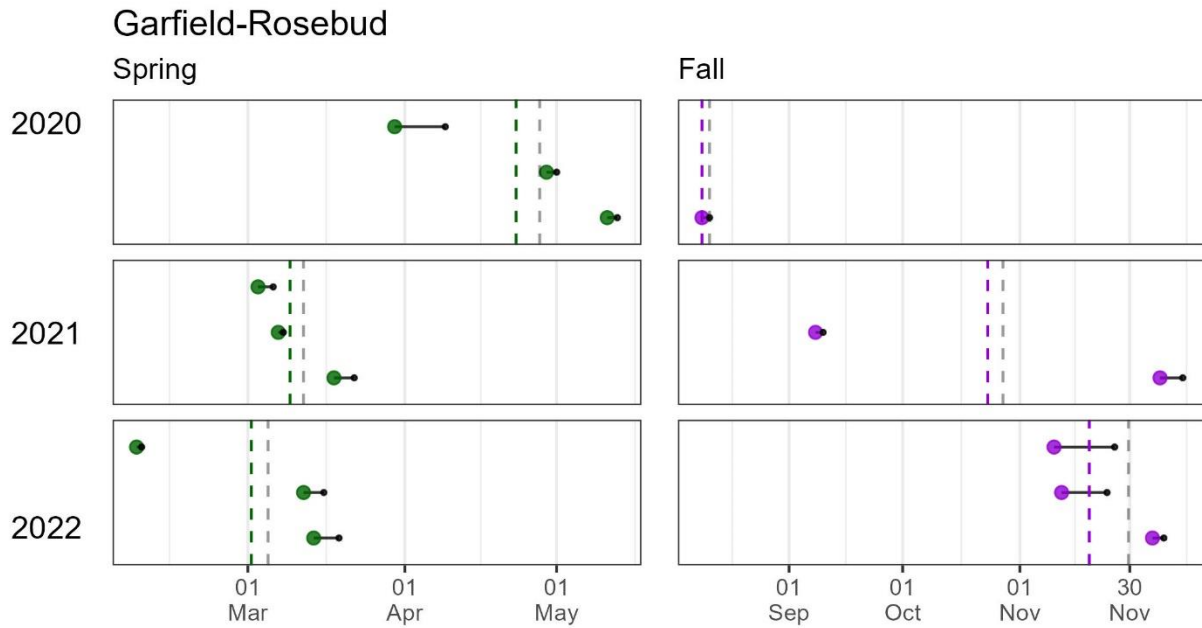


Figure 42. Timing of spring and fall migrations for individuals (y-axis) in the Garfield-Rosebud study population for 2020 - 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

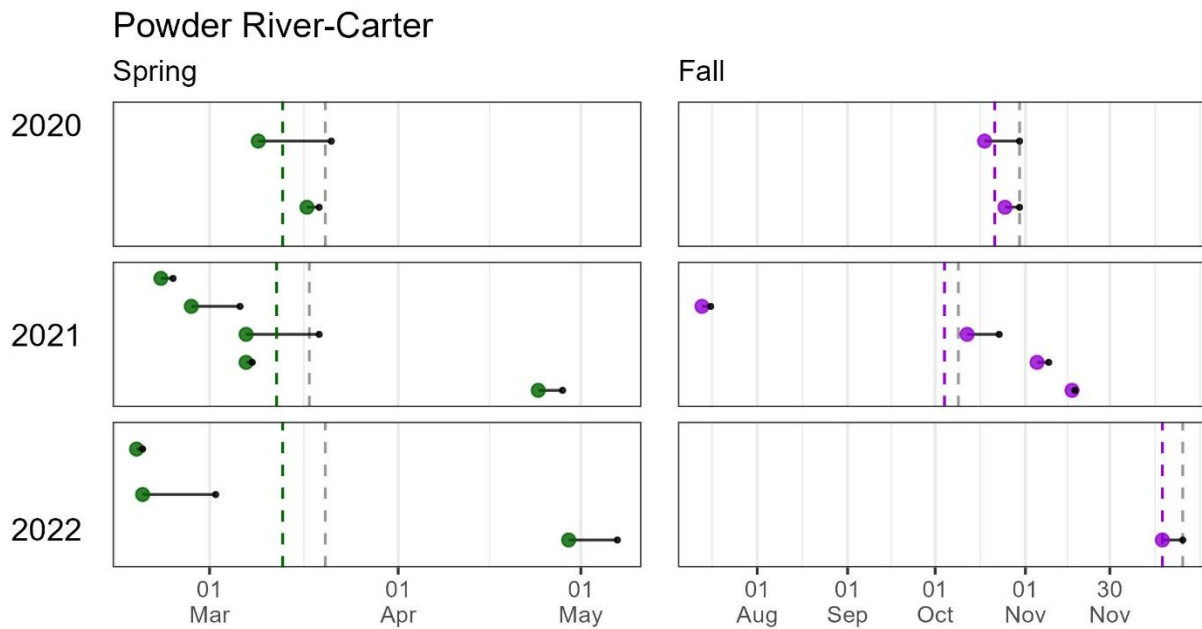


Figure 43. Timing of spring and fall migrations for individuals (y-axis) in the Powder River-Carter study population for 2020 - 2022. Points and horizontal bars represent individual pronghorn departure (green/purple) and arrival (black) dates. Dashed vertical bars represent the average departure and arrival date for each season and year. Note different x-axis scales between spring and fall panels.

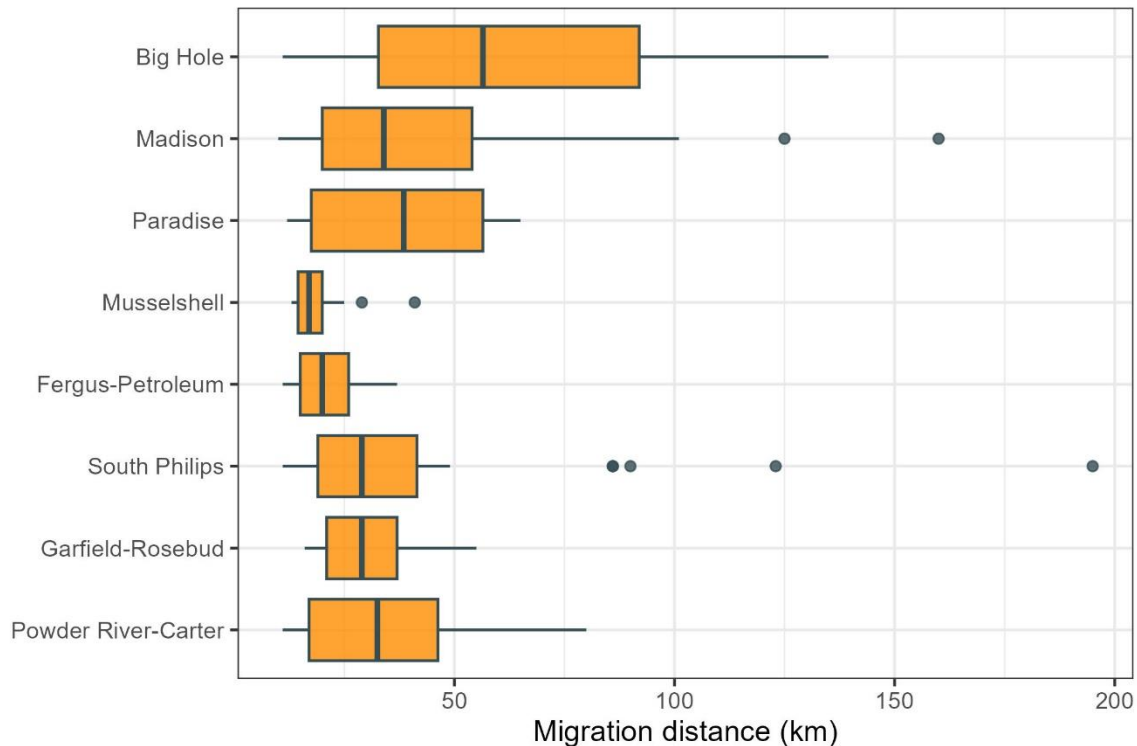


Figure 44. Distributions of migratory distances of migratory individuals in each study area of pronghorn during 2020 – 2023 (2019 – 2023 in Madison) in Montana, USA. Distances were measured following the animal’s spring migratory pathway to its furthest summer range. Vertical lines through boxes represent median values, the length of the box represents the interquartile range (IQR; i.e., the middle 50% of observations) and horizontal lines represent values within 1.5x the IQR.

Across all study areas and years, most individuals ($n = 782$, 77.3%) did not distinctly depart their initial winter range during the summer, with over half of all pronghorn ($n = 593$, 58.7% of total) remaining as residents, 114 (11.3% of total) exhibiting gradual range shifts as gradual movers, and 75 (7.4% of total) departing to new winter ranges during the fall (i.e., fall dispersers; Figure 45). The percent of individuals classified as either resident, gradual mover, or fall disperser each year ranged from 25.0% in Big Hole to 95.8% in Fergus-Petroleum (Table 8).

The remainder of individuals, comprising nearly a fourth of all pronghorn ($n = 160$, 23.3%), distinctly departed their initial winter range and moved to summer range, with 148 (64.6% of those departed) returning to the initial winter range and 81 (35.4% of those departed) dispersing to a new winter range. Of those that returned to their initial winter range, 117 (79.1% of total) were classified as dual-range migrants, 26 (17.6% of total) were classified as multi-range migrants, and 5 (0.3% of total) were classified as commuter migrants. Proportions of migratory classifications varied by study area and year (Figure 46 – 48; Table 8).

Across all migratory strategies, the percent of individuals returning to their initial winter range each year ranged from 57.8% in South Philips to 100% in Paradise and Fergus-Petroleum. Of the individuals that had enough data to determine summer range fidelity in subsequent years ($n = 496$), the percent of individuals

returning to their initial summer range each year ranged from 89.7% in Big Hole to 100% in Big Hole, Madison, Paradise, Musselshell, Fergus-Petroleum, Garfield-Rosebud, and Powder River-Carter.

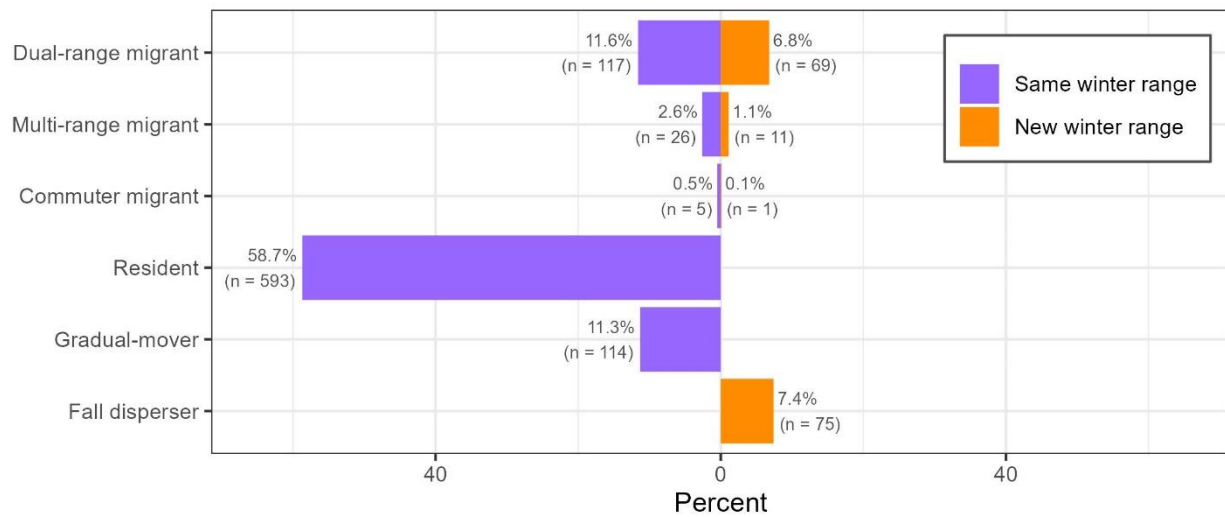


Figure 45. Percent of animals classified into migratory strategy classes and whether they returned to their original (purple) or a new (orange) winter range summarized across years and study areas of pronghorn during 2020 – 2023 (2019 – 2023 in Madison) in Montana, USA.

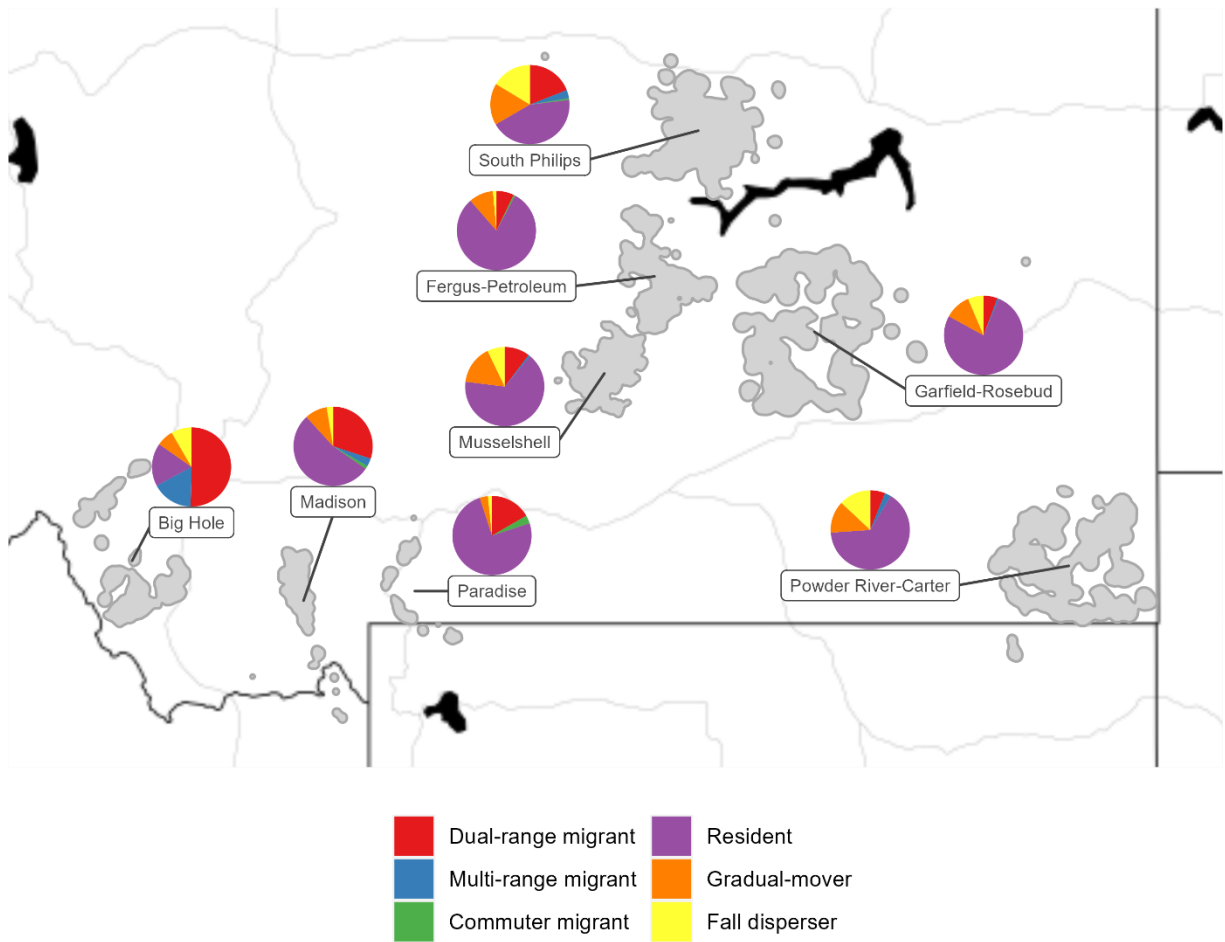


Figure 46. Map of the proportion of migratory behaviors in each study area across all study years (2020-2022; the Madison also includes 2019).

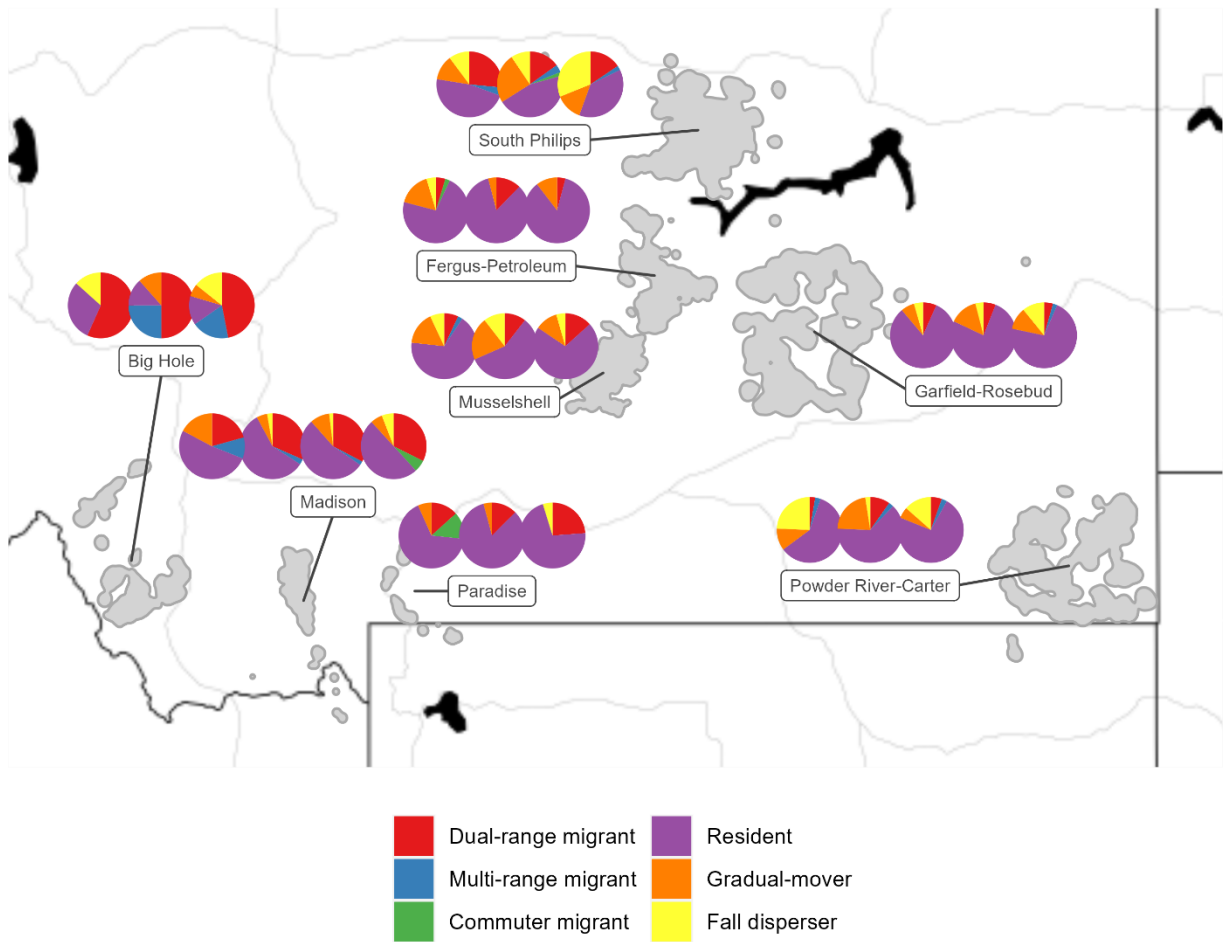


Figure 47. Map of the proportion of migratory behaviors in each consecutive study year (2020-2022) and study area (the Madison includes an extra chart for 2019).

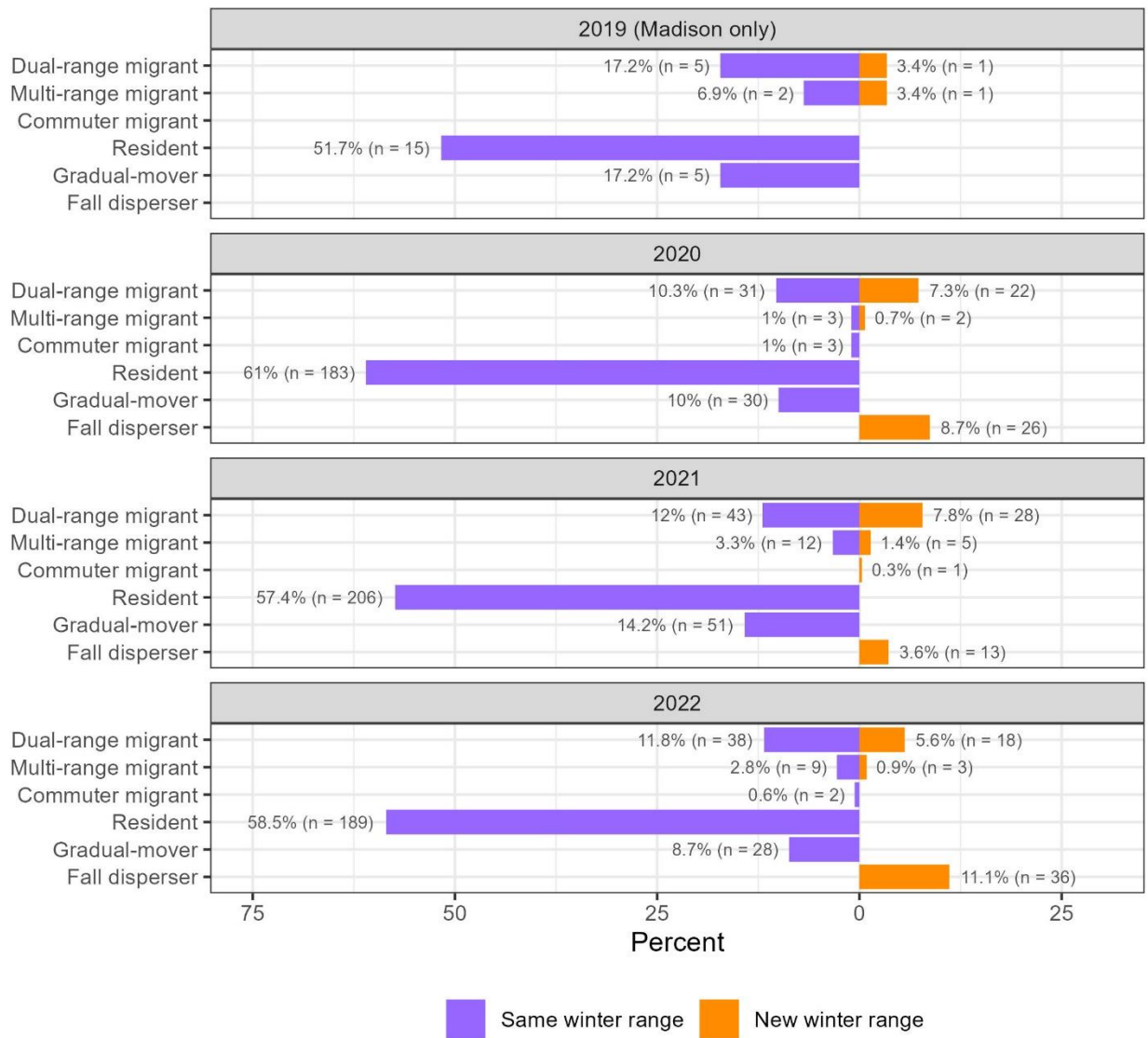


Figure 48. Proportion of animals classified into migratory strategy classes and whether they returned to their original (purple) or a new (orange) winter range for each year across pronghorn study areas in Montana, USA.

Table 8. Number and proportion of animals classified into each migratory class for each year and pronghorn study area in Montana, USA.

Study area	Migration behavior	2019	2020	2021	2022
Big Hole	Dual-range migrant	--	17 (0.57)	26 (0.50)	21 (0.45)
	Multi-range migrant	--	--	13 (0.25)	9 (0.19)
	Resident	--	9 (0.30)	7 (0.13)	7 (0.15)
	Gradual-mover	--	--	6 (0.12)	3 (0.06)
	Fall disperser	--	4 (0.13)	--	7 (0.15)
	Total	--	30	52	47
Madison	Dual-range migrant	6 (0.21)	12 (0.32)	17 (0.33)	11 (0.32)
	Multi-range migrant	3 (0.10)	1 (0.03)	1 (0.02)	--
	Commuter migrant	--	--	--	2 (0.06)
	Resident	15 (0.52)	22 (0.58)	28 (0.54)	17 (0.50)
	Gradual-mover	5 (0.17)	2 (0.05)	5 (0.10)	2 (0.06)
	Fall disperser	--	1 (0.03)	1 (0.02)	2 (0.06)
Total	29	38	52	34	
Paradise	Dual-range migrant	--	2 (0.13)	3 (0.12)	5 (0.24)
	Commuter migrant	--	2 (0.13)	--	--
	Resident	--	10 (0.67)	20 (0.83)	15 (0.71)
	Gradual-mover	--	1 (0.07)	1 (0.04)	--
	Fall disperser	--	--	--	1 (0.05)
	Total	--	15	24	21
Musselshell	Dual-range migrant	--	3 (0.07)	4 (0.11)	6 (0.13)
	Multi-range migrant	--	1 (0.02)	--	--
	Resident	--	29 (0.67)	22 (0.58)	32 (0.71)
	Gradual-mover	--	7 (0.16)	8 (0.21)	5 (0.11)
	Fall disperser	--	3 (0.07)	4 (0.11)	2 (0.04)
	Total	--	43	38	45
Fergus-Petroleum	Dual-range migrant	--	2 (0.05)	6 (0.12)	2 (0.04)
	Commuter migrant	--	1 (0.02)	--	--
	Resident	--	31 (0.72)	41 (0.84)	41 (0.85)
	Gradual-mover	--	7 (0.16)	2 (0.04)	5 (0.10)
	Fall disperser	--	2 (0.05)	--	--
	Total	--	43	49	48
South Philips	Dual-range migrant	--	13 (0.27)	8 (0.15)	7 (0.16)
	Multi-range migrant	--	2 (0.04)	2 (0.04)	1 (0.02)
	Commuter migrant	--	--	1 (0.02)	--
	Resident	--	23 (0.47)	24 (0.45)	17 (0.38)
	Gradual-mover	--	6 (0.12)	13 (0.25)	6 (0.13)
	Fall disperser	--	5 (0.10)	5 (0.09)	14 (0.31)
Total	--	49	53	45	
Garfield-Rosebud	Dual-range migrant	--	3 (0.07)	3 (0.06)	2 (0.04)
	Multi-range migrant	--	--	--	1 (0.02)
	Resident	--	37 (0.84)	38 (0.76)	33 (0.72)
	Gradual-mover	--	2 (0.05)	7 (0.14)	5 (0.11)
	Fall disperser	--	2 (0.05)	2 (0.04)	5 (0.11)
	Total	--	44	50	46
Powder River-Carter	Dual-range migrant	--	1 (0.03)	4 (0.10)	2 (0.05)
	Multi-range migrant	--	1 (0.03)	1 (0.02)	1 (0.03)
	Resident	--	22 (0.59)	26 (0.63)	27 (0.73)
	Gradual-mover	--	4 (0.11)	9 (0.22)	2 (0.05)
	Fall disperser	--	9 (0.24)	1 (0.02)	5 (0.14)
	Total	--	37	41	37

We observed 160 instances of individuals switching migratory strategies from one year to the next (Figures 49 - 51). From a total of 22 individuals classified into a migratory strategy for 2019 and 2020 (i.e., Madison study area only), 5 (21.7%) individuals switched, including 1 from dual-range migrant to multi-range migrant, 1 from dual-range migrant to resident, 2 from gradual-mover to resident, and 1 from gradual-mover to dual-range migrant. Of these, 15 individuals were also classified for 2021 from which 4 (26.7%) switched, including 1 from dual-range migrant to fall disperser, 1 multi-range migrant to dual-range migrant, and 2 residents to gradual-movers.

From a total of 229 individuals classified for 2020 and 2021, 78 (34.1%) animals switched. The majority of these animals switched from resident to gradual-mover ($n = 16$, 20.5%), gradual-mover to resident ($n = 17$, 21.8%), and fall disperser to dual-range migrant ($n = 11$, 14.1%). The remainder included 13 (16.9%) switches between migrant and non-departure classes (5 dual-range migrant to gradual-movers, 4 dual-range migrant to resident, 2 dual-range migrant to fall disperser, 1 multi-range migrant to resident, and 1 gradual-mover to multi-range migrant), 12 (15.4%) switches between non-migrant classes (5 resident to fall disperser, 3 fall disperser to gradual-mover, 3 fall disperser to resident, and 1 gradual-mover to fall disperser), and 9 (11.7%) switches between migrant classes (4 dual-range to multi-range, 1 dual-range to commuter, 2 multi-range to dual-range, 2 commuter to dual-range).

From a total of 244 individuals classified for 2021 and 2022, 77 (31.6%) animals switched. The majority of these switched from gradual-mover to resident ($n = 13$, 16.9%), gradual-mover to fall disperser ($n = 12$, 15.6%), resident to fall disperser ($n = 8$, 10.4%), and dual-range migrant to fall disperser ($n = 8$, 10.4%). The remainder included 18 (23.4%) switches between migrant and non-migrant departure classes (7 dual-range to resident, 2 dual-range to gradual-mover, 1 commuter to fall disperser, 3 fall disperser to dual-range migrant, 2 fall disperser to multi-range migrant, and 3 resident to dual-range migrant), 11 (14.3%) switches between migrant classes (2 dual-range to multi-range, 2 dual-range to commuter, and 7 multi-range to dual-range), and 7 (9.1%) switches between non-migrant classes (6 resident to gradual-mover, 1 fall disperser to resident).

Of the 78 individuals that switched migratory strategies between 2020 and 2021, 31 (39.7%) switched again in 2022. The majority of these animals switched from resident to gradual-mover to resident ($n = 6$, 19.4%), resident to dual-range migrant to fall disperser ($n = 4$, 12.9%), and fall disperser to dual-range migrant to fall disperser ($n = 5$, 16.1%), dual-range migrant to multi-range migrant to dual-range migrant ($n = 2$, 6.5%), dual-range migrant to commuter migrant to fall disperser ($n = 2$, 6.5%), dual-range to gradual-mover to fall disperser ($n = 2$, 6.5%), dual-range migrant to gradual-mover to resident ($n = 2$, 6.5%), and dual-range migrant to fall disperser to dual-range migrant ($n = 2$, 6.5%).

A total of 11 individuals had 4 years (2019 - 2022) of migratory data (i.e., Madison animals only), of which 5 demonstrated migratory switching strategy at some point during the study. Two individuals were residents for 2019 and 2020, switched to gradual-mover in 2021, and returned to residents in 2022. One individual switched every year, from gradual-mover to dual-range migrant to fall disperser to dual-range migrant. One individual switched from a dual-range migrant in 2019 to a resident in both 2020 and 2021 and then switched to a fall disperser in 2022. One individual remained a dual-range migrant for the first 3 years before switching to a commuter migrant in 2022.

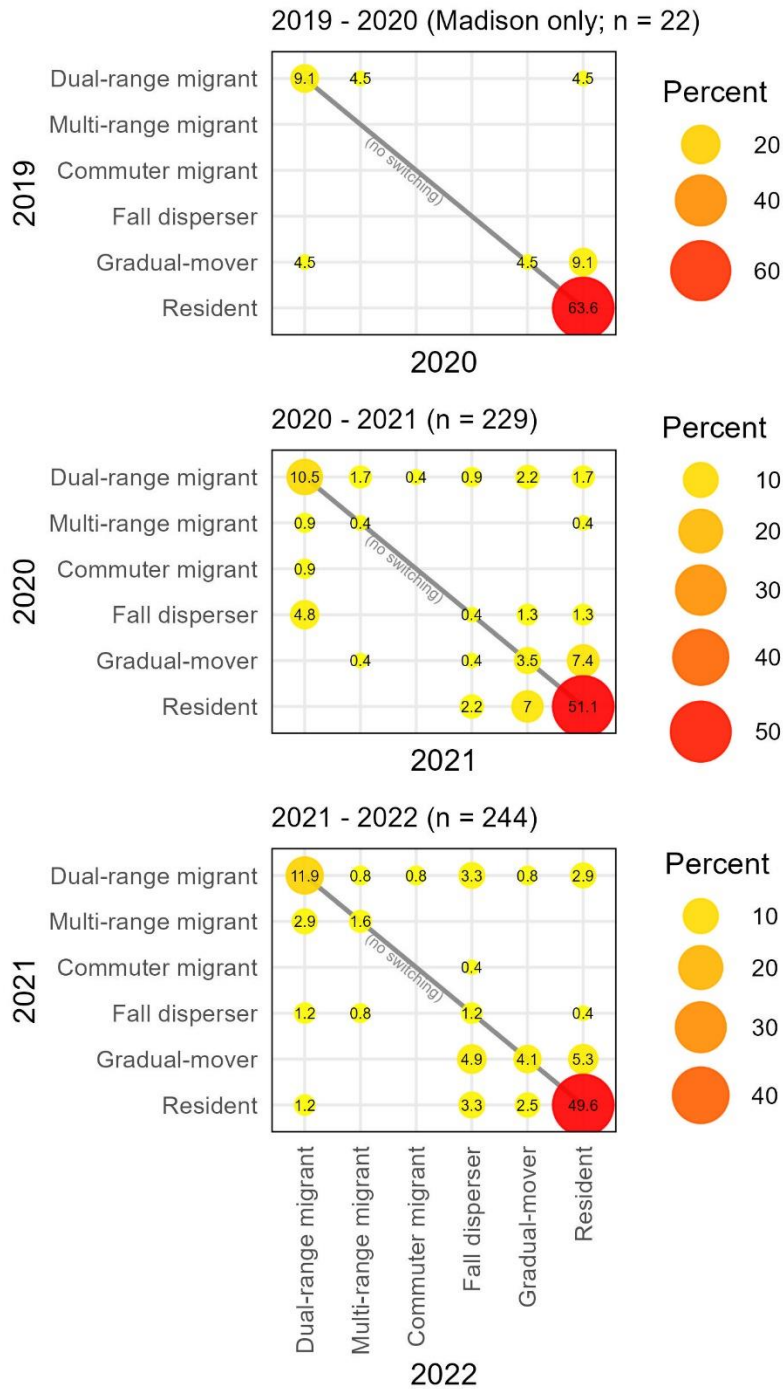


Figure 49. Percent of migratory strategy classification switches between pairs of years from 2019 – 2022 in Montana, USA. The migratory strategies occurring in the first year are displayed on the y-axis and in the second year on the x-axis. Values occurring along the diagonal line represent proportions of individuals that did not switch between the years (i.e., the “no switching” line). Sample sizes (n) represent total number of individuals (i.e., including both switching and non-switching individuals).

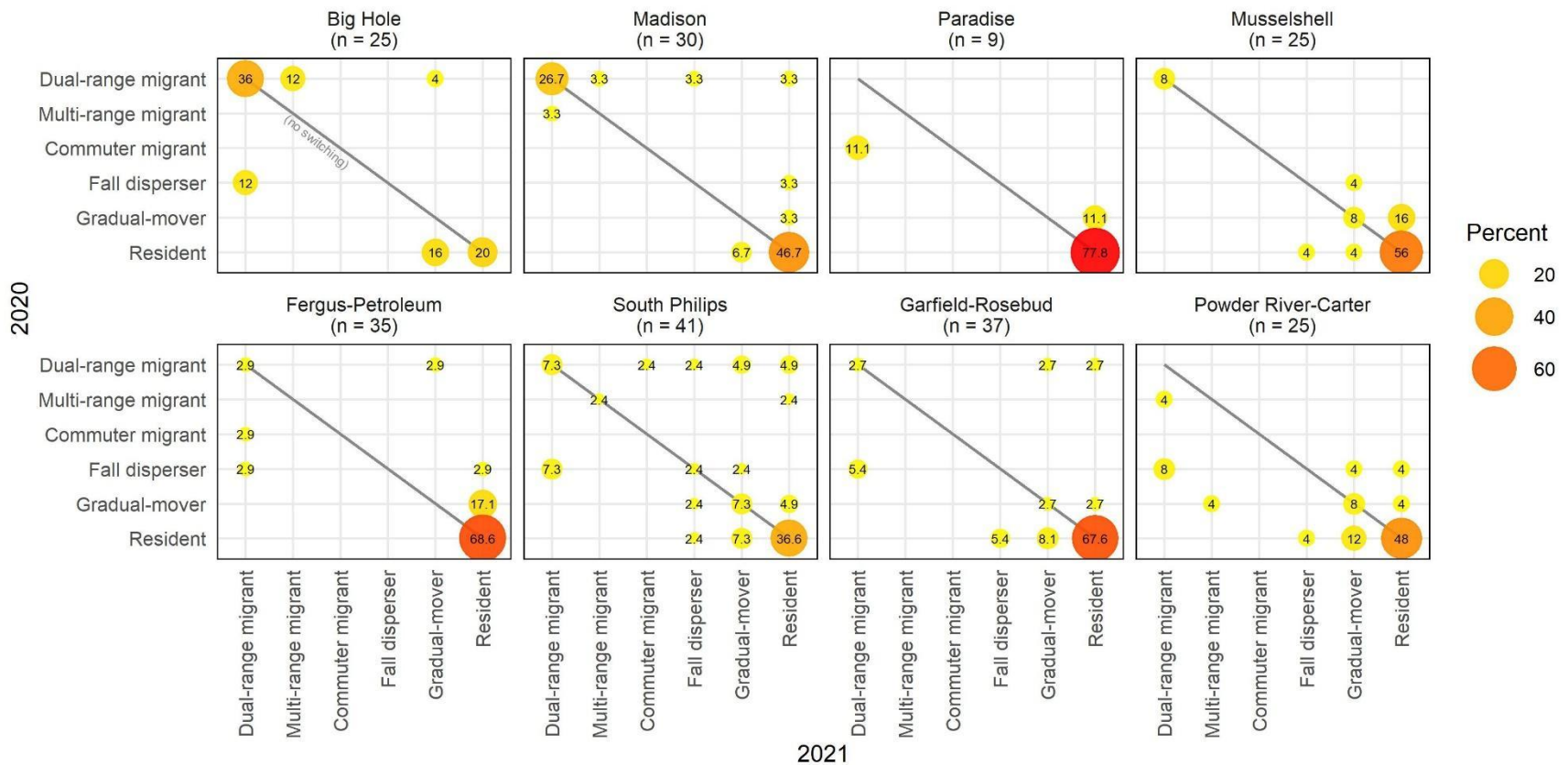


Figure 50. Percent of migratory strategy classification switches between years 2020 (y-axis) and 2021 (x-axis) in each study area of pronghorn captured between 2019 and 2023 in Montana, USA. Values occurring along the diagonal line represent proportions of individuals that did not switch between the years. Sample sizes (n) represent total number of individuals in each study area (i.e., including both switching and non-switching individuals) with sufficient data to classify.

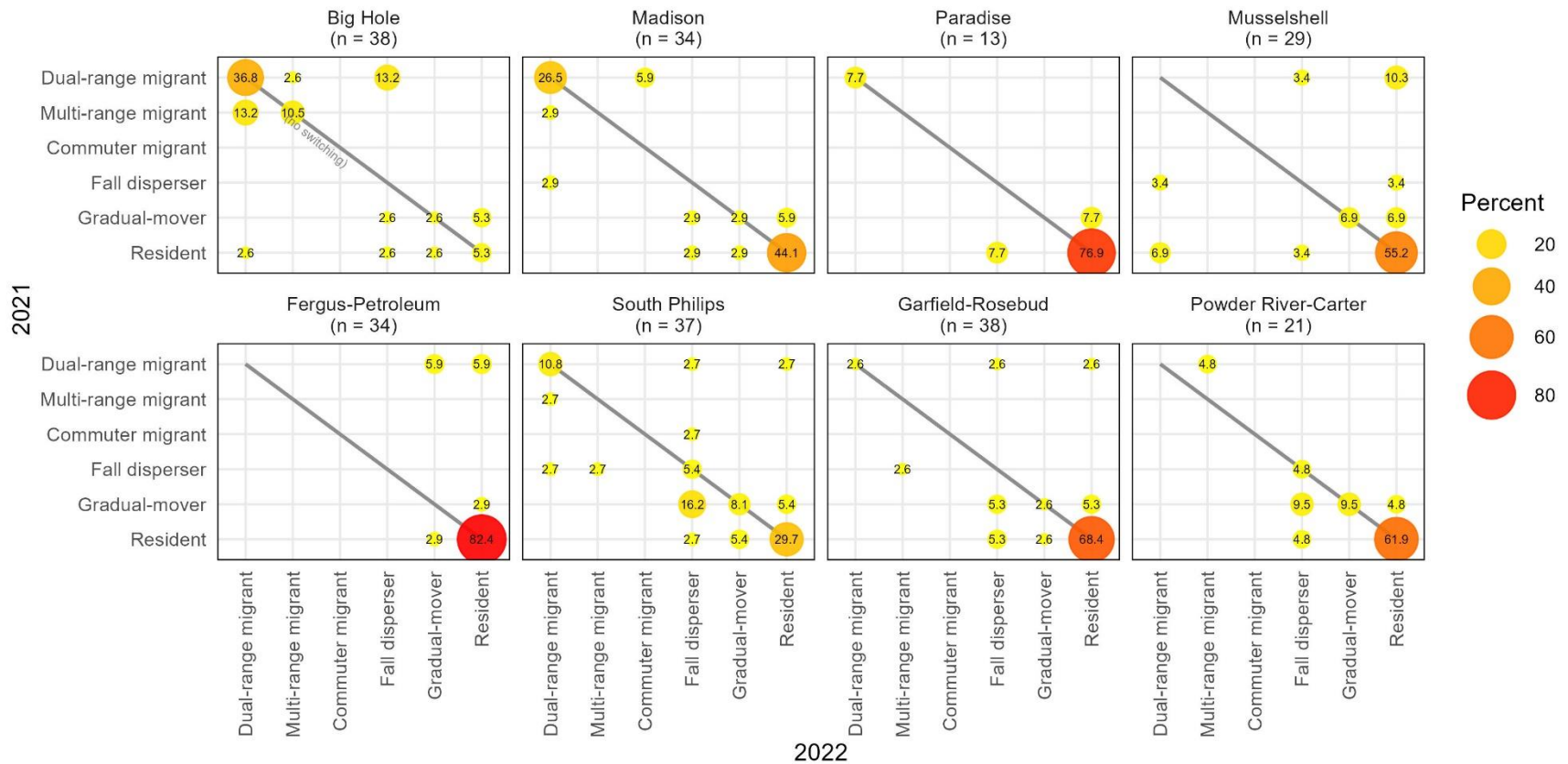


Figure 51. Percent of migratory strategy classification switches between years 2021 (y-axis) and 2022 (x-axis) in each study area of pronghorn captured between 2020 (2019 in Madison) and 2023 in Montana, USA. Values occurring along the diagonal line represent proportions of individuals that did not switch between the years. Sample sizes (n) represent total number of individuals in each study area (i.e., including both switching and non-switching individuals) with sufficient data to classify.

Objective #2: Create and distribute maps of seasonal range and movement areas for pronghorn

Since the initiation of the collar location data collection, we generated monthly summary reports of animal distributions and movements specific to each study area (Figure 52). These reports included population- and individual-level maps, with individual-level maps showing seasonal movements. On a monthly basis, we distributed these reports to state and federal agency biologists, non-profit conservation organizations, and private landowners. We generated these reports in lieu of a web-based platform but have made location data available to FWP and BLM wildlife staff associated with each study area on an ArcGIS Online platform (see Section 3.1). All animal movement data sharing associated with this project was aligned with FWP policy and directions for data sharing.

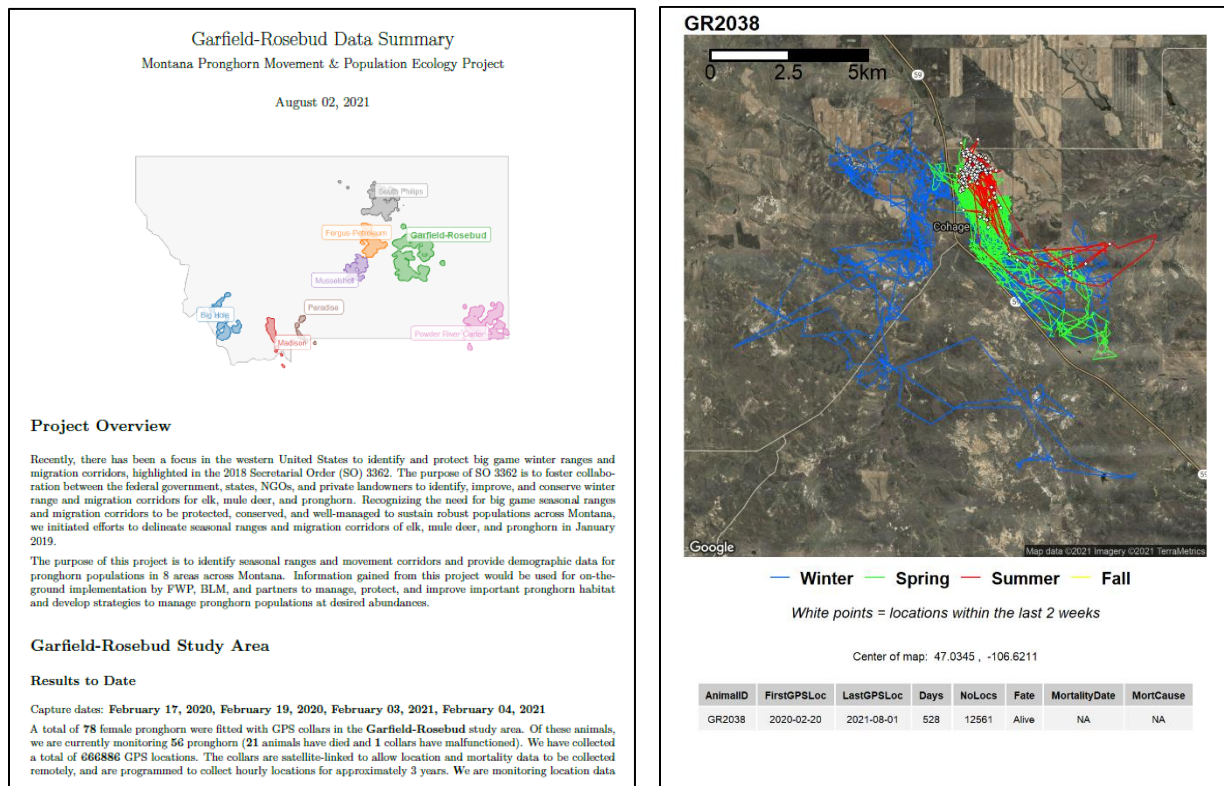


Figure 52. Example pages from the Garfield-Rosebud monthly summary report generated for distribution to agency biologists and collaborators. Reports were updated and distributed monthly for each of the 8 study areas of the Montana Pronghorn Movement and Population Ecology Project for the duration of the study.

Objective #3: Use seasonal range and movement data to identify potential barriers to movements, inform management decisions, and prioritize locations for habitat improvement projects

3.1 Identification of potential barriers to movements

The monthly reports summarizing pronghorn movement information (Section 2.1) have been used by area biologists to identify movement barriers and prioritize fence removal and modification projects for improving landscape permeability for pronghorn. At the time this study concluded, some projects were still in progress or scheduled for completion within the next year (see Section 3.3). To facilitate the identification of potential barriers to pronghorn movements, we developed 2 tools, including 1) an online platform based in ArcGIS Online for mapping fences and recording fence attributes and 2) interactive maps that display fence permeabilities based on relative frequencies of altered behavioral responses to mapped fences. We discuss each of these products below.

ArcGIS Online: Montana Fence Mapping

The ArcGIS Online platform for fence mapping is a collaboration between FWP, the BLM (Montana/Dakotas) State-wide Wildlife Program, and University of Montana that was initiated summer 2021 to collect and aggregate spatial fence data (Figure 53). Accurate spatial data and attribute information for fences provides critical information for management and conservation of pronghorn and other important species, such as sage grouse; however, such information is lacking for the vast majority of Montana. The overall objective of the fence mapping project was to collect and aggregate spatially precise fence locations into a centralized database that could be updated and accessed simultaneously by multiple users for research and conservation applications. To accomplish this, we developed an ArcGIS Online web map which provided a platform for adding fence and attribute data to a line feature layer, as well as other point location information, such as gates or pronghorn crossings, to a point feature layer. This information was added by drawing fences in the office based on aerial maps and in the field using tablets. When in the field, users added attributes to mapped fences, verified and moved positions of mapped fences, and mapped any additional fences. We created an ArcGIS Online group that permits BLM staff to collaborate on these same, centralized data. The original intent of the project was to map fences in each of the 8 pronghorn study areas (represented by annual ranges from the GPS collared pronghorn); however, given expressed interest and need by BLM, data was and will continue to be collected by BLM staff at a broader scale outside the study areas. In addition, fence data has also been contributed to this dataset by the National Wildlife Federation (Buzzard et al. 2022).

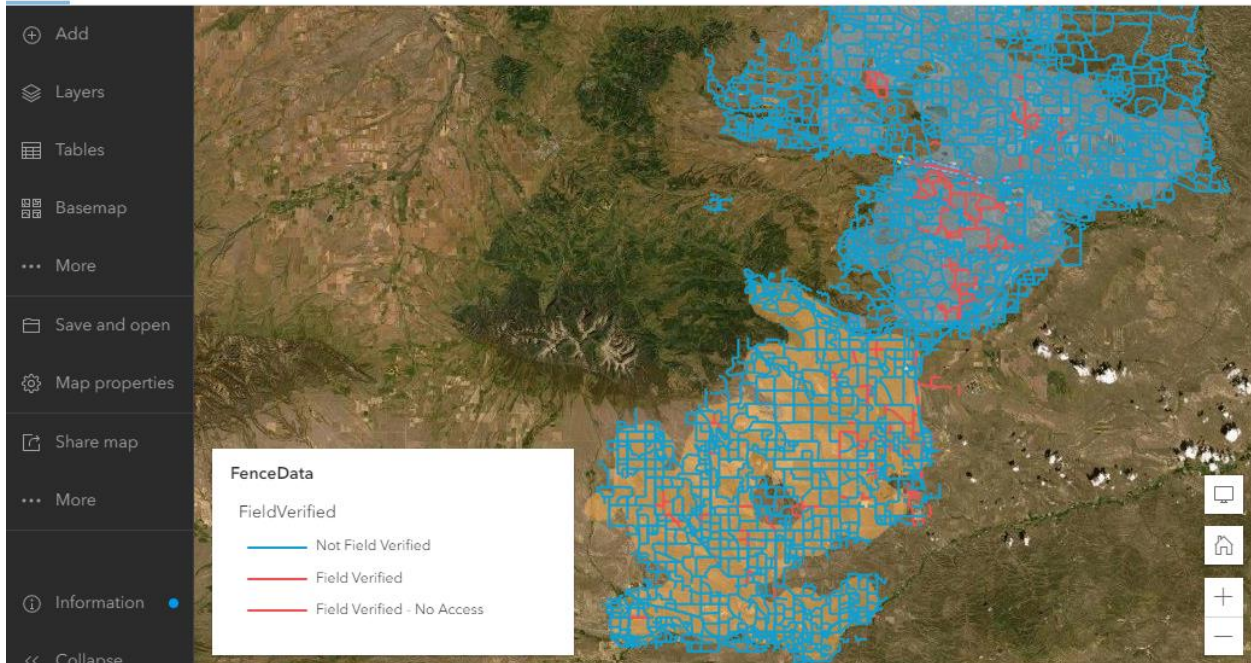


Figure 53. Example of fence spatial data recorded in the field within annual ranges of each population using the online platform on ArcGIS Online as part of the Montana Pronghorn Movement and Population Ecology Project. Red and blue lines represent mapped fences with and without fence characteristics measured in the field, respectively.

Fences were added to the fence data feature layer such that each line was mapped as spatially precise as possible, either drawn from aerial imagery base maps in the office or from GPS equipped handheld computers in the field. Each line feature was drawn to represent a segment of fence (e.g., a stretch of fence between corner fence posts, fence intersections, or substantial directional changes in the overall fence) that should have all the same characteristics (wire type, height, etc.). Upon visitation in the field, attributes could then be added to each line feature, or the line feature could be relocated to a more precise location if needed. Our protocol for field visitation included recording the primary and bottom wire type, number of total strands, and bottom and top wire height. The wire height attributes were calculated from the average distance from the ground to the lowest wire based on at least 5 measurements along the fence segment, making each measurement at every 3rd midpoint (middle location of each post-to-post section) and trying to ensure the measurements are as representative of the entire fence segment as possible. Visited line features were then marked as field verified.

We mapped a total of 82,132 fence segments, with 2,244 (5%) verified in the field, equating to approximately 48,694 km and 2,496 km of total and field verified fences, respectively (Figure 54). Of the field verified fences, we classified the majority of the primary wire type as barbed (2,062 km, 82.6%) and woven (404 km, 16.2%). Of those classified as barbed primary wire type, we recorded approximately 2,017 km of barbed bottom strand and 45 km of smooth bottom strand fences (with varying number of strands).

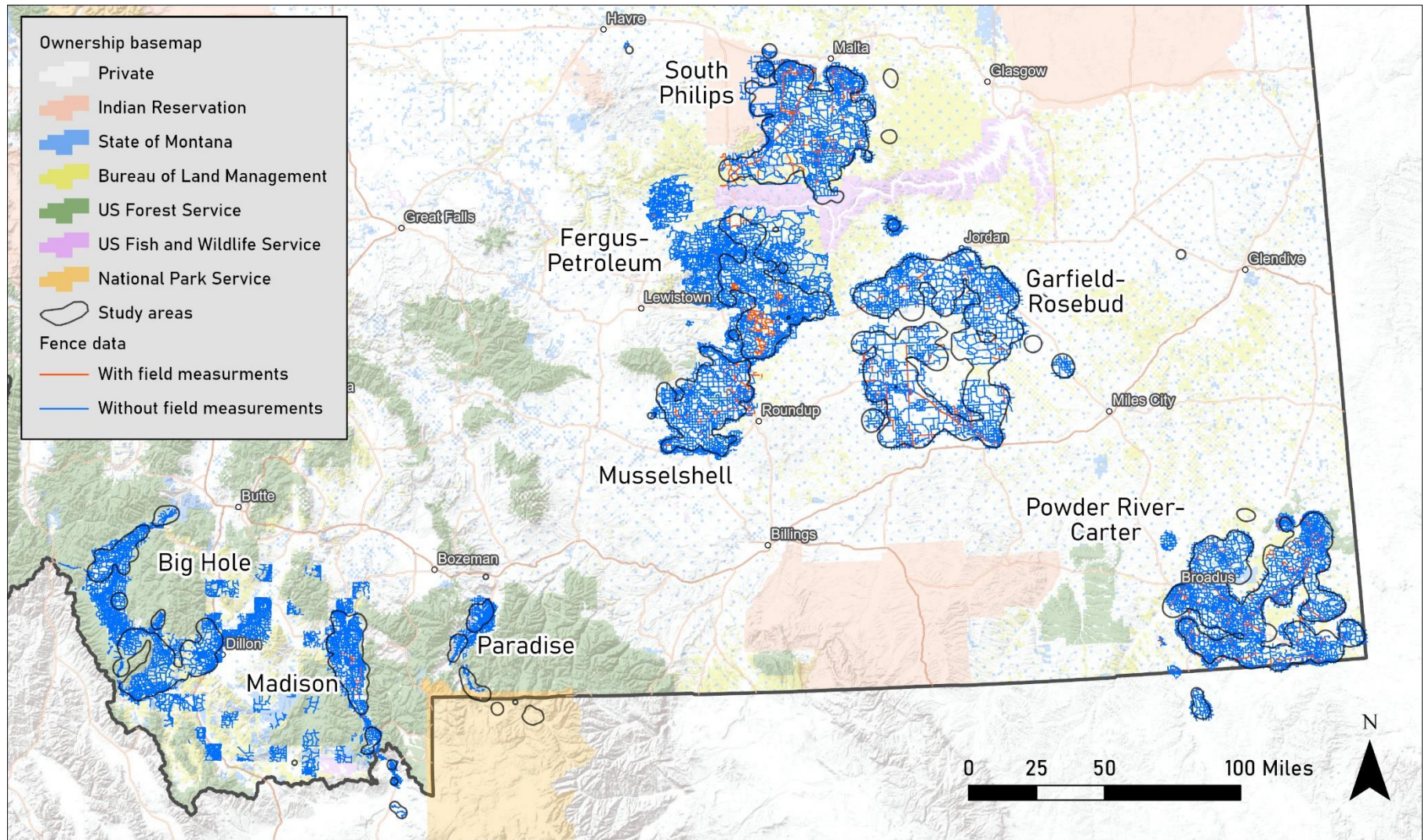


Figure 54. Fence spatial data collected as part of the Montana Pronghorn Movement and Population Ecology Project. Red and blue lines represent mapped fences with and without fence characteristics measured in the field, respectively. Black-bordered polygons represent the annual range of collared pronghorn in each study area.

Using this fence mapping data in combination with location data from collared pronghorn, we used methods developed by Xu et al. (2021*b*) to produce a tool that ranked and mapped fences based on relative levels of altered fence encounters of pronghorn (Section 3.1.3). In addition, we evaluated the effects of different fence types on pronghorn movement behaviors (DeVoe et al. 2023; Section 3.2).

Fence permeability analysis & interactive maps

The interactive map for displaying fence permeabilities based on pronghorn behavioral responses combines the fence data collected from the ArcGIS Online platform and the collar location data to provide an additional tool to identify, prioritize, and monitor fence modifications in each study area. The tool uses the Barrier Behavior Analysis (Xu et al. 2021*b*) to identify pronghorn encounters with fence segments and categorize their subsequent movement responses into behavioral types (Figure 55). The BaBA method defines encounters based on collar locations that occur within a user-specified buffer distance from the fence segments. We specified this buffer as 50 m, which we considered to represent a distance that pronghorn may perceive and interact with a fence. Although Xu et al. determined a 110 m buffer to be optimal for 2-hour fix interval data, we considered 50 m adequate given our finer fix interval data of 1-hour (DeVoe et al. 2022). Regardless of the chosen buffer, if the start or end points (collar locations) of an individual pathway feature do not occur within the buffer of the fence, these will not be identified as an encounter or a crossing. The BaBA method categorizes movement responses to fence encounters into 7 behavior types that include: *quick cross* (animal quickly crosses the fence), *average movement* (animal does not notably change its movement pattern), *bounce* (animal moves quickly away from the fence), *back-and-forth* (animal moves back and forth along the fence), *trace* (animal moves parallel to the fence), *trapped* (animal is located constantly near a fence), and *unknown* (unable to classify movement response). These behavioral types were then classified into unaltered (i.e., quick cross and average movement) and altered (i.e., bounce, back and forth, trace, and trapped) encounter types. We used the barrier ranking tool provided as part of the BaBA framework to calculate the relative permeability of each fence segment based on the number of encounters of each behavior type and the number of unique individuals encountering the fence segment. Specifically, the barrier ranking tool calculates a permeability index representing the ratio of altered encounters (i.e., bounce, back-and-forth, trace, and trapped) to total encounters weighted by the number of unique individuals encountering the fence segment (Figure 56). The index value is then scaled between 0 and 1 using the values of all fence segments in the study population, with values closer to 1 representing a higher relative barrier effect (i.e., lower permeability) for a given fence segment. Fence segments with no encounters are not included in this calculation. It is important to note that although the index value is adjusted based on the number of unique animals encountering the fence segment, the values are sensitive to the sample size and distribution of collared pronghorn in the area. In addition, the index values are sensitive to the spatial accuracy, lengths, and distribution of the drawn fence segments. Lastly, because index values are relative to encounters occurring within the study area, index values cannot be compared across study areas. Therefore, caution must be used when interpreting the results from this tool and we suggest its use to be in combination with local knowledge of the landscape and other resources to guide prioritization of projects.

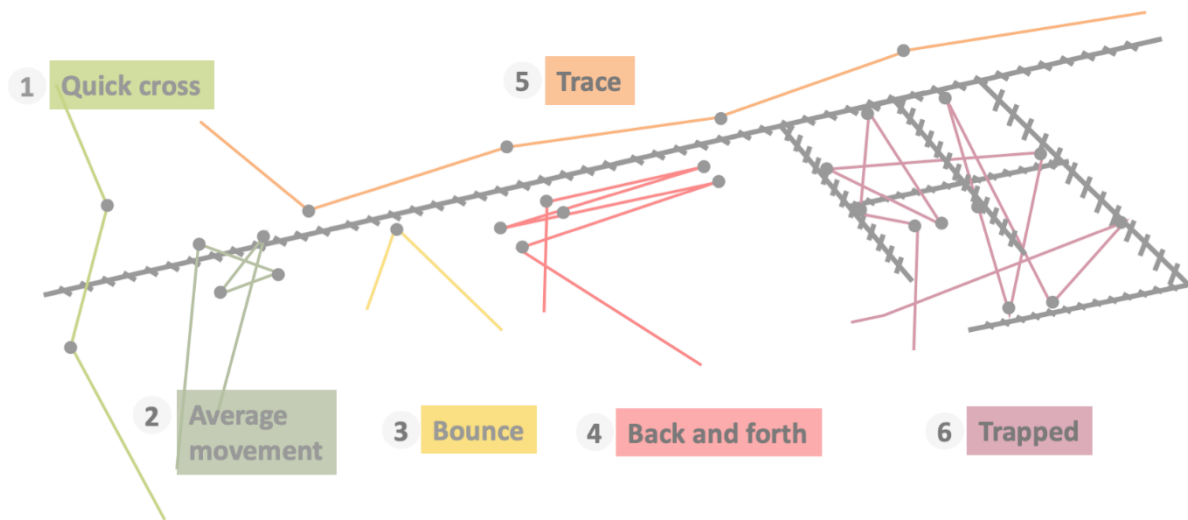


Figure 55. Schematic diagram reproduced from Xu et al. (2021) showing 6 behavioral types identified in the Barrier Behavioral Analysis. Behavioral types are then classified into unaltered (i.e., quick cross and average movement) and altered (i.e., bounce, back and forth, trace, and trapped) to calculate fence segment permeability values.

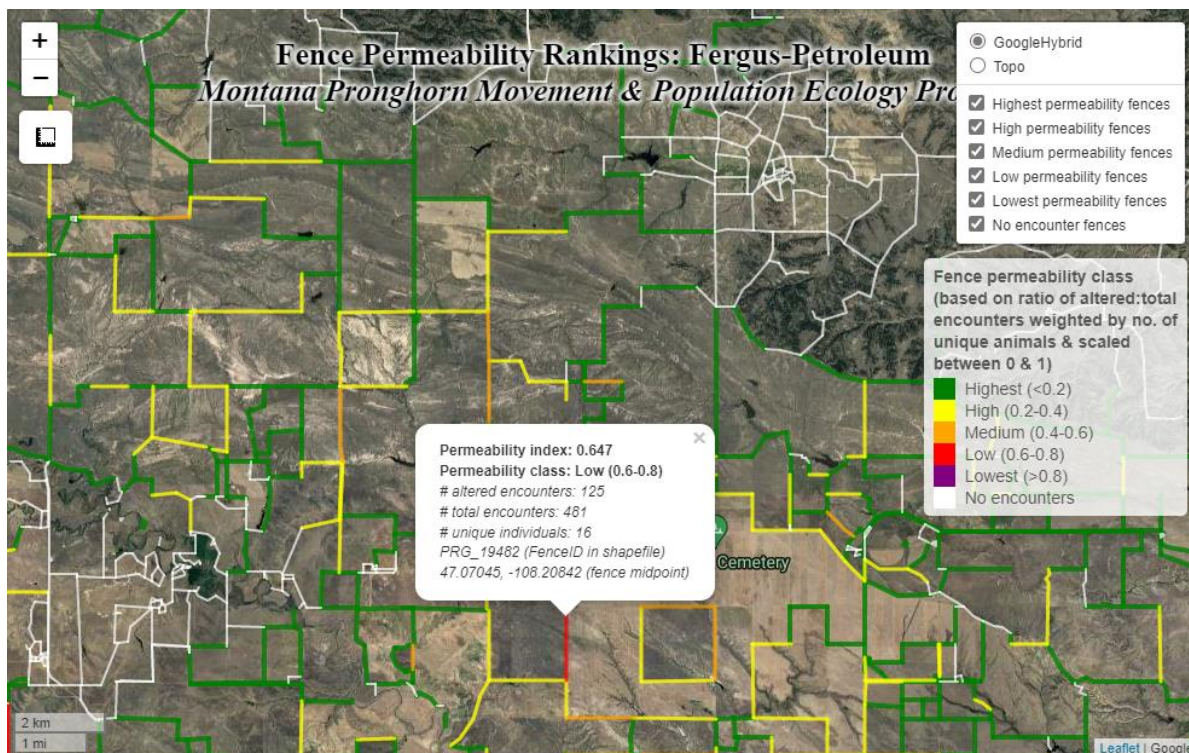


Figure 56. Screenshot of the fence permeability analysis interactive map displaying mapped fences by levels of permeability based on encounters and responses of collared pronghorn. Permeability classes were categorized based on equal quantiles, and do not represent any statistically significant quantification of permeabilities.

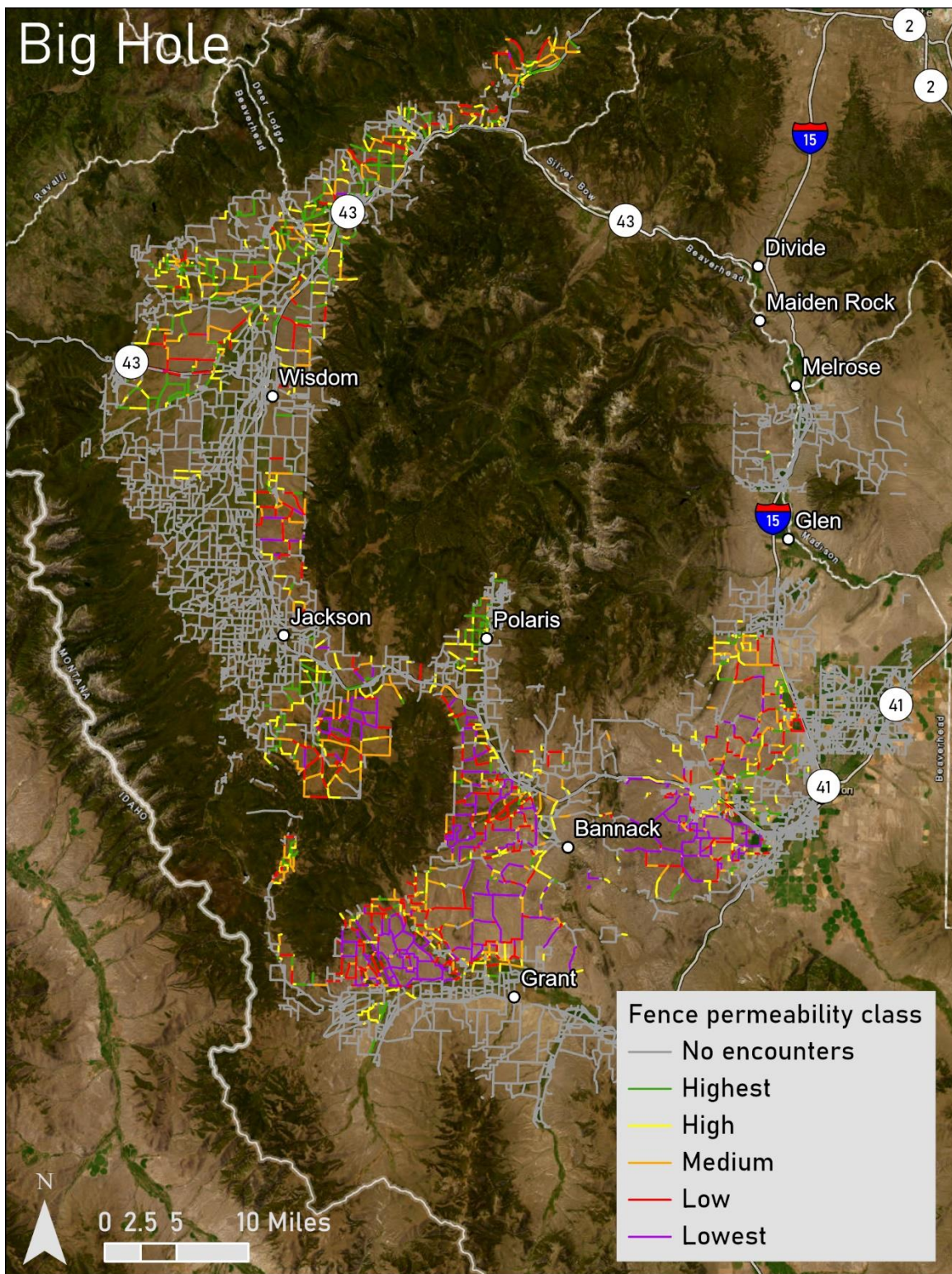


Figure 57. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the Big Hole study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

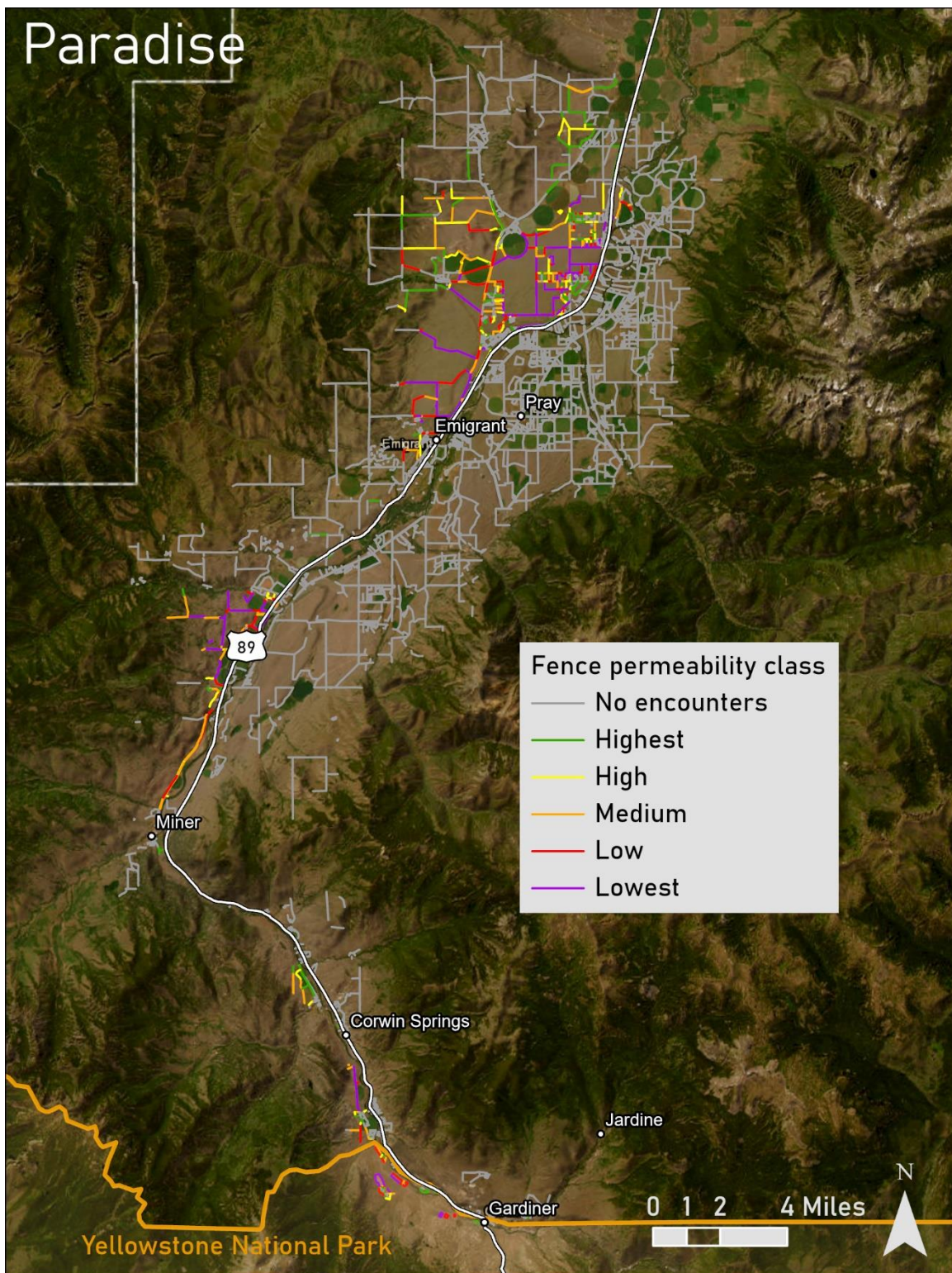


Figure 59. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the Paradise study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

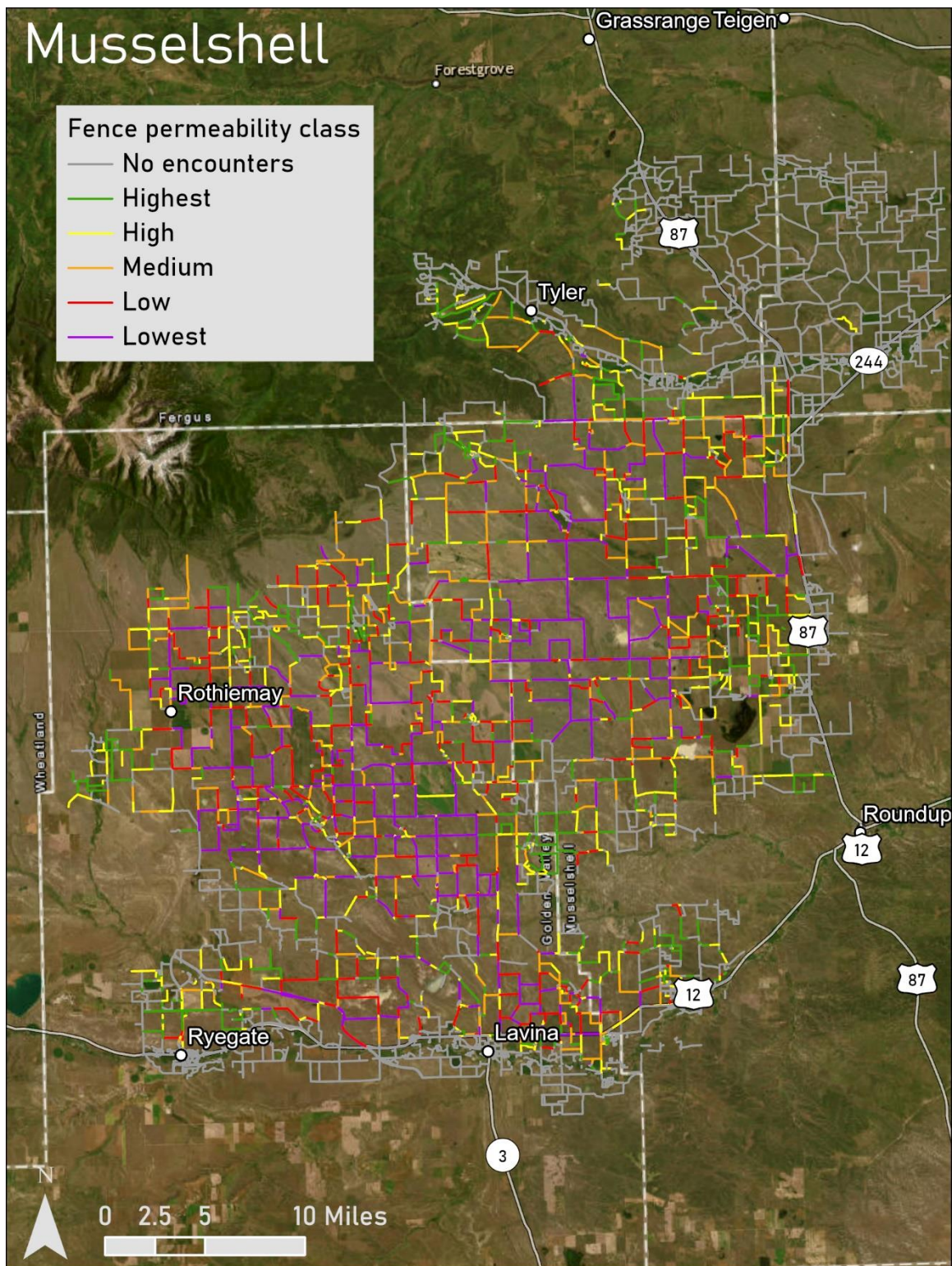


Figure 60. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the Musselshell study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

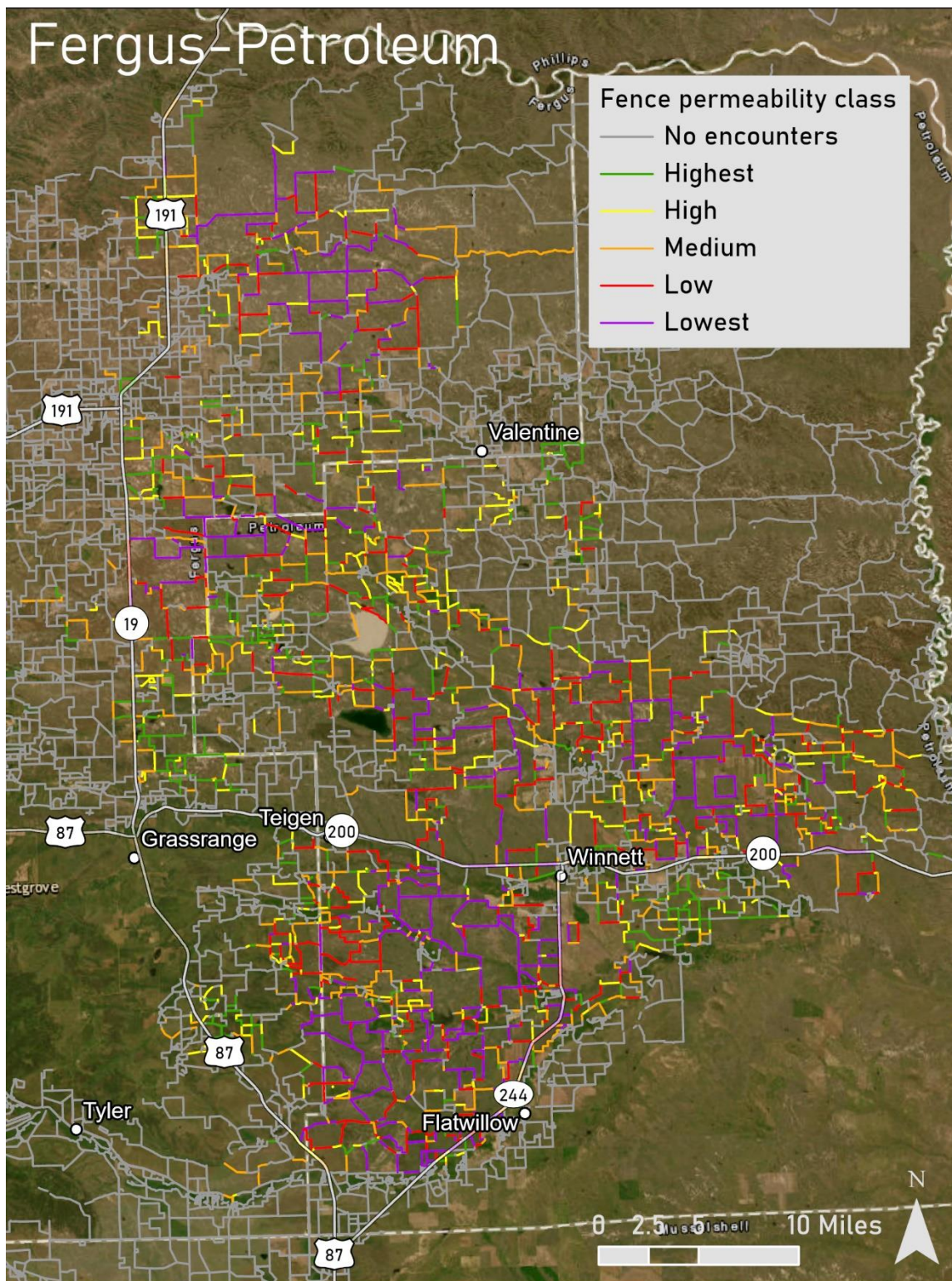


Figure 61. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the Fergus-Petroleum study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

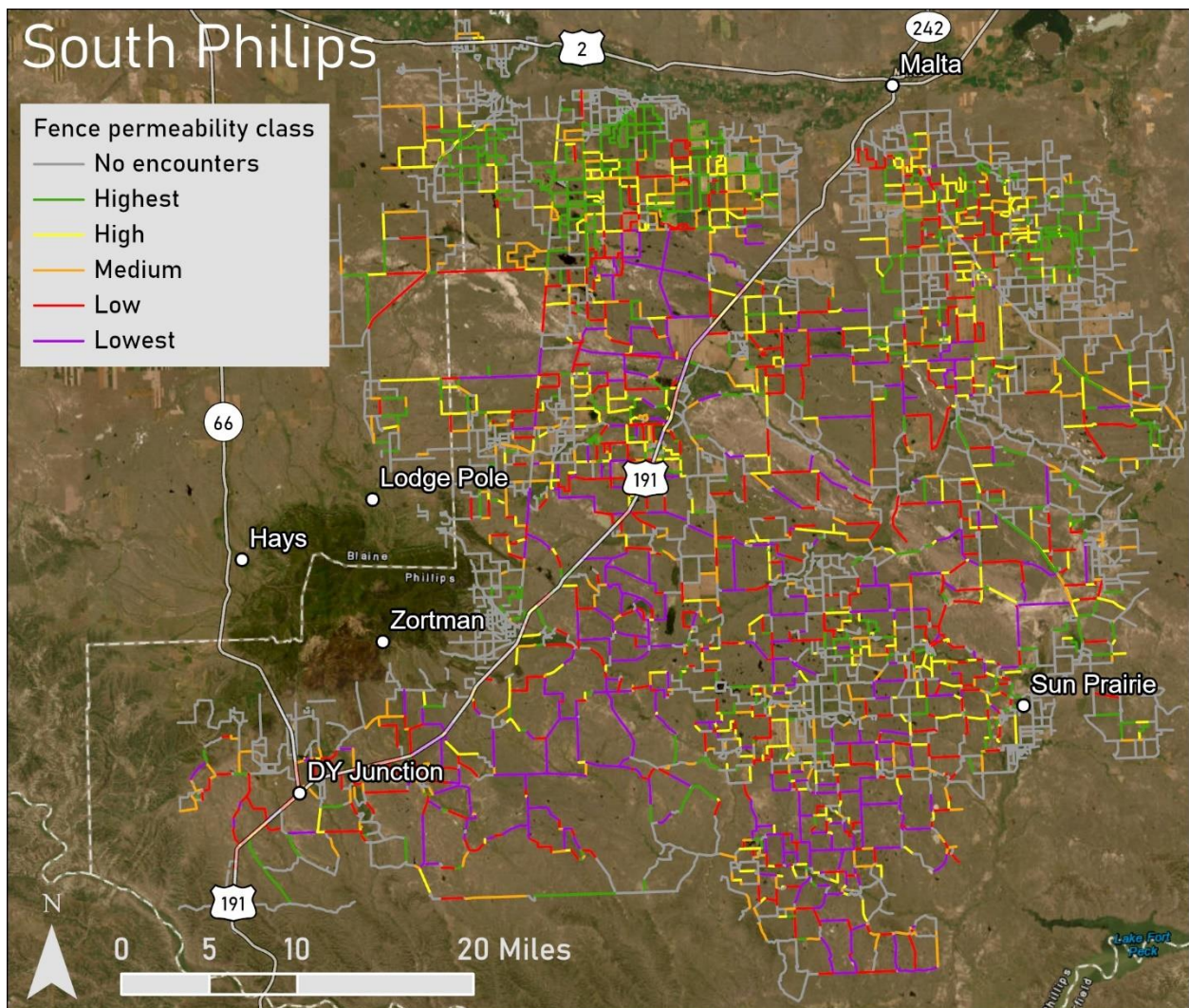


Figure 62. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the South Philips study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

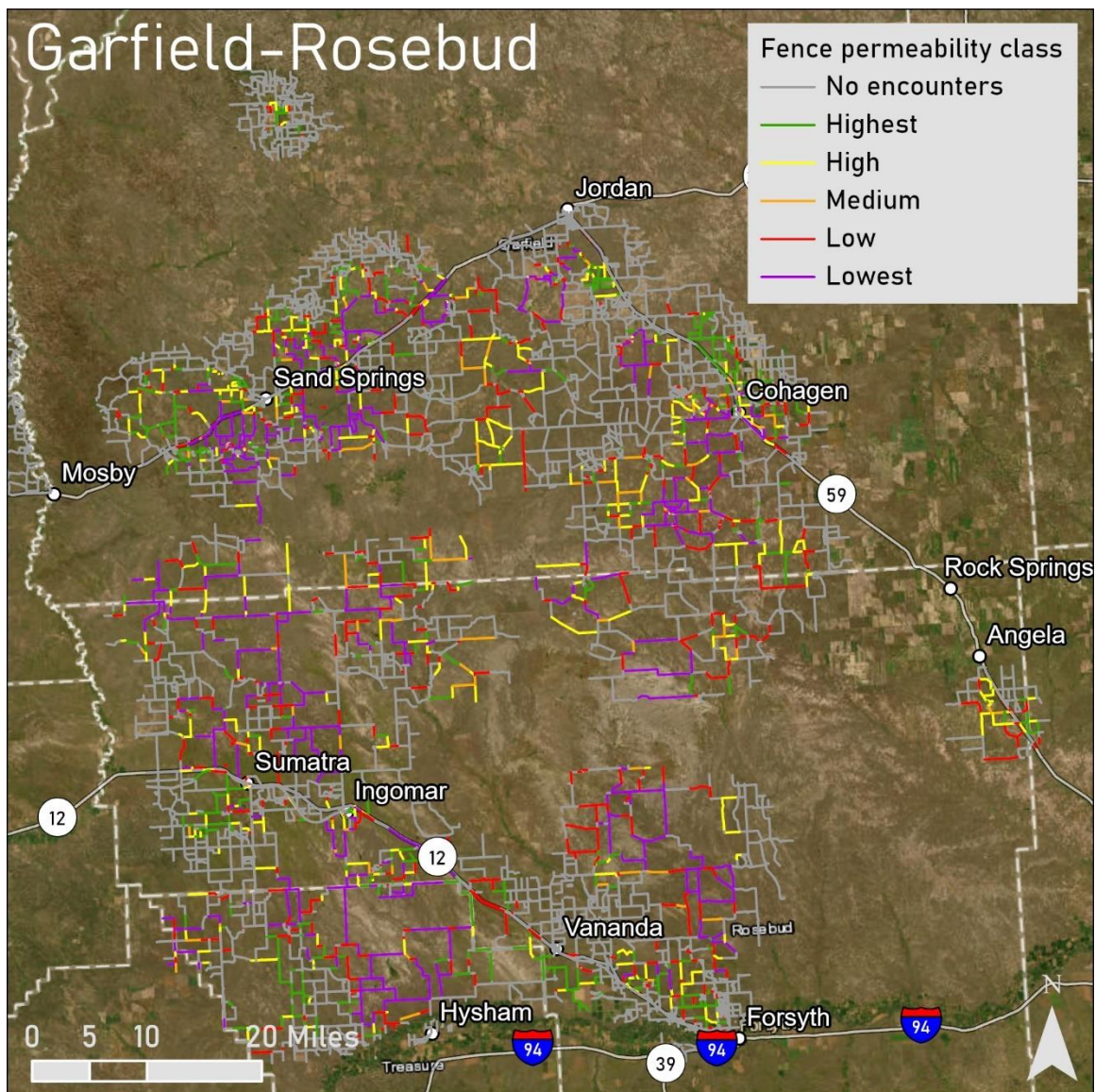


Figure 63. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the Garfield-Rosebud study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

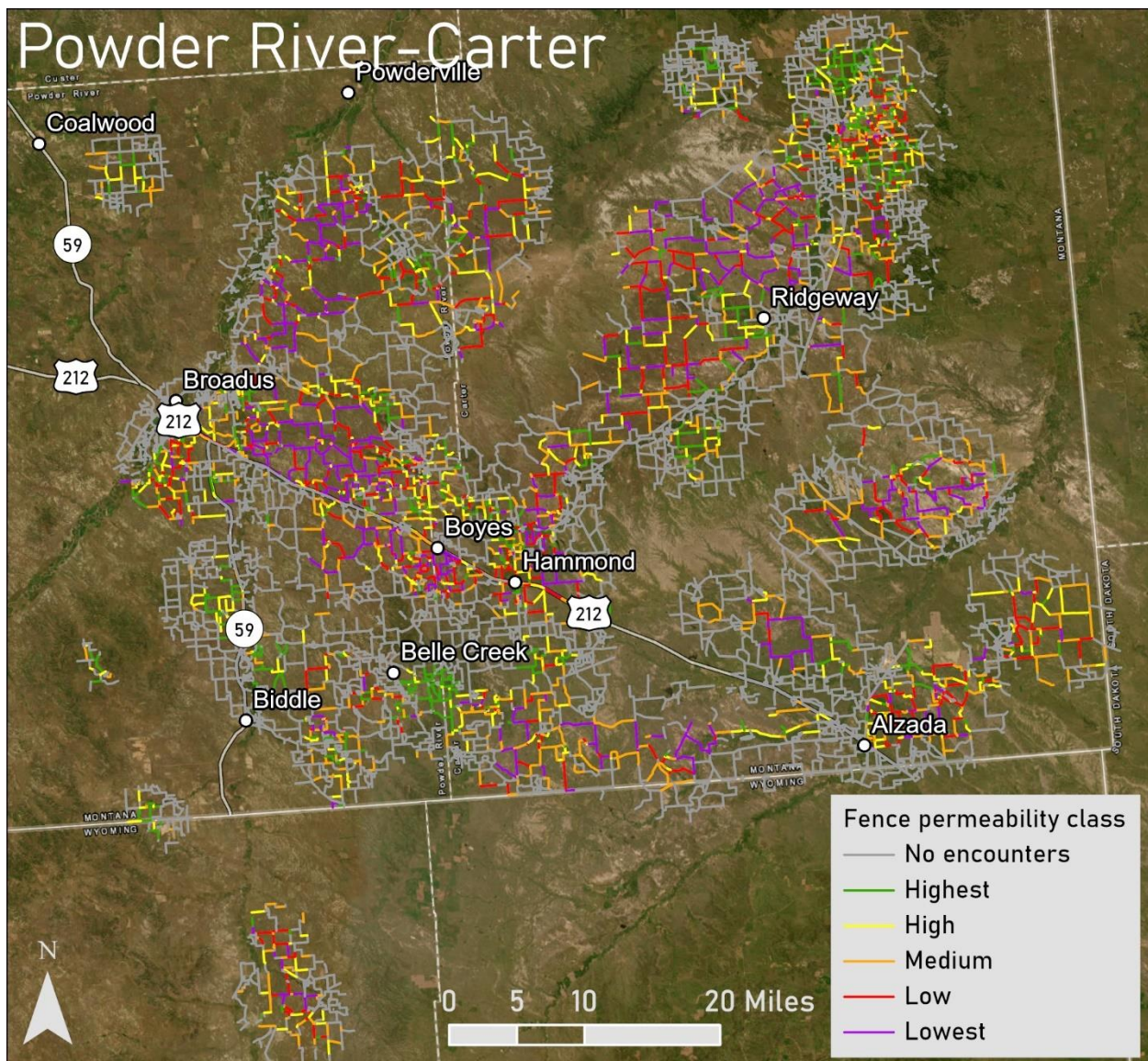


Figure 64. Fence permeability classes based on encounters and responses of collared pronghorn to fence segments in the Powder River-Carter study area. Higher levels of permeability indicate fences with relatively fewer altered behavioral responses by collared pronghorn. Movement data collected from January 2020 to June 2023 as part of the Montana Pronghorn Movement and Population Ecology Project.

3.2 Evaluating the effect of varying fence types on pronghorn movements behaviors

In addition to the tools designed to assist in identifying potential barriers to pronghorn movements, we completed an analysis that combines the collar and fence data to evaluate the effect of different fence types on pronghorn movement behaviors. This analysis has been published as a research article in the peer-review journal *Ecosphere* (DeVoe et al. 2023). Understanding pronghorn movement responses to fences is essential for improving landscape permeability; however, prior studies provide only limited insight due to lack of information on fence characteristics and small sample sizes. This analysis used the hourly collar locations in 6 of the study areas (Madison, Musselshell, Fergus-Petroleum, South Philips, Garfield-Rosebud, and Powder River-Carter) and identified encounters with the mapped fences based on Xu et al. (2021b) to evaluate 3 movement responses (i.e., probability of an unaltered initial response, probability of crossing following an altered initial response, and passage time following an altered initial response) as a function of fence and landscape attributes. We combined our fence mapping data with fence data collected prior to the study in FWP Regions 6 and 7, and classified fences into 3 types, including low strand (average lowest wire height <41 cm), high strand (average lowest wire height \geq 41 cm), and woven wire.

Based on 5,581 encounters identified from movement pathways of 265 collared pronghorn and 979 km of mapped fences, we found that variability in pronghorn fence response was correlated with fence type (Figure 65). Woven wire fences substantially reduced unaltered initial and crossing responses and increased passage times as compared to low (i.e., average lowest wire height <41 cm) or high (i.e., average lowest wire height \geq 41 cm) strand fences. Both low and high strand fences elicited similar responses of being relatively permeable at the initial encounter with reduced permeability thereafter. Fence crossing probabilities following altered initial responses increased through time modestly for strand fences but only negligibly for woven wire fences, with passage times averaging approximately 14 hours. Pronghorn knowledge of and fidelity to specific permeable locations along fences, which may be due to inconsistent fence and landscape characteristics along the fence stretch, likely allow some woven wire fences and most strand fences, regardless of the average lowest wire height, to be permeable. To improve landscape permeability, these results indicate that managers should prioritize removing woven wire fences, replacing woven wire fences with strand fences, and incorporating variation in lowest wire heights into new fence designs or modifications of existing fences.

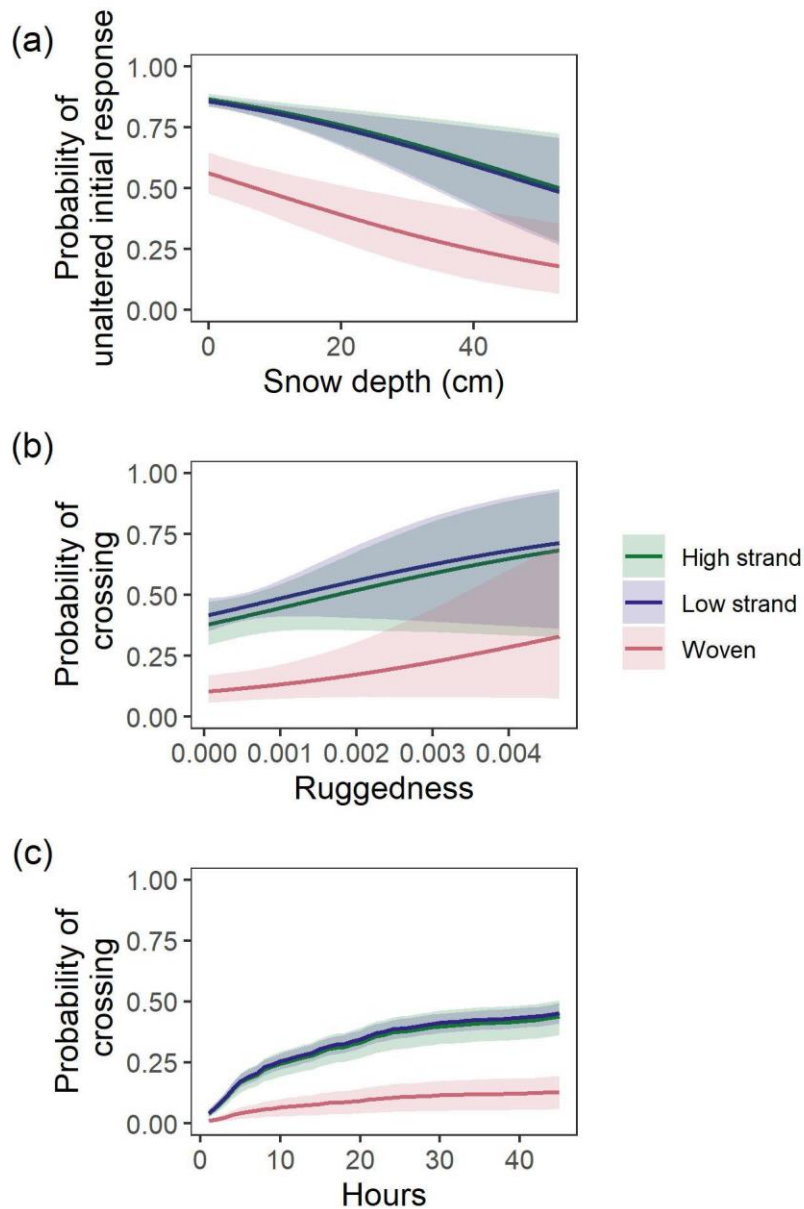


Figure 65. Predicted relationships of the probability ($\pm 95\%$ CI) of unaltered initial response (panel a), probability of crossing following an altered initial response (panel b), and passage time (i.e., probability of crossing through time) following an altered initial response (panel c) of pronghorn fence encounters for different fence types in 6 study areas in southwest, central, and southeast Montana, 2019 – 2021. Displayed relationships are based on averaged top models from each respective analysis and contain the range of the observed covariate values while keeping all other covariates constant at their mean value. Low and high strand fences are defined as wire fences with lowest wire height < 41 cm and ≥ 41 cm, respectively. Reproduced from DeVoe et al. (2023).

3.3 Collaborative efforts to remediate movement barriers

Biologists from multiple organizations have been using and continue to use the collar movement information to inform efforts to remediate movement barriers, which have primarily included fence removals and replacements with wildlife friendly designs (Figure 66 – 67; Table 9). In total, 12 projects have been completed (totaling 23 miles), 6 are ongoing (totaling 33 miles), and 3 are in preparation (totaling 10 miles). In addition to the partnerships of often multiple agencies to accomplish individual projects, FWP biologists have presented the collar movement and fence barrier information in various meetings with stakeholders, including other state and federal agencies, city and county commissioners, non-profit groups, and individual landowners.

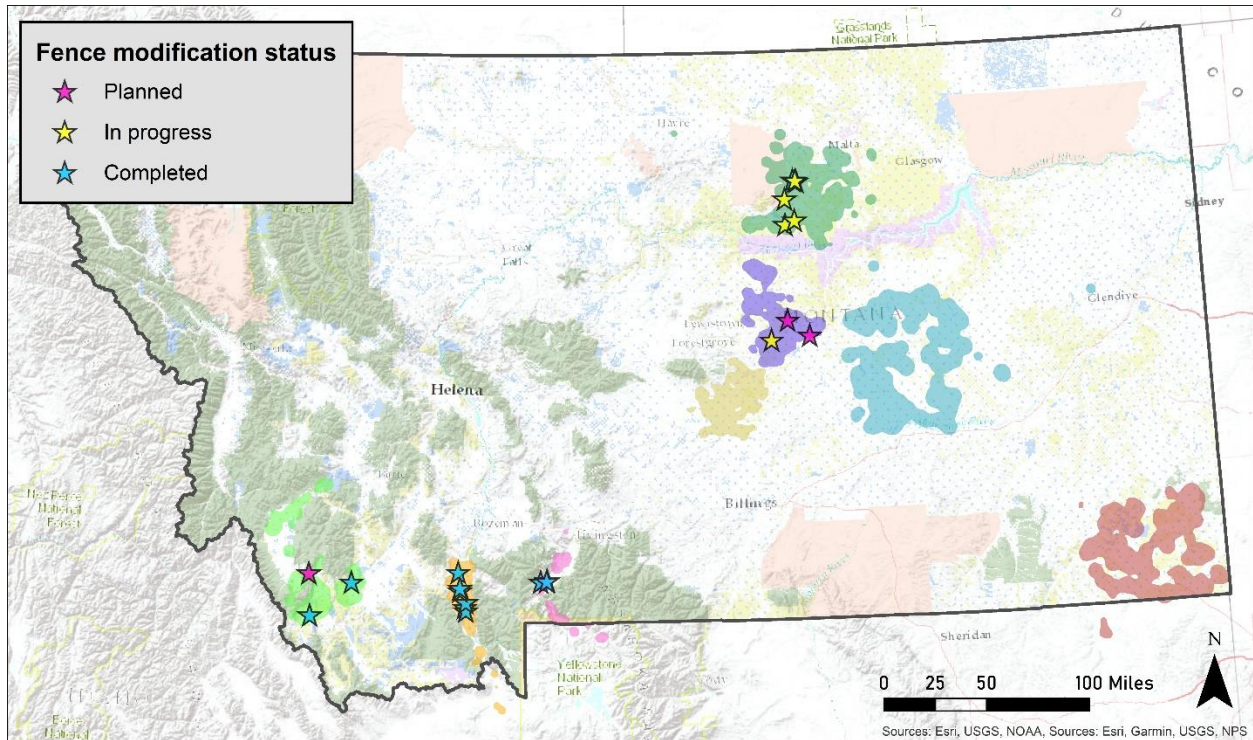


Figure 66. Locations of planned, in progress, and completed fence modification efforts informed by the pronghorn collar movement data collected as part of the Montana Pronghorn Movement and Population Ecology Project



Wildlife Friendly Fencing

This land is being managed with wildlife friendlier fences, allowing pronghorn antelope and other wildlife opportunities to move through this critical wildlife migration route.

This project is a collaboration between private landowners, state wildlife managers and non-profit conservation organizations.



Granger Ranches



Figure 67. Examples of fence modification projects informed by the pronghorn collar data and completed by partners of the Montana Pronghorn Movement and Population Ecology Project. Top left photo: modifying a 5-strand fence to a 4-strand fence with smooth bottom wire in the Paradise study area (photo credit: National Parks Conservation Association). Top right photo: new 4-strand fence with smooth bottom wire replacing 5-strand barbed wire fencing in the Fergus-Petroleum study area (photo credit: BLM). Middle photo: installing metal panels to replace 5-strand barbed wire fence in the Paradise study area (photo credit: National Parks Conservation Association). Bottom left image: signage used for outreach in the Madison study area. Bottom right photo: removing barbed bottom wires in the South Philips study area (photo credit: BLM).

Table 9. List of completed, ongoing, and planned remediation projects to improve landscape permeability for pronghorn initiated based on pronghorn collar data from the Montana Pronghorn Movement and Population Ecology Project.

Project name	General area	Status	Completion year	Type of modification (WF = wildlife friendly)	Length (mi)	Ownership	Lead agency*
Indian Creek	Madison Valley	Completed	2019	Old: jackleg w/ barbed New: post-and-wire WF	0.25	Private/BLM	BLM
Indian Creek	Madison Valley	Completed	2020	Old: jackleg w/ barbed New: post-and-wire WF	0.65	Private/State /BLM	BLM
SW MT Fencing for Wildlife Program	Horse Prairie	Completed	2021	Old: 4-6 strand barbed/woven New: removed/modified to WF	8.5	Private/BLM	NWF
SW MT Fencing for Wildlife Program	Frying Pan Basin	Completed	2021	Old: 4-6-strand barbed/woven New: removed/modified to WF	3.4	Private/BLM	NWF
Creek Bottom Project	SW of Malta	Completed	2021	Old: 4-strand barbed New: 4-strand barbed WF	2.33	Private	RSA
GYCC West	Paradise Valley	Completed	2022	Old: 5-strand barbed New: 4-strand WF	0.2	Private	NPCA
Creek/Mountain Sky	Paradise Valley	Completed	2022	Old: 5-strand barbed New: 4-strand WF w/ wildlife passage post-rail section.	0.3	Private	NPCA
GYCC Big Creek	Paradise Valley	Completed	2022	Old: 5-strand barbed New: WF panel configuration	0.2	Private	NPCA
GYCC Antelope Basin	Paradise Valley	Completed	2022	Old: 5-strand barbed New: 4-strand WF suspension fence	2.5	Private	NPCA
Black Mountain Ranch	Madison Valley	Completed	2020	Old: 5-strand barbed New: 4-strand WF suspension fence	2.5	Private	NPCA
Granger Ranches	Madison Valley	Completed	2020	Old: 5-strand barbed New: 4-strand WF suspension fence	1.3	Private	NPCA
Goggins N. Ennis	Madison Valley	Completed	2021	Old: 5-strand barbed New: 3-strand high tensile, elect. lay-down	1	Private	NPCA
Granger Ranches	Madison Valley	Completed	2021	Old: 5-strand barbed New: 4-strand WF suspension fence	4.5	BLM	BLM
BLM Malta Field Office	Dry Fork Rd	In progress	2022	Removal of bottom strands	2.5	Private/BLM	BLM
2021 MCC Project	South Phillips	In progress	2022	Old: 5-strand barbed New: 4-strand WF	2	BLM	BLM
Outcome Based Grazing Fence Mods Phase 1	SW of Winnett	Planned	2022	Old: 5-strand barbed New: 4-strand WF	0.75	Private/BLM	BLM/NRCS
Marks Individual Fence Mods Phase 1	N of Winnett	Planned	2022	Old: 5-strand barbed New: 4-strand WF	9.42	Private	RSA
RCCP Fence	SE of Winnett	Planned	2022	Old: 5-strand barbed New: 4-strand WF			
South Phillips Project (LBWR)	SW of Malta	In progress	2023	Old: 4-strand barbed New: 4-strand barbed WF			

Project name	General area	Status	Completion year	Type of modification (WF = wildlife friendly)	Length (mi)	Ownership	Lead agency*
Turbine Project	SW of Malta	In progress	2023	Old: 4-strand barbed New: 4-strand barbed WF	2.25	Private	RSA
Chinook Winds Project	SW of Malta	In progress	2023	Old: woven New: 4-strand barbed WF	6	TNC	RSA
FlyBoy Project	SW of Malta	In progress	2023	Wire height adjusted to WF	8	Private	RSA
Carroll Hill	Big Hole	Planned	2023	Old: 5-strand barbed New: 4-strand WF	7.5	Private/USFS	NWF

*NWF = National Wildlife Federation, NPCA = National Parks Conservation Association, RSA = Rangeland Stewardship Alliance.

Objective #4: Develop a population model to identify important vital rates affecting population growth rates and describe important demographic differences between populations that are growing or stable, versus those that are limited in their population performance

Background & objectives

Integrated population models (IPMs) can integrate known-fate survival from marked adults, recruitment and abundance data from count and classification surveys, and harvest data to provide estimates of vital rates and population abundance and improve inferences into the underlying drivers of variation of these processes (Kéry and Schaub 2011, Schaub and Abadi 2011). Management decisions can be improved by the use of IPMs in several ways that include: sensitivity and elasticity analyses for determining the vital rate most important in driving population abundance and targeting management actions specific to that vital rate (Johnson et al. 2010a, Eacker et al. 2017); retrospective analyses for estimating vital rates (Proffitt et al. 2021) and population abundances, while assessing the factors influencing annual variability in vital rates (Paterson et al. 2021); and prospective analyses for projecting population abundances under different management scenarios under consideration (e.g., what harvest rates increase or decrease populations by how much and over what amount of time; Johnson et al. 2010b, Mitchell et al. 2018). Integrated population models, therefore, can be a powerful learning tool that may help resource managers to understand the mechanisms driving population performance and to adapt management strategies accordingly.

Our objective is to develop a pronghorn IPM based on abundance and production estimates from count and classification surveys and harvest data collected for each study area (Figure 68). We are using a state-space IPM approach, wherein the model consists of a biological process model and an observation model (Buckland et al. 2004). We will use this model to 1) identify important vital rates affecting population growth rate, 2) contrast important vital rates between populations that are increasing and decreasing at different rates, and 3) develop hypotheses to explain why some pronghorn populations experience limitations on population growth rate. The population model will provide information towards developing more focused investigations into ecological and/or anthropogenic factors influencing pronghorn populations in Montana.

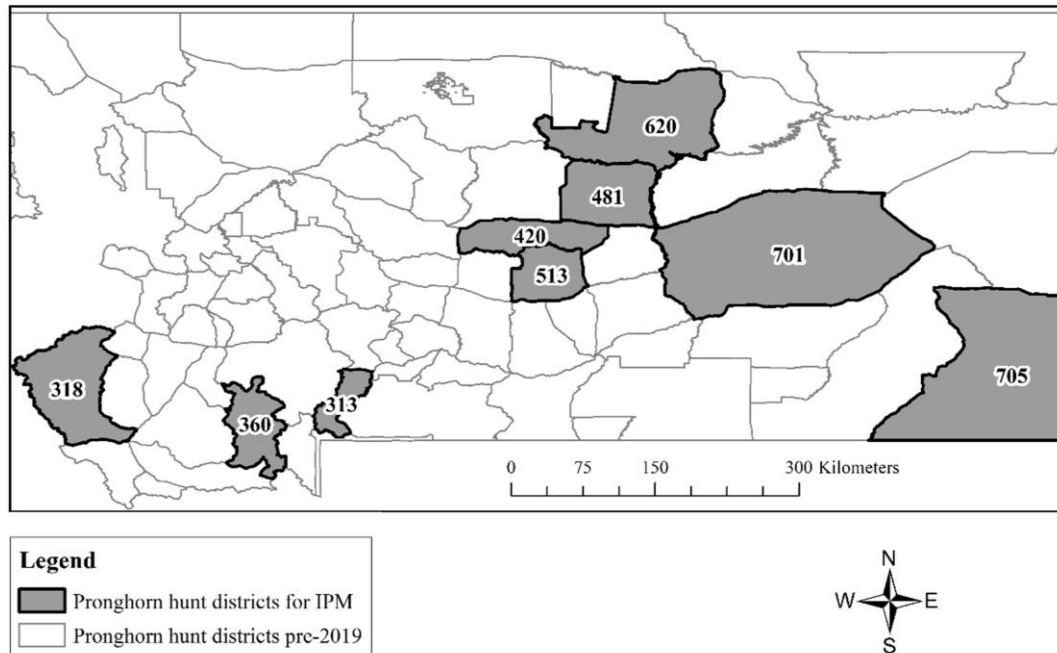


Figure 68. The nine pronghorn hunting districts (shaded gray) within the pronghorn study areas included in the integrated population model for the Pronghorn Movement and Population Ecology Project.

Methods

Process model and vital rates

We defined a pronghorn ecological year from 01 Oct of year $t-1$ to 30 Sep of year t to account for post-parturition count and age-sex ratio surveys in July, and the timing of population reconstruction estimates immediately prior to October harvest (Figure 69). We chose to use the beginning of the pronghorn rifle season as our model anniversary because we assume most animals are harvested with rifles, and thus archery mortality is relatively minimal. Pronghorn age classes are defined as fawn: 0–3 months, juvenile: 3–15 months, and adult: 15+ months. Fawns advance to the juvenile age class in September of their first year, prior to hunting season. Therefore, a fawn cannot be harvested, but could be harvested as a juvenile. This designation aligns with the way in which FWP stores fall harvest data (two stages, two sexes).

The biological process model is a discrete time (i.e., 01 Oct of year $t-1$ to 30 Sep of year t), three-stage (i.e., fawn, juvenile, adult) and two-sex (i.e., male, female) matrix projection model. We assumed that fawns were recruited into the juvenile age class in September at a rate similar to the age-sex counts observed during July aerial surveys. We further assumed that the sex ratio at birth was equal. In this manner, we were able to use the fawn:doe ratio data collected during summer aerial surveys as a measure of reproductive output (i.e., recruitment), which better aligns the biological process with data collection (e.g., White and Lubow 2002). We included demographic stochasticity in the process model with a Poisson distribution for fawns and Binomial distribution for juveniles and adults.

In juvenile and adult survival process models, we compartmentalized mortality into harvest and natural mortality through a multi-state survival model. A multi-state survival model allowed estimation of survival

(S), harvest mortality (H), and other mortality (O), where $S + H + O = 1$. In this framework, survival estimates reflected survival from both harvest as well as natural causes of death.

Our recruitment and survival models examined environmental variables thought to affect pronghorn population vital rates. To account for potential lag-effects on survival and recruitment, we examined vegetation and climatic conditions from both the current and previous model year (Figure 69; Figure 70). We hypothesized that annual variation in fawn recruitment may be driven by maternal body condition during gestation, through fat accumulation and subsequent fat loss in the summer and winter season prior to parturition (Garrott et al. 2003, Cook et al. 2004, Hurley et al. 2014, Paterson et al. 2019). In addition, recruitment may be affected by environmental conditions post-parturition that affect fawn nutrition through maternal provisioning or forage productivity (Beale and Smith 1970, Von Gunten 1978, Griffin et al. 2011, Bender et al. 2013). Thus, we included pronghorn population-level annual mean net primary productivity (NPP; MODIS Terra Net Primary Productivity: <https://lpdaac.usgs.gov/products/mod17a3hgv006/>), annual mean precipitation (PRISM), and winter snow depth (SNOWDAS: <https://nsidc.org/data/g02158>) in linear models predicting recruitment. We also included a temporal random effects structure to allow for random variation in recruitment across years.

We hypothesized that annual variation in juvenile and adult survival may be driven by body condition throughout the ecological year via the additive effects of accumulated fall fat reserves, subsequent winter fat loss (Cook et al. 1996, 2004, Garrott et al. 2003, Reinking et al. 2018), and fat accumulation in the following growing season (Miller and Drake 2003, O’Gara 2004). Thus, we included NPP and winter snow depth in linear models predicting juvenile and adult survival. We also included a temporal random effects structure to allow for random variation in juvenile and adult survival across years.

During 2021 and 2022, we estimated survival for collared pronghorn within each pronghorn population (see *Survival monitoring & analysis* section, p.16). We related these survival estimates (ϕ , σ) to associated survival parameters within the IPM (S) using a normal distribution:

$$\phi_t \sim \text{Normal}(S_t, \sigma) \quad \text{Eq. 1}$$

We hypothesized that harvest rate would be affected by the number of permits issued in a hunting district (i.e., “hunting effort”), so we included hunting effort in linear models predicting juvenile and adult harvest rate. Specifically, we included the number of either-sex permits issued as the hunting effort value for adult male harvest, and the total number of either-sex and doe/fawn permits issued as the hunting effort value for adult female and juvenile harvest.

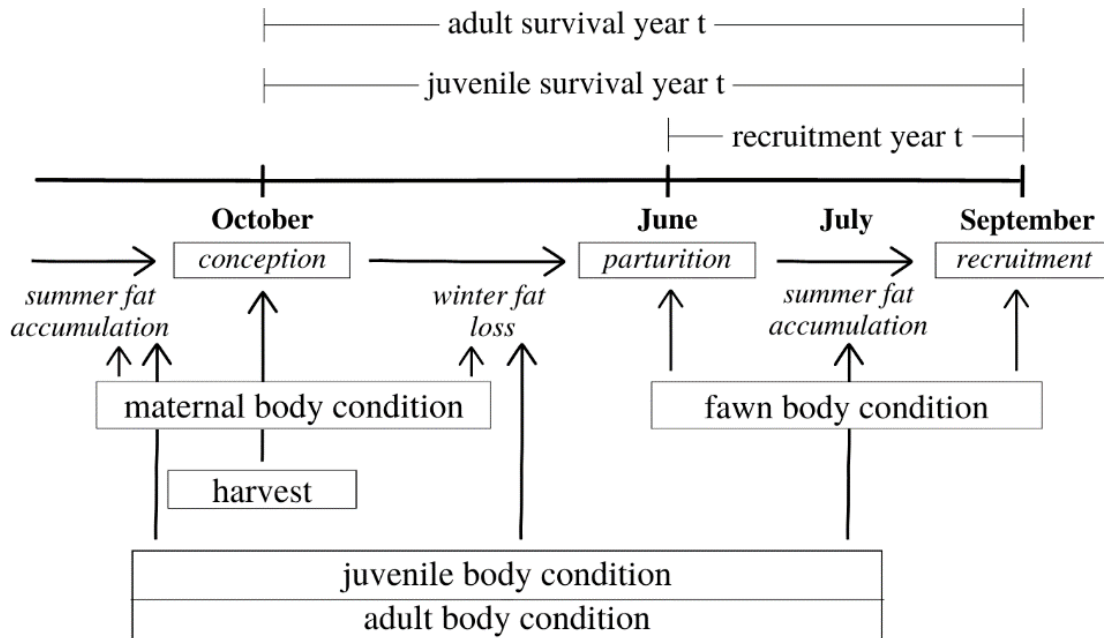


Figure 69. Conceptual diagram explaining the ecological year experienced by pronghorn and associated covariates in our survival (juvenile and adult) and recruitment process models. Model year is 01 Oct year $t-1$ to 30 Sep year t , where fawn and adult count and ratio surveys occur in July after parturition, and adult and juvenile harvest occurs in October. Age classes are defined as fawn: 0–3 months, juvenile: 3–15 months, and adult: 15+ months. Fawn recruitment into the population is affected by maternal body condition during gestation and fawn body condition post-parturition. Juvenile and adult survival are affected by body condition throughout the model year and harvest.

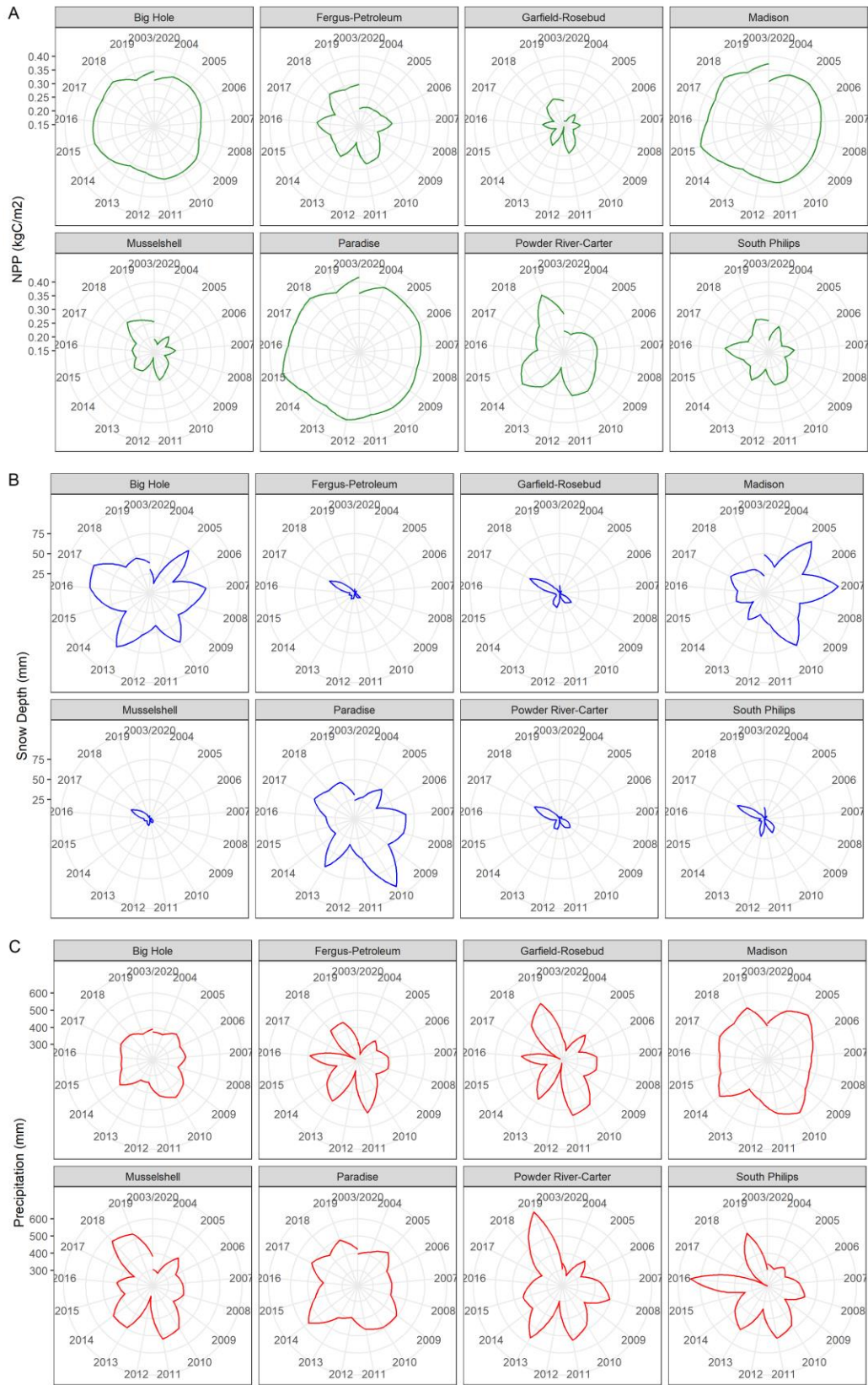


Figure 70. Net primary productivity (NPP; panel A), mean winter snow depth (panel B), and mean annual total precipitation (panel C) across 8 pronghorn populations in Montana from 2003 – 2021. Values were used as covariates in linear models predicting pronghorn recruitment and survival.

Observation models

Observation models link empirical field data to biological parameters in an IPM (Schaub and Abadi 2011). Observation data for the pronghorn IPM consisted of population counts from aerial surveys and harvest estimates from FWP harvest surveys. Pronghorn count data are collected during surveys that occur at two times of year and in two different structures (Table 10). The first type of count data is a total count, collected through complete coverage surveys or trend extrapolated surveys. While complete coverage surveys aim to count and classify all pronghorn in the hunting district (HD), trend surveys count and classify only those pronghorn within trend area(s). Trend areas in each hunting district were selected based on the 1-3 subunit(s) whose population trends were most representative of the total population, wherein trend area counts can be used to accurately predict the total population. Mean pronghorn density from trend areas is extrapolated to the HD level using the area of pronghorn habitat delineated by the FWP pronghorn habitat layer. Further details can be found in the FWP evaluation of survey protocols report (Newell 2013). The second type of data are stage and sex structured counts (Table 10), collected through summer age-sex ratio surveys as either complete or trend extrapolated counts.

Counts occurred in both the summer and winter seasons, depending on the hunting district region (Table 10). Thus, we adjusted model-estimated latent true population size to match timing of observations by subtracting harvest from model anniversary (01 Oct) population estimates, then multiplying by annual natural survival estimates, exponentiated by either $6/12$ (for winter counts) or $9/12$ (for summer counts).

For hunting districts with complete summer counts, we assumed counts represented a minimum of the true population size. Thus, we modeled counts as binomial random variables with the number of “trials” equal to the latent true population size in summer (N), the probability of “success” equal to the proportion of individuals in the population that were counted (p), and the variance equal to $N * p(1-p)$:

$$\text{Count}_t \sim \text{Binomial}(N_t^{\text{Summer}}, p_t) \quad \text{Eq. 2}$$

We assumed trend extrapolated summer counts could be above or below the true population size. Thus, for hunting districts with trend extrapolated counts, we modeled counts as normal random variables with the mean equal to the latent true population size in summer (N), and a model-estimated standard deviation (σ):

$$\text{Count}_t \sim \text{Normal}(N_t^{\text{Summer}}, \sigma) \quad \text{Eq. 3}$$

For hunting districts with complete, total winter counts, we modeled counts as gamma-Poisson random variables, assuming counts followed an over-dispersed Poisson distribution:

$$\begin{aligned} \text{Count}_t &\sim \text{Poisson}(N_t^{\text{Winter}} * \text{extra}) \\ \text{extra} &\sim \text{Gamma}(0.001, 0.001) \end{aligned} \quad \text{Eq. 4}$$

For hunting districts with stage and sex structured counts in summer, we modeled fawn counts as Binomial random variables with the number of “trials” equivalent to the number of adult females counted and the probability of “success” equivalent to the model-estimated recruitment (R):

$$\text{Count}_t^{\text{Fawn}} \sim \text{Binomial}(C_t^{\text{Adult female}}, R_t) \quad \text{Eq. 5}$$

Further, we modeled adult male counts as Binomial random variables with the number of “trials” equivalent to the number of adult females counted and the probability of “success” equivalent to the model-estimated summer sex ratio:

$$\text{Count}_t^{\text{Adult male}} \sim \text{Binomial}(C_t^{\text{Adult female}}, \text{sex ratio}_t) \quad \text{Eq. 6}$$

Table 10. Pronghorn count data from 2004–2022, collected across 9 hunting districts (HDs) in Montana. Pronghorn count data are collected during surveys that occur at two times of year: summer or winter. Total count surveys are further divided into two survey methods: complete coverage (CC) or trend extrapolated (TE) where surveys are conducted in specific trend areas. Values included for TE survey types represent the trend extrapolated count that was later included in integrated population models (i.e., trend area counts extrapolated to the area of pronghorn habitat in the hunting district). Additionally, stage and sex structured counts are collected during summer surveys in certain HDs.

HD	Year	Survey Month	Survey Type	Trend Areas	Total	Bucks	Does	Fawns	Unk
313	2007	March	CC	--	51	--	--	--	--
	2008	April	CC	--	71	--	--	--	--
	2009	May	CC	--	82	--	--	--	--
	2010	--	CC	--	58	--	--	--	--
	2011	May	CC	--	62	--	--	--	--
	2012	--	CC	--	95	--	--	--	--
	2013	--	CC	--	105	--	--	--	--
	2014	--	CC	--	121	--	--	--	--
	2015	--	CC	--	95	--	--	--	--
	2016	--	CC	--	112	--	--	--	--
	2017	July	CC	--	199	37	91	71	0
	2018	July	CC	--	99	33	53	13	0
	2019	July	CC	--	107	30	59	18	0
	2020	July	CC	--	71	12	50	9	0
2021	July	CC	--	51	10	34	7	0	
2022	July	CC	--	77	14	51	12	0	
318	2007	July	CC	--	1430	319	665	335	0
	2009	July	CC	--	1968	340	1072	555	0
	2011	July	CC	--	1027	178	528	201	0
	2013	July	CC	--	1466	229	771	321	0
	2015	July	CC	--	1758	374	834	510	0
	2017	July	CC	--	1490	340	797	353	0
	2019	July	CC	--	1141	246	631	232	0
	2021	July	CC	--	942	160	513	391	12
360	2004	March	CC	--	2001	--	--	--	--
	2005	February	CC	--	2216	--	--	--	--
	2005	August	CC	--	1935	309	1091	533	2
	2007	April	CC	--	2146	--	--	--	--
	2008	April	CC	--	2210	--	--	--	--
	2009	April	CC	--	1899	--	--	--	--
	2009	July	CC	--	757	184	346	227	0
	2010	April	CC	--	1843	--	--	--	--
	2010	July	CC	--	1160	285	559	316	0

HD	Year	Survey Month	Survey Type	Trend Areas	Total	Bucks	Does	Fawns	Unk
	2011	July	CC	--	1464	407	742	313	--
	2012	July	CC	--	900	274	416	195	15
	2013	March	CC	--	1715	--	--	--	--
	2013	July	CC	--	1331	195	770	354	12
	2014	April	CC	--	1610	--	--	--	--
	2014	July	CC	--	1280	371	547	339	23
	2015	April	CC	--	1556	--	--	--	--
	2015	August	CC	--	1435	331	718	368	18
	2016	March	CC	--	2480	--	--	--	--
	2016	July	CC	--	1166	245	610	291	20
	2017	February	CC	--	1959	--	--	--	--
	2017	July	CC	--	1003	243	460	249	51
	2018	March	CC	--	1351	--	--	--	--
	2018	August	CC	--	1111	293	497	306	15
	2019	April	CC	--	1540	--	--	--	--
	2020	March	CC	--	1567	--	--	--	--
	2020	July	CC	--	471	96	248	127	0
	2021	March	CC	--	1850	--	--	--	--
	2021	July	CC	--	499	96	267	136	0
	2022	March	CC	--	2035	--	--	--	--
	2022	July	CC	--	400	75	192	133	0
420	2004	July	TE	Yellow Water Triangle	2323	587	1184	553	0
	2005	July	TE	Yellow Water Triangle	2566	555	1239	773	0
	2006	July	TE	Yellow Water Triangle	1666	398	796	472	0
	2007	July	TE	Yellow Water Triangle	2014	542	1137	335	0
	2008	June	TE	Yellow Water Triangle	1546	341	864	341	0
	2009	July	TE	Yellow Water Triangle	917	214	536	167	0
	2010	July	TE	Yellow Water Triangle	1165	294	678	193	0
	2012	July	TE	Yellow Water Triangle	716	142	423	150	0
	2013	July	TE	Yellow Water Triangle	608	127	345	136	0
	2014	July	TE	Yellow Water Triangle	686	136	354	195	0
	2015	July	TE	Yellow Water Triangle	1090	358	485	248	0
	2016	July	TE	Yellow Water Triangle	1006	299	462	241	0
	2017	July	TE	Yellow Water Triangle	1124	303	466	356	0
	2018	July	TE	Yellow Water Triangle	855	231	500	125	0
	2018	July	CC	--	1504	408	791	305	0
	2019	July	TE	Yellow Water Triangle	1398	326	715	356	0
	2020	July	TE	Yellow Water Triangle	1125	246	648	231	0
	2021	July	TE	Yellow Water Triangle	1196	299	695	203	0
	2021	July	CC	--	1312	301	720	291	0
481	2004	July	TE	Warhorse	6177	1347	2816	2015	0
	2005	July	TE	Warhorse	6621	1539	2950	2132	0
	2006	July	TE	Warhorse	5178	1566	2137	1475	0
	2006	July	CC	--	7492	1611	3196	2385	0
	2007	July	TE	Warhorse	3238	748	1828	663	0
	2008	July	TE	Warhorse	3318	705	1806	705	0

HD	Year	Survey Month	Survey Type	Trend Areas	Total	Bucks	Does	Fawns	Unk
	2010	July	TE	Warhorse	1341	289	898	155	0
	2010	July	CC	--	1760	371	1107	282	0
	2012	July	TE	Warhorse	786	80	545	160	0
	2013	July	TE	Warhorse	689	102	470	118	0
	2014	July	TE	Warhorse	1149	176	652	321	0
	2015	July	TE	Warhorse	1069	267	545	256	0
	2015	July	CC	--	965	174	525	266	0
	2016	July	TE	Warhorse	1405	342	657	406	0
	2017	July	TE	Warhorse	1133	171	604	358	0
	2017	July	CC	--	1351	265	642	444	0
	2018	July	TE	Warhorse	908	283	470	155	0
	2019	July	TE	Warhorse	1571	310	689	572	0
	2020	July	TE	Warhorse	2388	395	1272	721	0
	2020	July	CC	--	1571	310	689	572	0
	2021	July	TE	Warhorse	1101	401	566	134	0
513	2004	July	TE	North	6898	1490	3060	2347	0
	2006	July	TE	North, South	4528	810	2120	1598	0
	2006	July	CC	--	4767	923	2255	1589	0
	2008	July	TE	North	4202	1110	2315	777	0
	2009	July	TE	North, North	5153	745	2854	1554	0
	2009	July	CC	--	2806	484	1612	710	0
	2010	July	TE	South	1742	266	1053	422	0
	2011	July	TE	North, South	1136	314	687	136	0
	2012	July	TE	North, South	996	127	619	250	0
	2013	July	TE	North, South	1556	318	975	263	0
	2014	July	TE	North, South	1403	191	805	407	0
	2014	August	CC	--	1921	290	1082	549	0
	2015	July	TE	North, South	1848	276	911	661	0
	2016	July	TE	North, South	2251	509	1157	585	0
	2017	July	TE	North, South	2658	411	1255	992	0
	2018	July	TE	North, South	2132	699	1085	348	0
	2019	July	TE	North, South	2959	555	1441	962	0
	2020	July	TE	North, South	3464	907	1946	610	0
	2020	July	CC	--	4214	1090	2210	914	0
	2021	July	TE	North, South	2149	585	1225	339	0
620	2004	July/August	TE	Count Unit 3, Count Unit 8	3106	602	1690	814	0
	2005	July/August	TE	Count Unit 3, Count Unit 8	6593	1239	3221	2133	0
	2006	July/August	TE	Count Unit 3, Count Unit 8	4478	1177	2124	1177	0
	2007	July/August	TE	Count Unit 3, Count Unit 8	9230	2478	4239	2513	0
	2008	July/August	TE	Count Unit 3, Count Unit 8	9142	2035	4655	2451	0
	2009	July/August	TE	Count Unit 3, Count Unit 8	7319	1761	3664	1894	0
	2010	July/August	TE	Count Unit 3, Count Unit 8	5487	1239	2655	1593	0
	2011	July/August	TE	Count Unit 3, Count Unit 8	2097	487	1221	389	0
	2012	July/August	TE	Count Unit 3, Count Unit 8	2150	451	1204	496	0
	2013	July/August	TE	Count Unit 3, Count Unit 8	1894	381	1062	451	0
	2014	July/August	TE	Count Unit 3, Count Unit 8	2938	611	1451	876	0

HD	Year	Survey Month	Survey Type	Trend Areas	Total	Bucks	Does	Fawns	Unk
	2015	July/August	TE	Count Unit 3, Count Unit 8	3097	690	1487	920	0
	2016	July/August	TE	Count Unit 3, Count Unit 8	2673	637	1319	717	0
	2017	July/August	TE	Count Unit 3, Count Unit 8	2912	655	1478	779	0
	2018	July/August	TE	Count Unit 3, Count Unit 8	1381	310	735	336	0
	2019	July/August	TE	Count Unit 3, Count Unit 8	4451	973	2062	1416	0
	2020	July/August	TE	Count Unit 3, Count Unit 8	5195	1088	2788	1319	0
	2021	July/August	TE	Count Unit 3, Count Unit 8	3779	858	2266	655	0
	2022	July/August	TE	Count Unit 3, Count Unit 8	4619	982	3009	628	0
701	2004	July	TE	Froze To Death, Plenty Creek, Sagehen	25479	6900	11157	7422	0
	2005	July	TE	Froze To Death, Plenty Creek, Sagehen	31445	7042	13895	10508	0
	2006	July	TE	Froze To Death, Plenty Creek, Sagehen	30226	6346	13024	10856	0
	2007	July	TE	Froze To Death, Plenty Creek, Sagehen	22757	6014	10271	6473	0
	2008	July	TE	Froze To Death, Plenty Creek, Sagehen	18785	4431	9551	4803	0
	2009	July	TE	Froze To Death, Plenty Creek, Sagehen	15723	3426	7351	4945	0
	2010	July	TE	Froze To Death, Plenty Creek, Sagehen	10872	2698	5895	2279	0
	2011	July, August, July	TE	Froze To Death, Plenty Creek, Sagehen	8198	2018	4534	1646	0
	2012	July, July, July	TE	Froze To Death, Plenty Creek, Sagehen	6196	1116	3347	1733	0
	2013	July, August, July	TE	Froze To Death, Plenty Creek, Sagehen	6575	1495	3861	1219	0
	2014	July, July, July	TE	Froze To Death, Plenty Creek, Sagehen	6639	950	2991	2698	0
	2015	August, August, July	TE	Froze To Death, Plenty Creek, Sagehen	7754	1836	3450	2469	0
	2016	August, July, July	TE	Froze To Death, Plenty Creek, Sagehen	10136	2255	4961	2920	0
	2017	July	TE	Froze To Death, Plenty Creek, Sagehen	8902	2073	3814	3015	0
	2018	July	TE	Froze To Death, Plenty Creek, Sagehen	6433	1796	3031	1606	0
	2019	July	TE	Froze To Death, Plenty Creek, Sagehen	10199	2121	4930	3149	0
	2020	July	TE	Froze To Death, Plenty Creek, Sagehen	8823	1954	4977	1891	0
	2021	July	TE	Froze To Death, Plenty Creek, Sagehen	5847	1416	2983	1448	0
	2022	July	TE	Froze To Death, Plenty Creek, Sagehen	11117	2318	6156	2643	0

HD	Year	Survey Month	Survey Type	Trend Areas	Total	Bucks	Does	Fawns	Unk
705	2004	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	13532	3441	5361	4730	0
	2005	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	18042	5662	6814	5566	0
	2006	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	19989	5045	8185	6759	0
	2007	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	26858	7924	10337	8596	0
	2008	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	24308	7732	9707	6869	0
	2009	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	18138	5278	7006	5786	0
	2010	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	14917	3619	5950	5347	0
	2011	August, July, July	TE	Medicine Rocks, South Deadboy, Thompson Creek	8281	2029	3647	2605	0
	2012	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	9816	2276	4058	3482	0
	2013	July, August, July	TE	Medicine Rocks, South Deadboy, Thompson Creek	12545	3496	5224	3825	0
	2014	August, July, July	TE	Medicine Rocks, South Deadboy, Thompson Creek	12558	3016	5100	4442	0
	2015	August, August, July	TE	Medicine Rocks, South Deadboy, Thompson Creek	17302	4332	7047	5923	0
	2016	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	19934	6142	7993	5799	0
	2017	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	19427	5388	7376	6622	0
	2018	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	21456	5100	8363	7993	0
	2019	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	26790	6293	10804	9583	110
	2020	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	25761	6060	10543	9158	0
	2021	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	15588	4730	6800	3866	192
	2022	July	TE	Medicine Rocks, South Deadboy, Thompson Creek	21429	4428	9268	7678	55

Pronghorn fall harvest data are collected each year within three age/sex classes (juvenile, adult female, adult male; Table 11). For each hunting district, we modeled harvest observations as Binomial random variables with the number of “trials” equal to the latent true population size of the age/sex class immediately before harvest (N) and the probability of “success” equal to the harvest rate of the age/sex class (h):

$$\text{Harvest}_t \sim \text{Binomial}(N_t, h_t) \quad \text{Eq. 7}$$

Table 11. Pronghorn harvest estimates and hunting effort (number of permits issued) for adult males (“Bucks”), adult females (“Does”), and juveniles, each year from 2004 – 2021 across nine hunting districts (HD) in Montana.

HD	Year	Harvest				Effort		
		Total	Bucks	Does	Juveniles	Bucks	Does	Juveniles
313	2016	10	10	0	0	10	10	10
	2017	9	9	0	0	10	10	10
	2018	7	6	1	0	11	11	11
	2019	17	17	0	0	21	21	21
	2020	10	9	0	1	11	11	11
	2021	15.1	15.1	0	0	10	10	10
318	2004	84	64	19	2	201	201	201
	2005	67	56	9	1	200	200	200
	2006	295	202	90	0	451	651	651
	2007	314	179	127	8	450	650	650
	2008	264	150	110	4	451	651	651
	2009	313	186	114	13	450	650	650
	2010	415	198	207	10	451	951	951
	2011	366	160	187	18	450	950	950
	2012	364	147	180	37	450	950	950
	2013	167	81	78	8	350	650	650
	2014	243	110	133	0	350	650	650
	2015	291	133	154	4	350	650	650
	2016	278	130	140	8	425	800	800
	2017	267	153	111	4	351	651	651
	2018	256	119	131	6	350	650	650
	2019	101	58	41	2	250	450	450
	2020	91	52	33	6	175	300	300
	2021	88.3	49.5	36.6	2.1	175	300	300
360	2004	305	203	89	9	400	400	400
	2005	360	209	144	7	400	500	500
	2006	359	213	133	13	499	599	599
	2007	476	241	234	2	501	679	679
	2008	444	261	174	9	500	600	600
	2009	412	222	177	12	500	600	600
	2010	469	228	231	10	501	701	701
	2011	412	236	167	10	502	602	602
	2012	390	234	150	6	500	600	600

HD	Year	Harvest				Effort		
		Total	Bucks	Does	Juveniles	Bucks	Does	Juveniles
	2013	368	186	181	2	500	601	601
	2014	379	203	173	2	500	600	600
	2015	406	228	178	0	501	601	601
	2016	424	250	171	2	501	652	652
	2017	399	222	174	4	500	650	650
	2018	387	234	146	7	500	650	650
	2019	259	163	94	3	500	526	526
	2020	251	148	97	6	500	525	525
	2021	161.2	101.3	59.9	0	500	500	500
420	2004	408	164	222	20	347	843	843
	2005	476	190	267	20	400	995	995
	2006	234	184	47	3	400	450	450
	2007	343	170	168	5	350	700	700
	2008	124	69	50	5	200	302	302
	2009	79	48	31	0	50	100	100
	2010	34	18	13	3	50	75	75
	2011	32	21	10	1	49	74	74
	2012	39	26	13	0	25	50	50
	2013	32	17	15	0	25	50	50
	2014	31	15	15	1	25	50	50
	2015	74	59	16	0	100	125	125
	2016	74	56	16	2	100	125	125
	2017	96	69	27	0	100	125	125
	2018	92	78	14	0	100	125	125
	2019	102	77	24	2	101	126	126
	2020	68	50	18	0	100	125	125
	2021	82.8	71	8	3.8	100	125	125
481	2004	858	381	431	40	750	1597	1597
	2005	959	461	448	47	1198	2200	2200
	2006	1022	503	470	34	1199	2199	2199
	2007	1082	476	589	17	1200	2201	2201
	2008	741	412	315	13	1200	2207	2207
	2009	231	157	69	6	400	500	500
	2010	52	38	15	0	100	125	125
	2011	48	35	13	0	100	125	125
	2012	22	15	8	0	50	75	75
	2013	15	11	4	0	25	50	50
	2014	22	14	8	0	25	50	50
	2015	26	16	10	0	25	50	50
	2016	35	30	6	0	25	50	50
	2017	26	15	11	0	25	50	50
	2018	26	21	5	0	25	49	49
	2019	32	19	11	2	25	50	50
	2020	150	93	53	5	150	350	350

HD	Year	Harvest				Effort		
		Total	Bucks	Does	Juveniles	Bucks	Does	Juveniles
	2021	224.7	107.2	114.9	2.6	150	350	350
513	2004	992	420	522	48	1000	1739	1739
	2005	923	447	432	44	1001	1651	1651
	2006	848	450	336	48	1000	1583	1583
	2007	863	395	437	31	1000	1576	1576
	2008	325	217	92	16	750	750	750
	2009	281	211	70	0	601	601	601
	2010	199	127	70	3	500	525	525
	2011	127	99	28	0	401	406	406
	2012	100	77	21	2	300	305	305
	2013	83	64	18	0	300	305	305
	2014	112	88	20	4	300	305	305
	2015	126	97	29	0	300	305	305
	2016	168	136	32	0	300	305	305
	2017	174	136	37	0	300	305	305
	2018	192	173	16	2	300	305	305
	2019	197	154	43	0	300	305	305
	2020	298	240	56	1	500	525	525
	2021	145.1	121.4	23.7	0	300	305	305
620	2004	330	235	86	5	502	602	602
	2005	385	280	95	9	499	599	599
	2006	535	429	93	11	800	900	900
	2007	1021	641	357	24	1200	1700	1700
	2008	807	516	270	20	1200	1748	1748
	2009	1012	703	287	22	1201	1701	1701
	2010	927	627	282	18	1200	1700	1700
	2011	296	230	63	3	600	700	700
	2012	248	205	36	6	503	553	553
	2013	170	135	36	0	300	350	350
	2014	284	225	56	3	500	550	550
	2015	259	194	65	0	501	551	551
	2016	253	202	48	3	501	551	551
	2017	296	245	43	8	500	550	550
	2018	142	119	23	0	200	250	250
	2019	176	145	29	2	201	251	251
	2020	383	333	51	0	600	650	650
	2021	355.1	301.1	54.1	0	600	650	650
701	2004	3843	2044	1666	123	12997	20992	20992
	2005	2599	1332	1143	121	12987	20983	20983
	2006	3427	1665	1524	157	13009	23025	23025
	2007	3399	1564	1732	103	13011	24040	24040
	2008	2384	1244	1077	64	13008	23042	23042
	2009	2482	1318	1118	47	13011	23013	23013
	2010	1595	1189	398	8	11014	13015	13015

HD	Year	Harvest				Effort		
		Total	Bucks	Does	Juveniles	Bucks	Does	Juveniles
	2011	610	480	130	0	6504	6753	6753
	2012	267	231	36	0	3008	3108	3108
	2013	208	161	47	0	3011	3111	3111
	2014	251	212	39	0	3011	3111	3111
	2015	411	336	75	0	5016	5116	5116
	2016	883	663	218	3	7514	9014	9014
	2017	657	505	146	6	7513	9013	9013
	2018	785	613	155	18	8010	9510	9510
	2019	781	560	199	23	8512	10012	10012
	2020	917	692	212	13	8501	10001	10001
	2021	713.5	589.3	121.8	2.4	6000	6150	6150
705	2004	2175	1075	943	129	12997	20992	20992
	2005	1736	809	834	86	12987	20983	20983
	2006	2592	1252	1199	92	13009	23025	23025
	2007	2950	1496	1391	63	13011	24040	24040
	2008	2195	1115	1006	74	13008	23042	23042
	2009	1896	948	892	57	13011	23013	23013
	2010	965	749	206	10	11014	13015	13015
	2011	571	477	91	2	6504	6753	6753
	2012	361	315	46	0	3008	3108	3108
	2013	333	304	29	0	3011	3111	3111
	2014	362	324	29	9	3011	3111	3111
	2015	612	546	65	1	5016	5116	5116
	2016	1112	908	194	10	7514	9014	9014
	2017	1239	1008	229	2	7513	9013	9013
	2018	1293	1087	200	5	8010	9510	9510
	2019	1255	1009	227	19	8512	10012	10012
	2020	1596	1229	339	28	8501	12277	12277
	2021	1134.7	827.3	300.4	7.1	6000	7150	7150

Model fitting

We used a Bayesian framework to fit the IPM, given its hierarchical structure. We assigned prior distributions for each parameter that were informed by past literature (see section below). We estimated posterior distributions of parameters by running three Markov Chain Monte Carlo (MCMC) chains, each for 100,000 iterations, with a burn-in of 50,000, and thinning of 10. We identified whether models converged by ensuring \hat{R} values were <1.1 and by visually inspecting posterior distributions for adequate mixing. We determined that covariates influenced vital rates if 95% credible intervals (between 2.5% and 97.5% quantiles) of posterior distributions of parameter estimates did not overlap zero.

Using the models described above, we estimated true population size for each sex/age class, as well as population growth rates, demographic rates, and correlations between demographic rates and population growth.

Literature review related to pronghorn vital rates

Population models

- Berger and Conner 2008
 - o Vital rates used to construct demographic models (not clarified but assume rates exclusive of human harvests):
 - 0.070 (variance = 0.006) summer survival of fawns 0-2 months (wolf sites)
 - 0.354 (variance = 0.006) summer survival of fawns 0-2 months (wolf-free sites)
 - 0.836 (variance = 0.005) winter survival of juveniles 2-12 months
 - 0.872 (variance = 0.006) annual survival of yearlings 1-2 years
 - 0.872 (variance = 0.006) annual survival of adults 2+ years
 - 0.95 (variance = 0.0003) fertility of adults 2+years

Age ratios

- Fawn:adult female ratio
 - o 53:100 during summer 1964 in Glasgow herd, Montana (Martinka 1967)
 - o 39:100 during summer 1965 after severe winter with substantial mortalities in Montana (Martinka 1967)
 - o 55:100 during summer 1965 after severe winter in Saskatchewan (Martinka 1967)
 - o 90-110:100 during most summers prior to 1965 in Montana & Saskatchewan (Martinka 1967)
 - o 90:100 during summer 1965 in Malta herd, Montana (Martinka 1967)
 - o 43-95:100 during August 1960-70s in Idaho (Bodie 1978)
 - o 58:100 during summer 1977 in Alberta (Barrett 1982)
 - o 42-115:100 during summers 1968-78 in Yellow Water Triangle, Montana based on aerial surveys (Pyrah 1987)
 - o 43 to >100:100 throughout pronghorn range (O'Gara 2004*c*)
 - o 20-117:100 during autumn 1985-1996 in Utah (Beale 1978)

- Yearling:adult female ratio
 - o 103:100 during summer 1963 in Glasgow herd, Montana (Martinka 1967)
 - No age class definitions, but based on aerial surveys, likely 1-1.5 years old
 - o 110:100 during summer in 1960's in Saskatchewan (Martinka 1967)
 - No age class definitions, but based on aerial surveys, likely 1-1.5 years old

Sex ratios

- Male fawn:female fawn ratio
 - o 1.1-1.2:1 from tagged fawns in Montana (Martinka 1967)
 - o 1:1 (Byers and Moodie 1990, Fairbanks 1993)
- Adult male:adult female ratio
 - o 86-93:100 during summer 1963-1964 in Glasgow herd, Montana (Martinka 1967)
 - >1.5 years old; based on aerial surveys
 - o 45:100 during summer 1965 after severe winter with substantial mortalities in Glasgow herd, Montana (Martinka 1967)
 - >1.5 years old; based on aerial surveys

Survival rates (sex- & age-class)

- Fawn survival
 - 0.379 surviving from birth until 01 Aug (n = 29 fawns) in Idaho, 1976 (Bodie 1978)
 - 0.354 surviving from birth until 60 days (n = 62 fawns) in Alberta 1975-76 (Barrett 1978, 1984)
 - 0.365 surviving from birth until 4 months (n = 200) in Utah, 1970's (Beale 1978)
 - 0.31 (0.19-0.43) average surviving from birth until 15 months during 1966-77 in Yellow Water Triangle, Montana based on aerial surveys (Pyrah 1987)
 - 0.433 (0.22-0.6) average marked fawns surviving from birth until weaning (n = 58) in Colorado, 1988-90 (Fairbanks 1993)
 - 0.42 (SE = 0.04) mean annual survival of radio-collared fawns during 2015-16 in Idaho (Western Association of Fish and Wildlife Agencies 2018)
 - In areas used by migratory pronghorn: At low elevations/winter snow, fawn survival positively associated with wolf density (0.0 – 0.42; average 0.25); At high elevations/winter snow, fawn survival unassociated with wolf density (0.70). Across average snow depths, fawn survival averaged 0.47 in low wolf density areas and 0.59 in high wolf density areas. Based on monitoring fawns of 44 GPS collared adult females in Yellowstone's northern range during spring, summer, and early fall 1999-2006. (Barnowe-Meyer et al. 2010)
 - 0.049 – 0.440 60-day survival rates of VHF collared neonatal fawns (n = 108) monitored from birth in 2002 & 2003 in Grant Teton National Park (Berger et al. 2008)
 - 0.082 (1st month), 0.429 (2nd month), 0.035 (2-month survival) for male fawns at wolf-free site (Berger and Conner 2008)
 - 0.168 (1st month), 0.631 (2nd month), 0.106 (2-month survival) for female fawns at wolf-free site (Berger and Conner 2008)
 - 0.292 (1st month), 0.777 (2nd month), 0.227 (2-month survival) for male fawns at wolf-abundant site (Berger and Conner 2008)
 - 0.484 (1st month), 0.888 (2nd month), 0.429 (2-month survival) for female fawns at wolf-abundant site (Berger and Conner 2008)
 - 0.58-0.71 annual survival, 0.66 6-month survival of marked fawns (n = 92). (Kauth 2017)
- Yearling survival
 - 0.92-0.95 post-hunt (Nov-Apr) survival of marked yearling (6-18 months) females 2002-05 in SD, no harvested individuals (Jacques et al. 2007)
- Adult survival
 - 0.82 & 0.68 annual survival of marked animals in hunted population during 1983 & 1984 in Colorado, 36% of mortalities were harvests (Firchow 1986).
 - Likely >1.5 years old, no indication of sex-specific rates
 - 0.858 (Feb 2016-Feb 2017) & 0.941 (Feb 2017-Feb 2018) annual survival of marked animals (sexes combined) in hunted population in CO, 12-16% of mortalities were harvested. (Stiver et al. 2018)
- Adult female survival
 - 0.73 (range during normal years: 0.77-0.97; as low as 0.19 in years with harsh winters) annual survival, 0.82 winter survival, 0.91 summer survival, 0.97 during mean 20-day spring migration period, & 1.0 during mean 10-day fall migration period in southeastern Alberta 2004-2007, northcentral MT and southwestern Saskatchewan, GPS collar study, 2004-2011.

Assume these are hunted populations (at least Montana populations), but not clarified in paper and no hunting related mortalities reported (Jones et al. 2020)

- 0.84 – 0.97 annual survival in WY, no hunting-related mortalities reported. (Sawyer and Lindzey 2000)
- 0.82 annual survival in TX, no hunting-related mortalities reported. (Canon and Bryant 2006)
- 0.801 annual survival of collared females (n=24) in unhunted population in Custer State Park, SD. Mortality due primarily to predation from lions and coyotes (Keller et al. 2013)
- 1.0 (winter; Nov-Mar), 0.791 (parturition; Mar-Jul), and 0.977 (breeding; Aug-Oct) seasonal survival rates of collared adult females (n=24) in unhunted population in Custer State Park, SD. (Keller et al. 2013)
- ~0.9 – 0.98 (during winter, spring, and summer) and ~0.8 fall (hunting season) survival of collared females (n=74) in ND (Kolar et al. 2012)
- 0.82 (1 yr; Jan-Dec 2015), 0.76 (2 yrs; Jan 2015-Dec 2016), 0.93 (in 3rd year given survival of first 2 years), 0.62 (across 31 months; Jan 2015-July 2017), GPS collar study in hunted population in Oregon, but no reporting of any cause of death data. (Larkins et al. 2018)
- 0.97 (Jan-May 2010), 0.53 (Oct-Apr 2010-11), 0.91 (Nov-Apr 2011-12) winter survival of GPS collared females (n = 47) in hunted population in Wyoming, 2 animals were harvested (Taylor et al. 2016)
- 0.73-0.94 annual survival in two hunted herds; 0.82-0.96 annual survival with harvest effects removed, based on collared animals (some yearlings included in the captures) in SW WY (Grogan and Lindzey 2010)
- 0.82 – 0.89 annual survival, 0.92-1.00 post-hunt (Nov-Apr) survival, 0.87-1.0 pre-hunt (May-Sep) survival, 0.90-1.00 hunt (Oct) survival of marked females 2002-05 in hunted populations in SD (Jacques et al. 2007)
- 0.85-0.89 annual survival of marked adult females (>18 months; n = 107) in hunted population in SD, 2 animals harvested. (Kauth 2017)
- Adult male survival
 - 0.76 (0.702 – 0.891) mean annual survival of collared males (n=26) in unhunted population in Custer State Park, SD. Mortality due primarily to predation from lions and coyotes (Keller et al. 2013)
 - 0.944 (winter; Nov-Mar), 0.837 (parturition; Mar-Jul), and 0.957 (breeding; Aug-Oct) seasonal survival rates of collared adult males (n=26) in unhunted population in Custer State Park, SD. (Keller et al. 2013)
 - ~0.9 – 0.98 (during winter, spring, and summer) and ~0.4 fall (hunting season) survival of collared males (n=60) in ND (Kolar et al. 2012)
 - 1.00 annual survival in TX, no hunting-related mortalities reported, collared males not permitted to be hunted. (Canon and Bryant 2006)

Harvest mortality rates

- Fawn
 - 10% (5-19%) average annual winter mortality during 1966-77 in Yellow Water Triangle, Montana based on aerial surveys (Pyrah 1987)
- Adults

- 23% (15–31%) average annual harvest mortality for both sexes during 1966–77 in Yellow Water Triangle, Montana based on aerial surveys (Pyrah 1987)
 - >10.5 months old
- 45% average annual mortality for both sexes in which an average of 52.2% of the summer population was harvested during 1960–63 in a population in Alberta (Mitchell 1980)
- 37.9% average annual mortality for both sexes in which an average of 18% of the summer population was harvested during 1960–64 in a population in Alberta (Mitchell 1980)
- 29% average annual mortality for both sexes in which an average of 7.9% of the summer population was harvested in 1964 in a population in Alberta (Mitchell 1980)
- Adult males
 - 41% (22–54%) average annual harvest mortality during 1966–77 in Yellow Water Triangle, Montana based on aerial surveys (Pyrah 1987)
 - >10.5 months old
- Adult females
 - 9% (5–19%) average annual harvest mortality during 1966–77 in Yellow Water Triangle, Montana based on aerial surveys (Pyrah 1987)
 - >10.5 months old

Natural mortality rates

- Fawn
 - 25% (10–48%) average annual winter mortality during 1966–77 in Yellow Water Triangle, Montana (Pyrah 1987)
 - 89 & 80% annual mortality during 1983 & 1984 in Colorado, mark-resight study (Firchow 1986)
 - 25–65% during first 2–3 months throughout most of their range (O’Gara 2004a)
 - Predation most common proximate cause of death for fawns (>67%; n = 28) on Yellowstone’s northern range (Barnowe–Meyer et al. 2009)
- Adults
 - 24% (9–53%) average annual winter mortality for both sexes during 1966–77 in Yellow Water Triangle, Montana (Pyrah 1987)
 - >10.5 months old
- Adult males
 - 10% (0–27%) average annual winter mortality during 1966–77 in Yellow Water Triangle, Montana (Pyrah 1987)
 - >10.5 months old
- Adult females
 - 10% (0–24%) average annual winter mortality during 1966–77 in Yellow Water Triangle, Montana (Pyrah 1987)
 - >10.5 months old
 - Predation most common proximate cause of death for adult female (59% of mortalities, n = 22) on Yellowstone’s northern range (Barnowe–Meyer et al. 2009)
 - Predation most common cause of death for adult female (69.5% of mortalities, n = 23) in Custer State Park, SD (Keller et al. 2013)

Pregnancy rates

- Fertility is high, both sexes achieve sexual maturity as yearlings (female fawns may conceive and produce young under favorable conditions). Evidence indicates a rather constant, high maternal investment into offspring by females and fecundity rates are not correlated strongly with weather, habitat, or physiological condition of the female (Kohlmann 2004)
- 98% in Colorado (Firchow 1986)

Litter size

- 1.4 – 1.8 fawns per adult female in Utah (Beale 1978)
- 1.84 – 1.98 fawns per adult female in Colorado, Wyoming, New Mexico, elsewhere (Ellis 1972)
- 1.85 – 1.97 fetal fawns per adult female (show little variation among years or regions across nearly all western states) (Kohlmann 2004)

Detection probabilities

- 0.643–0.666 unconditional parameter estimates for resighting probabilities of pronghorn based on spring (May–June) aerial flights of marked adult females in SD across 3 years (Jacques et al. 2014)

Results

We are currently considering all options for fitting models (i.e., different observation models, temporal structure, inclusion of covariates), given each hunting district has a unique data structure that needs to be fully considered before interpreting results. Uncertainty in the representativeness of counts, as well as pronghorn movements between aerial counts and harvest add additional uncertainty to the model that needs to be fully explored before interpreting findings. Once model specifications are finalized, we will fit the IPM for each hunting district and compare demographic parameter estimates across years both within and among study areas. In addition, we will examine which vital rates have the greatest effect on population growth rate for each hunting district study area. After working through these final stages of IPM development we envision rapid iteration and routine meetings to facilitate communication with field staff. Final models will be fit and results interpreted in 2023/2024.

Objective #5: Evaluate the effect of vegetation and other landscape features on pronghorn resource selection

Objectives

Understanding resource selection is important for the management of species and their associated habitat. For pronghorn, the growing season, ranging from mid-March through July in Montana, encompasses the biological period of late gestation and early lactation, which is energetically expensive and important for annual reproductive output (O'Gara 2004c). Our research objectives are to 1) identify important spring and summer forage species, 2) evaluate pronghorn selection in relation to ground-based measurements of forage and fawn security resources, and 3) evaluate how selection behavior changes correspond with changing biological needs and spatiotemporal variations in plant communities within the summer. Here, we provide an overview of this study which has been incorporated into a manuscript for submission into a peer-review journal (Crane et al. *in prep*).

Methods

From mid-March through the end of July 2021 and 2022, we collected fine-scale vegetation data in the Musselshell, Fergus-Petroleum, and South Philips study areas. Vegetation data were collected at used locations of collared pronghorn as well as at randomly assigned available locations throughout the study areas. Used locations were identified as GPS collar locations of pronghorn and were sampled within 48-hours of pronghorn use. Available locations were sampled in proportion to available landcover types (i.e., grassland, shrubland, forest, and agriculture) within the annual range. We paired used and available sites based on sampling date to compare resources at used sites with resources available to pronghorn during the same time. At each sampling site, we measured and recorded vegetation attributes including species-specific percent cover, species-specific phenology, biomass of shrubs/forbs, and shrub/herbaceous plant height. At each sampling site, we collected forage samples consisting of the earliest two available phenological stages of forbs/shrubs. Given evidence from previous studies that indicate grass species are not an important part of pronghorn diet (Kessler et al. 1981, Pyrah 1987, Yoakum 2004b, Jacques et al. 2006), we excluded grasses from sampling. These samples were then analyzed to determine forage quality using in-vitro dry matter digestibility (DairyOne 2020) to estimate digestible energy (kcal/g).

In addition, we also collected fecal samples at known pronghorn collar locations and/or opportunistically within the study area. To identify all important food items consumed by pronghorn during the spring and summer, we combined fecal pellets into composite samples to achieve spatially and temporally balanced sampling. To distribute samples temporally, each year we targeted sampling of 5 composite samples during each of 9 sampling periods, each lasting 16 days, beginning late March (approximately on the 16th of each year). To distribute sampling across the study area, we prioritized collecting at least 1 sample from each of the 3 hunting districts overlapping the study area during each sampling period. We combined collected fecal pellets into composite samples such that each composite sample consisted of two pellets from each of 5 piles (>1 m apart). We combined composite samples in two separate ways: 1) we combined pellets from piles found within a 500 m² area or 2) we combined pellets collected during the same sampling period and within the same hunting district if there were not enough pellets collected within a 500 m² area. The composite fecal samples were then analyzed using DNA metabarcoding (Species From Feces, Northern Arizona University).

The DNA metabarcoding results were used in a frequency of occurrence (FOO) analysis to develop a list of important forage species for pronghorn. FOO is generally considered a conservative approach to developing forage species lists as it limits the effect of taxa specific biases that impact marker signal (Deagle et al. 2018, Snobl et al. 2022). For each food item identified, we calculated the percentage of samples which contained that forage item within each sampling period as well as the percentage of yearly samples containing that forage item. We developed thresholds of 5% yearly FOO and 40% sampling period FOO. To be included in the forage species list, each forage item had to meet the 5% yearly threshold during at least one year or the 40% sampling period threshold during at least one sampling period. This removed any forage items that appeared in two or fewer samples over an entire summer, unless that forage item appeared in multiple samples from within a single sampling period.

To evaluate pronghorn resource selection during the summer, we compared resources at sites known to be used by pronghorn with those generally available in the study area. Using a combination of remotely-sensed and field data, we developed 19 covariates categorized into 5 groups containing variables related to time, anthropogenic features, forage availability, forage quality, and fawn security (Table 11). Covariates representing forage availability, forage quality, and fawn security were based on vegetation measurements and samples taken at vegetation sampling sites (Crane et al. *in prep*).

We correlated anthropogenic features and vegetation characteristics with relative probability of pronghorn selection using resource selection functions within a used-available study design (Manly et al. 2002). We paired used and available sites based on sampling date within a conditional logistic regression model framework to compare resources at used sites with resources available to pronghorn during the same time. Using a multi-stage modelling approach, we separately addressed research objectives. To understand overall pronghorn resource selection during summer, we developed a best-fit model without consideration of temporal variation (hereinafter referred to as the summer resource selection model). Next, to determine whether pronghorn resource selection varied during the spring and summer season, we built a time-varying model which included time interaction terms allowing selection to vary as a function of time (Wilson et al. 2014).

Table 11. Description of each covariate developed to represent variables expected to influence the summer resource selection of adult female pronghorn in central Montana, USA, 2021–2022. Covariates are divided into groups, each containing variables related to anthropogenic features, forage availability, forage quality, fawn security cover, and time. Each covariate is listed with a description of what the covariate value indicates. Covariates from all groups, excluding time, are listed with biological hypothesis associated with that covariate (“+” indicating selection, “-” indicating avoidance).

Covariate (units)	Description	Biological hypothesis (+/-)
Anthropogenic features		
Road density 500 m (m/km ²)	Density of paved/unpaved roads within 500m of a sampling site	-
Road density 1 km (m/km ²)	Density of paved/unpaved roads within 1km of a sampling site	-
Road density 2 km (m/km ²)	Density of paved/unpaved roads within 2km of a sampling site	-
Distance to road (m)	Distance (m) to nearest paved/unpaved road from a sampling site	-
Fence density 500 m (m/km ²)	Density of fences within 500m of a sampling site	-
Fence density 1 km (m/km ²)	Density of fences within 1km of a sampling site	-
Fence density 2 km (m/km ²)	Density of fences within 2km of a sampling site	-
Distance to fence (m)	Distance (m) to the nearest fence from a sampling site	-
Forage availability		
Forage cover (%)	Additive percent cover of forage species ^a	+

Forb biomass (g/m ²)	Biomass of annual and perennial forbs	+
Shrub biomass (g/m ²)	Biomass of shrubs	+
Forage quality		
Forb DE (kcal/g)	Digestible energy (DE) of forbs	+
Shrub DE (kcal/g)	DE of shrubs	+
Emergent forage cover (%)	Percent cover of emergent forage species at each sampling site	+
Fawn security cover		
Vegetation height (cm)	Maximum height of any vegetation (woody or herbaceous)	+
Shrub cover (%)	Additive percent cover of shrub species	+
Bare ground cover (%)	Additive percent cover of exposed soil, rock, litter, and lichen/moss/crust	-
Time		
Day of season (days)	Number of calendar days since beginning of sampling season starting with 1 on March 15 of each year	
Phenological day (days)	Number of calendar days until (negative values) or since (positive values) peak spring. Peak Spring (day 0) was identified each year by evaluating the relationship between forb biomass and day of season.	

^aForage species defined using fecal sample analysis.

Results

We sampled vegetation at 284 used and 284 available sampling sites resulting in 141 and 143 paired samples in 2021 and 2022, respectively. We identified 296 plant species from within 168 genera across all sampling sites. Common species included fringed sagewort (*Artemisia frigida*), Wyoming big sagebrush (*Artemisia tridentata*), common dandelion (*Taraxacum officinale*), scarlet globemallow (*Sphaeralcea coccinea*), western wheatgrass (*Pascopyrum smithii*), and Sandberg bluegrass (*Poa secunda*).

From the DNA metabarcoding of 87 fecal samples, we identified 74 species in 54 genera as forage species, including 54 forb, 14 shrub, and 6 grass species (Table 12). Of the forage species identified in the fecal samples, 56 species in 49 genera were sampled at the vegetation sites, consisting of 41 forb, 10 shrub, and 5 grass species. The number of forage species varied by sampling period, with the fewest average number of species occurring in late March (\bar{x} = 13.0 species) and early April (\bar{x} = 12.5 species; i.e., the first and second sampling periods) and increasing through time to a peak in June, with an average number of species of 31 in early June and 34 in late June (Table 13, Figure 70). Across this same time frame, the average number of forb species increased dramatically from ~3 to 26 species compared to shrub species that increased only from ~5 to 8 species and grass species that decreased from ~4 to 2 species.

Table 12. Summary of species composition of samples across years 2020 and 2021 for fecal samples analyzed using DNA metabarcoding. The percent mean for each species represents the average across years of the number of samples in which the species was detected divided by the total number of samples analyzed for each respective year (dashes occurring for standard deviation [SD] indicate the species was detected in only one year).

Species	Growth Form	Percent (%)				No. of Periods	No. of Samples
		Mean	SD	Min	Max		
<i>Artemisia</i> sp.	Shrub	72.4	1.3	71.4	73.3	18	72
<i>Artemisia cana</i>	Shrub	60.9	1.9	59.5	62.2	16	53
<i>Rosa</i> sp.	Shrub	56.2	5.4	52.4	60.0	15	49
<i>Taraxacum</i> sp.	Forb	55.3	5.9	51.1	59.5	15	48
<i>Symphotrichum</i> sp.	Forb	36.7	1.5	35.7	37.8	13	35

Species	Growth Form	Percent (%)				No. of Periods	No. of Samples
		Mean	SD	Min	Max		
Sphaeralcea coccinea	Forb	34.6	4.9	31.1	38.1	11	30
Oenothera suffrutescens	Forb	33.6	9.8	26.7	40.5	12	29
Poa nemoralis	Grass	31.2	6.4	26.7	35.7	11	27
Comandra umbellata	Forb	29.8	5.1	26.2	33.3	12	26
Eriogonum sp.	Forb	29.8	1.8	28.6	31.1	12	26
Atriplex sp.	Shrub	29.1	16.1	17.8	40.5	13	27
Tragopogon pratensis	Forb	29.0	9.5	22.2	35.7	10	25
Geocaulon lividum	Forb	28.7	3.5	26.2	31.1	11	25
Poa sp.	Grass	28.5	10.0	21.4	35.6	10	30
Medicago sp.	Forb	25.5	7.7	20.0	31.0	13	22
Lactuca sp.	Forb	23.1	4.4	20.0	26.2	10	20
Sarcobatus vermiculatus	Shrub	22.9	2.1	21.4	24.4	12	20
Tragopogon dubius	Forb	20.9	7.5	15.6	26.2	8	18
Atriplex patula	Shrub	19.7	5.8	15.6	23.8	9	17
Convolvulus arvensis	Forb	19.5	0.7	19.0	20.0	8	17
Glycyrrhiza lepidota	Forb	19.5	0.7	19.0	20.0	9	17
Polygonum aviculare	Forb	18.3	2.4	16.7	20.0	9	16
Dalea purpurea	Forb	17.5	9.0	11.1	23.8	7	15
Rumex acetosella	Forb	15.1	5.6	11.1	19.0	6	13
Lomatium sp.	Forb	14.8	7.4	9.5	20.0	8	13
Ericameria sp.	Shrub	13.9	3.9	11.1	16.7	9	12
Poa pratensis	Grass	13.3	--	13.3	13.3	4	6
Potentilla sp.	Forb	13.3	--	13.3	13.3	3	6
Erigeron pumilus	Forb	11.9	--	11.9	11.9	2	5
Bromus sp.	Grass	11.5	0.6	11.1	11.9	8	11
Eriogonum pauciflorum	Forb	11.1	--	11.1	11.1	4	5
Euphorbia sp.	Forb	10.2	4.4	7.1	13.3	5	10
Rhus sp.	Shrub	10.2	4.4	7.1	13.3	5	9
Achillea sp.	Forb	9.5	--	9.5	9.5	3	4
Heterotheca sp.	Forb	9.5	--	9.5	9.5	2	4
Juniperus communis	Shrub	9.5	--	9.5	9.5	3	4
Opuntia fragilis	Forb	9.5	--	9.5	9.5	3	4
Symphyotrichum novae-angliae	Forb	9.5	--	9.5	9.5	3	4
Triticum aestivum	Grass	8.9	--	8.9	8.9	3	4
Oenothera sp.	Forb	8.1	2.0	6.7	9.5	5	17
Chamaesyce sp.	Forb	7.1	--	7.1	7.1	2	3
Gutierrezia sp.	Shrub	7.1	--	7.1	7.1	3	3
Lygodesmia juncea	Forb	7.1	--	7.1	7.1	2	3
Packera sp.	Forb	7.1	--	7.1	7.1	2	3
Sphaeralcea sp.	Forb	7.1	--	7.1	7.1	3	8
Chenopodium sp.	Forb	6.9	0.3	6.7	7.1	5	7
Erigeron sp.	Forb	6.9	0.3	6.7	7.1	4	6
Geum sp.	Forb	6.9	0.3	6.7	7.1	5	6
Androsace sp.	Forb	6.7	--	6.7	6.7	3	3
Astragalus gracilis	Forb	6.7	--	6.7	6.7	2	3
Bassia scoparia	Forb	6.7	--	6.7	6.7	2	3
Carex sp.	Grass	6.7	--	6.7	6.7	2	3
Chenopodium album	Forb	6.7	--	6.7	6.7	2	3
Helianthus tuberosus	Forb	6.7	--	6.7	6.7	2	3
Lepidium sp.	Forb	6.7	--	6.7	6.7	2	3
Ribes aureum	Shrub	6.7	--	6.7	6.7	2	3
Ribes sp.	Shrub	6.7	--	6.7	6.7	2	3
Symphoricarpos occidentalis	Shrub	6.7	--	6.7	6.7	3	3

Species	Growth Form	Percent (%)				No. of Periods	No. of Samples
		Mean	SD	Min	Max		
Vicia sp.	Forb	6.7	--	6.7	6.7	2	3
Astragalus sp.	Forb	4.8	--	4.8	4.8	1	3
Penstemon sp.	Forb	4.8	--	4.8	4.8	1	1
Scorzonera laciniata	Forb	4.8	--	4.8	4.8	1	2
Scorzonera sp.	Forb	4.8	--	4.8	4.8	1	2
Tetranneuris acaulis	Forb	4.8	--	4.8	4.8	1	2
Helianthus sp.	Forb	4.6	0.2	4.4	4.8	2	4
Bassia sp.	Forb	4.4	--	4.4	4.4	1	2
Grindelia sp.	Forb	4.4	--	4.4	4.4	1	2
Lepidium densiflorum	Forb	4.4	--	4.4	4.4	1	2
Viola purpurea	Forb	4.4	--	4.4	4.4	1	2
Picradeniopsis oppositifolia	Forb	3.4	1.5	2.4	4.4	2	3
Salsola sp.	Forb	3.4	1.5	2.4	4.4	2	3
Juniperus sp.	Shrub	2.4	--	2.4	2.4	1	2
Convolvulus sp.	Forb	2.2	--	2.2	2.2	1	4
Rumex sp.	Forb	2.2	--	2.2	2.2	1	2

Table 13. Summary (percent mean and range) of forage species for each sampling period across years 2020 and 2021 for fecal samples analyzed using DNA metabarcoding. The percent mean for each species and period represents the average across years of the number of samples in each period in which the species was detected divided by the total number of samples analyzed in that period for each respective year. “Early” month timings generally represent the 1st to the 15th day of each month.

Taxon	Growth Form	Mean percent (%) and range (min – max)								
		Late March	Early April	Late April	Early May	Late May	Early June	Late June	Early July	Late July
<i>Artemisia cana</i>	Shrub	90 (80-100)	80 (80-80)	100 (100-100)	80 (80-80)	30 (20-40)	60 (60-60)	40 (40-40)	60 (60-60)	20 (20-20)
<i>Artemisia</i> sp.	Shrub	90 (80-100)	80 (80-80)	100 (100-100)	90 (80-100)	60 (40-80)	80 (80-80)	70 (60-80)	90 (80-100)	90 (80-100)
<i>Rosa</i> sp.	Shrub	20 (20-20)	20 (20-20)	40 (40-40)	70 (60-80)	70 (40-100)	80 (60-100)	90 (80-100)	90 (80-100)	65 (50-80)
<i>Taraxacum</i> sp.	Forb	20 (20-20)	30 (20-40)	70 (60-80)	60 (40-80)	100 (100-100)	80 (60-100)	80 (80-80)	60 (60-60)	100 (100-100)
<i>Poa nemoralis</i>	Grass	70 (40-100)	70 (40-100)	50 (40-60)	20 (20-20)	80 (80-80)	20 (20-20)	20 (20-20)	20 (20-20)	--
<i>Atriplex</i> sp.	Shrub	50 (40-60)	60 (60-60)	50 (20-80)	60 (60-60)	40 (40-40)	60 (60-60)	20 (20-20)	20 (20-20)	--
<i>Eriogonum</i> sp.	Forb	40 (20-60)	40 (40-40)	20 (20-20)	80 (80-80)	40 (20-60)	50 (40-60)	60 (60-60)	20 (20-20)	--
<i>Medicago</i> sp.	Forb	--	30 (20-40)	20 (20-20)	30 (20-40)	70 (60-80)	40 (20-60)	20 (20-20)	20 (20-20)	50 (50-50)
<i>Atriplex patula</i>	Shrub	30 (20-40)	60 (60-60)	40 (40-40)	40 (20-60)	20 (20-20)	60 (60-60)	20 (20-20)	--	--
<i>Symphotrichum</i> sp.	Forb	20 (20-20)	--	--	20 (20-20)	30 (20-40)	70 (60-80)	70 (60-80)	100 (100-100)	65 (50-80)
<i>Tragopogon pratensis</i>	Forb	20 (20-20)	--	20 (20-20)	--	60 (40-80)	90 (80-100)	40 (40-40)	60 (60-60)	50 (50-50)
<i>Sarcobatus vermiculatus</i>	Shrub	--	--	50 (40-60)	40 (40-40)	20 (20-20)	40 (20-60)	20 (20-20)	30 (20-40)	35 (20-50)
<i>Comandra umbellata</i>	Forb	--	--	40 (40-40)	60 (20-100)	50 (40-60)	50 (40-60)	40 (20-60)	40 (40-40)	35 (20-50)
<i>Geocaldon lividum</i>	Forb	--	--	40 (40-40)	60 (20-100)	50 (40-60)	40 (40-40)	60 (60-60)	40 (40-40)	45 (40-50)
<i>Ericameria</i> sp.	Shrub	--	--	20 (20-20)	20 (20-20)	40 (40-40)	20 (20-20)	40 (40-40)	20 (20-20)	60 (20-100)
<i>Poa</i> sp.	Grass	80 (60-100)	70 (40-100)	70 (60-80)	60 (60-60)	--	--	--	40 (20-60)	20 (20-20)
<i>Lomatium</i> sp.	Forb	--	20 (20-20)	40 (40-40)	60 (60-60)	30 (20-40)	20 (20-20)	20 (20-20)	--	--
<i>Convolvulus arvensis</i>	Forb	--	--	20 (20-20)	--	20 (20-20)	30 (20-40)	40 (40-40)	80 (80-80)	40 (40-40)
<i>Oenothera suffrutescens</i>	Forb	--	--	--	30 (20-40)	30 (20-40)	80 (60-100)	60 (40-80)	60 (60-60)	60 (20-100)
<i>Sphaeralcea coccinea</i>	Forb	--	--	--	30 (20-40)	40 (40-40)	50 (40-60)	90 (80-100)	70 (60-80)	55 (50-60)
<i>Bromus</i> sp.	Grass	40 (40-40)	20 (20-20)	--	30 (20-40)	--	20 (20-20)	20 (20-20)	--	--
<i>Geum</i> sp.	Forb	20 (20-20)	20 (20-20)	20 (20-20)	40 (40-40)	--	--	20 (20-20)	--	--
<i>Rumex acetosella</i>	Forb	--	--	60 (60-60)	20 (20-20)	30 (20-40)	80 (80-80)	--	--	40 (40-40)
<i>Glycyrrhiza lepidota</i>	Forb	--	--	--	--	40 (40-40)	50 (20-80)	30 (20-40)	40 (20-60)	45 (40-50)
<i>Lactuca</i> sp.	Forb	--	--	--	--	30 (20-40)	50 (20-80)	40 (20-60)	60 (60-60)	35 (20-50)
<i>Polygonum aviculare</i>	Forb	--	--	--	--	20 (20-20)	40 (40-40)	50 (40-60)	30 (20-40)	45 (40-50)
<i>Tragopogon dubius</i>	Forb	--	--	--	--	20 (20-20)	80 (80-80)	40 (40-40)	60 (60-60)	50 (50-50)
<i>Poa pratensis</i>	Grass	60 (60-60)	--	--	--	--	--	20 (20-20)	20 (20-20)	20 (20-20)
<i>Rhus</i> sp.	Shrub	20 (20-20)	--	--	--	--	40 (40-40)	40 (40-40)	40 (20-60)	--
<i>Eriogonum pauciflorum</i>	Forb	--	--	--	40 (40-40)	20 (20-20)	20 (20-20)	--	--	20 (20-20)
<i>Oenothera</i> sp.	Forb	--	--	--	40 (40-40)	60 (60-60)	80 (60-100)	80 (80-80)	--	--
<i>Dalea purpurea</i>	Forb	--	--	--	--	--	40 (40-40)	50 (40-60)	50 (40-60)	60 (20-100)
<i>Chenopodium</i> sp.	Forb	--	--	--	--	--	20 (20-20)	60 (60-60)	20 (20-20)	35 (20-50)
<i>Juniperus communis</i>	Shrub	40 (40-40)	20 (20-20)	20 (20-20)	--	--	--	--	--	--

Taxon	Growth Form	Mean percent (%) and range (min – max)									
		Late March	Early April	Late April	Early May	Late May	Early June	Late June	Early July	Late July	
<i>Opuntia fragilis</i>	Forb	20 (20-20)	--	20 (20-20)	40 (40-40)	--	--	--	--	--	
<i>Gutierrezia</i> sp.	Shrub	--	20 (20-20)	--	20 (20-20)	20 (20-20)	--	--	--	--	
<i>Sphaeralcea</i> sp.	Forb	--	20 (20-20)	--	--	--	60 (60-60)	80 (80-80)	--	--	
<i>Achillea</i> sp.	Forb	--	--	20 (20-20)	--	40 (40-40)	20 (20-20)	--	--	--	
<i>Androsace</i> sp.	Forb	--	--	--	20 (20-20)	20 (20-20)	20 (20-20)	--	--	--	
<i>Potentilla</i> sp.	Forb	--	--	--	20 (20-20)	--	--	60 (60-60)	40 (40-40)	--	
<i>Symphoricarpos occidentalis</i>	Shrub	--	--	--	20 (20-20)	20 (20-20)	--	20 (20-20)	--	--	
<i>Erigeron</i> sp.	Forb	--	--	--	--	20 (20-20)	--	--	30 (20-40)	40 (40-40)	
<i>Symphyotrichum novae-angliae</i>	Forb	--	--	--	--	--	40 (40-40)	20 (20-20)	20 (20-20)	--	
<i>Triticum aestivum</i>	Grass	--	--	--	--	--	40 (40-40)	20 (20-20)	--	20 (20-20)	
<i>Euphorbia</i> sp.	Forb	--	--	--	--	--	--	30 (20-40)	50 (40-60)	40 (40-40)	
<i>Carex</i> sp.	Grass	20 (20-20)	--	40 (40-40)	--	--	--	--	--	--	
<i>Vicia</i> sp.	Forb	--	--	20 (20-20)	--	--	--	40 (40-40)	--	--	
<i>Ribes aureum</i>	Shrub	--	--	--	40 (40-40)	20 (20-20)	--	--	--	--	
<i>Ribes</i> sp.	Shrub	--	--	--	40 (40-40)	20 (20-20)	--	--	--	--	
<i>Astragalus gracilis</i>	Forb	--	--	--	20 (20-20)	--	--	40 (40-40)	--	--	
<i>Lepidium</i> sp.	Forb	--	--	--	--	20 (20-20)	--	40 (40-40)	--	--	
<i>Lygodesmia juncea</i>	Forb	--	--	--	--	20 (20-20)	40 (40-40)	--	--	--	
<i>Erigeron pumilus</i>	Forb	--	--	--	--	--	60 (60-60)	40 (40-40)	--	--	
<i>Heterotheca</i> sp.	Forb	--	--	--	--	--	40 (40-40)	--	40 (40-40)	--	
<i>Chenopodium album</i>	Forb	--	--	--	--	--	20 (20-20)	40 (40-40)	--	--	
<i>Bassia scoparia</i>	Forb	--	--	--	--	--	--	40 (40-40)	20 (20-20)	--	
<i>Helianthus</i> sp.	Forb	--	--	--	--	--	--	40 (40-40)	40 (40-40)	--	
<i>Helianthus tuberosus</i>	Forb	--	--	--	--	--	--	40 (40-40)	--	20 (20-20)	
<i>Picradeniopsis oppositifolia</i>	Forb	--	--	--	--	--	--	40 (40-40)	--	50 (50-50)	
<i>Salsola</i> sp.	Forb	--	--	--	--	--	--	40 (40-40)	--	50 (50-50)	
<i>Chamaesyce</i> sp.	Forb	--	--	--	--	--	--	20 (20-20)	40 (40-40)	--	
<i>Packera</i> sp.	Forb	--	--	--	--	--	--	20 (20-20)	40 (40-40)	--	
<i>Juniperus</i> sp.	Shrub	--	40 (40-40)	--	--	--	--	--	--	--	
<i>Astragalus</i> sp.	Forb	--	--	--	--	--	60 (60-60)	--	--	--	
<i>Scorzonera laciniata</i>	Forb	--	--	--	--	--	40 (40-40)	--	--	--	
<i>Scorzonera</i> sp.	Forb	--	--	--	--	--	40 (40-40)	--	--	--	
<i>Tetranneuris acaulis</i>	Forb	--	--	--	--	--	40 (40-40)	--	--	--	
<i>Bassia</i> sp.	Forb	--	--	--	--	--	--	40 (40-40)	--	--	
<i>Grindelia</i> sp.	Forb	--	--	--	--	--	--	40 (40-40)	--	--	
<i>Lepidium densiflorum</i>	Forb	--	--	--	--	--	--	40 (40-40)	--	--	
<i>Viola purpurea</i>	Forb	--	--	--	--	--	--	40 (40-40)	--	--	
<i>Convolvulus</i> sp.	Forb	--	--	--	--	--	--	--	80 (80-80)	--	
<i>Penstemon</i> sp.	Forb	--	--	--	--	--	--	--	--	50 (50-50)	
<i>Rumex</i> sp.	Forb	--	--	--	--	--	--	--	--	40 (40-40)	

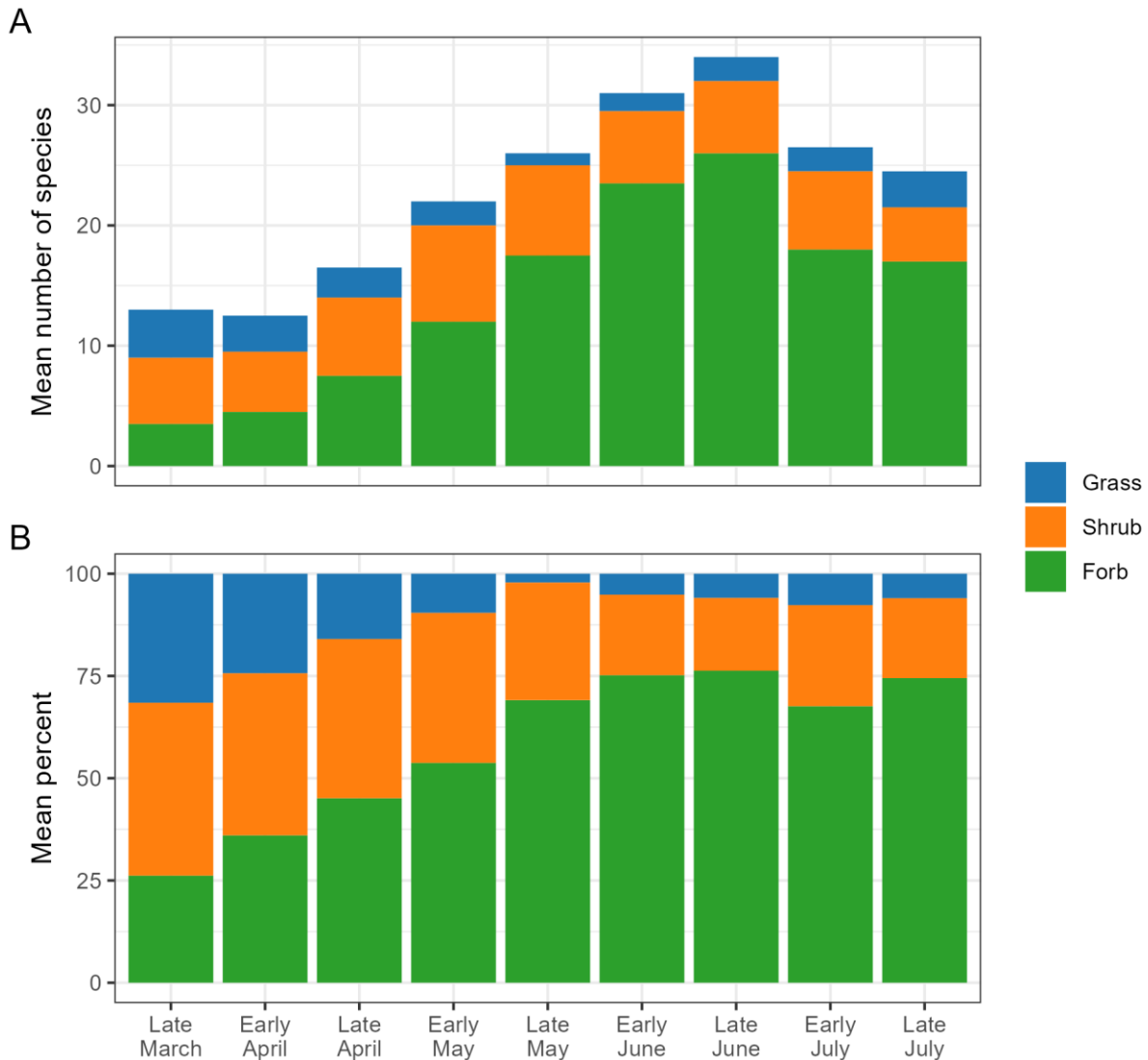


Figure 70. Mean number of species by growth form (panel A) and mean percent of each growth form in each summer sampling period across years 2020 and 2021 for fecal samples analyzed using DNA metabarcoding.

Forb forage quality, estimated as digestible energy (in kilocalories per gram), averaged 3.5 ± 0.9 kcal/g (\pm SD) across all available (i.e., excluding ‘used’) sampling sites and varied across sampling sites in different land cover classes (Fig. 72). Forb forage quality was highest in both grassland ($\bar{x} = 3.6$, SD = 0.6) and shrubland ($\bar{x} = 3.6$, SD = 0.7) and lowest in agriculture ($\bar{x} = 3.0$, SD = 1.6), averaged across summer sampling periods. Generally, forb forage quality declined through summer across and within all land cover types, with the highest values estimated during early May ($\bar{x} = 3.8$, SD = 0.3) and lowest during late July ($\bar{x} = 3.1$, SD = 0.4). In agriculture, forb forage quality averaged highest during early May ($\bar{x} = 3.9$, SD = 0.1) and lowest during late April ($\bar{x} = 1.8$, SD = 2.0). In grassland, forb forage quality averaged highest during early April ($\bar{x} = 3.7$, SD = 1.0) and lowest during late July ($\bar{x} = 3.1$, SD = 0.2). In shrubland, forb forage quality averaged highest during late April ($\bar{x} = 3.9$, SD = 0.6) and lowest during early July ($\bar{x} = 3.2$, SD = 0.4). We did not summarize forb forage quality for forest cover types due to lack of sufficient data.

Shrub forage quality, estimated as digestible energy (in kilocalories per gram), averaged 2.7 ± 1.7 kcal/g (\pm SD) across all available (i.e., excluding 'used') sampling sites and varied across sampling sites in different land cover classes (Fig. 72). Shrub forage quality was highest in shrubland ($\bar{x} = 3.8$, SD = 0.4) and lowest in grassland ($\bar{x} = 2.4$, SD = 1.8), averaged across summer sampling periods. Generally, shrub forage quality declined throughout summer, with the highest values estimated during late March ($\bar{x} = 3.6$, SD = 1.3) and lowest during late June ($\bar{x} = 2.3$, SD = 1.8). In grasslands, shrub forage quality averaged highest during late July ($\bar{x} = 3.4$, SD = 0.4) and lowest during late June ($\bar{x} = 1.8$, SD = 1.8). In shrubland, shrub forage quality averaged highest during late March ($\bar{x} = 4.1$, SD = 0.4) and lowest during early July ($\bar{x} = 3.3$, SD = 0.3). We did not summarize shrub forage quality for agriculture or forest cover types due to lack of sufficient data.

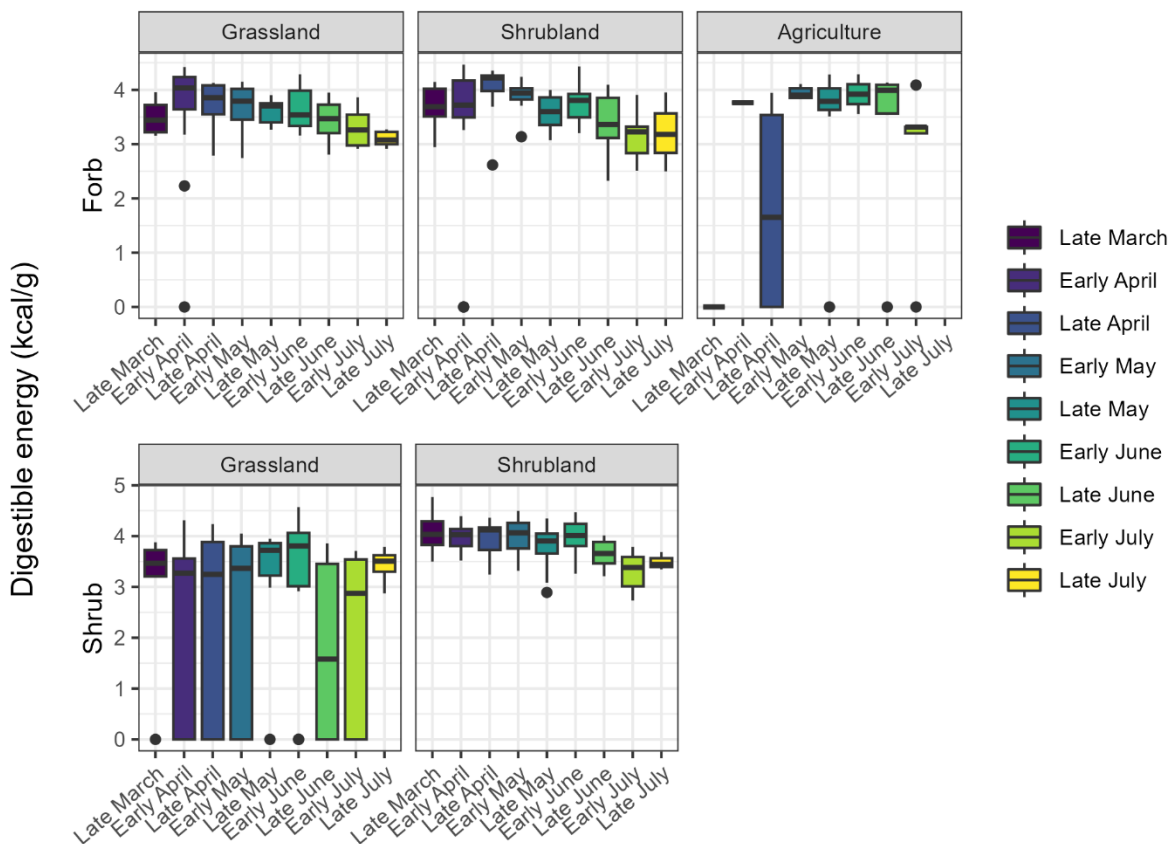


Figure 71. Summer digestible energy (i.e., forage quality; kilocalories per gram) of forbs (top 4 panels) and shrubs (bottom 2 panels) measured in each landcover type and sampling period. Data is summarized across 'available' sampling sites only (i.e., excluding 'used' sites). We removed panels for forest land cover type for forbs and agriculture and forest landcover types for shrubs due to lack of data. Horizontal lines through boxes represent median values, the length of the box represents the middle 50% of observations (IQR), vertical lines represent observations within 1.5x the range of the IQR, and points outside the vertical lines represent observations >1.5x the range of the IQR.

The most supported summer resource selection model indicated the covariates representing emergent forage cover and bare ground cover were potentially important in pronghorn resource selection. Pronghorn selection was correlated with higher emergent forage cover (Fig. 73A). There was a quadratic relationship between Pronghorn Movement & Population Ecology Project: 2023 Annual Report

relative probability of selection and percent cover of bare ground, with selection for bare ground peaking at 70% bare ground cover and declined at higher and lower levels of bare ground (Fig. 73B). This peak in selection occurred below the median value of bare ground cover observed at available sampling sites (77.5%, interquartile range: 63.9–86.5%).

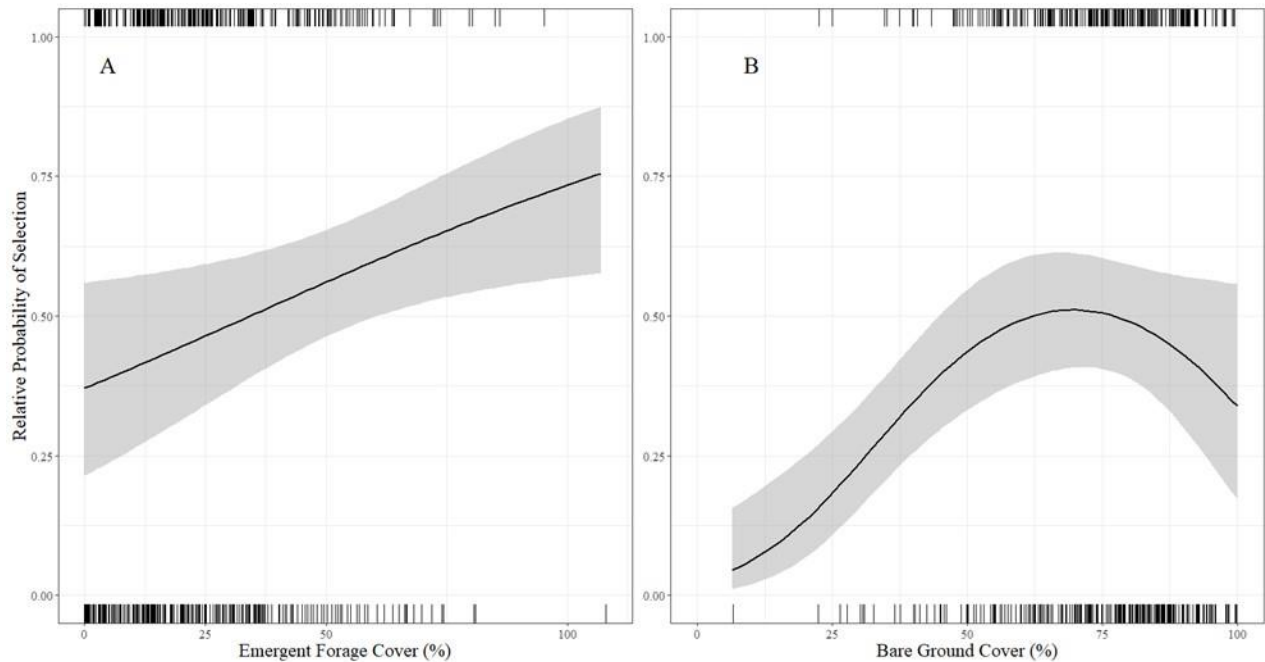


Figure 72. Predictive relationship of relative probability of selection (black line) and 95% confidence interval (shaded gray) across the range of observed values of (A) percent cover of emergent forage and (B) percent cover of bare ground estimated by holding all other covariates constant at their mean and using the final summer resource selection model for female pronghorn in central Montana, 2021–2022. The distributions of covariate values of used and available sites are represented by the upper and lower rug, respectively. Reproduced from Crane et al. (in preparation).

The time-varying resource selection model indicated that pronghorn selection of forage cover, forb DE, and shrub cover varied during the summer (Fig. 74). Pronghorn selection showed a significant positive correlation with forage cover briefly during the early part of the season (49–32 days before peak spring) but was not significantly associated with forage cover during the remainder of the summer (Fig. 74B). Although initially showing an avoidance of forb digestible energy, pronghorn selection of forb DE increased during the beginning of the season, until selection for forb DE peaked just prior to the peak of spring conditions. Pronghorn selected for shrub cover during the early parts of the season, with selection strength slightly increasing during and immediately following the fawning period. During late summer, pronghorn exhibited avoidance of shrub cover.

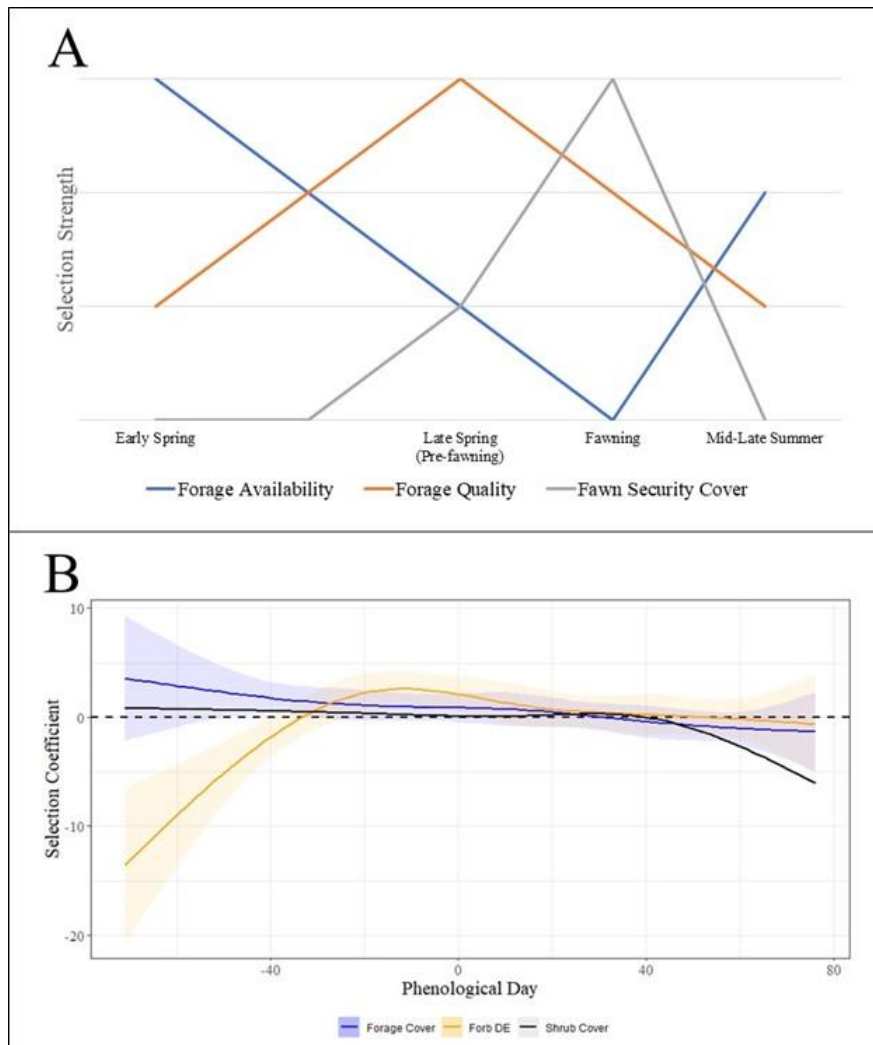


Figure 73. Plots of time-varying resource selection of female pronghorn during the summer in central Montana, USA, 2021–2022. Panel A depicts predicted temporal variation in resource selection. Panel B shows the selection coefficients (solid lines) and corresponding 95% confidence intervals (shaded area) of each covariate with a temporal interaction term in the time-varying resource selection global model. Phenological day represents number of days until (negative values) or after (positive values) ‘peak spring’ each year. Coefficient estimates >0 (dashed line) indicate a positive relationship with that covariate during the given time, whereas values <0 indicate a negative relationship. Shrub cover was evaluated using the quadratic functional form, while forage cover and forb DE were evaluated using the linear functional form, with each interacted with a natural cubic spline function of time with four degrees of freedom. Reproduced from Crane et al. (in preparation).

Discussion

Resource selection by pronghorn during the summer in central Montana correlated with forage quality (i.e., emergent forage cover, forb DE) and fawn security (i.e., bare ground cover, shrub cover). Forage availability (i.e., forage species cover and biomass of forbs and shrubs) and anthropogenic features (i.e., roads and fences) did not correlate with pronghorn resource selection in the summer, which contrasts with other studies reporting that pronghorn avoid these features (Jones et al. 2019, 2022, Reinking et al. 2019, Opatz et al. 2023). Further, the time-varying model suggested pronghorn selection for forb digestible energy varied temporally, with the peak in selection for forb digestible energy occurring during the last month of gestation for pronghorn (i.e., late April – early May), which is nutritionally demanding. As such, we conclude that observed pronghorn selection of forage quality aligned with changing vegetation resources and biological needs associated with late gestation nutrition.

Female pronghorn also appeared to select resources to meet fawn security needs. Our summer resource selection model indicated that pronghorn selected for areas with less bare ground cover than generally available but appeared to avoid areas with lower amounts of bare ground cover (which were predicted to provide greater cover for fawns). Our time-varying resource selection model indicated a slight increase in selection for shrub cover during the fawning period, this selection rapidly decreased, and pronghorn selected strongly against shrub cover during the late summer. Our results may indicate that female pronghorn must balance between fawn security cover and predation risk, as areas with more shrub cover and less bare ground cover may provide hiding cover for fawns, as well as provide predators with more stalking cover (Bodie 1978, Yoakum 2004c). Our study suggests pronghorn may be balancing these risks through their selection of resources (i.e., by selecting areas with only slightly less bare ground than available) and varying their selection for shrub cover during the summer to avoid shrub cover once fawns become reliant on early detection to avoid predation.

Management Implications

Management actions affecting forage quality and fawn security cover will likely have the greatest influence on pronghorn resource selection. Habitat improvement strategies focused on providing a consistent availability of highly nutritious forbs and newly emergent forage species will likely have the greatest influence on pronghorn resource selection. Since pronghorn selection for fawn security cover varied significantly during the summer, managers should consider a mosaic approach to managing shrub cover, and provide a landscape containing areas with heavy, moderate, and minimal shrub cover.

Literature Cited

- Barnowe-Meyer, K. K., P. J. White, T. L. Davis, and J. A. Byers. 2009. Predator-specific mortality of pronghorn on Yellowstone's northern range. *Western North American Naturalist* 69:186–194.
- Barnowe-Meyer, K. K., P. J. White, T. L. Davis, D. W. Smith, R. L. Crabtree, and J. A. Byers. 2010. Influences of wolves and high-elevation dispersion on reproductive success of pronghorn (*Antilocapra americana*). *Journal of Mammalogy* 91:712–721.
- Barrett, M. W. 1978. Pronghorn fawn mortality in Alberta. Pages 429–444 *Proceedings of the 8th Biennial Pronghorn Antelope Workshop*. Jasper, Alberta, Canada.
- Barrett, M. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *Journal of Wildlife Management* 46:991–1002.
- Barrett, M. W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. *Journal of Wildlife Management* 48:542.
- Beale, D. M., and A. D. Smith. 1970. Forage use, water consumption and productivity of pronghorn antelope in western Utah. *Journal of Wildlife Management* 34:570–582.
- Beale, D. M. 1978. Birth rate and fawn mortality among pronghorn antelope in western Utah. Pages 445–448 *Proceedings of the 8th Biennial Pronghorn Antelope Workshop*.
- Bender, L., J. Boren, H. Halbritter, and S. Cox. 2013. Factors influencing survival and productivity of pronghorn in a semiarid grass-woodland in east-central New Mexico. *Human-Wildlife Interactions* 7:313–324.
- Berger, K. M., and M. M. Conner. 2008. Recolonizing wolves and mesopredator suppression of coyotes: Impacts on pronghorn population dynamics. *Ecological Applications* 18:599–612.
- Berger, K. M., E. M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecology* 89: 818–828.
- Boccardi, S. J. 2002. Effects of winter range on a pronghorn population in Yellowstone National Park. Montana State University, Bozeman, MT.
- Bodie, W. L. 1978. Pronghorn fawn mortality in the upper Pahsimeroi River drainage of central Idaho. Pages 417–428 in *Proceedings of the 8th Biennial Pronghorn Antelope Workshop*. Jasper, Alberta, Canada.
- Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, J. Gude, J. Herbert, K. Hersey, M. Hurley, P. M. Lukacs, S. McCorquodale, E. McIntire, J. Nowak, H. Sawyer, D. Smith, and P. j. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. *Journal of Applied Ecology* 50:295–305.
- Brown, D. E., and M. R. Conover. 2011. Effects of large-scale removal of coyotes on pronghorn and mule deer productivity and abundance. *Journal of Wildlife Management* 75: 876–882.
- Buckland, S. T., K. B. Newman, L. Thomas, and N. B. Koesters. 2004. State-space models for the dynamics of wild animal populations. *Ecological Modelling* 171:157–175.
- Bunnfeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- Buzzard, S. A., A. F. Jakes, A. J. Pearson, and L. Broberg. Advancing fence datasets: Comparing approaches to map fence locations and specifications in southwest Montana. *Frontiers in Conservation Science* 3:958729.
- Byers, J. A., and J. D. Moodie. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioral Ecology and Sociobiology* 26:157–164.
- Cagnacci, F., S. Focardi, A. Ghisla, B. van Moorter, E. H. Merrill, E. Gurarie, M. Heurich, A. Mysterud, J. Linnell, M. Panzacchi, R. May, T. Nygård, C. Rolandsen, and M. Hebblewhite. 2016. How many routes lead to migration?

- Comparison of methods to assess and characterize migratory movements. *Journal of Animal Ecology* 85:54–68.
- Canon, S. K., and F. C. Bryant. 2006. Home range and survival of pronghorn in the Trans-Pecos region of Texas. Page in K. A. Cearley and S. Nelle, editors. *Pronghorn Symposium 2006*. Texas Cooperative Extension, College Station, Amarillo, USA.
- Deagle, B. E., A. C. Thomas, J. C. McInnes, L. J. Clarke, E. J. Vesterinen, E. L. Clare, T. R. Kartzinel, and J. P. Eveson. 2018. Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data? *Molecular Ecology* 28:391–406.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1–61.
- Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. *Journal of Wildlife Management* 60:528–541.
- DairyOne. 2020. Analytical Procedures. <<https://dairyone.com/download/forage-forage-lab-analytical-procedures/?wpdmdl=13889&refresh=6201552e509591644254510>>.
- DeVoe, J. D., K. M. Proffitt, and J. J. Millsaugh. 2023. Fence types influence pronghorn movement responses. *Ecosphere* e4285.
- Dubay, S. A., T. H. Noon, J. C. deVos, and R. A. Ockenfels. 2006. Serologic survey for pathogens potentially affecting pronghorn (*Antilocapra americana*) fawn recruitment in Arizona, USA. *Journal of Wildlife Diseases* 42:844–848.
- Dunn, S. J., and J. A. Byers. 2008. Determinants of survival and fecundity through a population bottleneck in pronghorn (*Antilocapra americana*). *Journal of Mammalogy* 89:1124–1129.
- Eacker, D. R., P. M. Lukacs, K. M. Proffitt, and M. Hebblewhite. 2017. Assessing the importance of demographic parameters for population dynamics using Bayesian integrated population modeling. *Ecological Applications* 27:1280–1293.
- Ellis, J. 1972. Observations on pronghorn population dynamics. Pages 55–65 *Proceedings of the 5th Biennial Pronghorn Antelope Workshop*.
- Fairbanks, W. S. 1993. Birthdate, birthweight, and survival in pronghorn fawns. *Journal of Mammalogy* 74:129–135.
- Firchow, K. M. 1986. Ecology of pronghorns on the Pinon Canyon Maneuver Site, Colorado. M.S. thesis, Virginia Polytechnic Institute and State University.
- Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology* 81:33–45.
- Gates, C. C., P. Jones, M. Sutor, A. Jakes, M. S. Boyce, K. Kunkel, and K. Wilson. 2012. The influence of land use and fences on habitat effectiveness, movements and distribution of pronghorn in the grasslands of North America. Pages 277–294 *in* *Fencing for Conservation*. Springer, New York, USA.
- Gray, S. S. 2013. Investigation of diseases occurring in pronghorn. Federal Aid Project W-127-R Segment 20. Big Game Research and Surveys, Texas Parks and Wildlife.
- Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *The Journal of Animal Ecology* 80:1246–1257.
- Grogan, R., and F. Lindzey. 2010. Pronghorn survival in Wyoming. Pages 46–64 *Proceedings of the 24th Biennial Pronghorn Workshop: Partnering for Pronghorn*.

- Hamlin, K. L., and R. J. Mackie. 1989. Mule deer in the Missouri Breaks, Montana: A study of population dynamics in a fluctuating environment. *Montana Fish, Wildlife and Parks*.
- Harrington, J. L., and M. R. Conover. 2007. Does removing coyotes for livestock protection benefit free-ranging ungulates? *Journal of Wildlife Management* 71:1555–1560.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–2363.
- Hurley, M. A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369: 20130196.
- Jacques, C. N., J. D. Sievers, J. A. Jenks, C. Sexton, and D. E. Roddy. 2006. Evaluating diet composition of pronghorn in Wind Cave National Park, South Dakota. *Prairie Naturalist* 38:239–250.
- Jacques, C. N., J. A. Jenks, J. D. Sievers, D. E. Roddy, and F. G. Lindzey. 2007. Survival of pronghorns in western South Dakota. *Journal of Wildlife Management* 71:737–743.
- Jacques, C. N., J. A. Jenks, T. W. Grovenburg, R. W. Klaver, and C. S. Deperno. 2014. Incorporating detection probability into northern Great Plains pronghorn population estimates. *Journal of Wildlife Management* 78:164–174.
- Jakes, A. F. 2015. Factors influencing seasonal migrations of pronghorn across the Northern Sagebrush Steppe. University of Calgary, Calgary, Alberta.
- Jakes, A. F., C. C. Gates, N. J. DeCesare, P. F. Jones, J. F. Goldberg, K. E. Kunkel, and M. Hebblewhite. 2018*a*. Classifying the migration behaviors of pronghorn on their northern range. *The Journal of Wildlife Management* 82:1229–1242.
- Jakes, A. F., P. F. Jones, L. C. Paige, R. G. Seidler, and M. P. Huijser. 2018*b*. A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. *Biological Conservation* 227:310–318.
- Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010*a*. Population-specific vital rate contributions influence management of an endangered ungulate. *Ecological Applications* 20:1753–1765.
- Johnson, H. E., L. S. Mills, J. D. Wehausen, and T. R. Stephenson. 2010*b*. Combining ground count, telemetry, and mark-resight data to infer population dynamics in an endangered species. *Journal of Applied Ecology* 47:1083–1093.
- Jones, P. F., A. F. Jakes, A. C. Telander, H. Sawyer, B. H. Martin, and M. Hebblewhite. 2019. Fences reduce habitat for a partially migratory ungulate in the Northern Sagebrush Steppe. *Ecosphere* 10:e02782.
- Jones, P. F., A. F. Jakes, D. R. Eacker, M. Hebblewhite. 2020. Annual pronghorn survival of a partially migratory population. *Journal of Wildlife Management* 84:1114–1126.
- Jones, P. F., A. F. Jakes, S. E. Vegter, and M. S. Verhage. 2022. Is it the road or the fence? Influence of linear anthropogenic features on the movement and distribution of a partially migratory ungulate. *Movement Ecology* 10:37.
- Kauth, A. 2017. Reassessing Survival, Movement, Resource Selection, and Slightability of Pronghorn in Western South Dakota. South Dakota State University.
- Keller, B. J., J. J. Millspaugh, C. Lehman, G. Brundige, and T. W. Mong. 2013. Adult pronghorn (*Antilocapra americana*) survival and cause-specific mortality in Custer State Park, South Dakota. *The American Midland Naturalist* 170:311–322.
- van de Kerk, M., R. T. Larsen, D. D. Olson, K. R. Hersey, and B. R. McMillan. 2021. Variation in movement patterns of mule deer: have we oversimplified migration? *Movement Ecology* 9:44.

- Kéry, M., and M. Schaub. 2011. Bayesian population analysis using WINBUGS: a hierarchical perspective. Academic Press, Inc., New York, USA.
- Kessler, W. B., W. F. Kasworm, and W. L. Bodie. 1981. Three Methods Compared for Analysis of Pronghorn Diets. *The Journal of Wildlife Management* 45:612–619.
- Kohlmann, S. G. 2004. Population dynamics and modeling. Pages 645–674 in B. W. O’Gara and J. D. Yoakum, editors. Pronghorn ecology and management. University Press of Colorado, Boulder, Colorado, USA.
- Kolar, J. L., J. J. Millspaugh, and B. A. Stillings. 2011. Migration patterns of pronghorn in southwestern North Dakota. *Journal of Wildlife Management* 75:198–203.
- Kolar, J. L., J. J. Millspaugh, and T. W. Mong. 2012. Survival and cause-specific mortality of pronghorn in southwestern North Dakota. *The American Midland Naturalist* 167:164–173.
- Larkins, A., S. M. Harju, and D. G. Whittaker. 2018. Pronghorn migration and survival: A statistical analysis of a southeastern Oregon population. Pages 19–35 2018 Proceedings of the Western States and Provinces Pronghorn Workshop: Volume 28.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: Statistical design and analysis for field studies. Second edition. Springer, Boston, Massachusetts, USA.
- Martinka, C. J. 1967. Mortality of northern Montana pronghorns in a severe winter. *Journal of Wildlife Management* 31:159–159.
- Merkle, J. A., J. Gage, and M. J. Kauffman. 2022. Migration mapper v2.3. University of Wyoming, Department of Zoology and Physiology, Migration Initiative. <<https://migrationinitiative.org/content/migration-mapper>>.
- Miller, W. H., and M. Drake. 2003. Nutritional concerns of pronghorn antelope on Anderson Mesa and Garland Prairie, Arizona. Arizona Game and Fish Department, Phoenix, USA.
- Mitchell, G. 1980. The pronghorn antelope in Alberta. Alberta Department of Lands and Forests, Fish and Wildlife Division and University of Regina, Saskatchewan, Canada.
- Mitchell, M. S., H. Cooley, J. A. Gude, J. Kolbe, J. J. Nowak, K. M. Proffitt, S. N. Sells, and M. Thompson. 2018. Distinguishing values from science in decision making: Setting harvest quotas for mountain lions in Montana. *Wildlife Society Bulletin* 42:13–21.
- Montana Fish Wildlife and Parks. 2012. Big game surveys and inventory, antelope, Region 5. Statewide Wildlife Inventory, Federal Aid Project W-130-R-26. Montana Fish, Wildlife, and Parks, Billings.
- Montana Fish Wildlife and Parks. 2020a. Montana harvest reports. <<https://myfwp.mt.gov/fwpPub/harvestReports>>. Accessed 30 Jun 2020.
- Montana Fish Wildlife and Parks. 2020b. Montana statewide elk management: population and distribution. <<http://fwp.mt.gov/fishAndWildlife/management/elk/>>. Accessed 30 Jun 2020.
- Montana Fish Wildlife and Parks. 2020c. Deer management: population and distribution. <<http://fwp.mt.gov/fishAndWildlife/management/deer/>>. Accessed 30 Jun 2020.
- Newell, J. 2013. Survey & Inventory Protocols for Big Game in Montana: Pronghorn Antelope. Montana Fish, Wildlife and Parks.
- O’Gara, B. W. 2004a. Mortality factors. Pages 379–408 in B. W. O’Gara and J. D. Yoakum, editors. Pronghorn ecology and management. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder, Colorado, Boulder Colorado.
- O’Gara, B. W. 2004b. Physical characteristics. Pages 109–144 in B. W. O’Gara and J. D. Yoakum, editors. Pronghorn ecology and management. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder, Colorado.

- O'Gara, B. W. 2004c. Reproduction. Pages 275–298 *in* B. W. O'Gara and J. D. Yoakum, editors. Pronghorn ecology and management. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder, Colorado, USA.
- O'Gara, B. W., and H. G. Shaw. 2004. Predation. Pages 337–377 *in* B. W. O'Gara and J. D. Yoakum, editors. Pronghorn ecology and management. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder, Colorado.
- Opatz, A. P., T. E. Fulbright, G. Mizer, R. W. DeYoung, W. C. Conway, S. S. Gray, and D. G. Hewitt. 2023. Influence of cropland on resource selection by pronghorn. *Journal of Wildlife Management* 87:e22372.
- Paterson, J. T., K. Proffitt, J. Rotella, and R. Garrott. 2019. An improved understanding of ungulate population dynamics using count data: Insights from western Montana. *PLoS ONE* 14:e0226492.
- Paterson, J. T., K. Proffitt, J. Rotella, D. McWhirter, and R. Garrott. 2021. Drivers of variation in the population dynamics of bighorn sheep. *Ecosphere* 12:e03679.
- Poor, E. E., C. Loucks, A. Jakes, and D. L. Urban. 2012. Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. *PLoS ONE* 7:e49390.
- Proffitt, K. M., A. B. Courtemanch, S. R. Dewey, B. Lowrey, D. E. McWhirter, Kevin. L. Monteith, J. T. Paterson, J. Rotella, P. J. White, and R. A. Garrott. 2021. Regional variability in pregnancy and survival rates of Rocky Mountain bighorn sheep. *Ecosphere* 12:e03410.
- Pyrah, D. B. 1987. American pronghorn antelope in the Yellow Water Triangle, Montana: a study of social distribution, population dynamics, and habitat use. Montana Department of Fish, Wildlife and Parks, Helena, Montana.
- Reinking, A. K., K. T. Smith, K. L. Monteith, T. W. Mong, M. J. Read, and J. L. Beck. 2018. Intrinsic, environmental, and anthropogenic factors related to pronghorn summer mortality. *The Journal of Wildlife Management* 82:608–617.
- Reinking, A. K., K. T. Smith, T. W. Mong, M. J. Read, and J. L. Beck. 2019. Across scales, pronghorn select sagebrush, avoid fences, and show negative responses to anthropogenic features in winter. *Ecosphere* 10:e02722.
- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323–335.
- Sawyer, H., and F. Lindzey. 2000. Jackson Hole pronghorn study. Final report. Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, Wyoming, USA.
- Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* 19:2016–2025.
- Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. *Journal of Animal Ecology* 80:1078–1087.
- Schaub, M., and F. Abadi. 2011. Integrated population models: A novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152:S227–S237.
- Seidler, R. G., R. A. Long, J. Berger, S. Bergen, and J. P. Beckmann. 2015. Identifying impediments to long-distance mammal migrations. *Conservation Biology* 29:99–109.
- Snobl, L. A., K. M. Proffitt, and J. J. Millspaugh. 2022. Wildfire extends the shelf life of elk nutritional resources regardless of fire severity. *Ecosphere* 13:e4178.
- Stiver, J., W. Biologist, and C. Parks. 2018. Pronghorn movement and survival in southeastern Colorado. Status Report 2017–2018, Colorado Parks and Wildlife.
- Taylor, K. L., J. L. Beck, and S. V. Huzurbazar. 2016. Factors influencing winter mortality risk for pronghorn exposed to wind energy development. *Rangeland Ecology & Management* 69:108–116.

- Thorne, E. T., E. S. Williams, T. R. Spraker, W. Helms, and T. Segerstrom. 1988. Bluetongue in free-ranging pronghorn antelope (*Antilocapra americana*) in Wyoming 1976 and 1984. *Journal of Wildlife Diseases* 24:113–119.
- Von Gunten, B. 1978. Pronghorn fawn mortality on the National Bison Range. University of Montana, Missoula, MT. <<https://scholarworks.umt.edu/etd/3324>>.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.
- Western Association of Fish and Wildlife Agencies. 2018. Proceedings of the Western States and Provinces 28 Biennial Pronghorn Workshop: Learning from the Past – Adapting for the Future.
- White, G. C., and B. C. Lubow. 2002. Fitting population models to multiple sources of observed data. *Journal of Wildlife Management* 66:300–309.
- Wilson, R. R., J. S. Horne, K. D. Rode, E. V. Regehr, and G. M. Durner. 2014. Identifying polar bear resource selection patterns to inform offshore development in a dynamic and changing Arctic. *Ecosphere* 5(10):136
- Xu, W., K. Barker, A. Shawler, A. Van Scoyoc, J. A. Smith, T. Mueller, H. Sawyer, C. Andreozzi, O. R. Bidder, H. Karandikar, S. Mumme, E. Templin, and A. D. Middleton. 2021a. The plasticity of ungulate migration in a changing world. *Ecology* 102:e03293.
- Xu, W., N. Dejid, V. Herrmann, H. Sawyer, and A. D. Middleton. 2021b. Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. *Journal of Applied Ecology* 58:690–698.
- Yoakum, J. D. 2004a. Distribution and abundance. Pages 75–105 in. *Pronghorn ecology and management*. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder, Colorado.
- Yoakum, J. D. 2004b. Foraging ecology, diet studies and nutrient values. Pages 447–502 *in*. *Pronghorn Ecology and Management*. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder Colorado.
- Yoakum, J. D. 2004c. Habitat characteristics and requirements. Pages 409–445 in. *Pronghorn ecology and management*. Wildlife Management Institute, Washington D.C. and University Press of Colorado, Boulder, Colorado.