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MONOGRAPH

Ecology of reintroduced Rocky Mountain bighorn sheep in Dinosaur National Monument

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Abstract

Translocations have been widely used to restore and conserve bighorn sheep (*Ovis canadensis*) populations in North America. Some translocations have been successful, but many populations remain small and genetically isolated. Population structure can influence the viability and long-term success of reintroductions. Social ungulates often function as interconnected subpopulations (metapopulations); however, few studies evaluate subpopulation sizes, connectivity, and genetic diversity within metapopulations. To address this gap, we conducted a comprehensive study of a reintroduced Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) population in Dinosaur National Monument in Colorado and Utah, USA, between 2006–2020. We analyzed global positioning system (GPS) radio-collar data, genetic samples, and results of health testing to evaluate abundance, distribution, genetic structure and diversity, habitat use, movement and connectivity, and presence of or exposure to respiratory pathogens. We integrated these analyses to evaluate the outcomes of a reintroduction effort that began in 1952, over 70 years ago, and to inform management decisions in Dinosaur National Monument. We also provide a framework for evaluating metapopulation processes, including a

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non-invasive approach that links genetic structure with Bayesian spatial capture-recapture analyses to estimate subpopulation sizes. Despite models indicating continuous suitable habitat, we found a spatially structured population with at least 4 subpopulations with constrained connectivity. Evidence from step selection and density analyses suggested that movement among subpopulations may be limited by semi-permeable barriers including rivers and human disturbance, which could contribute to maintenance of spatial structure over time. In 2006, antibody to *Mycoplasma ovipneumoniae* was detected in all geographically and genetically distinct subpopulations. Widespread clinical signs of disease and a confirmed exposure to *M. ovipneumoniae* in 2019 indicate a long-term disease challenge. Proximity to domestic sheep creates repeated opportunities for introduction of new *M. ovipneumoniae* strains. We estimated abundance in 2019 at 109 (95% CrI = 87–133), composed of subpopulations ranging from 18–39 animals (95% CrIs from 11–50). Genetic diversity was relatively high compared to other reintroduced and native Rocky Mountain bighorn sheep populations, which is likely a consequence of multiple translocations from different sources. Three of 4 subpopulation centers generally aligned with the locations of original translocation release sites. Persistence in the presence of pathogens may be facilitated by metapopulation structure and moderately high genetic diversity. Conversely, metapopulation structure can also facilitate pathogen persistence. Our approach offers a path to advance understanding of the population ecology of reintroduced bighorn sheep and can inform effective conservation and management of their populations.

KEYWORDS

abundance, Bighorn sheep, Dinosaur National Monument, genetics, metapopulation dynamics, movement, population structure, resource selection, spatial capture-recapture

La Ecología de Borrego Cimarron de las Montañas Rocosas Reintroducido en el Monumento Nacional de Dinosaurio Resumen

Las translocaciones han sido utilizadas ampliamente para restaurar y conservar las poblaciones de Borrego Cimarrón en América del Norte. Algunas translocaciones han sido exitosas pero muchas

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poblaciones quedan pequeñas y genéticamente aisladas. La estructura poblacional puede influir la viabilidad y el éxito a largo plazo de las reintroducciones. Ungulados sociales frecuentemente funcionan como subpoblaciones interconectadas (metapoblaciones); sin embargo, pocas investigaciones evalúan el tamaño de las subpoblaciones, conectividad y diversidad genética dentro de las metapoblaciones. Para abordar esta brecha, realizamos una investigación comprehensiva de una población reintroducida de Borrego Cimarrón de Las Rocosas (*Ovis canadensis canadensis*) en el Monumento Nacional Dinosaurio, en Colorado y Utah entre 2006–2020. Analizamos datos de collares con sistema de posicionamiento global (GPS), muestras genéticas y resultados de pruebas de salud para evaluar la abundancia, la distribución, la estructura y la diversidad genética, el uso del hábitat, el movimiento y la conectividad, y la presencia de o la exposición a patógenos respiratorios. Integramos estos análisis para evaluar los resultados de un esfuerzo de reintroducción que comenzó en 1952 —hace más de 70 años— y para formar las decisiones de dirección en el Monumento Nacional Dinosaurio.También proporcionamos un marco de investigación para evaluar los procesos de metapoblación, que incluye un método que relaciona la estructura genética con análisis Bayesiano de captura-recaptura espacial para estimar los tamaños de las subpoblaciones. A pesar de que los modelos indican la existencia de un hábitat continuo apropiado, encontramos una población espacialmente estructurada, compuesta por al menos cuatro subpoblaciones con una conectividad restringida. La evidencia derivada del modelo de selección de hábitat y análisis de densidad sugirió que el movimiento entre subpoblaciones podría ser limitado por barreras semipermeables, incluyendo ríos y perturbaciones humanas, lo cual podría contribuir al mantenimiento de la estructura espacial con el paso del tiempo.En 2006, se detectaron anticuerpos contra *Mycoplasma ovipneumoniae* en todas las subpolaciones geográficamente y genéticamente distinctas. La presencia generalizada de signos clínicos de enfermedad y la exposición confirmada a *M. ovipneumoniae* en 2019 indican un desafío sanitario persistente a largo plazo. La proximidad a ovejas domésticas genera oportunidades repetitivas para la introducción de nuevas cepas de *M. ovipneumoniae*. Para el año 2019, estimamos la abundancia en 109 individuos (intervalo de credibilidad del 95%: 87–133) cifra

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compuesta por subpoblaciones que oscilaban entre 18 y 39 animales (intervalos de credibilidad del 95%: 11-50). La diversidad genética fue relativamente elevada comparada a otras poblaciones de Borregos Cimarrones de las Montañas Rocosas reintroducidos y nativos, lo cual probablemente consecuencia de múltiples translocaciones de distintas fuentes. Tres de los 4 centros de subpoblación, por lo general, están de acuerdo con la ubicación de los sitios originales de liberación de translocaciones. La persistencia en presencia de patógenos puede ser facilitada por la estructura de metapoblación y una diversidad genética moderadamente alta. Por el contrario, la estructura de metapoblación también puede facilitar la persistencia de los patógenos. Nuestro enfoque ofrece una vía para promover la comprensión de la ecología poblacional del borrego cimarrón reintroducido, y puede informar conservación y gestión eficaces de sus poblaciones.

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INTRODUCTION

The reintroduction or restoration of wildlife by translocation is a globally applied conservation strategy intended to reestablish or augment declining wildlife populations (Griffith et al. 1989, Batson et al. 2015). In North America, many translocations aimed to restore large wild herbivore populations that declined from the mid-1800s to the early 1900s because of overexploitation and habitat loss associated with Euro-American settlement (Griffith et al. 1989). Large wild herbivores are ecologically and culturally important, influencing nutrient cycling and vegetation dynamics (Zamin and Grogan 2013, Geremia et al. 2019) and providing cultural, recreational, and economic value (Reo and Whyte 2012, Cooper et al. 2015). Despite conservation advances, the largest herbivores (≥100 kg) continue to be threatened with extinction globally and have the highest extinction risk among all mammals, in part due to slow life histories and relatively small population sizes (Ripple et al. 2015, Atwood et al. 2020). Small populations, especially if isolated, can face increased extinction risk (Fagan and Holmes 2006, Bulman et al. 2007, Kurland et al. 2023).

Bighorn sheep declines and environmental stressors

Bighorn sheep (*Ovis canadensis*) exemplify the challenges facing large herbivore conservation. Although they occupy diverse environments, bighorn sheep depend on open, steep, and rugged terrain for predator avoidance (Buechner 1960). Many populations function as metapopulations with subpopulations partially isolated from each other by the patchy distribution of suitable habitat (Bleich et al. 1990, Singer et al. 2000a). Like other large herbivores, bighorn sheep populations declined severely during Euro-American settlement, likely because of market hunting, forage depletion, and diseases introduced by domestic livestock (Buechner 1960, Wishart 1978). Though historical abundance estimates are uncertain, bighorn sheep likely numbered in the hundreds of thousands prior to European contact, with many populations declining to a fraction of historical numbers by the 1970s (Schmidt and Gilbert 1978, Whiting et al. 2023, Bleich and Holl 2026). In response, over 1,450 translocation projects moved 21,500 animals across the United States and Canada between 1922 and 2015 in efforts to restore populations (Whiting et al. 2023). As of 2022, the combined population of bighorn sheep across subspecies in the United States and Canada was estimated at approximately 70,000 animals (Wild Sheep Initiative 2023).

Many factors likely contribute to the ongoing suppression of bighorn sheep abundance, persistence, and expansion into suitable habitat. Factors may also interact, with their relative influence varying by population and context (Singer et al. 2000c, Whiting et al. 2023). Epizootic outbreaks are a well-documented limitation (Gross et al. 2000). Infection with *Mycoplasma ovipneumoniae* can predispose bighorn sheep to polymicrobial pneumonia (Cassirer and Sinclair 2007, Besser et al. 2013). This disease may cause die-offs of 10–90% of individuals at all ages followed by years of reduced lamb recruitment (Cassirer et al. 2018, Besser et al. 2021). Respiratory pathogens can be transmitted from exposure to

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domestic livestock or other bighorn sheep carrying the pathogen (Wolfe et al. 2010, Wehausen et al. 2011, Cassirer et al. 2018). Thus, restoration and translocation efforts can be complicated by the presence of domestic sheep and the potential introduction of new pathogens (Cassirer and Sinclair 2007, Wehausen et al. 2011, Cassirer et al. 2018, Besser et al. 2021, Whiting et al. 2023).

Die-offs and low recruitment may also result from resident pathogens becoming virulent when environmental conditions favor disease, such as when populations approach carrying capacity or experience forage limitations (Butler et al. 2018, Wagler et al. 2023). Forage can be reduced under drought conditions, through water diversion, following incursions of invasive species, or along with other land cover change (Wagler et al. 2023). Predation by mountain lion (*Puma concolor*) may further restrict survival across the species' range (Rominger et al. 2004, Proffitt et al. 2021).

Post-translocation or natural expansion into suitable habitat can be limited by both habitat fragmentation and bighorn sheep movement behavior. Metapopulation structure in bighorn sheep results from a mix of natural and anthropogenic causes influencing demographic and genetic connectivity among subpopulations (Creech et al. 2014, Tosa et al. 2023). Rivers and thick forests can pose partial barriers to connectivity (Epps et al. 2024, Flesch et al. 2026). Human infrastructure including highways can limit dispersal between suitable habitats and reduce gene flow via influences on movement or mortality (Epps et al. 2005). Bighorn sheep may avoid human activities including hikers and campers (Keller and Bender 2007, Longshore et al. 2013). Sociality and herding behaviors can also shape habitat use and movement (Festa-Bianchet 1991, Creech et al. 2014, Tosa et al. 2023). Reintroduced and augmented populations may have fewer and less diverse migratory behaviors and higher site fidelity compared to native populations, even when suitable habitat is available (Lowrey et al. 2019, 2020, Lula et al. 2020). However, migratory behavior can emerge decades after reintroduction (Jesmer et al. 2018).

Translocation outcomes and metapopulation dynamics

Despite extensive translocation efforts, bighorn sheep restoration and management outcomes have been mixed (Singer et al. 2000c, Whiting et al. 2023). Augmentations and reintroductions can bolster small populations and introduce new genetic diversity but sometimes also introduce new pathogens or pathogen strains (Hogg et al. 2006, Jamieson 2011, Olson et al. 2013, Jahner et al. 2019). Bighorn sheep abundance has increased only modestly compared to species such as elk (*Cervus canadensis*) for which there have been similar efforts (Griffith et al. 1989, Witmer 1990). Of 217 Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) populations across the subspecies' range, 58% increased from 2014 to 2017, but most augmented and some reintroduced populations were more likely to have declined (Donovan et al. 2020). A separate study found that 15 of 17 managed populations in Wyoming and Montana, USA, had marginal population performance (geometric mean growth rates ≤1) and that factors affecting vital rates varied among populations, suggesting that effective management interventions need to be population-specific (Paterson et al. 2021).

Many bighorn sheep populations that received translocations remain small and genetically isolated (Flesch et al. 2020). Genetic diversity outcomes for both Rocky Mountain and desert bighorn sheep (*O. c. nelsoni*) are influenced by many aspects of translocations including founder population size, fitness effects of individual genetic variants, the number of translocated individuals, and source population genetics (Jahner et al. 2019, Flesch et al. 2022, Love Stowell et al. 2020). Strategic translocations from multiple source populations have facilitated genetic rescue of small populations (Miller et al. 2012, Olson et al. 2012, Poirier et al. 2019). For example, augmentations of Rocky Mountain bighorn sheep at the National Bison Range in Montana resulted in selective retention of beneficial genes from translocated animals, with 57% of loci showing evidence of natural selection favoring introduced alleles, and subsequent increased reproduction (Miller et al. 2012). Translocations to Ram Mountain in Alberta, Canada, also rescued a bottlenecked population, with admixed lambs showing higher allelic diversity and improved fitness compared to non-admixed lambs (Poirier et al. 2019).

Metapopulation processes, occurring within and among subpopulations, interact in complex ways to influence population viability from both demographic and genetic perspectives (Ceballos et al. 2017, Frankham 2022).

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Thus, long-term and comprehensive assessments of subpopulation sizes, population structure, genetics, disease exposure, and connectivity within populations are needed to disentangle multiple hypotheses for these interactions (Paolini et al. 2023, Whiting et al. 2023). Decades of research on the reintroduced Hells Canyon metapopulation in Oregon and Idaho, USA, revealed how movement, connectivity, and population structure can shape disease and demographic outcomes, with connectivity facilitating both population persistence and pathogen spread (Manlove et al. 2016; Cassirer et al. 2013, 2017). Spatial structure and partial isolation may benefit pathogen-exposed metapopulations by slowing disease transmission and buffering against synchronous population-wide outbreaks (Cross et al. 2005, Dekelaita et al. 2023). To demonstrate trade-offs for *M. ovipneumoniae* infection susceptibility, recent work on a native desert bighorn sheep metapopulation integrated spatial genetic, disease, and demographic data (Dugovich et al. 2023). More genetically diverse and connected subpopulations showed stronger immune responses to respiratory pathogens, despite being at higher risk of disease transmission than more isolated subpopulations (Dugovich et al. 2023). Epps et al. (2024) conducted a similar systematic assessment, integrating non-invasive genetic sampling with movement and disease data to evaluate how the distribution and abundance of Grand Canyon desert bighorn sheep are influenced by fragmentation and gene flow.

Management challenges and innovative approaches

While partial isolation may benefit pathogen-exposed bighorn sheep metapopulations, excessive isolation can lead to pathogen persistence or small subpopulations vulnerable to local extinction via inbreeding depression, Allee effects, reduced immune response, or local catastrophes (Hagenaars et al. 2004, Borg et al. 2017, Cassirer et al. 2018). Managers must often balance these competing benefits and risks with incomplete information, weighing the benefits of connectivity against pathogen transmission risk and concerns such as outbreeding depression (Paolini et al. 2023, Whiting et al. 2023). Yet frameworks for cohesively assessing these processes across various environments and translocation histories remain underdeveloped, in part because of sparse long-term health and movement data and a lack of robust abundance estimates (Donovan et al. 2020, Lula et al. 2020, Paolini et al. 2023).

Comprehensive assessments require substantial resources, especially for metapopulations with cryptic or small subpopulations in remote terrain. Managers of protected areas face additional constraints including limited funding for ungulate management, few personnel with species-specific expertise, and restrictions on the use of aerial surveys. Recent developments pairing fecal sample collection with spatial capture-recapture models offer an alternative approach to understanding metapopulations that addresses some of these constraints (e.g., Schmidt et al. 2022, Epps et al. 2024).

Here, we used global positioning system (GPS)-collar data, genetic samples, and pathogen datasets to conduct a comprehensive spatially explicit assessment of a reintroduced Rocky Mountain bighorn sheep population in Dinosaur National Monument (hereafter the Monument) in Colorado and Utah, USA. We expand on prior integrated assessments by estimating both total abundance and subpopulation sizes and synthesizing ecological datasets to evaluate metapopulation processes (Figure 1). Bighorn sheep in the Monument were extirpated by 1950, and the current population was established by at least 5 translocations occurring from 1952 to 2000 (Barmore 1962, Singer and Gudorf 1999). Past monitoring has included ground and helicopter counts, but no previous study has rigorously evaluated the population, in part because of protected area constraints (George et al. 2009). Several stressors discussed above likely challenge this population, including pathogens introduced through translocations or ongoing overlap with domestic sheep and cattle grazing allotments, human recreation, and barriers to movement and gene flow.

We integrated information on pathogen exposure, movement and habitat use, population structure, genetics, and abundance to answer the following questions: 1) What is the spatial distribution and structure of this population? Is it continuous along steep canyons, or divided into discrete subpopulations by landscape features, anthropogenic activities, or translocation history? 2) What is the current size of the population and potential subpopulations? 3) What respiratory pathogens has the population been exposed to, particularly those associated with die-offs and livestock, and is there

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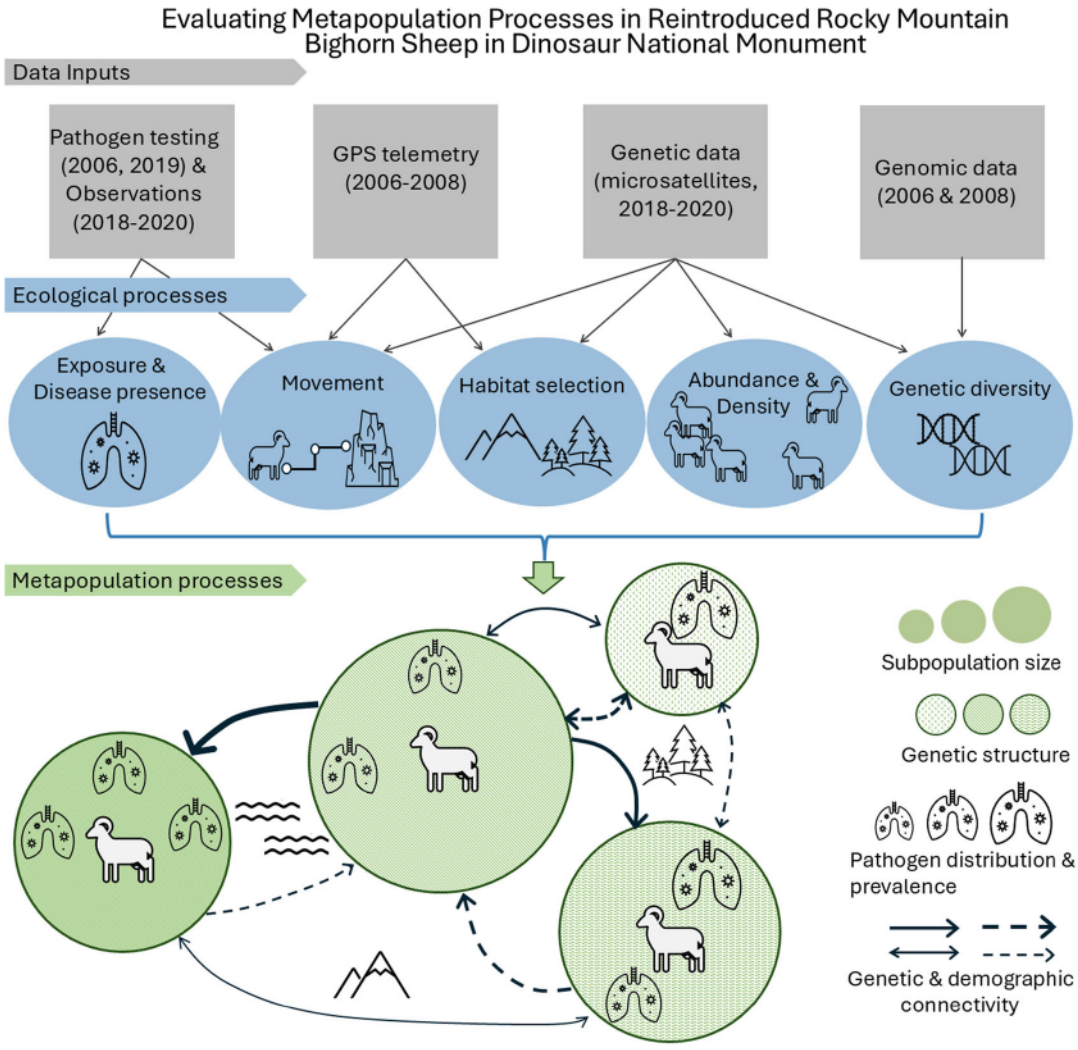


FIGURE 1 Conceptual framework for evaluating metapopulation processes in reintroduced Rocky Mountain bighorn sheep in Dinosaur National Monument, Colorado and Utah, USA. We analyzed multiple datasets (upper, gray panel) to assess different ecological processes (middle, blue panel), which we then integrated to inform metapopulation processes represented in the bottom, green panel. For example, combining genetic diversity and structure analyses with spatially explicit density models allowed us to evaluate the distribution and structure of the population and how environmental and genetic factors may shape this structure, and to estimate the size of genetically distinct subpopulations. The bottom panel shows subpopulations as nodes with bighorn, where node size corresponds to subpopulation size within a metapopulation. Patterning of nodes reflects variation in genetic structure among subpopulations. Lung icons depict how the number of different respiratory pathogens and the prevalence (depicted as size of lung icon) of different pathogens may vary among subpopulations. Arrows between subpopulations depict genetic (solid) and demographic (dashed) connectivity. Arrow weight reflects variation in levels of connectivity between subpopulations and variation in directionality of connectivity, indicating unidirectional or reciprocal connections (depicted by one-headed vs. double-headed arrows).

evidence of respiratory disease? If so, is evidence of pathogen exposure isolated by subpopulation or distributed throughout the population? 4) What influences bighorn sheep habitat selection in the semi-arid Monument given source populations inhabited more mesic, alpine environments? and 5) Do predictions of suitable habitat based on habitat selection align with population densities? By integrating these analyses across ecological scales, we sought to evaluate

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the outcomes of a reintroduction effort that began in 1952, establish baseline information for future monitoring, inform management decisions in Dinosaur National Monument, and advance a framework for comprehensive assessments of similar reintroduced bighorn sheep populations that evaluate metapopulation processes. This includes development of a novel, efficient approach for estimating subpopulation size.

STUDY AREA

The study area comprised Dinosaur National Monument (~850 km^2) in northwest Colorado and northeast Utah (Figure 2). The Monument is centered on the confluence of the Green and Yampa rivers and is dominated by rugged canyons and mesas with elevation ranging from 1,500 to 2,740 m (NASA 2020). The climate is semi-arid to sub-humid with average annual precipitation of 203–406 mm across elevations (NASA 2020). Riparian tree and shrub communities in river canyons are dominated by willow (*Salix* spp.), boxelder (*Acer* spp.), and tamarisk (*Tamarix* spp.), whereas drier and higher elevation sites are dominated by sage (*Artemesia* spp.) and rabbitbrush (*Ericameria* spp.; Perryman et al. 2002). Rocky canyon slopes are dominated by pinyon-juniper (*Pinus* spp. and *Juniperus* spp.), pine woodlands, or mountain mahogany (*Cercocarpus* spp.) partially owing to a history of fire suppression, which favors

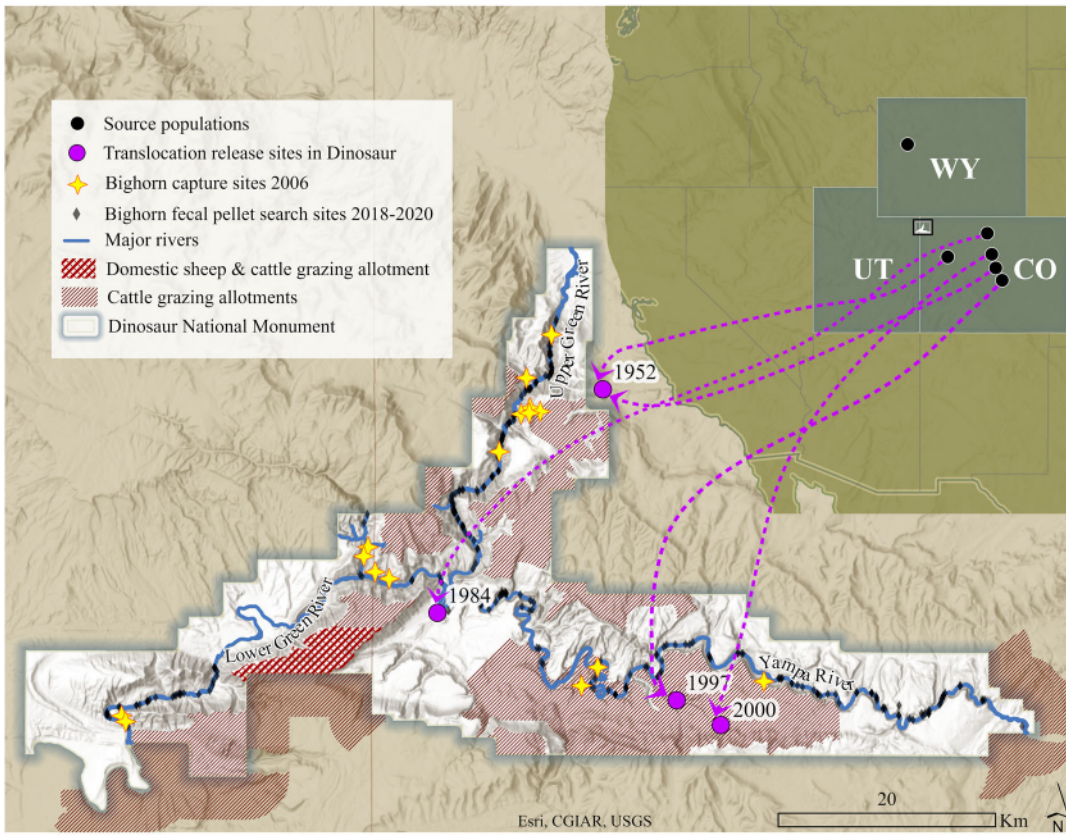


FIGURE 2 The study area showing Dinosaur National Monument, Colorado and Utah, USA, locations in Wyoming (WY) and Colorado (CO) of source populations from which bighorn were released either inside (purple dots) or within 100 km of Dinosaur National Monument (inset map; study area is depicted on the inset with a black box and white profile), bighorn capture locations in 2006, and bighorn sampling locations during 2018–2020. Background layer credits: Environmental Systems Research Institute (Esri 2024), Consultative Group on International Agricultural Research (CGIAR; Jarvis et al. 2008), and United States Geological Survey (USGS 2021).

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conifers (Perryman et al. 2002). Because of the steep terrain, human access to bighorn sheep habitat is limited to a few trails and the river corridors. Human recreational activities include rafting, hiking, and camping, with average annual total visits of approximately 292,000 and average total overnight stays of about 54,000 from 2000–2023 (National Park Service [NPS] 2025). Livestock grazing is also permitted on 9 cattle grazing allotments ranging in size from 2 km^2 to 131 km^2. One allotment permits cattle (50 animals) from May to November and domestic sheep (500 animals) from late June to late July (Figure 2; E. Spencer, Dinosaur National Monument, unpublished data). Land surrounding the Monument includes Bureau of Land Management (BLM) units, privately owned cattle and domestic sheep ranches, and additional active grazing allotments on BLM units to the southwest (Figure 2).

Archeological evidence including rock art and animal remains in the Monument suggest that bighorn sheep (*Ovis* spp.) occupied the region as far back as 450–1250 CE (Burgh and Scoggin 1948). Domestic sheep were first reported around 1920 (Barmore 1962). Native bighorn sheep were locally extirpated during 1933–1950, likely because of disease-associated die-offs, with the last observation of small, apparently sick groups of animals in 1944 (Barmore 1962, George et al. 2009). The first reintroduction occurred in 1952 when Colorado Parks and Wildlife (CPW) released 32 animals about 2 km outside the Monument (Figure 2). Three additional augmentations inside the Monument occurred in 1984, 1997, and 2000, ranging from 15–27 individuals each, totaling 99 animals across all 4 attempts (Figure 2; George et al. 2009). Other translocations from Wyoming (Whiskey Mountain herds; Figure 2) with release sites near the Monument (within ~100km) at Sawmill Draw on Bear Mountain and Big Spring (Sheep Creek) Canyon occurred in 1977, 1983, and 1984, and genetic evidence suggests dispersal from at least one of those translocations to the Monument population (Singer and Gudorf 1999, Flesch et al. 2020). Bighorn sheep also occur outside the boundary to the east in Cross Mountain Canyon upstream on the Yampa River and adjacent to the northwest border in the Diamond Mountain region of Utah. Colorado Parks and Wildlife conducted ground and helicopter counts in the Monument from 1989 to 2007 and used these counts to approximate herd size. The last flight, in June 2007, had a minimum count of 91 animals (49 adult females, 12 adult males, 1 yearling, 29 lambs), which led to an approximation of 165 animals; no new counts of the population have occurred until this study (George et al. 2009, Carroll et al. 2025). Mountain lions are present in the region, but their densities are unknown and they are considered rare. Other ungulates found in the Monument at low densities are mule deer (*Odocoileus hemionus*), elk, and pronghorn (*Antilocapra americana*; Barmore 1962).

Given multiple translocations from different source populations and early reports of bighorn sheep far from original release sites, we hypothesized a single, continuously distributed, and genetically diverse population of approximately 165 animals. However, disease risk from domestic sheep allotments (Cassirer et al. 2018), documented deaths during early data collection, and evidence that rivers restrict connectivity (Epps et al. 2024) provided reasoning for a contrasting hypothesis of spatial structuring into smaller, potentially isolated subpopulations with low genetic diversity. Research demonstrates that translocations can be successful even when source and release habitats differ, and bighorn sheep typically exhibit consistent habitat use patterns across environments (e.g., selection for escape terrain; DeCesare and Pletscher 2006, Lula et al. 2020, Werdel et al. 2023). We therefore hypothesized that habitat use and selection in the Monument would be consistent with patterns documented in previous studies.

METHODS

Data collection

Capture, pathogen testing, and GPS collaring of bighorn sheep in 2006

In December 2006, the United States Geological Survey (USGS), National Park Service, and Colorado Parks and Wildlife partnered to deploy GPS collars on 20 animals (10 males, 10 females) distributed across the Monument. Bighorn sheep were captured using helicopter net-gun protocols approved by the Animal Care and Use Committee at the USGS Northern Rocky Mountain Science Center (#2006-01), aged from horn annuli, and fit with Telonics

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TGW-3500 store-on-board radio-collars with GPS recording locations every 2.5 hours (Telonics, Mesa, AZ, USA). Collars collected data for up to roughly 18 months, until 30 June 2008. To test for pathogens and parasites, biologists collected oropharyngeal swabs, fecal samples, and blood samples during captures and other samples opportunistically, primarily from mortalities. The contribution of *M. ovipneumoniae* to bighorn sheep disease outbreaks was identified in Besser et al. (2007). Therefore, we submitted archived blood serum samples ($n = 15$; 14 were of sufficient quantity for testing) collected during 2006 to the Washington Animal Disease Diagnostic Laboratory in 2017 for enzyme-linked immunosorbent assay (ELISA) tests for detection of *M. ovipneumoniae* antibodies.

Genetic sampling and observations 2018–2020

To estimate population size, assess movements, and evaluate genetic structure, diversity, and gene flow in the Monument's rugged terrain, we collected non-invasive genetic samples (fecal pellets) along rivers and one trail. Sampling was conducted by Monument biologists, researchers, and volunteers on river float trips on the Green and Yampa rivers and hikes up the Jones Hole trail during the summer months (June–August) in 2018, 2019, and 2020 (Figure 2; Table 1). Trained observers attended all bighorn sheep-focused trips to classify and count sightings of animals. Researchers stopped at riverbanks where rafts could safely stop and searched for fecal pellets on foot in accessible surrounding areas. Bighorn sheep had been observed in many but not all sites during previous river trips. Each sample consisted of several fecal pellets collected in a coin envelope. Most bighorn sheep pellets were collected during 2 trips in 2018, and 3 trips in both 2019 and 2020. Sampling in 2020 occurred only on the Yampa River because of COVID-19 pandemic restrictions. Additional river trips with other primary goals (e.g., weed pulling) wherein trained staff searched only limited sites also yielded a few samples. During sampling, researchers and Monument staff recorded observations of symptomatic animals (e.g., violent coughing, nasal discharge), and in 2019 observed and sampled a symptomatic lamb for a full necropsy including a *M. ovipneumoniae* polymerase chain reaction (PCR) test of pneumonic lung tissue.

Data analysis

Disease

Diagnostic testing of serum samples occurred at the Montana Veterinary Diagnostic Laboratory (Montana State University, Bozeman, MT, USA). Oropharyngeal swabs were kept cool until plated within 2 days of collection and

TABLE 1 Summary of sites where non-invasive searches were conducted for bighorn sheep fecal pellets (sampling effort) and sample numbers in Dinosaur National Monument in Colorado and Utah, USA, from 2018-2020.

Year	River trips (Bighorn focus)	Trip dates	Total sites searched	Lower green river sites	Upper green river sites	Yampa river sites	Total samples collected
2018	3 (2)	11–14, 18–23 Jun; 22–25 Jul	35	17	14	4	126
2019	6 (3)	10–14, 19–24 Jun; 30 Jun–2 Jul; 29 Jul–2 Aug; 9–12, 25 Sep	140	28	95	17	397
2020	3 (3)	10–15 Jun; 26 Jun–2 Jul; 7–12 Jul	94	0	0	95	265

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then cultured at the Caine Veterinary Teaching Center (University of Idaho, Caldwell, ID, USA). Larval counts of lungworm (*Protostrongylus* spp.) in fecal pellets were conducted by the Colorado Veterinary Diagnostic Laboratories, College of Veterinary Medicine and Biomedical Sciences, Colorado State University, Fort Collins, Colorado (Diagnostic Laboratory Accession #067-41563).

Typically, the ELISA test for *M. ovipneumoniae* is used only for characterizing exposure for the population. Prevalences of other pathogens identified from the serological and oropharyngeal samples were estimated as the number of positive samples divided by the total number of samples with confidence bounds calculated using the incomplete beta function ratio (Johnson et al. 1993:129–130). Where all samples tested negative, the estimated prevalence was zero and 95% confidence bounds were estimated as in Johnson et al. (1993:131), where n is the number of samples examined:

$$0 \leq \text{prevalance} \leq 1 - 0.05^{1/n}$$

To shed light on potential age-structured pathogen susceptibility, for each pathogen we tested the null hypotheses that prevalence did not vary with age or sex using logistic regression for age and Fisher's exact test for sex (Plowright et al. 2017; Appendix A). Variance of prevalence among different geographic segments of the population could not be addressed statistically because of the small sample size, but we mapped results to assess visual patterns.

Genotyping

We used fecal samples collected during float trips to genotype and sex individuals. We scraped the exterior of pellets to collect epithelial cells and extracted DNA using the AquaGenomic Stool and Soil protocol (Wehausen et al. 2004; Multitarget Pharmaceuticals, Salt Lake City, UT, USA; Appendix B). To identify individuals, we attempted to amplify 10 markers (9 microsatellites and 1 sex identification marker) for each sample using PCR and 3 replicate reactions per sample. We tabulated allele frequencies and determined that a minimum of 6 loci were required to maintain a cumulative probability of identity (P_{ID}) of 1×10^{-4} and P_{IDsibs} of 1×10^{-2}. We removed samples with fewer than 6 loci and identified recaptures in the remaining sample set (Appendix B, Table B1-B2).

Genetic structure and diversity analyses

To evaluate population genetic structure, we extended genotypes for 120 individuals (of 152 total) to 16 microsatellites (Appendix B, Table B2; Carroll et al. 2025). We selected 40 individuals with 9-locus genotypes sampled from each of the 3 areas bisected by rivers (i.e., between the Yampa and upper Green, between the Yampa and lower Green, and on river right of the Green). We used 16 microsatellite loci previously used in genotyping fecal, blood, and tissue samples for evaluating genetic structure and diversity and identifying individual bighorn sheep across their range (Epps et al. 2018, 2024; Spaan et al. 2021). We repeated the probability of identity and matching analyses for individuals with extended genotypes to verify individual identifications across the full dataset.

To evaluate whether subpopulation structure existed, we assessed support for a range of genetic clusters (K), from 2 to 10. We used program STRUCTURE (Pritchard et al. 2000) with no prior information on population or sampling location to assign individual ancestry proportionally across multiple potential subpopulations. STRUCTURE uses a Bayesian framework and assumes Hardy-Weinberg and linkage equilibrium across populations. We used a burn-in of 50,000 iterations and 100,000 Markov chain Monte Carlo (MCMC) sampling iterations with 5 replicate runs. We averaged assignment probabilities, q, across these runs in CLUMPAK (Kopelman et al. 2015). To determine the largest substantiated number of clusters (subpopulations) in the dataset, we used the High Assignment Criterion (HAC), which supports the highest value of K at which at least 1 individual is assigned at high confidence ($q > 0.90$) to each cluster (Epps et al. 2018). We also compared the difference in the likelihoods across K (ΔK; Evanno et al. 2005).

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We mapped the average assignment probabilities for each sampled individual in our dataset at increasing values of K to evaluate alternative hypotheses that STRUCTURE assignment had spatial cohesion (i.e., formed mostly discrete groups). We defined spatially discrete coherent clusters as subpopulations based on visual inspection of assignment tests and geographic locations and then estimated genetic distance (F_{ST}) among subpopulations using the R package GENEPOP (Rousset 2008). We tested for deviations from Hardy-Weinberg equilibrium by population and locus to check for evidence of selection processes or further population structuring. To test for isolation by distance, we created minimum convex polygons to define subpopulation distributions. Each polygon contained all sampling locations associated with individuals assigned to each subpopulation. We measured the nearest-edge Euclidean distance and the nearest-edge river kilometer distance between each polygon and performed a Mantel test of F_{ST} against each distance measurement (Legendre and Fortin 2010). We identified migrants between spatially cohesive subpopulations as individuals for which our STRUCTURE analyses assigned an average $q > 0.80$ to a subpopulation other than the one in which it was spatially located.

Microsatellite markers (short, tandem DNA repeats) can provide valuable information about genetic diversity and relatedness and can be extracted from samples with degraded or limited DNA, including fecal pellets, but provide limited resolution regarding population structure and genome-wide diversity (Blouin 2003, Liu et al. 2005, Taylor 2015). Because genomic data composed of thousands to millions of single nucleotide polymorphisms (SNPs) can provide more power given enough individuals, we used genomic data from an earlier study to assess kinship between individuals and compared those patterns with the microsatellite-based analyses for consistency (Pool et al. 2010, Kopps et al. 2015, Flesch et al. 2018). Flesch et al. (2022) calculated kinship using 7,728 SNPs from the Illumina High Density (HD) Ovine array (San Diego, CA, USA) for blood samples from 19 of the animals captured in 2006 and a tissue sample from a natural mortality in 2008 (Kijas et al. 2009, 2014; Manichaikul et al. 2010; Flesch et al. 2022). These data also represented genetic characteristics of the population about 2 generations (~12 years) before the microsatellite dataset. We calculated average kinship within and between individuals captured in locations associated with subpopulations identified using microsatellite genotypes.

Environmental data

We developed a suite of environmental variables from terrain, hydrological, vegetation, land use, and infrastructure datasets to evaluate bighorn sheep habitat selection, distribution, and abundance (Table 2). Because model parameters across these analyses describe processes occurring at different spatial and ecological scales, we selected covariates for use in specific analyses based on their expected ecological relevance informed by previous studies. For the broader scale processes of range selection and density, we focused on landscape variables indexing habitat suitability, resource availability, and anthropogenic disturbance that we expected could structure distribution. We evaluated localized terrain and vegetation features in addition to potential barriers to movement in our fine-scale site and step selection models to evaluate influences on bighorn sheep movement decisions. For continuous variables, we tested multiple functional forms (linear, quadratic, and pseudo-threshold) to capture potential non-linear relationships and we selected linear forms when performance was similar to transformed versions for better interpretability. We created pseudo-threshold transformations by log-transforming variables and used them to model potential relationships such as distance to grazing allotments where animals may show little response to a variable until a critical value is reached, after which selection or avoidance may be pronounced (Tosa et al. 2023).

Habitat selection modeling

We used GPS-collar relocations to evaluate both home range selection and fine-scale habitat selection and movement. For both scales of selection, we fit separate models for summer (1 June–31 August) and winter (1

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TABLE 2 List of variables tested in range selection, integrated step selection (iSSA), and spatial-capture recapture (SCR) analyses hypothesized to influence habitat selection, movement, detection, and density of bighorn sheep in Dinosaur National Monument, Colorado and Utah, USA. All raster-sourced data variables and distance to vector features were analyzed at a 30-m resolution. NASA JPL = National Aeronautics and Space Administration Jet Propulsion Laboratory; USGS = United States Geological Survey; N/A indicates not tested in that model set.

Variable description	Habitat selection parameters tested	SCR parameters tested	Terms[a]	Data source	Evidence
Elevation	site selection	N/A	L	NASA JPL 30-m digital elevation model (NASA 2020)	Smith et al. (1991), DeCesare and Pletscher (2006), Lula et al. (2020)
Standard deviation of terrain curvature (terrain complexity)	site selection	detection, density	L, P, Q	NASA JPL 30-m digital elevation model	
Distance to escape terrain (slope ≥40 degrees)	site selection	detection, density	L, P, Q	NASA JPL 30-m digital elevation model	
Eastness: cosine transformation of aspect and northness: sine transformation of aspect	site selection	N/A	L	NASA JPL 30-m digital elevation model	Keating et al. 2007, Semenzanto et al. 2021, Lula et al. 2020, Zhou et al. 2022, Brushett et al. 2023
Elevation change (m)	step selection (movement)	N/A	L	NASA JPL 30-m digital elevation model	
Solar radiation (kWh/m^2)	site selection	N/A	L	NASA JPL 30-m digital elevation model	
Distance to permanent water (m)	site selection	density	L, P, Q	National Hydrography Dataset NHDPlus (USGS 2022)	Epps et al. 2006, Lowrey and Longshore 2017
Distance to intermittent water	site selection	density	L, P, Q	National Hydrography Dataset NHDPlus	
(m) Distance to Green or Yampa River (m)	site selection	density	L, P, Q	National Hydrography Dataset NHDPlus	
River reach (categorical, upper Green, lower Green, or Yampa)	N/A	density	L	National Hydrography Dataset NHDPlus	Epps et al. (2024)
Distance to recreational campsites (m)	summer site selection	density	L,P,Q	National Park Service (NPS): Points of Interest (NPS 2023a)	Keller and Bender (2007), Longshore et al. (2013), Werdel et al. (2023), Brushett et al. (2023)
Distance to paved and unpaved roads	summer site selection	density	L,P,Q	National Park Service: Public Roads (NPS 2023b)	

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TABLE 2 (Continued)

Variable description	Habitat selection parameters tested	SCR parameters tested	Terms[a]	Data source	Evidence
Distance to hiking trails (all unpaved, m)	summer site selection	density	L,P,Q	National Park Service: Public Trail Centerlines (NPS 2023c)	
Distance to domestic sheep grazing allotment edge and center (m)	N/A	density	L,P	Dinosaur National Monument	Singer et al. (2000c), Brown et al. (2010), Garrison et al. (2016)
Distance to nearest livestock grazing allotment (domestic sheep and cattle)	N/A	density	L, P	Dinosaur National Monument	
Grazing allotment presence-absence	site selection	density		Dinosaur National Monument	
Distance to stock water points inside allotments	site selection		L,P,Q	Dinosaur National Monument	
Burned since 1996 (burned or not burned)	Site selection	density		Monitoring Trends in Burn Severity (MTBS) Burned Areas Boundaries Dataset (MTBS 2017)	Greene et al. 2012, Proffitt et al. 2019
Categorical land cover 1) grassland 2) shrubland 3) woodland 4) non-vegetated	site selection	density		Geospatial data for the Vegetation Mapping Inventory Project of Dinosaur National Monument (NPS 2004)	DeCesare and Pletscher (2006), Lula et al. (2020), Lowrey et al. (2021), Werdel et al. (2023)
Percent canopy cover	step selection (movement)	detection, density	L,Q, P	LANDFIRE; Forest Canopy Cover (Soluk 2024)	
Green or Yampa River crossing	step selection (movement)	N/A	N/A	National Hydrography Dataset NHDPlus	Epps et al. (2018, 2024)
Relative probability of home range selection		detection, density	L	this study	

[a]Terms represent transformations of variables tested in models: linear (L), pseudo-threshold (P), and quadratic (Q).

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September–31 May) because we expected seasonal variation in space use based on previous studies that found Rocky Mountain bighorn sheep use higher elevation habitat in the summer driven by forage and water access but are more likely to use lower elevation areas during winter to avoid snow and regulate body temperature (DeCesare and Pletscher 2006, Lowrey et al. 2020). To evaluate seasonal home range selection, we applied a biased-random bridge model to estimate 95% utilization distributions for each collared individual to represent home ranges (Benhamou 2011). We modeled home range selection with a use-availability design, and for each collared animal, sampled the estimated seasonal home ranges with 1,000 used locations paired with 10,000 randomly sampled points across the Monument to define available locations (Johnson 1980, Johnson et al. 2006). We tested distance to escape terrain defined as slopes >40° as a covariate because bighorn sheep use locations in and near rugged terrain to escape predators (Smith et al. 1991, Singer et al. 2000b, DeCesare and Pletscher 2006, Lula et al. 2020), and northness calculated as the sine of the topographic aspect as an index of the thermal landscape because we hypothesized that bighorn sheep may select seasonal ranges to minimize thermal stress (Keating et al. 2007, Semenzanto et al. 2021, Zhou et al. 2022). We derived both variables from 30-m resolution digital elevation model (DEM) data (Table 2) and calculated them using the Spatial Analyst toolbox in ArcGIS Pro v3.4 (Esri 2024).

We extracted the hydrology network from the National Hydrography Dataset (NHDPlus High Resolution; USGS 2022) and calculated the Euclidean distance to the Green and Yampa rivers because we expected that access to permanent water would influence bighorn sheep range selection in the semi-arid study area (Lowrey and Longshore 2017). We evaluated vegetation influence on range selection by comparing use of grassland, shrubland, and woodland cover types to non-vegetated areas (reference category) using the categorical Dinosaur National Monument vegetation classification dataset (Table 2; NPS 2004). We also calculated continuous percent tree cover extracted from LANDFIRE data (Soluk 2024) to account for canopy density because previous research found that bighorn sheep select for short vegetation and avoid closed canopy habitat (Smith et al. 1991, DeCesare and Pletscher 2006; Table 2). We used burned area polygons from the Monitoring Trends in Burn Severity dataset (MTBS 2017) to evaluate the effect of recent fires on range selection because they select for open habitat for increased visibility (Mysterud and Østbye 1999, DeVoe et al. 2015; Table 2). Outside of breeding, bighorn sheep typically form sex-segregated herds, with males having larger home ranges and dispersing farther from natal herds than females (Festa-Bianchet 1991). Therefore, we tested for sex-specific range selection because females tend to prioritize predator avoidance during lambing, but males are likely to prioritize access to high-quality forage (Geist and Petocz 1977, Lowrey and Longshore 2017, Brushett et al. 2023).

We modeled fine-scale selection using integrated step selection analysis (iSSA; Avgar et al. 2016). The iSSA approach expands habitat selection functions that compare used locations to random, unused locations assumed to be available by including a movement model informed by the observed transitions (steps) between successive GPS relocations (Arthur et al. 1996, Avgar et al. 2016). This allows for simultaneous analysis of how environmental variables affect both habitat selection and movement and reduces bias in habitat selection coefficients because the effect of movement choices on site selection is modeled explicitly (Forester et al. 2009). We applied a matched case-control logistic regression to evaluate site selection and movement, matching each observed used location and observed step (3 successive relocations) with 10 randomly sampled available locations and steps sampled from the distribution of observations, resulting in an analysis of 477,620 data points (Fieberg et al. 2021).

We tested additional variables indexing local environmental conditions that we expected could influence site and step selection (Table 2). Because of the greater number of possible variable combinations to test in iSSA models, we organized variables into 4 categories representing key ecological processes informed by previous studies and employed a hierarchical model selection approach to reduce the total number of models (Hebblewhite and Merrill 2008). We considered distance to escape terrain as described above, canopy cover, and terrain complexity as variables indexing security from predators (Table 2; Smith et al. 1991, DeCesare and Pletscher 2006, Lula et al. 2020). We calculated the standard deviation in total terrain curvature in a 300-m^2 window of each data point using focal statistics in ArcGIS to index terrain complexity (Ironside et al. 2017). We calculated the minimum distance to intermittent and permanent water from each location as described above and also extracted vegetation cover type as indices of resource availability using

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the data sources described above. To test for the influence of thermal stress on bighorn sheep movement decisions, we evaluated elevation because temperatures can differ by several degrees from the canyon rim to the canyon floor, included northness and eastness as described for range selection models, and calculated winter and then summer solar radiation at each data point from a DEM using the Area Solar Radiation tool in ArcGIS Pro, which incorporates latitude, time, elevation, slope, and aspect to model direct and diffuse radiation (Table 2). To evaluate the potential influence of anthropogenic disturbance, we calculated Euclidean distance to roads, recreational campsites, and hiking trails for the summer model only because recreational use during winter is limited. We used the minimum distance to campsites on both the Yampa and Green rivers from 1 June–15 July and then used the minimum distance to only camps located on the Green River between 16 July and 31 August because the Yampa River is often not floatable because of low late summer flows, whereas the Green River is controlled via an upstream dam and maintains flows and campers well into September (USGS 2025; E. Spencer, personal observation).

Finally, we used livestock grazing allotment vector layers provided by Monument resource managers to create a binary livestock allotment presence-absence variable and a distance to stock water variable using point water sources within active grazing allotments, where we hypothesized livestock to congregate. To evaluate potential barriers to movement, we evaluated maximum percent tree canopy cover along the step, elevation gain between the start and end of the step, and whether the step included a river crossing (Table 2). We did not evaluate sex-based differences in fine-scale selection analyses. We also identified potential movements across rivers and between putative subpopulations directly. To address location uncertainty in the canyon environment, we considered only multiple consecutive locations with at least one location on each side having low dilution of precision in these direct assessments.

For range selection models, we used an all-combinations approach to fit candidate models from all combinations of covariates described above and ranked competing models using Akaike's Information Criterion (AIC) to identify the most supported fixed-effect range selection models for summer and winter (Hebblewhite and Merrill 2008; Appendix C, Tables C2–C3). We evaluated model performance of range selection models by calculating the area under receiver operating characteristic curve (AUC) for all data as a measure of model fit and the AUC for each animal using a leave-one-out cross-validation strategy as a measure of predictive performance (Roberts et al. 2017). For site selection models, we first tested variables within each of the above categories (security, resources, thermoregulation, and disturbance) in univariate models and ranked competing models using AIC. We used the best-ranked model for each category to develop a global model and tested all possible combinations of supported variables to identify the best supported habitat selection model structure. We added movement parameters to the best supported habitat selection model to evaluate support for the movement-integrated model versus the habitat-only selection model. For all regressions, we omitted the weaker variable if any 2 supported variables showed significant collinearity ($|r| > 0.7$; Dormann et al. 2013), and the final models included a random intercept for each individual to account for individual heterogeneity. We implemented analyses in the R programming environment (v.4.3.0; R Core Team 2023) and fit regressions using the packages lme4 and mclogit (Elff 2022).

Because the extreme terrain in the Monument influenced GPS data collection, we modeled the spatial probability of a successful GPS fix (acquisition probability) as a function of vegetation cover, aspect, and terrain openness and ruggedness following the approach developed in Ironside et al. (2017; Appendix C, Figure C3). We then extracted predicted acquisition probabilities for each GPS location and used these values to weight GPS locations in all selection models (Ironside et al. 2017). Weighting GPS locations by the inverse of their predicted acquisition probability reduces bias in coefficient estimates due to missed fixes in habitats with poor satellite visibility such as deep canyons (Ironside et al. 2017).

Abundance and density modeling

To estimate bighorn sheep abundance and density, we used individual encounter histories from genotyped fecal pellets to fit spatially explicit, hierarchical capture-recapture models (Royle and Dorazio 2008, Royle and

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Young 2008). Spatial capture-recapture (SCR) models estimate the observation process separately from the ecological processes (density, abundance) by conditioning a model for individual encounter data on a spatially explicit point process of individual activity centers (s_i) distributed across a discrete space (state space,) that contains all capturable individuals in the target population (Royle and Young 2008, Efford et al. 2009, Royle et al. 2013b). The activity centers of every individual in the target population are latent variables estimated by the model and represent the center of an individual animal's home range during the study period. Population density is calculated by dividing the number of estimated individual activity centers by the area of the state space and can be modeled as either a homogeneous point process or as an inhomogeneous point process as a function of spatial covariates measured at the resolution of the state space. We modeled detection (and non-detection) of i individuals at j = 269 pellet search sites with coordinates x_j across k = 3 years as Bernoulli random variables with site-specific detection probabilities such that y_{ijk}~ Bernoulli (p_{ijk}). We modeled encounter probability using a half-normal function in which the probability of detecting an individual at a particular detector (p_{ij})varies as a function of distance from that individual's activity center, s_i, to the detector location, x_j, such that

$$p_{ij} = p_0 \times \exp[\text{dist}_{euc}(x_j, s_i)^2/2\sigma^2],$$

where p_0 is the baseline encounter probability and σ is the spatial scale parameter that determines the rate of decline in detection probability as the Euclidean distance between activity center and detector increases. We defined the state space as the area encompassing all pellet search locations buffered by 4 km to ensure inclusion of animals near the edge of the study area, and we set the resolution of the state space at 500 m^2 following the recommendation that the resolution should be smaller than the estimated spatial scale parameter (σ; Royle et al. 2013b).

Analogous to habitat selection analyses, we developed variables indexing escape terrain and terrain complexity, water availability, vegetation cover and structure, anthropogenic disturbance, cattle grazing, and domestic sheep grazing that we expected could influence either the detection of pellets, variation in density, or both (Table 2). We tested many of the same variables considered in home range selection analyses (Table 2), but in the SCR framework, we evaluated these variables for their potential to explain spatial heterogeneity in density and pellet detection. Additionally, we tested the predicted relative probability of home range selection as an integrated indicator of habitat quality that we expected could influence density. Because SCR models explicitly relate variation in model parameters to spatial covariates, we evaluated these covariates at multiple spatial scales to avoid arbitrary selection of a single scale, consistent with recommendations that spatial scale optimization can improve inference and prediction (Ash et al. 2021; Appendix D). We used a multi-stage model selection approach to build ecologically relevant candidate models to evaluate mechanisms leading to variation in density and detection model parameters and used AIC to rank competing models (Appendix D, Tables D2–D4). Because sampling effort was highly variable across years, our reference detection model used a year-specific term that assumes independence in baseline detection probability ($p0$) across years. Because males typically range over larger areas, we included a sex-specific effect on σ, the spatial scaling parameter, in our reference model for detection, estimating sex-specific density (Edelhoff et al. 2023). We tested all other covariates that we expected could influence detection as univariate additions to the reference model and eliminated uninformative spatial covariates with similar log-likelihood values and equal or lesser AIC weights than that of the reference model. We followed the same procedure to test variation in density, adding spatial covariates on density as univariate additions to the reference detection model and then selecting the most supported variables based on AIC for final candidate models (Appendix D, Tables D2–D4).

For candidate model selection, we fit SCR models using maximum likelihood estimation in the package oSCR v.0.42.0 (Sutherland et al. 2019). After identifying the most supported model structures based on AIC, we fit the final SCR models used for inference in a Bayesian modeling framework in NIMBLE v.1.0.1 (De Valpine et al. 2017).

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We opted for Bayesian inference for our final abundance and density estimates to 1) have full flexibility to account for sampling variation across years, river reaches, and sex, and 2) directly quantify the uncertainty of our estimates for specific subpopulations in a probabilistic framework. We implemented all covariate creation and statistical analyses in the R programming environment (v.4.3.0; R Core Team 2023). To fit the Bayesian model in NIMBLE, we ran 3 independent MCMC chains for 30,000 iterations and discarded the first 6,000 samples resulting in 72,000 total posterior samples for each parameter used for inference. We examined trace plots of MCMC chains to ensure mixing and assessed convergence by calculating the Gelman-Rubin statistic for each model parameter (Hobbs and Hooten 2015). We conducted posterior predictive checks and evaluated the fit of our final models by simulating new observations from the likelihood and conducting discrepancy goodness-of-fit tests between observed and simulated data (Hobbs and Hooten 2015; Appendix D4). We conducted processing and visualization of spatial data using ArcGIS Pro (v3.4; Esri 2024).

We estimated subpopulation abundances as derived quantities from the SCR model (Hobbs and Hooten 2015). We partitioned the state space comprised of 500 x 500-m pixels into 4 discrete polygons defined by the K = 4 genetic subpopulation structure results. In the SCR model, we modeled the activity center of each individual as a discrete location assigned to a specific pixel using a categorical distribution sampled from the full set of available pixels in the state space. After model fitting, we summed the predicted activity centers within each polygon at each MCMC iteration to obtain posterior distributions of abundance for each subpopulation.

RESULTS

Pathogen exposure and evidence of disease presence

Thirteen of 14 testable serum samples submitted for antibody testing for *M. ovipneumoniae* had high levels of antibodies; thus, we considered this as evidence of exposure across the metapopulation in 2006 (Figure 2). Serum sample testing of 19 samples revealed exposure to 8 of the 18 other pathogens, with estimated prevalence ranging from 5.3–100% (Appendix A, Table A1). The upper bound of 95% confidence intervals for estimated prevalence of the 10 pathogens with no antibody detections ranged up to 15.3%, indicating that sample sizes were too small to conclude that these pathogens were absent from the metapopulation. Four of the other pathogens of interest were detected in >1 serum sample (n = 19), including parainfluenza 3 (prevalence = 100%), bovine respiratory syncytial virus (prevalence = 47.4%), *Leptospira autumnalis* (prevalence = 42.1%), and epizootic hemorrhagic disease (prevalence = 21.1%). We did not find support for age, sex, or spatial variation in pathogen exposure (Appendix A, Table A1).

Cultures of oropharyngeal swabs detected 9 microbial species of interest with prevalences of 5.3–78.9%, and multiple strains of Pasteurellaceae, Staphylococcus, and Streptococcus (Appendix A, Table A2). Upper 95% confidence intervals of 26% prevalence do not allow us to infer absence from the population for *Moraxella* sp. Two pathogens sometimes associated with respiratory disease had moderate prevalence across all strains: *Mannheimia haemolytica* (prevalence = 36.8%, spread evenly across all strains detected) and *Bibersteinia trehalosi* (prevalence = 78.9%, strain with highest prevalence = 42.1% for 4^{CDS} non-hemolytic). Prevalence increased with host age for *M. haemolytica* all strains (odds ratio = 2.2), *M. haemolytica* type U $^{\alpha BD}$ β-hemolytic (odds ratio = 3.5), and *Neisseria* sp. (odds ratio = 3.5), but we did not detect variation by age or sex otherwise. We detected *Pasteurella multocida b* only in the 2 animals in the Split Mountain area, in the southwest corner of the Monument. In contrast, *Trueperella pyogenes was* detected in 9 of 15 animals tested along the Green River, but none of the 4 animals from the Yampa River. We detected no other spatial patterns in pathogens cultured from oropharyngeal samples.

We detected lungworm larvae (*Protostrongylus* spp.) in all 18 fecal samples (average = 73.7 ± 11.5 [SE] larvae per gram [lpg]; range = 15–176). We detected levels exceeding 100 lpg in 3 individuals (17%) and no spatial pattern was obvious. Loads increased weakly with age, although no lambs or yearlings were sampled (linear regression $r^2 = 0.20$, $P = 0.07$, $\beta_0 = 13.7$, $\beta_1 = 11.1$; Appendix A, Table A3).

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In 2005, a full-curl male was observed coughing, grew thinner, and eventually died. In 2007, biologists found one male that died 6 months post-capture and multiple dead lambs during collar retrieval without signs of predation, poaching, or falls, leading to disease as the suspected cause of death (Appendix C, Figure C1). Additionally, biologists received periodic reports of animals with clinical signs of pneumonia (e.g., coughing) in Jones Hole. During pellet sampling, researchers observed weak-acting animals 3 times near Split Mountain in 2019, and a clinical lamb (coughing, emaciated, and smaller than its peers) sampled at this location presented with severe pneumonia and a lung swab tested positive by PCR for *M. ovipneumoniae*. We documented one collared male from 2006 on the domestic sheep allotment while domestic sheep were present. A ranch southwest of the Monument reported 15 domestic Suffolk sheep-bighorn hybrid lambs with photos dated 2000, shortly after the 1997 translocations along the Yampa River.

GPS telemetry, habitat selection, and movement

Three of 20 collars could not be retrieved, and 3 collared bighorn sheep died before collar release, though the collar of one individual (06-19) collected approximately 6 months of relocation data, resulting in 15 animals (8 females, 7 males) with sufficient data for analysis of GPS locations. The topography of the Monument reduced GPS fix success such that locations deep in canyons were often preceded or followed by missed fixes, resulting in fix success ranging from 71.3–87.7% and 60,351 locations.

Home range selection

The best supported range selection models indicated that bighorn sheep home range selection was similar across seasons, showing positive selection for areas nearer to rivers and escape terrain, and with low canopy cover in both summer and winter (Figure 3; Appendix C, Tables C2–C3). Additionally, they showed consistent positive selection for shrubland and woodland cover over non-vegetated areas. We found evidence of minor differences in the slope-aspect of home ranges between males and females, where females selected for more northerly slopes in both seasons, whereas males selected for southerly slopes in winter but without clear preference during the summer (Figure 3; Appendix C, Tables C2–C3). Model validation indicated strong predictive capabilities of the best models, with an overall AUC of 0.91 for the summer model and 0.92 for the winter model (Appendix C, Table C4). Leave-one-out validation showed an AUC range of 0.84–0.95 for individuals when the summer model was trained on all other animals, and 0.86–0.96 for the winter model. We used the regression coefficients to predict the relative probability of range selection across the study area using the means of male and female selection probabilities during the summer (Figure 3; winter map not visually distinct from summer map). The predicted selection map shows the highest probabilities in and along river corridors and canyons.

Fine-scale habitat selection (site and movement)

The best supported fine-scale habitat selection models for both summer and winter indicated strong positive selection for locations near escape terrain, that had burned in the previous decade, with moderate variation in local terrain complexity, and with lower solar radiation (Figure 4). In the winter, bighorn sheep were more likely to select locations near permanent water (major rivers) and farther from intermittent water. Variables indexing thermoregulation were supported and differed by season; in the winter, they were more likely to use south-facing slopes that get more sun but selected more westerly and northerly slopes in the summer and were overall

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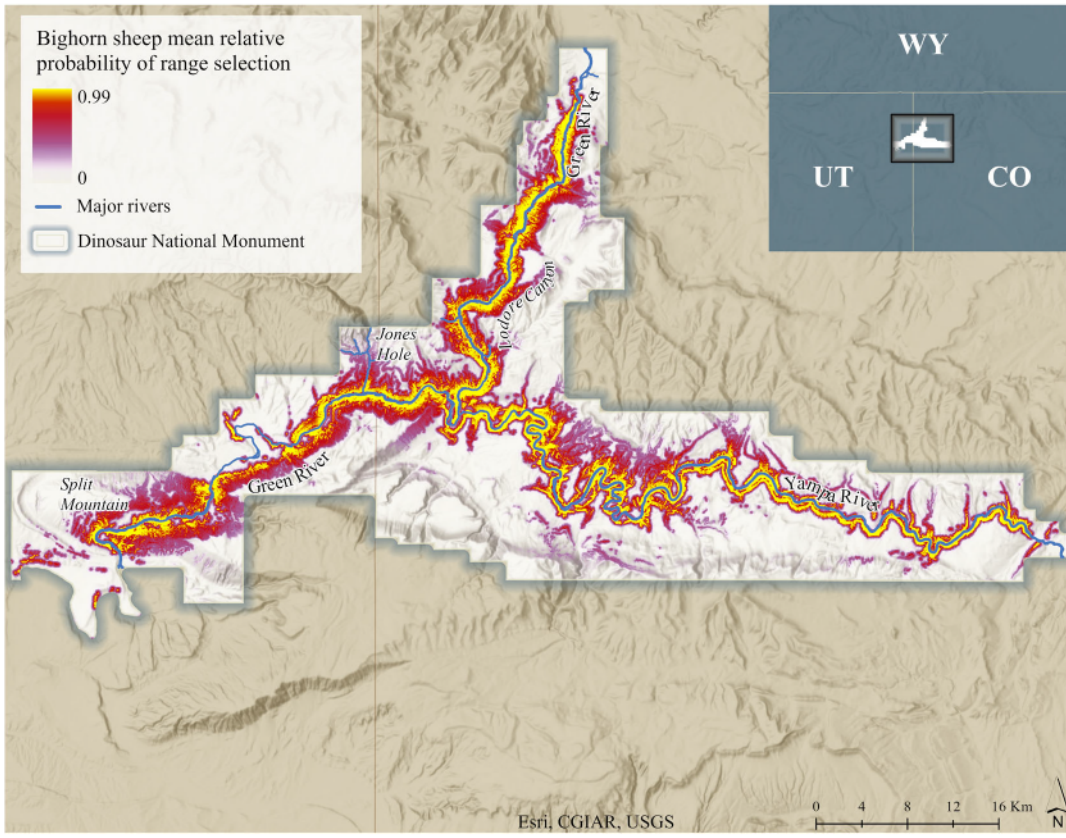


FIGURE 3 Mean relative probability of male and female range selection by bighorn sheep in Dinosaur National Monument in Colorado and Utah, USA, estimated from global positioning system (GPS) tracking data collected during summer (1 June–31 August) from 2006–2008. Background layer credits: Environmental Systems Research Institute (Esri 2024), Consultative Group on International Agricultural Research (CGIAR; Jarvis et al. 2008), and United States Geological Survey (USGS 2021).

more likely to select sites deep in river canyons that likely have lower solar radiation in both seasons (Figure 4; Appendix C, Tables C5–C6).

Model selection indicated strong support for the iSSA models that include movement parameters (step length and turning angle) for both seasons (iSSA model weight = 1.0, habitat site selection only model weight = 0.0; winter model ΔAIC = 775.47, summer ΔAIC = 58.61; Appendix C, Tables C7–C8). In both seasons, individuals generally avoided river crossings when moving and were more likely to move through areas with lower canopy cover. Bighorn sheep were 3.70 times more likely to stay on the same side of a river than cross in the winter, and 2.13 times more likely to stay on the same river side than cross in the summer. Additionally, the winter model indicated slight avoidance of elevation gain during movement and across seasons; animals were more likely to travel through locations farther from escape terrain, indicating the opposite response observed for site selection (Figure 4).

Genetic structure and diversity

We successfully genotyped 590 bighorn sheep pellet samples collected from 2018-2020 with 9-locus genotypes and identified 152 individuals. After extending genotypes for 120 individuals to 16 loci, we excluded 1 individual

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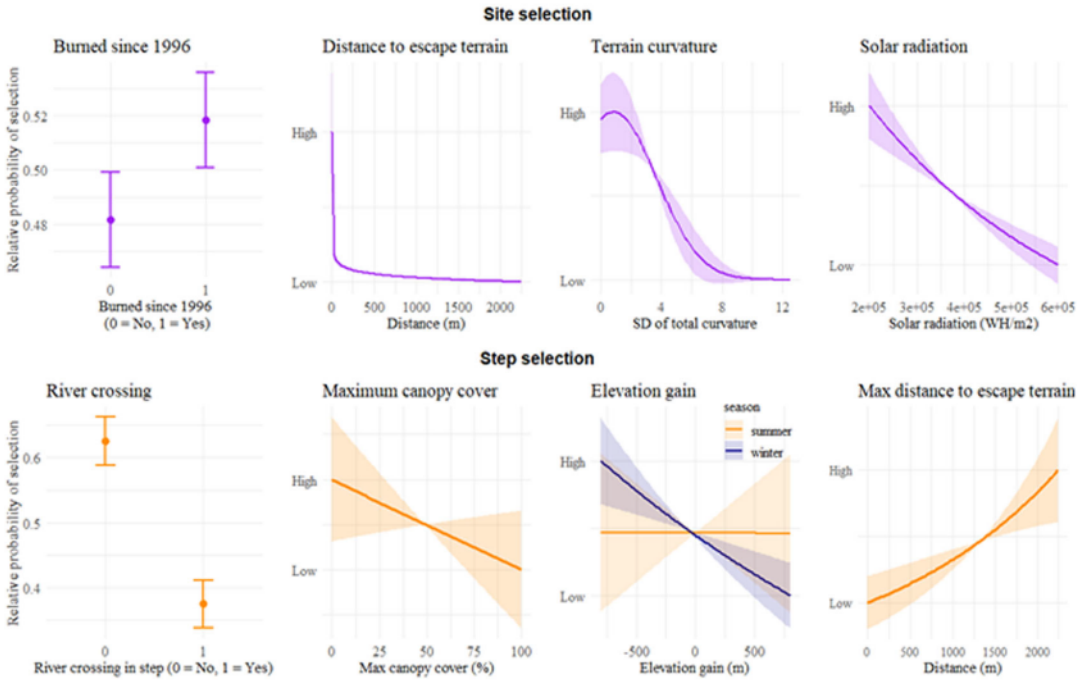


FIGURE 4 Predicted summer site (top row) and step (bottom row) relative selection probabilities associated with a subset of environmental variables that most influenced summer habitat selection by bighorn in Dinosaur National Monument in Colorado and Utah, USA, from 2006–2008, ordered by relative effect size from left to right. Winter predictions are included only when substantially different from summer (bottom panel, navy prediction).

because of an inconsistent genotype and reclassified 2 individuals into 1 based on the information from the added loci, yielding 118 individuals with extended genotypes. We found support for both K = 4 (by ΔK criterion) and K = 5 (by HAC) subpopulations using STRUCTURE. Defining genetic clusters into spatially cohesive subpopulations at K = 4 and K = 5 showed identical groupings for 3 of the subpopulations (Lower Green, Upper Green, and Yampa; Figure 5). The fourth subpopulation in K = 4, situated in the center of the Monument around the confluence of the Green and Yampa rivers, was split along the Green River in the K = 5 results, with 1 subpopulation containing the individuals on the eastern side, or river left, and a separate subpopulation farther north on river right of the Green River that extended up Jones Hole Creek. The Upper Green and Yampa subpopulations extended across the rivers for both K = 4 and K = 5. Individuals within the Lower Green subpopulation for both K = 4 and K = 5 only had detections on river left. Tests for deviation from Hardy-Weinberg equilibrium of spatially defined subpopulations at K = 5, after Bonferroni correction for 16 tests, showed no loci with consistent global violations. No subpopulations had significant departures from Hardy-Weinberg equilibrium. At K = 4 only the Confluence subpopulation showed a single locus (MAF209) out of Hardy-Weinberg proportions.

For K = 4 subpopulations, genetic diversity metrics were slightly higher for the centrally located Confluence subpopulation (observed heterozygosity [H_{obs}] = 0.65, expected heterozygosity [H_{exp}] = 0.61, allelic richness [Ar] = 3.92) and the Yampa (H_{obs} = 0.61, H_{exp} = 0.58, Ar = 3.67), than the Lower and Upper Green subpopulations (both H_{obs} = 0.55, H_{exp} = 0.53, Ar = 3.5; Appendix B, Table B4). After assigning the 20 individuals for which we had high density ovine array genotypes from 2006–2008 to the area for the putative subpopulation identified in the microsatellite-based K = 4 analysis, we found higher average pairwise kinship within ($\overline{x}$ = 0.028–0.081, *n* pairwise individuals = 3–21 individuals) than between putative subpopulations ($\overline{x}$ = −0.001 to 0.020, *n* pairwise individuals = 15–35 individuals) aside from the Confluence to Lower Green pair ($\overline{x}$ = 0.059; Flesch et al. 2022;

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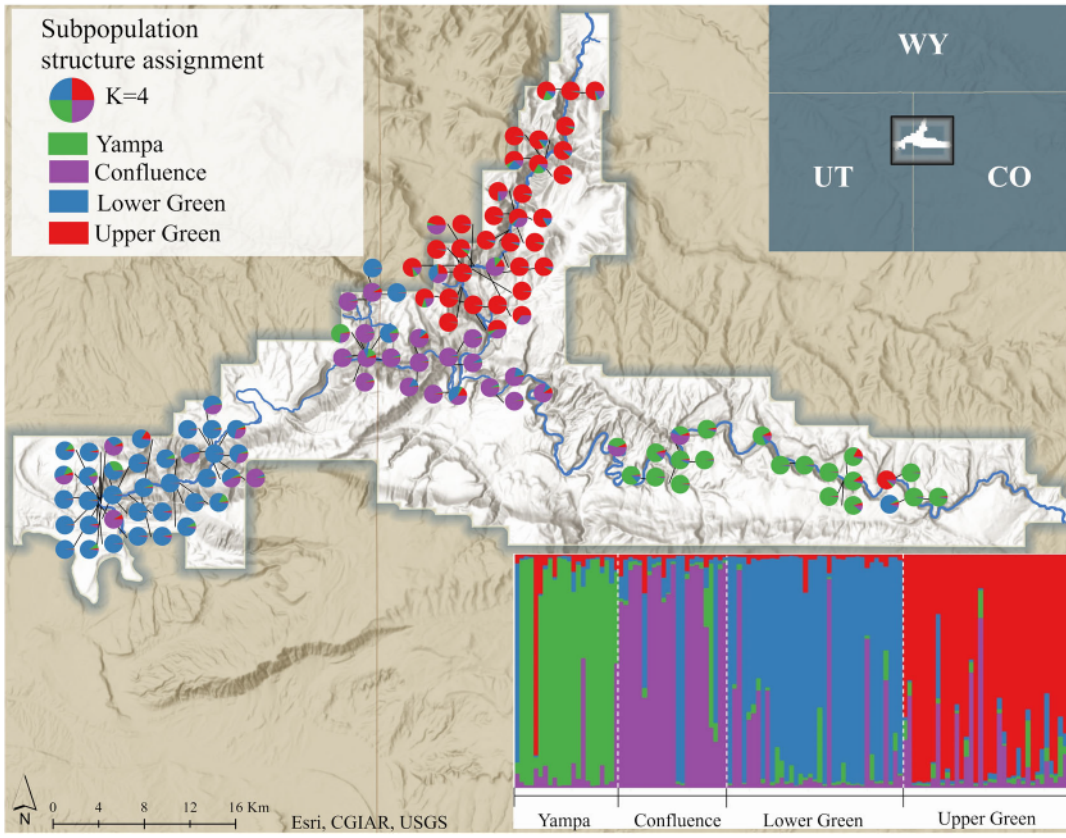


FIGURE 5 Assignments to 4 genetic clusters for Rocky Mountain bighorn in Dinosaur National Monument in Colorado and Utah, USA from fecal pellets collected 2018-2020. Each pie chart and each bar illustrates ancestry for an individual bighorn (n = 118) with 16 locus microsatellite genotypes. Pie charts are offset from the sample location for visibility; therefore, the distances between samples from different subpopulations are larger than they appear here. All Lower Green samples were collected south of the Green River. Background layer credits: Environmental Systems Research Institute (Esri 2024), Consultative Group on International Agricultural Research (CGIAR; Jarvis et al. 2008), and United States Geological Survey (USGS 2021).

Appendix B, Table B4). The Yampa and Confluence subpopulations had average pairwise kinship <0.044, a threshold for considering individuals unrelated on average (Manichaikul et al. 2010).

Abundance and density

The 590 successfully genotyped samples collapsed into 390 spatially distinct detections of 152 individual bighorn sheep (91 females, 56 males, and 6 unsexed individuals) from 2018–2020 (Table 3). Of the 152 individuals detected, 93 were spatially recaptured (61%). We report the ratio of individuals with simple (i.e., same site) recaptures to spatial (i.e., >1 site) recaptures, the number of unique individuals with spatial recaptures, and the average distance moved between spatial recaptures because these data characteristics and sample sizes of each have the potential to affect the accuracy and precision of SCR parameter estimates (Table 3; Schmidt et al. 2022).

The best-supported model structure for detection probability in SCR models included separate intercepts for the combination of the search effort for the site (site searched or not) and the river reach where the site was

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TABLE 3 Cumulative summary of spatial-capture recapture (SCR) data for bighorn sheep in Dinosaur National Monument in Colorado and Utah, USA, from 2018–2020, used to estimate abundance and density.

	Total detections	Total recaptures	Individuals detected	Individuals with spatial recaptures	All recaptures: spatial recaptures	Max distance moved (km)	Mean of max distance moved (km)
All	390	238	152[a]	93	0.61	14.63	4.60
Females	254	163	91	62	0.68	8.23	3.83
Males	128	78	56	30	0.44	14.63	6.20

[a]6 bighorn were not assigned a sex, so females + males does not sum to the reported total.

located across years, in addition to the standard deviation of terrain curvature averaged in a 900-m radius around the search site and a sex-specific effect (Appendix D, Table D5). Across years and river reaches, mean detection probabilities ranged from 0.27 (95% CrI = 0.19–0.37) on the Lower Green River in 2018 to 0.07 (95% CrI = 0.05–0.11) on the upper Green River in 2019. Some detection estimates, particularly for areas sampled in 2018, had low precision indicating high spatial variation in detection rates. Terrain complexity had a small positive effect indicating a marginal increase in detection probability at search sites surrounded by more complex terrain ($\beta_{trap\ curvature\ ewes}$ = 0.21 [95% CrI = 0.09–0.32]). The posterior mean difference in detection probability between females and males suggested lower detection rates for males overall, but low precision for the coefficient suggests limited evidence for this difference ($\beta_{trap\ rams}$ = −0.18 [95% CrI = −0.59 to 0.20]). Posterior mean σ estimates (spatial scaling parameters) were similar for females (σ_{ewes}= 3.56 km [95% CrI = 3.15–4.03 km]) and males (σ_{rams}= 3.16 km [95% CrI = 2.67–3.77 km]).

The 2 best-supported models included a single covariate on density indicating an increase in density with greater distance from recreational campsites (model weight = 0.50) followed by a model including only distance to grazing allotments predicting increasing density with greater distance from allotments (ΔAIC = 1.56, weight = 0.23; Appendix D, Table D4). These indices of anthropogenic activity were the only supported covariates; the next best-ranked model was the homogeneous density model (no spatial covariates; ΔAIC = 6.12). We thus advanced 1) a heterogeneous density model including effects of both campsites and grazing allotments, and 2) a homogeneous model without density covariates for evaluation as final models with Bayesian inference.

The heterogeneous model indicated a posterior mean density of 0.57 (95% CrI = 0.46–0.70) bighorn sheep/km^2, with density increasing with distance from recreational campsites ($\beta_{dist\ to\ camps}$ = 0.36 [95% CrI = 0.02 – 0.69]) and with distance from livestock grazing allotments ($\beta_{dist\ to\ allotments}$ = 0.30 [95% CrI = −0.04 to 0.57]). The 95% credible interval for the effect of grazing allotments included zero, though the 90% credible interval did not ([90% CrI = 0.05 – 0.55]; Appendix D, Figure D1). For the homogeneous model, posterior mean density was 0.56 (95% CrI = 0.45–0.66) animals/km^2; thus, mean density was not substantially different between models. However, because no campgrounds are outside the Monument, the heterogeneous model exhibited edge effects, predicting unrealistically higher densities in locations without bighorn sheep at the boundary as the distance from campsites increased. Resulting point estimates of abundance were sensitive to the assigned boundary of the state space. Given that sensitivity, we focus on interpretation of abundance and density estimates from the homogeneous model (Figure 6; Table 4).

Predicted density ranged from a low of 0.16 to a high of 1.54 bighorn sheep/km^2 in 2019 and was spatially structured with hotspots of higher density (Figure 6). Predicted density maps were similar for all years indicating limited annual variation in density during the study period (Appendix D, Figure D2). Annual posterior mean abundance estimates ($\hat{N}$) from 2018–2020 ranged from 105 (95% CrI = 84–130) to 117 (95% CrI = 94–142; Table 4). Because the most robust sampling occurred in 2019, we consider the point estimate from 2019 indicating $\hat{N}$ = 109 (95% CrI = 87–133) animals

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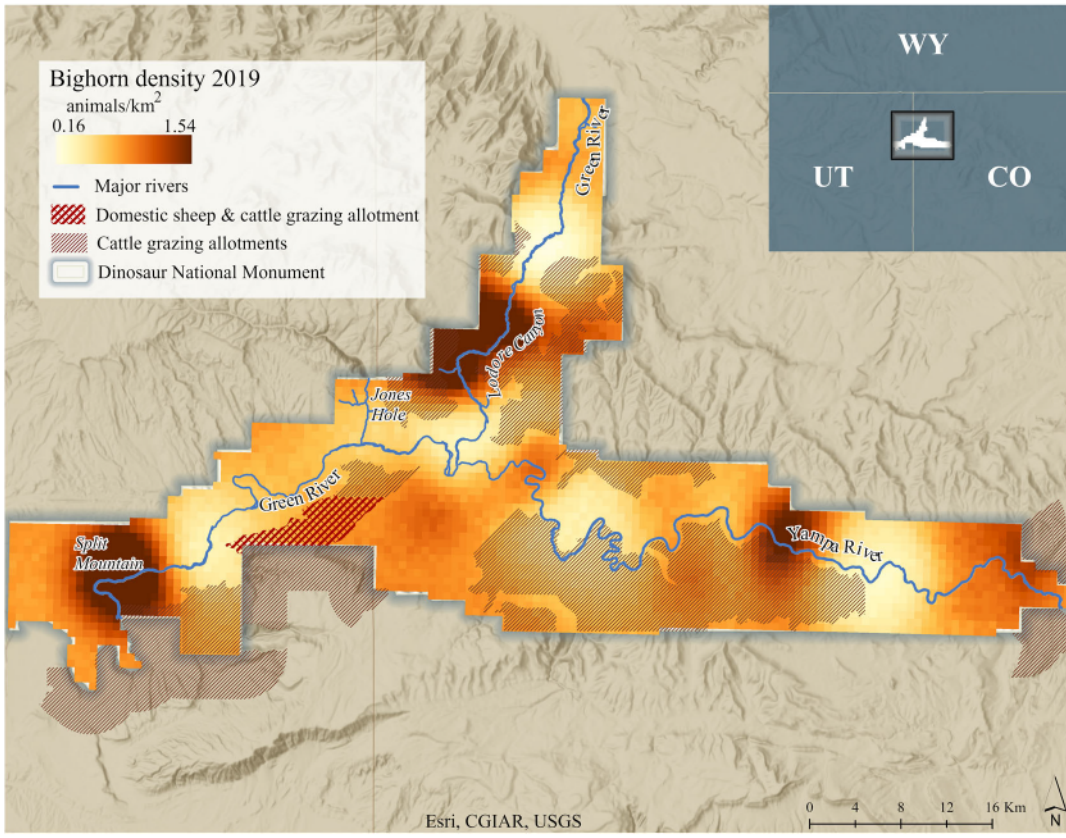


FIGURE 6 Posterior mean bighorn density (bighorn/km^2) for 2019 in Dinosaur National Monument in Colorado and Utah, USA, estimated from a Bayesian sex-specific spatial capture recapture model with no density covariates. Background layer credits: Environmental Systems Research Institute (Esri 2024), Consultative Group on International Agricultural Research (CGIAR; Jarvis et al. 2008), and United States Geological Survey (USGS 2021).

(48 males and 61 females; Table 4) as the best estimate of summer abundance in Dinosaur National Monument. We calculated subpopulation-specific abundances as derived parameters for the genetically differentiated subpopulations identified in the structure analyses. Across years, point estimates of mean abundance were highest from the Yampa River subpopulation ($\hat{N}_{\text{Yampa},2019} = 37$ [95% CrI = 26–50]), though significant overlap of credible intervals suggests a similar size herd at the Confluence subpopulation where the Yampa River joins the Green River ($\hat{N}_{\text{Confluence},2019} = 28$ [95% CrI = 19–39]). Our analysis indicated that the Upper Green River and Lower Green River subpopulations likely are slightly smaller, with estimates for 2019 having means of 21 and 23 animals, respectively (Table 4).

Connectivity

We assessed demographic connectivity with observed movements in the GPS telemetry and pellet data and assessed genetic connectivity with the calculated genetic distances (F_{ST}) among subpopulations. The GPS data showed one male collared in the Lower Green subpopulation crossed the Green River, spending 2 days on river right in the Jones Hole subpopulation in early November. Another male collared in Jones Hole crossed the Green River repeatedly, spending the rut and winter on the west side of the Green River and the remainder of the collar-life on the east side of the river. We recorded multiple crossings of the Yampa River for each of the 3 females collared in the eastern third of the Monument, with GPS locations recorded on both the north and south banks. In the pellet data, we detected 19

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TABLE 4 Annual bighorn sheep posterior mean abundance ($\hat{N}$) estimates and 95% credible intervals (in parentheses) for Dinosaur National Monument for each year from 2018 to 2020 in Colorado and Utah, USA, and genetic subpopulations identified in the K = 4 cluster analysis.

Year	Males	Females	Total $\hat{N}$	Sex ratio (Proportion male)	Genetic subpopulation			
					Lower green $\hat{N}$	Confluence $\hat{N}$	Upper green $\hat{N}$	Yampa $\hat{N}$
2018	50 (33–71)	67 (51–85)	117 (94–142)	0.432 (0.327–0.539)	27 (19–36)	32 (22–43)	19 (11–27)	39 (27–51)
2019	48 (32–68)	61 (46–78)	109 (87–133)	0.435 (0.330–0.542)	23 (16–31)	28 (19–39)	21 (14–28)	37 (26–50)
2020	50 (35–70)	55 (40–72)	105 (84–130)	0.463 (0.355–0.571)	24 (14–34)	30 (20–40)	18 (10–27)	34 (20–40)

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animals on both sides of the Yampa River across sampling years from 2018–2020, but no individuals on both sides of the Green River. Genetic distances (F_{ST}) among K = 4 subpopulations ranged from as high as 0.16 between the Upper Green and Lower Green subpopulations to 0.06 between the Lower Green and Confluence subpopulations. For K = 5, the lowest F_{ST} value was 0.08 between the Jones Hole subpopulation on the western side of the Green River and both the Confluence and the Lower Green subpopulations. We identified migrants in all subpopulations for K = 4 and in all but the Confluence subpopulation for K = 5 (here constrained to the eastern side of the Green River; Appendix B, Table B6). Although both Euclidian distance and river-kilometer distance had positive correlations with population pairwise F_{ST}, Mantel tests were not statistically significant for either K = 4 or K = 5 (Mantel r range = 0.51–0.64, P-value range = 0.12–0.21), likely due to low power from only 4–5 subpopulations (Appendix B, Table B4). Both datasets suggest differences in permeability of the Yampa and Green rivers, but detection of migrants in most subpopulations indicated that even the Green River presents only a partial barrier.

DISCUSSION

We provide the first scientific evaluation of the reintroduced bighorn sheep population in the Monument since the last release of translocated animals in 2000, over 2 decades prior. Multiple lines of evidence indicate that the population is spatially structured into at least 4 genetically distinct subpopulations with relatively high genetic diversity. Estimated subpopulation sizes ranged from 18–39 individuals (95% CrIs from 11–50). These small abundances suggest each subpopulation may be vulnerable to genetic drift and extirpation. Three of 4 subpopulation centers generally align with the locations of original translocation release sites despite home range selection models indicating continuous suitable habitat. This suggests lasting effects of initial translocations on population distribution. Evidence from step selection and density analyses indicate that movements among subpopulations are limited by seasonal and semi-permeable barriers including rivers and human disturbance. We also found evidence of widespread exposure to pathogens known to cause respiratory disease in 2006 and active infections in 2019, yet our 2018–2020 annual abundance estimates were similar across years and do not indicate large declines during this period. Collectively, our results suggest that translocation history, habitat structure, partial connectivity, and disease interact to influence population size and genetic structure and diversity in the Monument. The apparent recent stability of the population despite small subpopulation sizes, pathogen exposure, and limited connectivity suggests that persistence may depend on partial connectivity sufficient to prevent genetic isolation but limited enough to reduce synchronous, Monument-wide disease outbreaks. Overall, our work demonstrates both the insights gained and challenges encountered when integrating multiple analytical approaches to better understand metapopulation processes and their implications for conservation and management of reintroduced populations.

Metapopulation metrics

Population distribution and structure

In contrast to our hypothesis that bighorn sheep would be continously distributed based on earlier reports (Barmore 1962, George et al. 2009), density and genetic structure analyses indicated high-density clusters reflecting subpopulations in a metapopulation. The clusters align with subpopulations from genetic analyses referred to as the Upper Green, Confluence, Lower Green, and Yampa. Bighorn sheep often form metapopulations, but the spatial scale of structuring varies. In alpine and desert-island environments, large distances (e.g., >100 km) occur between distinct genetic subpopulations (Singer et al. 2000a, Epps et al. 2018, Love Stowell et al. 2020, Dekelaita et al. 2023). However, spatial structuring at finer scales has been reported in other riverine systems. In Hells Canyon, distinct subpopulations occur at geographic distances of 15–60 km along the Snake River (Cassirer and Sinclair 2007, Cassirer and Besser 2025). Similarly, in the Grand Canyon metapopulation, adjacent subpopulations separated by 40–150 km showed genetic

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differentiation (Epps et al. 2024). Along with our findings of structure at distances of 27–55 km in the Monument, this suggests riverine systems may promote fine-scale structure, perhaps via the concentration of water, forage, and escape terrain near rivers, semi-permeable river barriers, and site fidelity— as evidenced by the alignment of subpopulation centers with original translocation release sites. The Green and Yampa rivers presented weak barriers to gene flow. Therefore, rivers themselves are not likely to be the sole driver of spatial structure in this population. Small subpopulation sizes could themselves maintain genetic structure through increased genetic drift (Hedrick 2014).

Anthropogenic activities may also influence population structure and distribution in the Monument. Our results suggest moderate evidence of a negative relationship between summer bighorn sheep density and the location of livestock (cattle and one domestic sheep) grazing allotments. It is possible that the domestic sheep allotment located between the most isolated subpopulation (Lower Green) and the others could influence structure through reduced survival in the adjacent small subpopulations. Few studies have directly investigated if bighorn sheep avoid cattle where they co-occur, though forage reduction and competition may limit their populations in arid environments (Buechner 1960, Garrison et al. 2016). The presence or grazing impacts of cattle can alter bighorn sheep foraging behavior (Brown et al. 2010, Garrison et al. 2016). Some evidence suggests that cattle grazing can negatively affect population growth of translocated populations (Singer et al. 2000c). Pathogen transmission from cattle may also occur (Wolfe et al. 2010). Bighorn sheep avoidance of grazing cattle or land with reduced forage could also contribute to spatial structure over time.

In alignment with previous work reporting that bighorn sheep avoid human recreation in some areas (Papouchis et al. 2001, Longshore et al. 2013, Brushett et al. 2023), our findings suggest human activities in the Monument in the summer months may influence bighorn sheep density and distribution. The SCR models predicted lower density near recreational campsites and, to a lesser extent, near livestock grazing allotments. However, both effects had low precision, particularly at large distances from those land uses.

Abundance and subpopulation sizes

Given limited gene flow between subpopulations, even small increases in mortality (e.g., disease or predation) could result in the local extinction of the small subpopulations we found, particularly for those more spatially isolated like the Lower Green subpopulation (Gilpin 1986, Gross et al. 2000). However, our estimates of total abundance (109 [95% CrI = 87–133] in 2019) suggest the population had no or small declines between 2018 and 2020 in the presence of pathogen exposure (Table 4). Because our study is the first estimate of abundance explicitly accounting for detection, our estimates are not directly comparable to historical approximations extrapolated from ground and aerial counts (Barmore 1962, George et al. 2009). Our abundance estimate corresponds to a density of 0.56 individuals/km^2, which falls within the range of other densities reported for free-ranging bighorn sheep populations, though comparision is complicated by differences in methodolgy and habitat definition (Bleich and Holl 2026). Our study area necessarily included some upland areas with low expected sheep occurrence, suggesting density in canyons could be somewhat higher.

Translocation records show 99 animals released in the Monument by 2000, and the latest historical approximation conducted in 2007 reported 165 animals based on a minimum count of 91 individuals (George et al. 2009; D. Finley, Colorado Parks and Wildlife, written communication, 6 Jan 2025). Although aerial counts are standard practice for bighorn sheep population monitoring, detection can vary widely given variation in topography, and in this case, no standard index of detection was used (Schmidt et al. 2022, Blum et al. 2024). We detected a minimum of 85 animals in 2019, slightly fewer than the 2007 aerial count, but our pellet-based minimum count method differed greatly.

Connectivity and barriers to movement

Our step selection results indicating avoidance of rivers align with studies in other ecosystems reporting water bodies as partial barriers to bighorn sheep movement (Tosa et al. 2023, Epps et al. 2024). This result likely reflects

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animals moving along versus across the dam-controlled Green River, which is cold and fast (minimum May peak flow ~314.32 m^3/sec, water temp = 10°C, minimum August peak flow ~ 65.98 m^3/sec, 20°C at Jensen gauge; USGS station number 09261000; USGS 2025). Movement across the Green River occurs rarely. We detected individuals on only one side of the river in the Lower Green subpopulation, and observed no movements across the Green River in the pellet dataset. There was evidence of a single short-term movement across this part of the Green River in the telemetry dataset. Some movement occurs near the confluence of the 2 rivers as supported by photographic evidence of a male crossing the Green River, multiple crossings of 2 telemetered males, and mixed support for 4 versus 5 subpopulations. The 5 subpopulation model splits the Confluence subpopulation along the Green River. Similarly, individuals from both sides of the Canyon of Lodore were assigned to the Upper Green subpopulation, indicating genetic connectivity. However, we did not detect movement directly in either pellet or telemetry data. Our results suggest the Yampa River is more permeable. Movement of collared animals across the Yampa River, detection of multiple individuals on both sides via pellets, and the lack of support for substructure within the Yampa subpopulation suggest both demographic and genetic connectivity. The fluctuations from peak flow in May–June (m^3/sec ~ 232.20) of the Yampa to late summer as flows decrease and temperatures rise (m^3/sec ~11.04, temp = 24°C) may influence the timing of connectivity and potentially pathogen transmission (USGS station number 092660050; USGS 2025).

Role of pathogens

Respiratory disease dynamics may influence the distribution, size, and genetics of this metapopulation. We detected individuals with exposure to multiple respiratory pathogens, including *M. ovipneumoniae*, in geographically and genetically distinct subpopulations throughout the Monument in 2006. Spatial patterns existed only for 2 pathogens, but small sample sizes limit inference. Ongoing reports of symptomatic animals and a positive *M. ovipneumoniae* test of an ill lamb in 2019 indicate that pathogens are a persistent challenge. Original sources of pathogens could include both translocated bighorn sheep and exposure to domestic sheep (Cassirer et al. 2018, Besser et al. 2012, 2021) and cattle (Wolfe et al. 2010). All-age die-offs can occur after contact with a novel strain of *M. ovipneumoniae* (Cassirer et al. 2018). Adult bighorn sheep that survive outbreaks can maintain immunity for several years, but immunity is strain-specific (Cassirer et al. 2017). Thus, continued contact with domestic sheep, or with conspecifics infected with different strains of *M. ovipneumoniae*, can trigger new cycles of mortality followed by suppressed recruitment that slows or prevents population growth (Manlove et al. 2016, Cassirer et al. 2017).

The high *M. ovipneumoniae* antibody prevalence in 2006 with continued clinical signs but stable abundance suggests the population may be in a chronic phase following an earlier epizootic with suppressed recruitment from ongoing infections in juveniles (Manlove et al. 2016, Cassirer et al. 2018, Besser et al. 2021). Because the most recent sampling was 13 years after the apparent initial outbreak, current adults may have developed immunity to resident *M. ovipneumoniae* strains or have genotypes supporting survival of existing pathogens (Cassirer et al. 2017, Dugovich et al. 2023). In either case, the spatial proximity and observed co-locations of bighorn sheep with domestic sheep indicate ongoing risk for exposure to new pathogens or strains (Besser et al. 2012, 2021; Cassirer et al. 2018). Additional data could help to distinguish between continuing transmission in a chronic state (Manlove et al. 2016, Cassirer et al. 2018), re-emergence of existing pathogens (Butler et al. 2018), or repeated introduction of new pathogen strains. If novel strains are introduced, pneumonia outbreaks could reduce both abundance of and dispersal among subpopulations (Gross et al. 2000, Singer et al. 2000b, Dekelaita et al. 2020). Fewer animals might be available to disperse, or dispersing animals could have high mortality or limited reproduction, restricting genetic connectivity (Gross et al. 2000). Disease can reduce horn growth (Martin et al. 2022) as well as overall health, which could influence successful competition with dominant males. If differences are apparent between males, those dispersing to breed may quickly leave if they are subdominant and do not succeed in mating attempts (Hogg and Forbes 1997, Lassis et al. 2022). This could provide enough contact to spread pathogens without spreading genes (Hagenaars et al. 2004).

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In bighorn sheep metapopulations, spatial structure can both support population viability by limiting disease transmission and create risks when subpopulations are small, isolated, or become sources of pathogen persistence (Dugovich et al. 2023, Epps et al. 2024). Previous studies evaluating abundance, persistence, and pneumonia outbreaks have advocated that improved resilience might best be achieved by promoting large, genetically diverse, and connected metapopulations (Hess 1996, De Castro and Bolker 2005, Cassirer et al. 2018, Dugovich et al. 2023). We found a spatially structured population for which persistence in the presence of disease may be facilitated by separation into several subpopulations with partial connectivity and moderately high genetic diversity originating in translocation history.

Genetic diversity and translocation legacy

Monument bighorn sheep subpopulations have slightly higher genetic diversity than many other Rocky Mountain bighorn populations (Gutiérrez-Espeleta et al. 2000, Gille et al. 2019, Love Stowell et al. 2020, Barbosa et al. 2021, Flesch et al. 2022). Translocations from multiple source populations likely created high diversity in the Yampa and Upper Green subpopulations initially. High diversity in the Confluence subpopulation may be the result of previous mixing. Statewide studies of genetic outcomes of Rocky Mountain bighorn translocations in Montana and Arizona found that populations that had received translocations were either similarly or more genetically diverse than native populations (Gille et al. 2019, Flesch et al. 2022). Flesch et al. (2022) calculated mean kinship, which is inversely correlated with genetic diversity. Monument bighorn sheep had the lowest mean kinship of the reintroduced populations evaluated, indicating high diversity. The microsatellite-based diversity metrics used to assess diversity herein, though relatively high for Rocky Mountain populations, are closer to the mean for previously measured desert bighorn sheep (Creech et al. 2020) and are far higher than estimates for California lineage bighorn sheep populations in Oregon (Spaan et al. 2021). Several of these populations were established by serial translocations from a small single founding population or its descendants (Olson et al. 2013).

The genetic differentiation between the Lower Green and Yampa (F_{ST} = 0.14) and the Upper Green and Yampa (0.12) subpopulations that are only 27 km and 55 river km apart, respectively, was unexpectedly high. Those genetic differences were greater than reported for riverine subpopulations of desert bighorn sheep in Grand Canyon National Park. There, subpopulations separated by Euclidean distances up to 150 km and a more extreme barrier exhibited F_{ST} ranging from 0.07–0.13 (Epps et al. 2024). Differentiation in the Monument is similar to Rocky Mountain bighorn populations in Wyoming that are more isolated such as between Kouba Canyon and Laramie Peak, approximately 240 km apart (Love Stowell et al. 2020). The high genetic diversity of Monument bighorn sheep resulting from diverse source populations, in combination with spatial structuring and partial connectivity, could support persistence as was demonstrated for desert bighorn in Dugovich et al. (2023). The Monument differs, however, in high risk of exposure to new pathogen strains. Although we expect rapid genetic drift in small subpopulations with limited movement, animals from different sources could also have had different genes shaping survival in the face of disease. If so, selection could also play a role in maintaining genetic diversity and structure.

Habitat selection

Bighorn sheep habitat selection in the Monument is consistent with reports from similar studies of both native and reintroduced populations. Collared animals selected ranges near rugged escape terrain as well as areas with intermediate terrain ruggedness and open habitat with lower canopy cover, including burned areas, similar to findings in DeCesare and Pletscher (2006), Lula et al. (2020), and Werdel et al. (2023). Wildfires can enhance forage quality in areas that recently (<5 years) burned (Greene et al. 2012, Proffitt et al. 2019). Previous studies of other mountain ungulates have found that non-vegetated areas can offer security from predators via increased visibility

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(Mysterud and Østbye 1999, DeVoe et al. 2015), which seems a more likely driver for Monument bighorn sheep, as we found they used areas that burned in the decade prior to 2003. However, unlike studies in Rocky Mountain alpine ecosystems (e.g., DeCesare and Pletscher 2006, Lula et al. 2020), thermoregulation indices indicating selection of cooler areas in summer months were important explanatory variables of habitat selection, indicating behavioral adaptations to a semi-arid environment.

Methodological considerations and future research directions

Our habitat selection analyses were based on GPS data collected from 15 collared animals. Although this sample size is consistent with similar studies from this era (e.g., DeCesare and Pletscher 2006), it limited our ability to detect rare dispersal events between subpopulations and precluded evaluations of sex-based differences in movement and site selection. We could not evaluate the influence of rare landscape features, such as the single domestic sheep allotment (versus all allotments), on habitat selection and movement. Future GPS telemetry studies that include more individuals could address these questions and support the evaluation of changes over time. Similarly, our serological testing for most pathogens was limited to the 19 samples from animals captured in 2006. This restricted our ability to evaluate spatiotemporal patterns in exposure and prevalence for most respiratory pathogens. Some datasets were temporally separated—GPS telemetry from 2006–2008 and abundance sampling from 2018–2020—spanning roughly 2 bighorn generations. Movement and habitat use patterns could have changed during this period. However, genetic structure results suggest that differences in dataset types and covariate scales likely explain discrepancies between habitat selection and density results.

Our baseline abundance estimates that quantify uncertainty can be used to support future metapopulation monitoring. We highlight the use of non-invasive genetic sampling and SCR models to estimate spatial patterns of bighorn density in rugged and remote environments (Epps et al. 2024). To assess future changes in abundance, identifying consistent pellet sampling locations along rivers that include both preferred habitat (i.e., river canyons) and lower quality areas (along roads, trails, and allotments) would increase statistical power for quantifying bighorn sheep distributions with SCR models. Limited sampling in allotments likely increased uncertainty around the grazing allotment effects. We aggregated detections to an artificial detector array for SCR analysis, similar to Royle et al. (2011), Bischof et al. (2016), and Epps et al. (2024). This approach coarsely approximates detection locations. Given the linear distribution of bighorn sheep in river canyons, an ecological distance kernel for detection could provide additional insights into movement and may potentially better align with the detection process (Royle et al. 2013a, Carroll et al. 2024). Recently developed flexible Bayesian SCR models that use a continuous inhomogeneous point process may also better represent the spatially continuous process of pellet searches (Zhang et al. 2023). Although our pellet-based approach does not provide data on age structure, it provided rigorous estimates for a population in a protected area with limited opportunity for aerial surveys. In this study area, innovative complementary surveys that record age and sex classifications could support identification of recruitment changes given restrictions on aerial surveys.

MANAGEMENT IMPLICATIONS

Our study provides a repeatable method and robust estimates of abundance for bighorn sheep in Dinosaur National Monument that can be used as a baseline to support future population monitoring. Our approach also describes population structure and provides subpopulation abundance estimates, enabling managers to implement subpopulation-specific monitoring. We found strong evidence that this reintroduced population is spatially structured with at least 4 small subpopulations that may be vulnerable to local extinction given their relative isolation and exposure to respiratory pathogens. Monitoring subpopulations could help managers to detect declines early and track demographic and genetic connectivity between partially isolated subpopulations. Managers could tailor

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interventions for specific subpopulations to support efficient allocation of resources. In Dinosaur National Monument, this could include priorities of reducing contact risk with domestic sheep for the Lower Green and Confluence subpopulations and managing human disturbance in locations where high recreation activity overlaps with the Upper Green subpopulation. Given the overlap of domestic sheep, cattle, and bighorn sheep, regular monitoring of population health and disease exposure could provide information about patterns of disease transmission and aid managers in balancing trade-offs between disease transmission risk and demographic and genetic connectivity.

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DATA AVAILABILITY STATEMENT

Data have been published in (Carroll et al. 2025).

ETHICS STATEMENT

Bighorn sheep were captured and tissue, blood, and pellet samples were collected following protocols approved by the Animal Care and Use Committee at the USGS Northern Rocky Mountain Science Center (2006-01).

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