Final Report WY01/21

State of Wyoming Department of Transportation

Investigating Potential Solutions to the Barrier Effect of Interstate 80 on Pronghorn Movements

By University of Wyoming
1000 East University Avenue, Dept. 3166
Laramie, Wyoming 82071

January 2021

Technical Report Documentation

Report No. WY-01/21	Government Accession No.	Recipients Catalog No.
Title and Subtitle Investigating Potential Solutions to the Barrier Effect of Interstate 80 on Pronghorn Movements		Report Date January 2021 Performing Organization Code
Authors Benjamin S. Robb (ORCID 0000-0003-1419-3918), William J. Rudd (ORCID 0000-0001-5207-5854), Matthew J. Kauffman (ORCID 0000-0003-0127-3900), Thomas Hart (ORCID 0000-0002-3246-7049), and Scott Gamo (ORCID 0000-0001-8672-3485)		Performing Organization Report No. RS06218
Performing Organization Name and Address University of Wyoming 1000 East University Avenue, Dept. 3166 Laramie, Wyoming 82071		Work Unit No. Contract or Grant No. 1003849-
Sponsoring Agency Name and Address Wyoming Department of Transportation 5300 Bishop Blvd. Cheyenne, WY 82009-3340 WYDOT Research Center (307) 777-4182		Type of Report and Period Covered: Final Report Sponsoring Agency Code: WYDOT
Supplementary Notes WYDOT Sponsor: Keith Compton, District 3 Engineer Thomas Hart, Wildlife Specialist Scott Gamo, Environmental Services Manager		

Abstract

Pronghorn rely on long-distance migrations to access seasonal resources and mitigate the consequences of severe winters and droughts. When barriers sever routes to alternative habitats then pronghorn populations may decline as a result of loss of habitat. Wyoming highways and interstates include woven-wire ROW fencing along the road. Such fencing can be effective deterrents to pronghorn and other ungulates from getting onto roads, which could otherwise pose a threat both to passengers and wildlife. However, this has also exacerbated the barrier effects faced by pronghorn. In our study, we sought to predict the most likely crossing locations for pronghorn across the Wyoming section of Interstate 80 (I80), given seasonal habitats and existing migratory habitat of pronghorn in southern Wyoming. We used a novel approach to develop connectivity models that assign the most likely estimates of movement costs as a function of landscape attributes to predict the probability of corridor use. By combining seasonal habitat predictions with our connectivity models, we simulated the most probable locations of historical corridors used by pronghorn prior to the development of I80. We evaluated the accuracy of our predicted corridors using locations of pronghorn carcasses from attempted crossings, as well as trail camera counts of pronghorn using underpasses, and professional review by wildlife biologists. Our results provide a large-scale assessment of pronghorn seasonal habitat, connectivity, and the identification of crossing structure locations that may best restore migratory behavior across a nearly impermeable barrier.

Key Words: pronghorn, migration, connectivity, underpass, Wyoming, mule deer; *Antilocapra americana*; *Odocoileus hemionus*		Distribution Statement This document is available through the National Transportation Library. Copyright © 2018. All rights reserved, State of Wyoming, Wyoming Department of Transportation, and University of Wyoming.	
Security Classif. (of this report) Unclassified	Security Classif. (of this page) Unclassified	No. of Pages 52	Price

Form DOT F 1700.7 (8-72) Reproduction of form and completed page is authorized.

SI* (MODERN METRIC) CONVERSION FACTORS

APPROXIMATE CONVERSIONS TO SI UNITS

Symbol	When You Know	Multiply By	To Find	Symbol
		LENGTH		
in	inches	25.4	millimeters	mm
ft	feet	0.305	meters	m
yd	yards	0.914	meters	m
mi	miles	1.61	kilometers	km
		AREA		
in^2	square inches	645.2	square millimeters	mm^2
ft^2	square feet	0.093	square meters	m^2
yd^2	square yard	0.836	square meters	m^2
ac	acres	0.405	hectares	ha
mi^2	square miles	2.59	square kilometers	km^2
		VOLUME		
fl oz	fluid ounces	29.57	milliliters	mL
gal	gallons	3.785	liters	L
ft^3	cubic feet	0.028	cubic meters	m^3
yd^3	cubic yards	0.765	cubic meters	m^3
		NOTE: volumes greater than 1000 L shall be shown in m^3		
		MASS		
oz	ounces	28.35	grams	g
lb	pounds	0.454	kilograms	kg
T	short tons (2000 lb)	0.907	megagrams (or "metric ton")	Mg (or "t")
		TEMPERATURE (exact degrees)		
°F	Fahrenheit	5 (F-32)/9 or (F-32)/1.8	Celsius	°C
		ILLUMINATION		
fc	foot-candles	10.76	lux	lx
fl	foot-Lamberts	3.426	candela/m^2	cd/m^2
		FORCE and PRESSURE or STRESS		
lbf	poundforce	4.45	newtons	N
lbf/in^2	poundforce per square inch	6.89	kilopascals	kPa

APPROXIMATE CONVERSIONS FROM SI UNITS

Symbol	When You Know	Multiply By	To Find	Symbol
		LENGTH		
mm	millimeters	0.039	inches	in
m	meters	3.28	feet	ft
m	meters	1.09	yards	yd
km	kilometers	0.621	miles	mi
		AREA		
mm^2	square millimeters	0.0016	square inches	in^2
m^2	square meters	10.764	square feet	ft^2
m^2	square meters	1.195	square yards	yd^2
ha	hectares	2.47	acres	ac
km^2	square kilometers	0.386	square miles	mi^2
		VOLUME		
mL	milliliters	0.034	fluid ounces	fl oz
L	liters	0.264	gallons	gal
m^3	cubic meters	35.314	cubic feet	ft^3
m^3	cubic meters	1.307	cubic yards	yd^3
		MASS		
g	grams	0.035	ounces	oz
kg	kilograms	2.202	pounds	lb
Mg (or "t")	megagrams (or "metric ton")	1.103	short tons (2000 lb)	T
		TEMPERATURE (exact degrees)		
°C	Celsius	1.8C+32	Fahrenheit	°F
		ILLUMINATION		
lx	lux	0.0929	foot-candles	fc
cd/m^2	candela/m^2	0.2919	foot-Lamberts	fl
		FORCE and PRESSURE or STRESS		
N	newtons	0.225	poundforce	lbf
kPa	kilopascals	0.145	poundforce per square inch	lbf/in^2

TABLE OF CONTENTS

CHAPTER 1. EXECUTIVE SUMMARY **1**
CHAPTER 2. INTRODUCTION **3**
  Migrations **3**
  Interstate 80 .... **4**
CHAPTER 3. MOVEMENTS AND MIGRATIONS OF PRONGHORN **5**
  Methods **5**
  Results and Discussion **6**
CHAPTER 4. PREDICTING MIGRATION ROUTES ACROSS I80 .... **11**
  Methods **12**
    GPS Data Organization **12**
    Resource Selection Functions **12**
    Cost-Distance Models and Validation **14**
    Historical Corridors and Validation **15**
  Results and Discussion **16**
CHAPTER 5. PRONGHORN AND MULE DEER USE OF UNDERPASSES **25**
  Methods **25**
  Results and Discussion **26**
CHAPTER 6. MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS **31**
  Recommendations **31**
APPENDIX A. IMAGES **33**
REFERENCES **41**

LIST OF FIGURES

Figure 1. Map. Pronghorn GPS collar data. 7
Figure 2. Map. Seasonal ranges of pronghorn in southwestern Wyoming. 8
Figure 3. Map. Full dataset of pronghorn winter movements. 9
Figure 4. Map. Modeled seasonal habitat of pronghorn north and south of Interstate 80. 16
Figure 5. Map. Predicted autumn corridors for the Sublette and Medicine Bow populations. 18
Figure 6. Map. Predicted spring corridors for the Sublette and Medicine Bow populations. 19
Figure 7. Maps. Predicted migration routes for pronghorn across Interstate 80. 21
Figure 8. Map. Areas along I80 that overlap with the highest autumn and spring connectivity with red dots illustrating attempted crossings by pronghorn. 22
Figure 9. Graph. Randomly sampled ratios of pronghorn crossings within predicted connectivity surfaces and the observed ratio of pronghorn attempted crossings (diamonds). 23
Figure 10. Map. Underpasses we monitored with trail cameras. 26
Figure 11. Maps. Pronghorn use of underpasses. 29
Figure 12. Maps. Mule deer use of underpasses. 30

LIST OF TABLES

Table 1. Beta coefficients of conductivity for connectivity models of pronghorn migrations. 20
Table 2. Cross-validation of connectivity model using held-out pronghorn migrations. 20
Table 3. Autumn counts of mule deer and pronghorn movements in underpasses. 27
Table 4. Spring counts of mule deer and pronghorn movements in the underpasses. 28

LIST OF ABBREVIATIONS

AIC — Akaike's information criterion
AICc — Akaike's corrected information criterion
ΔAIC — change in Akaike's information criterion
CI — confidence interval
GIS — geographic information systems
GPS — Global Positioning System
I80 — Interstate 80
KM — kilometer
M — meter
NSD — net-squared displacement
ROW — right-of-way (fence)
RSF —resource selection function
WYDOT — Wyoming Department of Transportation

CHAPTER 1. EXECUTIVE SUMMARY

Migrations provide wildlife access to seasonal habitats while evading harmful conditions, such as severe winters. For pronghorn (*Antilocapra americana*), severe winters with high snowpack can be one of the leading causes of herd die-offs. Such die-offs are caused because pronghorn are poorly adapted to move through snow and will lose access to buried vegetation during storms. Thus, pronghorn rely on long-distance movements to access forage and mitigate the consequences of severe winters.

Pronghorn are inhibited by movement barriers, such as roads and fences, and when such barriers intersect migration corridors, pronghorn can lose access to seasonal habitats vital to their survival. Barriers effectively cut off habitat that would otherwise be accessible to pronghorn. During severe winters or droughts, losing access to seasonal habitats can cause increased mortality because pronghorn depend on the ability to move to alternative habitats to alleviate harsh conditions. Because pronghorn rely on movement, the viability of pronghorn populations can be threatened when barriers sever routes to alternative habitats.

Interstate 80 (I80) has become a formidable barrier to seasonal movements for ungulates across southern Wyoming. From previous research, we know that pronghorn are 300 times less likely to successfully cross I80 than other highways in the state. Although the added barrier effect of woven-wire, right-of-way (ROW) fencing, and game-proof fencing have helped minimize the number of animal-vehicle collisions, the barrier effect of I80 has cost wildlife the ability to freely move. I80 has likely severed the ability of migratory ungulates, particularly pronghorn and mule deer (*Odocoileus hemionus*), to exploit seasonal habitats.

The Wyoming Department of Transportation (WYDOT) has been working to conserve migratory connectivity throughout Wyoming. Crucial to these efforts is an understanding of where seasonal habitats and corridors are located, or once were prior to the development of I80. Existing underpasses along I80 were primarily designed for either vehicle or cattle use, with several designed for wildlife, as well. Understanding whether movement continues through these existing underpasses will contribute to management efforts to conserve migrations across I80 and identify where such underpasses could be redesigned to better incorporate wildlife. Since the interstate has acted as a barrier for over 50 years, it is challenging to understand where animals may have historically migrated and where managers might place structures to most effectively reestablish movement corridors. Our research objective was to assess where the Wyoming section of I80 likely had the greatest effect on pronghorn movements by identifying locations along I80 most similar to migration routes today. Such efforts will contribute information on where migratory connectivity once was, thus, where connectivity could be restored through crossing structures, as well as where migratory connectivity still exists, thus, where connectivity can be conserved by redesigning underpasses.

We collected Global Positioning System (GPS) collar data of pronghorn movements between 2017 and 2020, and organized a collaborative GPS collar dataset from previous research led by Jeffrey Beck, Fred Lindzey, and Hall Sawyer, to predict pronghorn seasonal habitats and migration routes across the Wyoming section of I80. We identified four networks across I80 that may have contained migration routes prior to I80: a) east of Lyman, b) north and south of Wamsutter, c) east of Rawlins, and d) west of Laramie, Wyoming. These areas overlap with the locations of pronghorn carcasses documented on I80 between 2009 and 2019.

We used camera trap data collected between autumn 2018 and spring 2019 from 23 and 24 underpasses across I80 to monitor present-day movements. We primarily monitored mule deer and pronghorn. We identified several hotspots for pronghorn and mule deer movements in Wyoming, including the Dana Ridge underpass at mile marker 243.9 in Carbon County, which remains a mule deer migration corridor. Likewise, the underpasses between mile markers 12 and 18 in Uinta County had a high amount of mule deer use in the autumn. Few pronghorn used underpasses, but pronghorn use was documented at underpasses that were unfenced at the entrances.

Our study reinforces that I80 is an effective barrier to pronghorn, although some pronghorn do cross successfully in very low numbers using existing underpass structures. Pronghorn are attempting to cross in many locations but are being killed within the I80 ROW. Using these results, we suggest that mitigation across the I80 barrier could include the removal or redesign of fenced entrances of underpasses — particularly along rivers, as well as at the Dana Ridge area in Carbon County and the Table Rock area in Sweetwater County — to improve connectivity for pronghorn. Pronghorn migration routes in southern Wyoming likely existed west of Green River, around Wamsutter, east of Rawlins, and west of Laramie, which agrees with patterns of where pronghorn are still trying to cross as indicated by carcass data. Corridor networks predicted by our connectivity models can help narrow down potential sites where crossing structures could effectively restore movement of pronghorn. Such management action will be a valuable contribution to the long-term conservation of pronghorn populations. Our results indicate that there are opportunities to redesign some existing structures in a manner to increase the numbers of crossings by pronghorn.

CHAPTER 2. INTRODUCTION

Migrations

Migration is defined as the repeated long-distance movement between distinct ranges,[1,2] and can benefit wildlife populations that rely on seasonal habitats to access forage. Migrating seasonally can benefit populations by minimizing exposure to costly conditions, such as excess snowfall,[3,4] while providing access to seasonal resources.[5,6] Likewise, migration can lower competition with conspecifics on seasonal ranges.[7,8] In seasonally predictable habitats, migration is often the optimal strategy to exploit resources,[9] with migrants sometimes outnumbering their resident (non-migratory) counterparts by an order of magnitude.[10]

Pronghorn often migrate to access habitats free of snow while also accessing nutritious forage.[11–13] Where, and how far, pronghorn migrate can be a result of resource availability and winter severity.[11] Because pronghorn are poorly adapted to move through snow,[14] many pronghorn populations rely on long-distance migrations to access seasonal resources and mitigate the consequences of severe winters and droughts. Pronghorn utilize open landscapes to move between a diversity of habitats including the "Path of the Pronghorn" between the Upper Green River Basin and Grand Teton National Park, in Wyoming.[15] Because pronghorn are adapted to large, open landscapes, the ability to move between different habitats can be crucial to their long-term viability.

Pronghorn survival relies on the ability to move freely across the landscape to best make use of available and important habitats. When barriers, such as fences and roadways, sever movements to these habitats, pronghorn populations may decline. Barriers that inhibit the migrations of pronghorn have contributed to population crashes by limiting access to available habitats during severe winters.[11,16–18] For example, in 1983, a winter storm in south-central Wyoming forced pronghorn to migrate to avoid snow, but a recently erected woven-wire fence severed access to alternative winter range. Pronghorn exhibit a low success rate of jumping over fences and often will either cross under the fence, if the bottom wire is high enough from the ground, or forgo crossing entirely.[19–21] Winter mortality that year was estimated at 35–70 percent of the population.[18] To mitigate such die-offs, management guidelines suggest modifying fences to be more permeable.[22] This raises the question of where to mitigate the negative effects of movement barriers.

Wyoming highways and interstates include woven-wire ROW fencing along the road. Such fencing can be effective deterrents to pronghorn and other ungulates from getting onto roads, which would otherwise pose a threat to both passengers and wildlife. Because of the risk of wildlife-vehicle collisions, it is not necessarily a practical solution to make ROWs more permeable to pronghorn movement. This has also exacerbated the barrier effects faced by pronghorn. Major highways can circumscribe the home ranges of pronghorn[23] and sever migration corridors.[24] When there are no alternative passageways over or under highways, traffic volume along with exclusionary ROW fencing can make roads impermeable to movement, which likely inhibits pronghorn from exploiting surrounding resources.

Interstate 80

Interstate 80 (I80), a transcontinental highway that extends east to west across the United States, was opened to traffic in Wyoming in 1970. Since that time, increasingly high traffic volumes, installed ROW fencing (usually 1.2 m in height),[25] and game-proof fencing (usually 2.4 m in height)[26] have effectively created a barrier to the short and long-distance movements of many ungulates in southern Wyoming.[15] Pronghorn rarely cross this nearly impermeable barrier.[27] This barrier effect in Wyoming has been well documented since Charles Sundstrom's work in the Red Desert.[28] Although enough pronghorn can cross to promote gene flow,[29] pronghorn, as well as mule deer, moose, and elk, have had their access to additional habitat essentially eliminated along much of this state-wide barrier.[15] The only known mule deer migrations across I80 are maintained by an open span bridge underpass (measuring 61 m by 9 m by 4.5 m) and associated game-proof fencing[30,31] on Dana Ridge, east of Walcott Junction, Wyoming. Pronghorn, however, are generally adverse to using underpasses.[31,32] Those few pronghorn that do use underpasses are slower to acclimate to underpasses compared to other ungulates.[24] Additionally, the placement of existing underpasses largely fail to facilitate pronghorn movement across I80. During severe winters, when pronghorn make facultative movements to alternative ranges, I80 often inhibits access to habitat with less snow.[17,33]

In our study, we sought to predict the most likely crossing locations for pronghorn across I80, given seasonal habitats and existing migratory habitat in southern Wyoming. We used a novel approach to develop connectivity models that calculate a probability of corridor use given the surrounding landscape and juxtaposition of seasonal habitats (Nuñez et al, *in prep*). By combining seasonal habitat predictions, at the home range and patch level of selection, with our connectivity models, we simulated the locations that were most likely linkages to pronghorn connectivity prior to the development of I80. We evaluated the accuracy of our predicted corridors using locations of pronghorn carcasses from attempted crossings as well as trail camera counts of pronghorn using underpasses and professional review by wildlife biologists. Our results provide a large-scale assessment of pronghorn seasonal habitat, connectivity, and the identification of crossing structures that may best restore migratory behavior across a nearly impermeable barrier.

CHAPTER 3. MOVEMENTS AND MIGRATIONS OF PRONGHORN

Previous studies on pronghorn movement in southern Wyoming were not designed to study the I80 barrier. Rather, these studies noted the barrier of I80 as an additional finding to their research. Such studies have created a patchwork of collected movement data on pronghorn. This patchwork has left large spatial gaps where there have been no recent studies on pronghorn movement. These gaps raise the question of whether I80 is a barrier across southern Wyoming, or only specific to certain areas. To help fill in these gaps, we specifically located pronghorn found along I80 in areas that have not been recently studied with the explicit goal of studying the barrier effect of I80. We used GPS collars on pronghorn to build a more comprehensive study of pronghorn movements and seasonal ranges throughout the area of Wyoming occupied by I80.

Methods

In March of 2017 and 2018, we placed GPS collars on a total of 89 pronghorn throughout southwestern Wyoming. These pronghorn were captured using helicopter net-gunning. We collared pronghorn found along I80 within a study area including five populations delineated by herd units from Wyoming Game and Fish Department: Carter Lease, Sublette, Bitter Creek, South Rock Springs, and Uinta-Cedar populations. This study area extends from the road junction with I80 and Wyoming State Highway 189 at the western most extent, and the Table Rock area west of Wamsutter, Wyoming, as the easternmost extent (Fig. 1, Fig. 2). Collars were collected either after mortality of the pronghorn, or after remote drop-off of the collars, programmed for either March of 2020 or March of 2021. To add to our dataset, we collaborated with Hall Sawyer, Western Ecosystems Technology, Inc., and Jeffrey Beck, University of Wyoming,[34,35] to create a larger dataset of pronghorn movements. This created a dataset spanning from 2002 to 2020, of 476 pronghorn, or 1010 unique animal years (separating every pronghorn into distinct categories when tracked for more than one year, e.g., pronghorn 1 2013 and pronghorn 1 2014). This added to our study extent from Highway 189 to Elk Mountain, Wyoming (Fig. 3).

Because GPS collars can collect erroneous points due to collar failure or a low number of satellites creating an unreliable fix location, we processed all GPS collar data, including the larger dataset of previous studies, to remove any GPS points with a speed greater than 20 m/s or exactly 0 m/s to the subsequent fix. Additionally, we removed erratic ‘spike’ points, which were also likely caused by poor satellite connection, by removing any point with a median or mean distance greater than 25 km or cosine step angle correlation greater than 0.97 from the previous fix and the subsequent fix.[36] The time intervals between subsequent GPS fixes varied by the study, so to standardize seasonal range estimation, we subsampled all GPS data to have 7 – 8 hour time intervals.

We mapped pronghorn long-distance movements using net-squared displacement (NSD) plots for each animal year. To be classified as a potential migration, pronghorn NSD within a five-day window had to exceed 701 km^2, the squared diameter of the largest reported home range of a female pronghorn.[20] Because pronghorn can make non-migratory facultative movements,[12] we differentiated between seasonal migrations and facultative movements by the behavior of the pronghorn following the extended movement: instances where the movement was immediately followed by an asymptote within our NSD threshold were mapped as a migration.

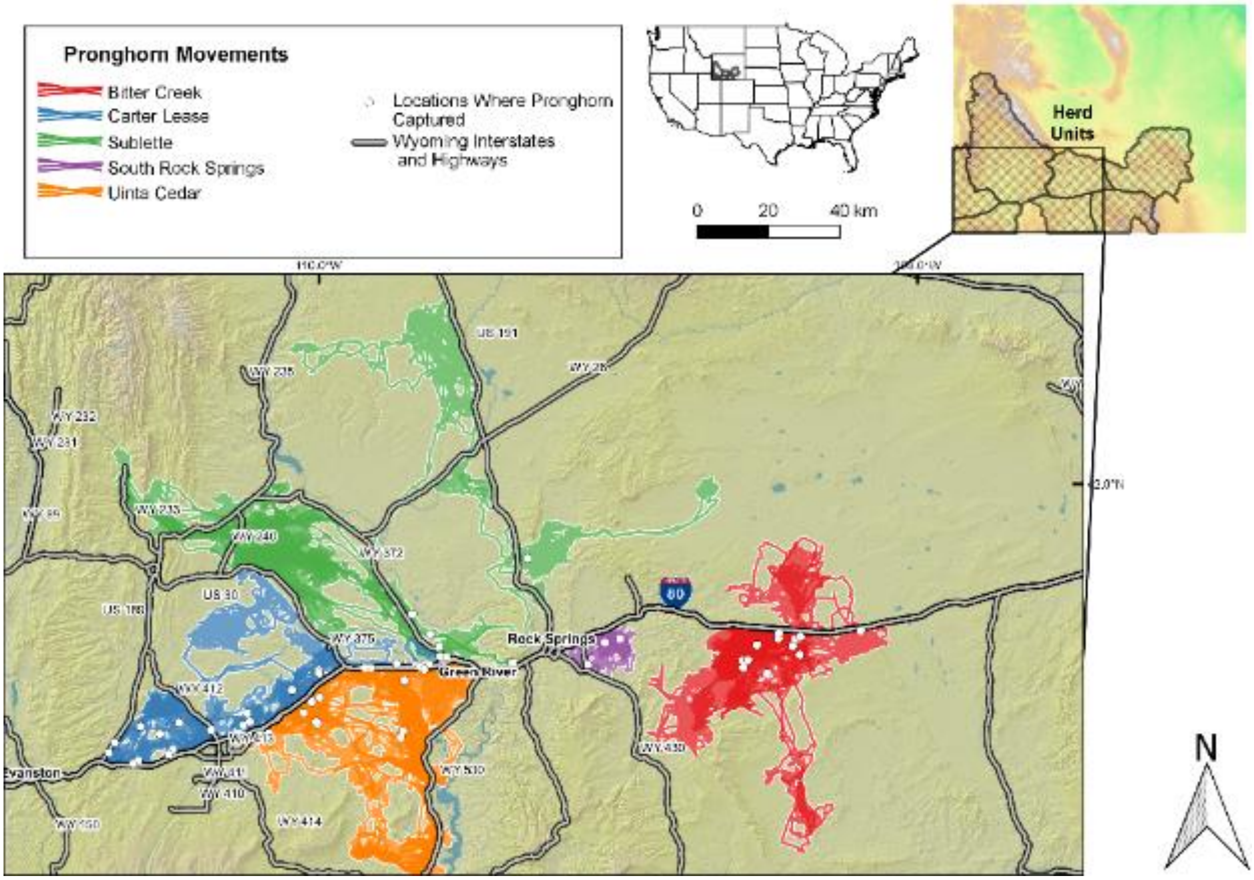
To calculate seasonal ranges, we removed all migrations and forays, and defined summer as June through September, and winter as December through February. To estimate seasonal ranges, we used the 99 percent kernel density estimate of each pronghorn with a bivariate normal distribution. Individuals with a time gap in GPS fixes greater than two days, within a season, were estimated separately, before and after the gap, then combined. We only estimated seasonal ranges on pronghorn tracked for at least seven days in a given season.

Results and Discussion

Our study design was tailored toward the Wyoming section of I80, and so the movements we observed are more representative of pronghorn along I80 rather than the entire populations. Nonetheless, we observed many short- and long-distance migrations across our study area, with the Sublette and Uinta-Cedar populations demonstrating the highest prevalence of seasonal movements. By population, pronghorn in the Carter Lease population, north of I80, often winter and summer along I80, and thus, are primarily residents. Pronghorn in Sublette will often summer near either Kemmerer, Wyoming, or the Hams Fork, if they successfully cross Wyoming State Highway 189. Pronghorn migrations in Sublette often parallel State Highway 372, near its junction with I80. Pronghorn winter range in Sublette is more variable, and can either be along I80 and the 372 junction, or closer to Opal, Wyoming. In the Bitter Creek population, a large number of resident pronghorn had seasonal ranges between I80 at the northern extent, and the Union Pacific railroad at the southern extent. However, some pronghorn did make southern migrations closer to Adobe Town, in southern Wyoming. In the Uinta-Cedar population, pronghorn most often had winter ranges either along I80, at the northern extent of the study area, or to the south closer to Manila, Utah. The migration route pronghorn followed to access the southern winter range tended to parallel I80 in the eastern direction, then paralleled State Highway 530 and the Green River in the southern direction. We had a low sample of pronghorn in the South Rock Springs population and so could not delineate seasonal ranges or migration routes across this population.

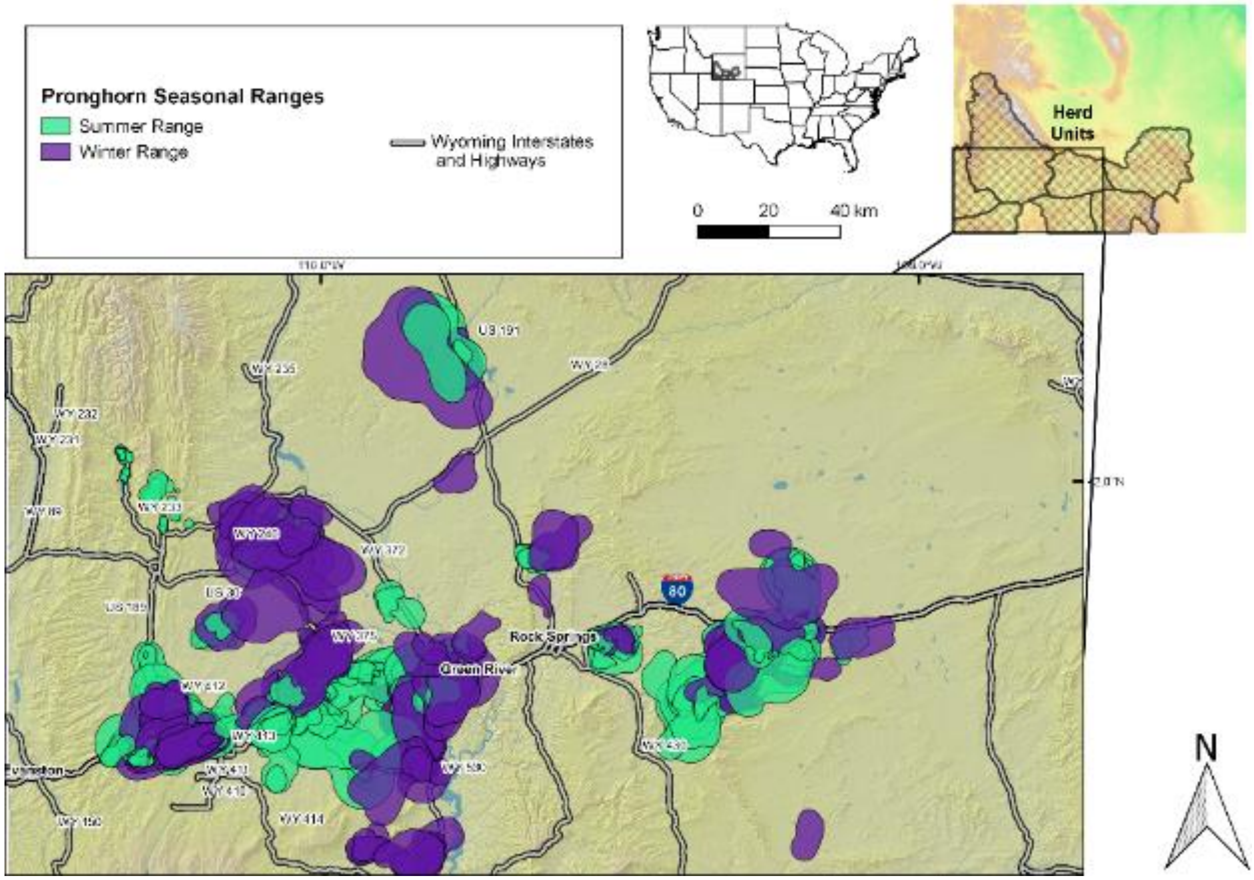
Of our collaborative dataset of 476 pronghorn, only 6 ever successfully crossed I80. We observed one pronghorn cross at Lyman between mile markers 46 and 47, two pronghorn crossed in the Table Rock area near mile marker 151, one crossed near Bar X road between mile markers 161 and 162, and two crossed next to Platte River around mile marker 229.

The effects of roads on pronghorn can extend beyond barriers, as pronghorn may be more vigilant along roads, creating an opportunity cost due to lost time foraging.[37] Thus, the costs of the barrier effect on pronghorn can also be a loss of foraging efficiency, although we did not measure this in our study. Likewise, pronghorn have been reported following along roads for up to 10.5 km.[38,39] GPS collar data in our study exhibited a similar trend, as we found that pronghorn ranges were elongated along roads. Such movements could occur because pronghorn are either seeking a location to cross the barrier, or are confined to habitat along the barriers.



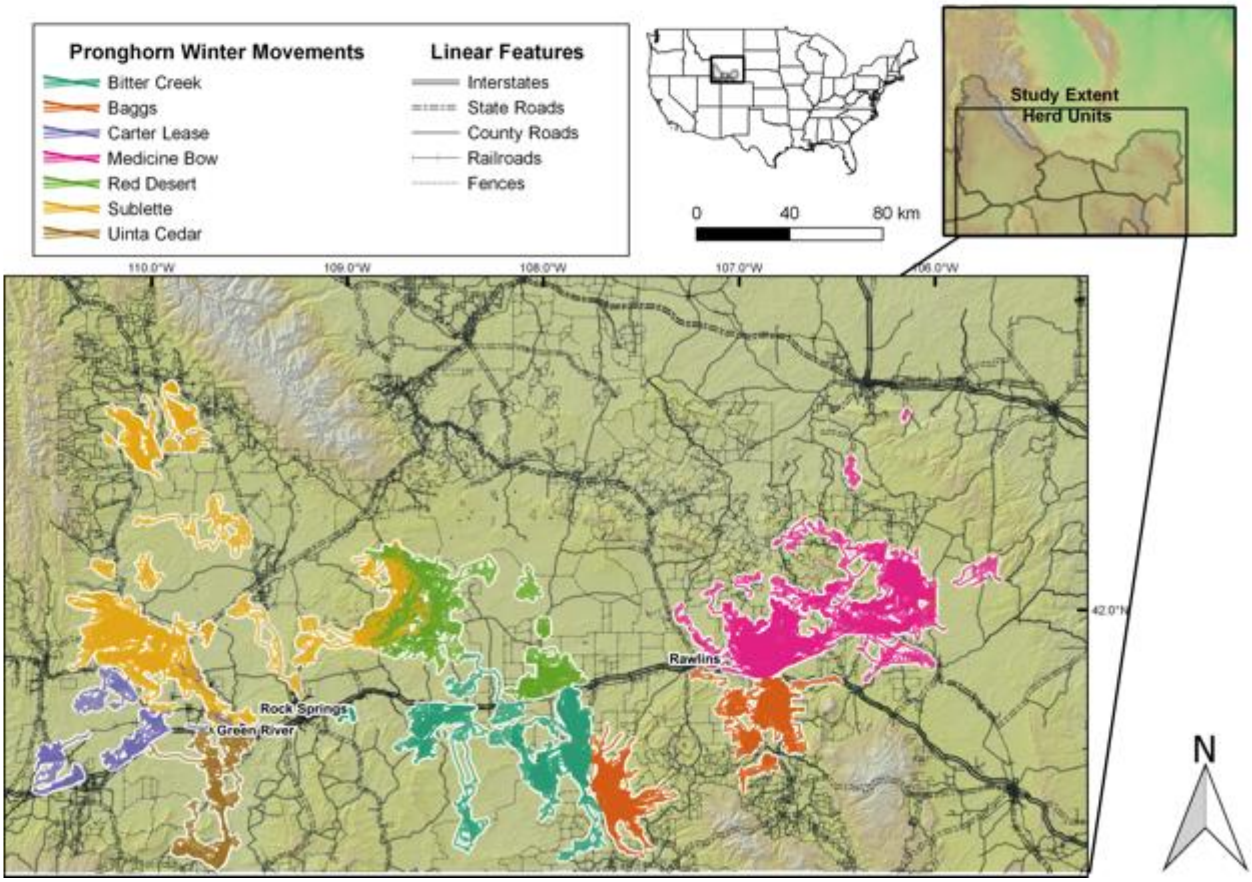
Source: Benjamin Robb

Figure 1. Map. Pronghorn GPS collar data.



Source: Benjamin Robb

Figure 2. Map. Seasonal ranges of pronghorn in southwestern Wyoming.



Source: Benjamin Robb

Figure 3. Map. Full dataset of pronghorn winter movements.

CHAPTER 4. PREDICTING MIGRATION ROUTES ACROSS I80

Wildlife crossing structures can restore movements through migration corridors severed by long-standing barriers.[40,41] The implementation of crossing structures have mostly been to protect seasonal movements of intact populations, and as such, uses of crossing structures have been successful across a diversity of taxa ranging from brown bears (*Ursus arctos*) to squirrel gliders (*Petaurus norfolcensis*).[40,42,43] Crossing structures have largely been motivated by the goal of minimizing road-related mortalities that pose a threat to both the viability of mobile populations and motorist safety. Nationwide, wildlife-vehicle collisions are estimated to cost $8.3 billion in property damage annually.[44] The economics of crossing structures are mostly motivated by this high-cost of property damage and threat to human life when wildlife get onto roads. Nonetheless, the expansion of anthropogenic barriers (e.g., roads, railways, fences) have already severed the migration corridors of many taxa.[15,45] Placing crossing structures within predicted locations that were likely historical corridors can provide population-level benefits by providing access to currently inaccessible habitats. Crossing structures can not only protect existing movements but may also restore movements lost from severe barriers.

When seasonal movements are lost due to long-standing barriers, it is a distinct challenge to identify the best locations to restore movement because migration corridors and the location of crossing structures are often delineated using GPS tracking data.[46,47] Most methods to identify locations of crossing structures depend on existing movement. Additionally, for some species the location of suitable habitat that animals will move through can be more important to the use of a crossing structure than its structural dimensions.[48] It is thus critical that corridor restoration be informed by the distribution of suitable habitat, especially when such habitats may no longer be used due to barriers. Moreover, the financial costs of designing and constructing crossing structures elevate the importance that managers locate these structures in the most optimal locations.[49] To restore seasonal movements, the location of crossing structures will need to be grounded in an understanding of the landscape attributes that promote these movements and the juxtaposition of seasonal ranges.

Because migration corridors are influenced by components of the landscape that facilitate movement,[50,51] the location of potential corridors can be identified by the landscape features that would facilitate movement, even when barriers prevent migration. Thus, methods to quantify landscape connectivity hold potential to identify where historically important — but now lost — movements can be retroactively identified to guide restoration efforts.

In this chapter, we sought to predict the locations that were likely most important for pronghorn movement across I80, given seasonal habitats and existing migratory habitat of pronghorn in southern Wyoming. Thus, we did three separate analyses to predict pronghorn migration routes:

1. Pronghorn winter range
    a. Estimated by resource selection functions at the home range and patch scale.
2. Pronghorn summer range
    a. Estimated by resource selection functions at the home range and patch scale.
3. Pronghorn migration routes
    a. Estimated by a cost-distance model.

By combining seasonal habitat predictions with our connectivity models, we simulated the most probable locations of historical corridors used by pronghorn prior to the development of I80. Our results provide a large-scale assessment of pronghorn seasonal habitat, connectivity, and the potential locations where crossing structures may best restore migratory behavior across a nearly impermeable barrier.

Methods

GPS Data Organization

We used the GPS dataset outlined in Chapter 2. Our general approach was to model winter and summer range habitats, then to simulate migrations between seasonal ranges and across the interstate with a rule-based connectivity model.

Data cleaning and identification of migrations are outlined in Chapter 3 methods. We removed seasonal migrations with less than 10 points. Due to low sample sizes, cost-distance analyses were only calculated on the Sublette and Medicine Bow populations, and migrations from all other populations (Carter Lease, Uinta-Cedar, Bitter Creek, Baggs, and Red Desert) were used for cross-validation because the datasets were too low for use in the modeling step.

We used seasonal ranges estimated from Chapter 3. Additionally, to reduce pseudoreplication, GPS data were randomly sampled to one point per day for each animal year. Finally, to avoid bias, we removed all pronghorn that ever came within 15 km of I80 from the resource selection functions.

Resource Selection Functions

To estimate resource selection functions (RSFs), we used ten predictors known to influence pronghorn resource selection:

- Slope. Calculated from a digital elevation model.
- Heat load index. Calculated from a digital elevation model.
- Topographic position. Calculated from a digital elevation model, where topographic position index was classified using a 90 m moving window.[52,53]
- Density of rivers. River data were available through the national hydrography dataset,[54] filtered to all named rivers in Wyoming as well as the Blacks Fork and the Hams Fork rivers.
- Sagebrush cover. Shrubland fractional component data from the Multi-Resolution Land Characteristics Consortium database.[55–57]
- Herbaceous cover. Shrubland fractional component data from the Multi-Resolution Land Characteristics Consortium database.[55–57]
- Annual cover. Shrubland fractional component data from the Multi-Resolution Land Characteristics Consortium database.[55–57]
- Integrated Normalized Difference Vegetation Index (integrated NDVI). NDVI is an informative proxy of high quality forage and ungulate resource selection.[58] The integrated

NDVI estimates the yearly sum of positive NDVI values within each pixel, which we averaged from 2002 to 2019.[59]

- Density of fences. We obtained fence data from the Wyoming Cooperative Fish and Wildlife Research Unit, as well as the Wyoming Game and Fish Department and Bureau of Land Management.
- Density of major highways. Highways were available from WYDOT. Any highway within 500 m of I80 was removed from the highways layer to avoid any habitat effect caused by I80.

We estimated resource selection at two different scales: the home range scale analyzed habitat within the larger population boundaries, and the patch scale analyzed habitat within the boundaries of the home range.[60,61] Thus, the two scales tried to incorporate coarse scale and fine scale definitions of habitat. For selection at the home range scale, we randomly sampled points within the 99 percent contour of each kernel density estimate as used points, and randomly sampled points within the population of that pronghorn as available, delineated by herd units created by the Wyoming Game and Fish Department. The number of used points for each animal year was equal to the number of GPS points used in the patch level resource selection analysis (see next paragraph). Available points were sampled within each population at a ratio of 1:1 to the number of used points within each population. We buffered all points by eight radii (0.25 km, 0.50 km, 1.00 km, 3.00 km, 5.00 km, 7.50 km, 10.00 km, and 15.00 km).[61] We extracted each predictor with each of the eight buffers, then fit a simple logistic regression to each predictor-buffer combination. We used corrected AIC (AICc) to select the optimal scale (buffer) of home range selection with a threshold of two AICc.[60] Any predictor where the AICc values of each buffer were all within two, or where the lowest AICc was at the upper-bound buffer (15 km), was removed prior to model selection. Predictors for which there were multiple buffers within two AICc of one another, but not all eight, were assumed to both be optimal and their scale was averaged.

We likewise estimated resource selection at the patch level within home range. This level of selection was analogous to our methods to quantify home range selection, except at a finer extent and grain of analysis. We defined availability as the 99 percent contour of the kernel density estimate within each animal year. Within a use-available framework, we used GPS points within each seasonal range contour as the used points, and we sampled random points within each home range as available. We sampled available points at a ratio of 1:1 for the number of used points by each animal year. Points were buffered by eight radii (50 m, 100 m, 150 m, 200 m, 300 m, 500 m, 1000 m, and 1500 m). Any predictor where either every buffer was within 2 AICc of one another, or where the lowest AICc was the upper-bound cutoff (1500 m), was removed from further model fitting.

To estimate resource selection at both the home range and patch levels of selection, we used mixed effects conditional Poisson models with a large, fixed variance of 10^3 to avoid shrinkage of the intercepts towards the overall mean.[62] We used a hierarchical random intercept structure with each animal year stratified by their respective population. We assigned a weight value of 1000 for available points and 1 for used points.[62] To assess the predictive accuracy of each RSF, we used k-folds cross validation with three folds.[63,64] We then compared the Spearman's rank correlations between predicted habitat quality (binned) and the number of GPS points within each habitat bin.

Cost-Distance Models and Validation

To fit a cost-distance model to migration routes, we used six predictors we expected to be important to pronghorn migration routes:

- Slope. See description in “Resource Selection Functions”.
- Aspect. This indicates the direction the slope is facing and was calculated from a digital elevation model.
- Distance to roads. See description in “Resource Selection Functions”. Excluding I80, we took the distance to highways in Wyoming with a decay function.[65] We used an alpha value of -0.001.
- Distance to rivers. See description in “Resource Selection Functions”. We took the distance to rivers in Wyoming with a decay function.[65] We used an alpha value of -0.001.
- Sagebrush cover. See description in “Resource Selection Functions”.
- Herbaceous cover. See description in “Resource Selection Functions”.

We fit cost-distance corridor models separately to the migration data for each of the two populations used to train the models (Sublette and Medicine Bow), for both spring and autumn migrations. The general approach to cost-distance corridor models is to assign values of movement “cost” to features of the landscape that influence the study animal.[66] Then, given a starting location (e.g., winter range) and ending location (e.g., summer range), the model can visualize the most likely corridor network the study animal would use to connect seasonal habitats. We used maximum likelihood to estimate the cost values to the above six features of the landscape we expected to influence pronghorn movement. For a brief outline of the method, please see the Master’s thesis from this project.[27] The value of this approach using maximum likelihood estimation is it can estimate the most likely cost values given GPS points of migrations, rather than make subjective assumptions of these cost values. Moreover, this method provides a probability surface of the locations of corridors, rather than a relative map of corridors.

To cross validate the accuracy of the cost-distance models, we predicted the probability surfaces of connectivity from seasonal movements held-out from model training. Thus, we validated the cost-distance models using pronghorn migrations outside of the Sublette and Medicine Bow populations. We used two different cross-validations based off of previous studies.[67] First, we assessed whether the cost-distance model was more accurate than a null model with no environmental effects (i.e., a straight line), where the more accurate model should require less area to conserve movement. We predicted a migration probability surface for each individual migration and compared against a null probability surface based on a straight line Euclidean model prediction, where the rate parameter was equal to the parameter from the compared model. We estimated area of each least-cost corridor that would encompass 95 percent of the GPS points by fitting splines to the percent of GPS points within each percentile of the predicted corridor. In our second cross-validation, we assessed whether the actual migration path was better predicted by our cost distance model than random paths, where, if the cost distance model accurately predicts migrations, then the accumulated cost of an actual migration track should be lower than the accumulated cost for a randomly sampled migration track. We randomly generated 99 paths for each migration by spinning the path around the centroid at a random angle.[68] We then jittered the x- and y-coordinates of each path by a random distance within 5 km. We then extracted the total cost given the cost surface predicted from our cost distance model across each migration track, buffered to 1 m. For each individual migration, we estimated the percentile of accumulated cost for the observed path compared to the distribution of accumulated cost for each available migration track.

Historical Corridors and Validation

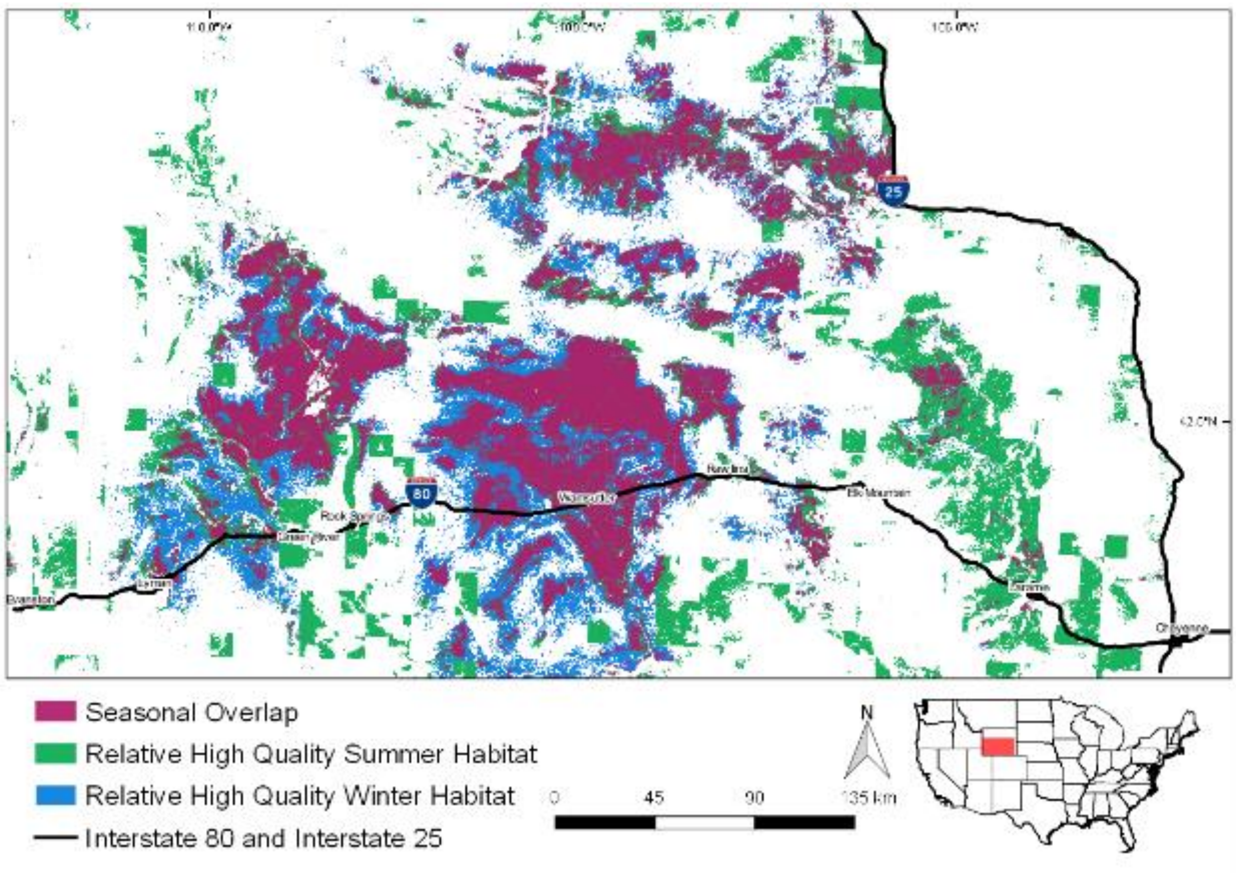
We randomly sampled 3000 points within the upper 75th percentile of pronghorn winter range and summer range, given the seasonal range maps of pronghorn unimpeded by I80. We then randomly connected each winter range point with one summer range point on the other side of the interstate within a distance between 30 km and 300 km. These random pairings were the start and end points for the spring simulation; analogous autumn migration simulations were conducted with random pairings starting with summer range points and ending with winter range points. Upon running each of the 3000 least cost simulations, we took the sum across each corridor to get one connectivity layer. Because our simulation could have been biased towards points in the center of the study area, we divided the summed connectivity layer by a null connectivity layer, where each of the same 3000 individual start-end points were predicted against a flat cost-distance layer, then summed. By dividing our summed connectivity layer by a null connectivity layer, we produced a normalized connectivity layer that controlled for the arrangement of start and end points.[69–71] Finally, we transformed the resulting connectivity layer into 5 percentile bins so that the highest predicted connectivity were values between the 80th and 100th percentiles.

To cross validate our predicted surface of likely corridors across I80, we used pronghorn carcass data collected between 2009 and 2019. Carcass data were collected by WYDOT. We expected that if our simulated historical corridor surface accurately estimated pronghorn corridors, then the frequency of pronghorn attempted crossings (i.e., locations of carcasses) should be highest within our predicted corridors along I80. We removed all carcass points east of Cheyenne, Wyoming, because this was outside our study area. We then estimated attempted crossings as the daily presence of a pronghorn carcass at each mile post on I80. We then used a permutation test to assess whether the observed frequency of crossing locations within our connectivity model predictions was statistically significant. To do this, first we estimated the ratio of pronghorn crossing locations inside versus outside the highest connectivity bin, 80th to 100th percentile, for autumn and spring maps. We then randomly sampled 3000 times an equal number of points along the interstate and compared the ratio of randomly distributed points inside versus outside the highest connectivity bin. We used the percentage of random iterations with a ratio greater than or equal to the observed ratio as an empirical estimate for a p-value.[72]

We did all analysis in program R (version 3.5.1 for estimating cost distance models, version 3.6.2 for all other analysis).[73] We calculated kernel density estimates from the package 'adehabitatHR',[74] Poisson conditional mixed effects models from the package 'glmmTMB',[75] and cost distance calculations from the package 'gdistance'.[76]

Results and Discussion

We found that winter ranges were confined to areas of relatively flat terrain with intermediate sagebrush cover and warmer facing slopes, and a higher density of rivers. Summer habitats were less flat, had higher herbaceous cover, and were in cooler areas. From our predicted map of habitat quality for pronghorn farther than 15 km from I80, summer ranges tended to be closer to the foothills of mountain ranges compared to winter ranges, which were closer to the center of our study area, characterized by lower elevation basins with nearby ridges providing insulation (Fig. 4). Additionally, pronghorn habitat in the summer was often within the vicinity of highways, but in the winter, pronghorn tended to avoid highways.

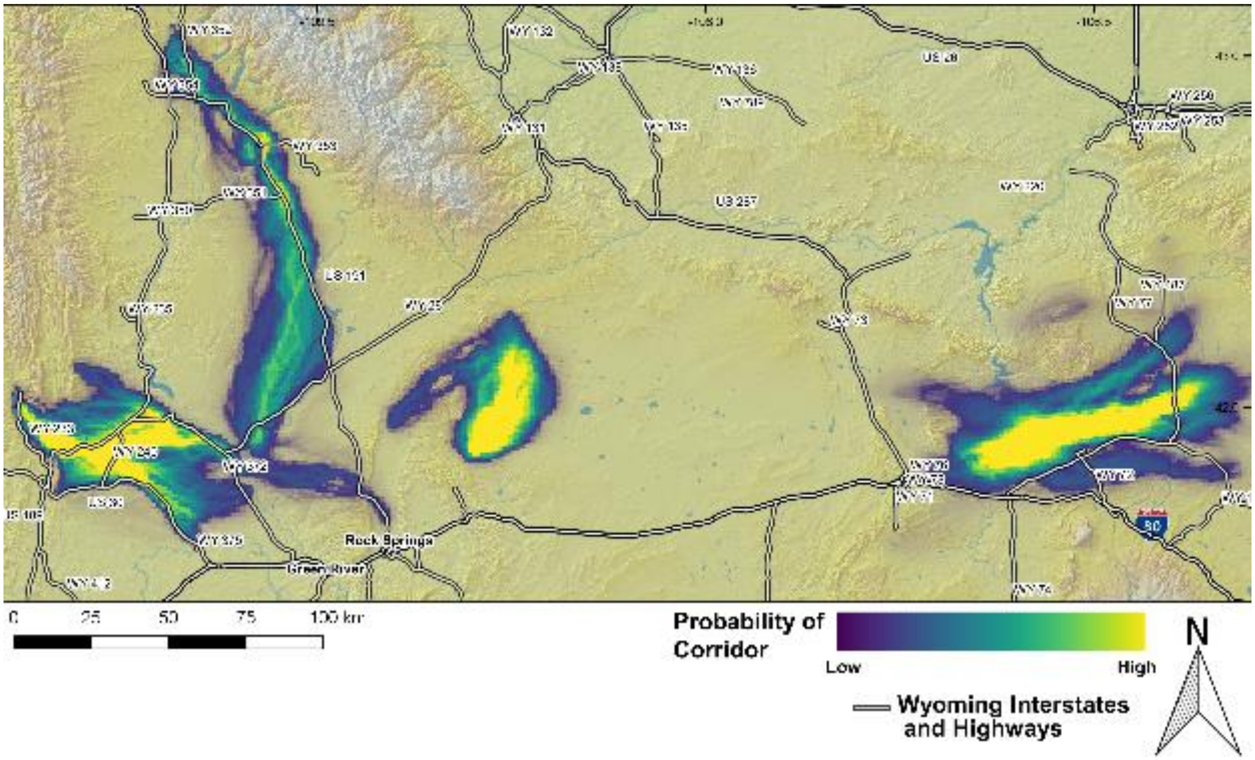


Source: Benjamin Robb

Figure 4. Map. Modeled seasonal habitat of pronghorn north and south of Interstate 80.

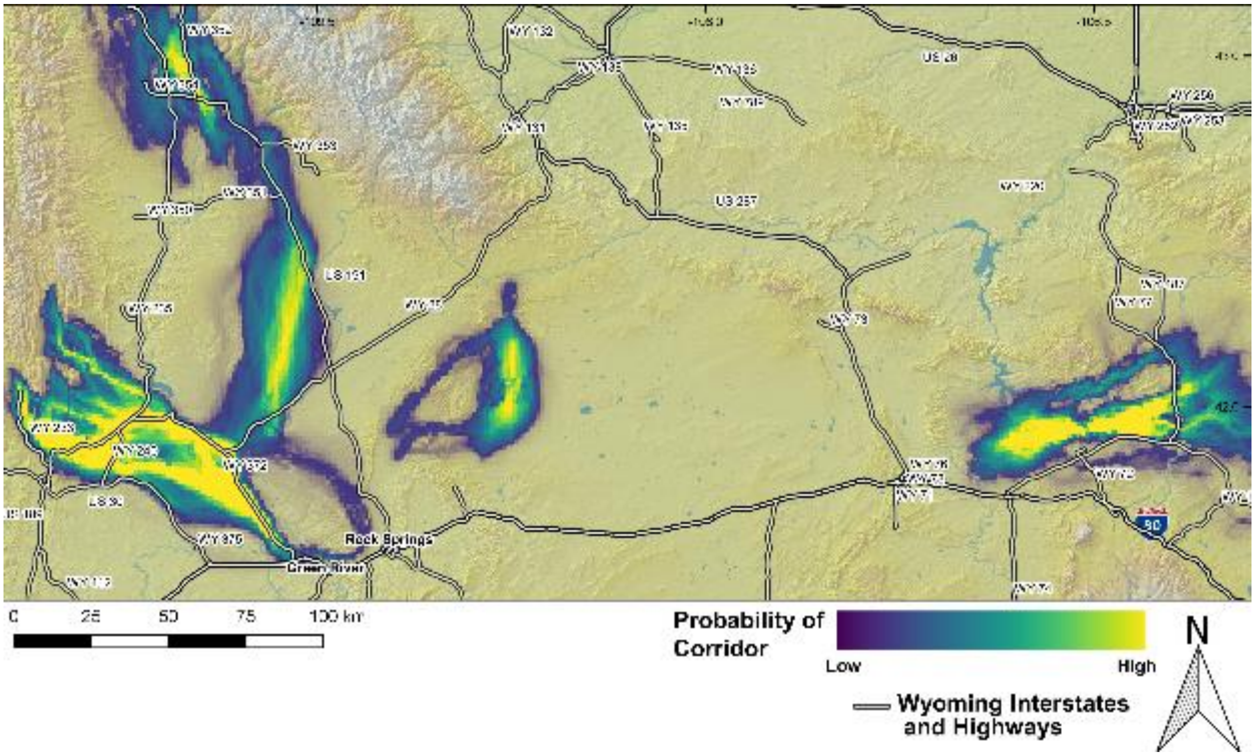
Pronghorn seasonal movements in the Sublette and Medicine Bow populations were best explained by the full connectivity model with six predictors (Fig. 5, Fig. 6), as the AICs of the full model were lower than the next-lowest AIC models with a ΔAIC ranging from 6 (Medicine Bow in the spring) to 124 (Sublette in the spring). Likewise, the full models had substantially lower AIC compared to the null connectivity models with ΔAIC ranging from 717 (Sublette in the autumn) to 1375 (Sublette in the spring). Across seasons and populations, migrating pronghorn were inhibited both by higher slope and areas closer to rivers (Table 1, coefficients not overlapping 0 at the 95 percent confidence interval in bold). Pronghorn migrations in the Sublette population in autumn were facilitated in habitats closer to roads, but pronghorn in the Medicine Bow population were inhibited closer to roads in both the autumn and spring. Pronghorn autumn migrations were not affected by vegetation, but in the spring, pronghorn were facilitated by sagebrush cover and inhibited by herbaceous cover. Cross-validating the connectivity models using held-out pronghorn migrations from other populations, pronghorn autumn migrations were significantly better predicted by each of the two connectivity models than by a null (straight line) model (paired t-test, p-value of 0.0006 using the Sublette model, and p-value of 0.0001 using the Medicine Bow model; Table 2). Autumn migration routes from the least cost corridor models were between 133 km^2 and 344 km^2 more efficient at containing 95 percent of GPS points as the null corridors predicted from the null model, indicating that the least cost model is more predictive than a straight line null.[27] In contrast, pronghorn spring migrations were not significantly better predicted compared to the null model (paired two sample t-test, p-value of 0.615 using the Sublette model, and p-value of 0.328 using the Medicine Bow model; Table 2). Pronghorn spring migrations used to cross validate were on average 20 km shorter than autumn migrations. In our second cross-validation, we compared the sum cost of the used migration track to 99 randomly sampled migration tracks. In the autumn, the percentiles for the cost of pronghorn migration tracks relative to the available costs were 0.031 (Sublette model) and 0.022 (Medicine Bow model). In the spring, the percentiles for the cost of pronghorn migration tracks relative to the available costs were 0.052 (Sublette model) and 0.073 (Medicine Bow model).

Predicting pronghorn migration routes across I80, we found four overall corridor networks linking seasonal ranges: a) east of Lyman, b) north and south of Wamsutter, c) east of Rawlins, and d) west of Laramie, Wyoming (Fig. 7, Fig. 8, where the areas overlapping with the spring connectivity layer are higher for visualization purposes). Of pronghorn crossing locations between 2009 and 2019, for the autumn and spring connectivity layers, there were significantly more pronghorn crossings within the highest predicted connectivity than expected by chance (Fig. 9). The number of attempted crosses within our predicted connectivity surface was significantly greater than a random distribution as no random iteration in the autumn, and only one iteration in the spring had a ratio greater than or equal to the observed ratio (autumn p-value less than 0.001, spring p-value less than 0.001).



Source: Benjamin Robb

Figure 5. Map. Predicted autumn corridors for the Sublette and Medicine Bow populations.



Source: Benjamin Robb

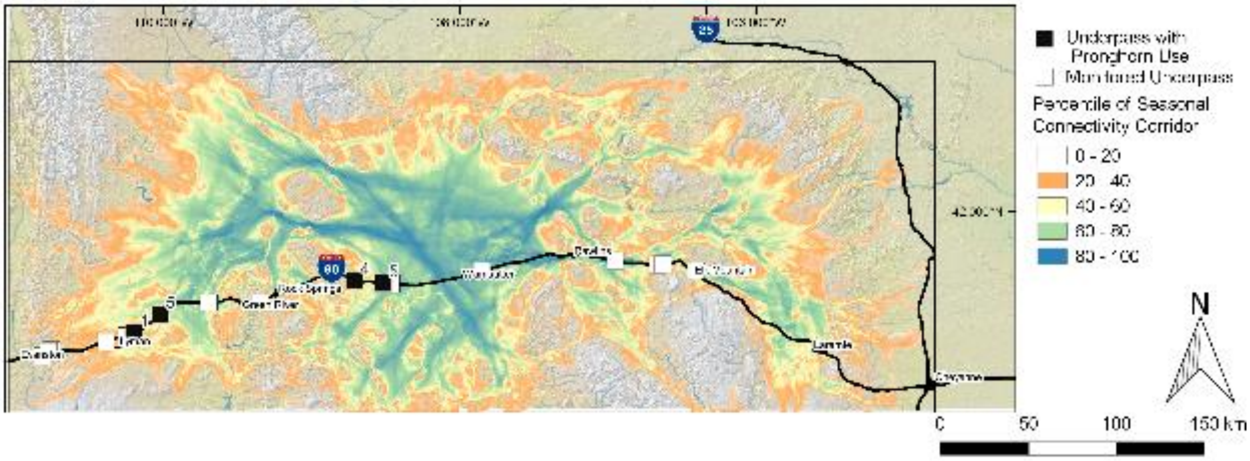
Figure 6. Map. Predicted spring corridors for the Sublette and Medicine Bow populations.

Table 1. Beta coefficients of conductivity for connectivity models of pronghorn migrations.

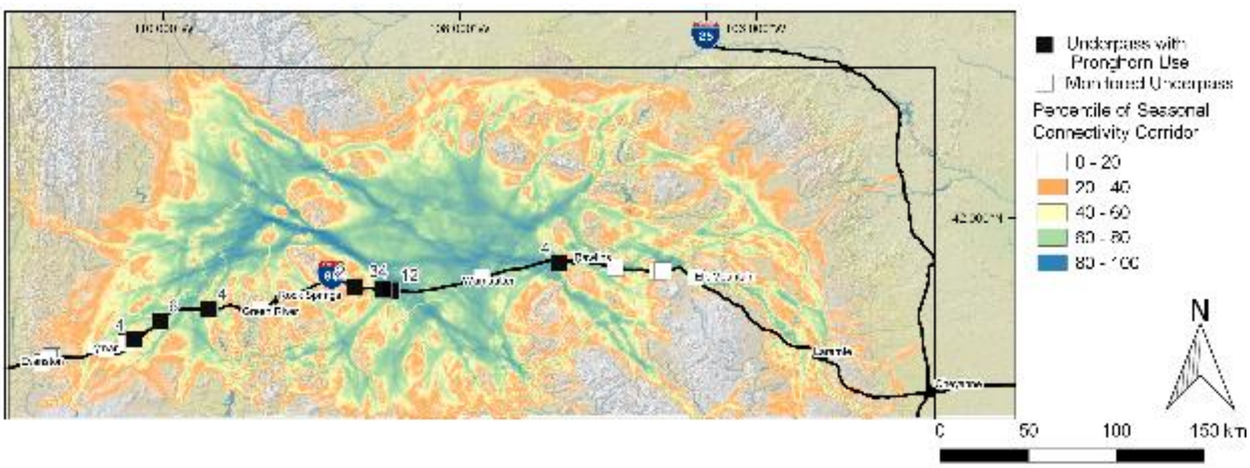
Season	Parameters	Sublette Coefficient	Confidence Interval	Medicine Bow Coefficient	Confidence Interval
Autumn					
	Slope	**-1.204**	**(-1.730, -0.678)**	**-0.618**	**(-0.770, -0.467)**
	Aspect	-0.019	(-0.146, 0.108)	0.043	(-0.029, 0.115)
	Distance to Rivers	**0.822**	**(0.507, 1.136)**	**0.601**	**(0.264, 0.938)**
	Distance to Roads	**-0.404**	**(-0.709, -0.099)**	**1.288**	**(1.041, 1.536)**
	Sagebrush Cover	0.075	(-0.171, 0.322)	-0.067	(-0.499, 0.364)
	Herbaceous Cover	-0.215	(-0.635, 0.204)	-0.231	(-0.521, 0.058)
Spring					
	Slope	**-0.820**	**(-1.124, -0.516)**	**-1.102**	**(-1.323, -0.882)**
	Aspect	-0.056	(-0.169, 0.057)	0.060	(-0.026, 0.145)
	Distance to Rivers	**0.814**	**(0.451, 1.176)**	**0.884**	**(0.570, 1.197)**
	Distance to Roads	-0.127	(-0.406, 0.151)	**1.603**	**(1.219, 1.986)**
	Sagebrush Cover	**0.371**	**(0.194, 0.548)**	**0.306**	**(0.057, 0.555)**
	Herbaceous Cover	**-0.455**	**(-0.796, -0.114)**	**-0.955**	**(-1.233, -0.678)**

Table 2. Cross-validation of connectivity model using held-out pronghorn migrations.

Season	Model Training Herd	Surface Type	Average Area (km^2) of Corridor	n	p-value
Autumn					
	Sublette	Null	1450.287	30	< 0.001
		Least Cost Surface	1106.317		
	Medicine Bow	Null	1450.287	30	< 0.001
		Least Cost Surface	1316.977		
Spring					
	Sublette	Null	388.412	50	0.615
		Least Cost Surface	395.028		
	Medicine Bow	Null	388.501	50	0.328
		Least Cost Surface	377.885		



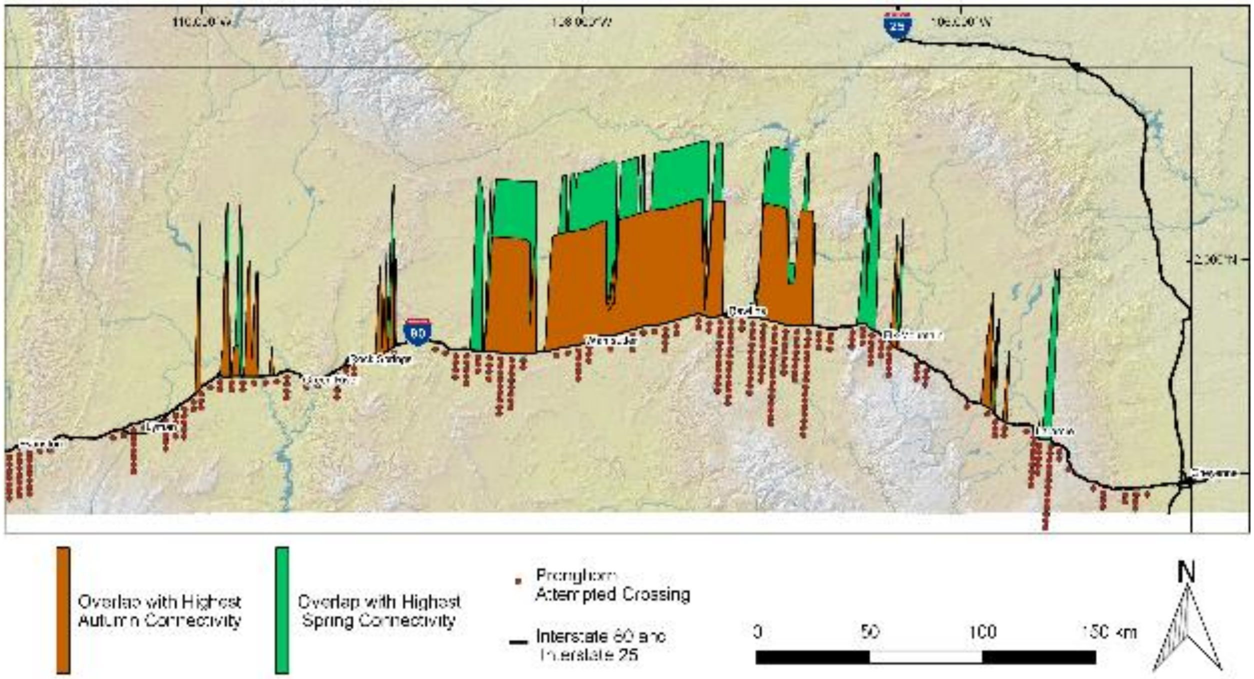
Subfigure A. Predicted migration routes in the autumn.



Source: Benjamin Robb

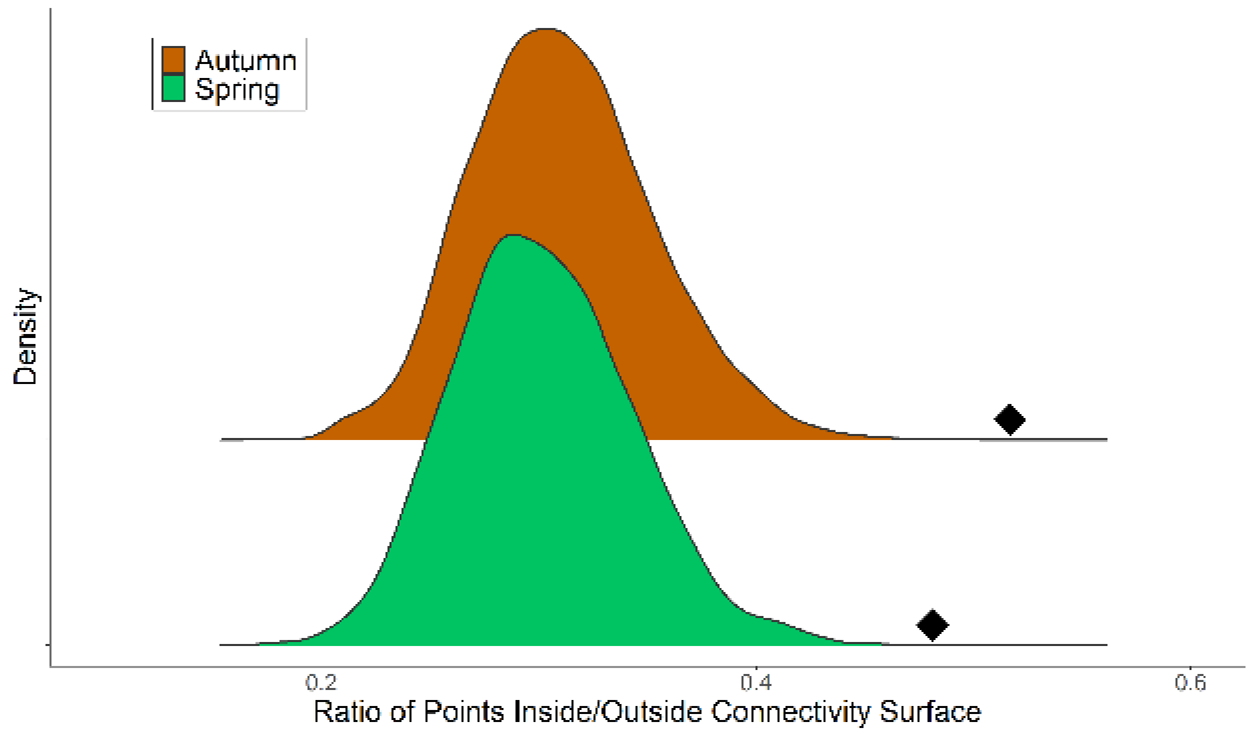
Subfigure B. Predicted migration routes in the spring.

Figure 7. Maps. Predicted migration routes for pronghorn across Interstate 80.



Source: Benjamin Robb

Figure 8. Map. Areas along I80 that overlap with the highest autumn and spring connectivity with red dots illustrating attempted crossings by pronghorn.



Source: Benjamin Robb

Figure 9. Graph. Randomly sampled ratios of pronghorn crossings within predicted connectivity surfaces and the observed ratio of pronghorn attempted crossings (diamonds).

CHAPTER 5. PRONGHORN AND MULE DEER USE OF UNDERPASSES

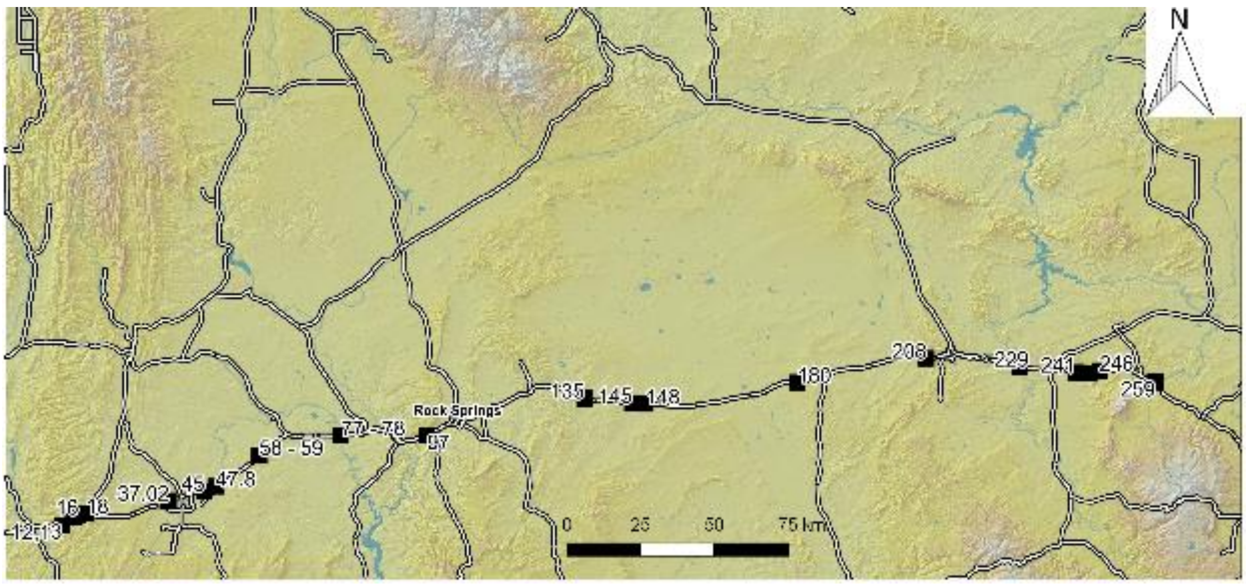
Several underpasses exist along I80, including machinery underpasses, box culverts, span bridges over drainages, and highway interchanges. These underpasses were designed for a variety of purposes from road interchanges, to river crossings, to wildlife structures. These underpasses vary considerably in size, design, and nearby topography, as well as associated fences. We visited each structure and selected a subsample of these for further monitoring for potential wildlife use. Some of these passageways were designed for wildlife, but at least initially, many of the passageways under I80 were implemented for livestock or traffic purposes. Nonetheless, even passageways not designed for wildlife can still be valuable contributions to wildlife movement. Studies on roe deer and moose in Sweden have noted that non-wildlife underpasses designed for humans or livestock can still be used by wildlife.[77] Often times, whether non-wildlife underpasses are located within habitat can be as important to their use by wildlife as the structural design of the underpass.[48] Regardless of their initial design and purpose, there could still be many non-wildlife underpasses used by wildlife along I80.

In the 1970s, Lorin Ward led research on mule deer movement along I80 between mile markers 238.1 and 246 at Dana Ridge (Appendix, Image 1). This research located a mule deer movement corridor facilitated by the machinery underpass at mile marker 243.9. Over two decades later, research led by Kelly Gordon and Stanley Anderson found that this machinery underpass was still an important bottleneck being traversed by migrating mule deer.[78] This section of I80 between Arlington and Walcott Junction has been extensively studied, yet the larger swath of I80 remains poorly understood. Whether, and where, similar migration bottlenecks might still exist for mule deer and pronghorn remains an important question to managers.

By monitoring underpasses for wildlife use, we can identify locations that could be important bottlenecks to wildlife movement. Locating and modifying such underpasses can be a cost-effective management solution to further promote wildlife movement. Although wildlife might already be using such underpasses, they can be prioritized to better promote movement by retroactively changing the structure and design of the underpass. Management actions to better promote movement can include expanding the 'openness' of the underpass and guiding game-proof fencing through or to the underpass, such as at mile marker 243.9. Moreover, because adjacent fencing may be discouraging use by pronghorn or deer, identifying these structures where fences can be modified or removed could further facilitate wildlife use.

Methods

We estimated counts of pronghorn using underpasses along the interstate between October and December 2018 (autumn, n of 23) and March and June of 2019 (spring, n of 24). These underpasses were selected because they had an opening to the sky in the middle, were not tunnels, were not paved roads, and had no cattle guards at the entrance (Fig. 10, numbers indicate nearest mile marker of the underpass). Three box culverts or tunnel underpasses were also monitored because they showed signs of use by wildlife. We used one or two Bushnell trail cameras to monitor use at each underpass, where cameras were set up on the eastern or western side of the structure, usually on the right-of-way fencing along the underpass. Cameras were installed facing perpendicular to the openings of the underpass to monitor any wildlife use. For each season we counted total pronghorn and mule deer using these underpasses facing in either direction, using a time threshold of three minutes between pictures to identify unique crossing events. Within each crossing event, we counted the maximum number of individual pronghorn within a given picture. We also counted the facing direction of each mule deer and pronghorn, north or south. To identify potential migration routes, we subtracted the number of mule deer or pronghorn moving north by the number moving south during the fall and compared this to net numbers observed in the spring. This gave us a net difference of movement, where a positive number shows net movement primarily north, while a negative number shows net movement primarily south.



Source: Benjamin Robb

Figure 10. Map. Underpasses we monitored with trail cameras.

Results and Discussion

Pronghorn rarely used underpasses, which confirms previous studies on pronghorn behavior (Table 3, Table 4). However, we observed some pronghorn use of machinery underpasses within the Bitter Creek area, and through span bridges along rivers. The highest-used underpass was at mile marker 145 near Table Rock, Wyoming, which had a total of 35 pronghorn moving through (Fig. 11, where each point above I80 illustrates one pronghorn that moved north and below I80 one pronghorn that moved south). This underpass was unfenced at the entrances, wide, and overlapped with both pronghorn seasonal habitats and corridors from Chapter 4. There were much greater numbers of mule deer using underpasses (Fig. 12, where each point above I80 illustrates ten mule deer that moved north and below I80 ten mule deer that moved south). The highest used underpass was at Dana Ridge at mile marker 243.9, which had a total of 627 mule deer move through in the autumn and 388 in the spring. This is consistent with prior studies by Ward and others[25,30] as previously described and is currently within a designated migration corridor. In the autumn, there was a net movement of 307 mule deer that moved north. In the spring, there was a net movement of 216 moving south. Potential underpasses between mile markers 12 and 18 were primarily used by resident mule deer, as there were relatively equal numbers of mule deer facing north as facing south. The underpasses in the area between Evanston, Wyoming, and Mountain View, Wyoming, had substantially less use in the spring, which was likely because snowdrifts blocked the passage of most of these underpasses, or there was a high winter mortality rate of deer within this population. From observation during camera retrieval, there was substantial ROW damage at the underpasses between mile markers 15 and 18, which may have contributed to the low use of the underpasses themselves. The use of these underpasses could be further improved by using game-proof fencing following the sides of the underpass, similar to the underpass at mile marker 243.9 (Image 1).

Overall, our results indicated that although pronghorn rarely used these underpasses, they mostly did so in areas predicted by our connectivity maps (Fig. 7, Fig. 11). Importantly, of the five underpasses within the highest connectivity from our connectivity maps, three had either completely or partially fenced entrances. To be most viable, pronghorn populations need to be able to move between habitats.[11] It would likely be a valuable management strategy to mitigate these fenced underpasses located within areas of high connectivity by raising the bottom-wire to no less than 16 inches and ensuring it is smooth wire to permit pronghorn passage.[79] Locations of carcasses and underpass crossings indicate that pronghorn are still attempting to access habitat on both sides of I80, but the barrier effect constrains the number of pronghorn and their success rate.

Table 3. Autumn counts of mule deer and pronghorn movements in underpasses.

Nearest Mile Marker	Longitude	Latitude	Type	Pronghorn North	Pronghorn South	Pronghorn Net	Pronghorn Total	Mule Deer North	Mule Deer South	Mule Deer Net	Mule Deer Total
12 - 13	-110.823	41.272	Machinery Underpass	0	0	0	0	122	102	20	224
15 - 16	-110.777	41.294	Machinery Underpass	0	0	0	0	78	57	21	135
16	-110.757	41.303	Machinery Underpass	0	0	0	0	260	228	32	488
18	-110.727	41.306	Box Culvert	0	0	0	0	105	93	12	198
37.02	-110.390	41.345	Machinery Underpass	0	0	0	0	0	0	0	0
45	-110.246	41.374	Span Bridge	0	0	0	0	0	0	0	0
47.8	-110.201	41.389	Span Bridge	1	0	1	1	0	0	0	0
58 - 59	-110.024	41.483	Machinery Underpass	1	4	-3	5	0	0	0	0
77 - 78	-109.694	41.543	Span Bridge	0	0	0	0	24	16	8	40
77 - 78	-109.694	41.543	Span Bridge	0	0	0	0	20	17	3	37
97	-109.346	41.543	Machinery Underpass	0	0	0	0	0	0	0	0
135	-108.711	41.655	Machinery Underpass	4	0	4	4	0	0	0	0
145	-108.517	41.641	Machinery Underpass	3	2	1	5	0	0	0	0
148	-108.463	41.638	Machinery Underpass	0	0	0	0	0	0	0	0
180	-107.850	41.703	Machinery Underpass	0	0	0	0	0	0	0	0
229	-106.949	41.751	Span Bridge	0	0	0	0	21	27	-6	48
229	-106.949	41.751	Span Bridge	0	0	0	0	8	5	3	13
241	-106.725	41.733	Box Culvert	0	0	0	0	91	72	19	163
242	-106.695	41.730	Box Culvert	0	0	0	0	7	7	0	14
243 - 244	-106.666	41.731	Machinery Underpass	0	0	0	0	467	160	307	627
246	-106.627	41.739	Machinery Underpass	0	0	0	0	5	18	-13	23
259	-106.402	41.704	Span Bridge	0	0	0	0	2	0	2	2
259	-106.402	41.704	Span Bridge	0	0	0	0	7	9	-2	16

Table 4. Spring counts of mule deer and pronghorn movements in the underpasses.

Nearest Mile Marker	Longitude	Latitude	Type	Pronghorn North	Pronghorn South	Pronghorn Net	Pronghorn Total	Mule Deer North	Mule Deer South	Mule Deer Net	Mule Deer Total
12 - 13	-110.823	41.272	Machinery Underpass	0	0	0	0	9	22	-13	31
15 - 16	-110.777	41.294	Machinery Underpass	0	0	0	0	24	19	5	43
16	-110.757	41.303	Machinery Underpass	0	0	0	0	18	37	-19	55
18	-110.727	41.306	Box Culvert	0	0	0	0	7	12	-5	19
37.02	-110.390	41.345	Machinery Underpass	0	0	0	0	0	0	0	0
45	-110.246	41.374	Span Bridge	0	0	0	0	0	0	0	0
47.8	-110.201	41.389	Span Bridge	1	3	-2	4	0	0	0	0
58 - 59	-110.024	41.483	Machinery Underpass	4	2	2	6	0	0	0	0
77 - 78	-109.694	41.543	Span Bridge	0	0	0	0	32	26	6	58
77 - 78	-109.694	41.543	Span Bridge	2	2	0	4	3	6	-3	9
97	-109.346	41.543	Machinery Underpass	0	0	0	0	0	0	0	0
135	-108.711	41.655	Machinery Underpass	1	1	0	2	0	0	0	0
145	-108.517	41.641	Machinery Underpass	20	14	6	34	0	0	0	0
148	-108.463	41.638	Machinery Underpass	6	6	0	12	0	0	0	0
180	-107.850	41.703	Machinery Underpass	0	0	0	0	0	2	-2	2
208	-107.327	41.776	Machinery Underpass	2	2	0	4	11	31	-20	42
229	-106.949	41.751	Span Bridge	0	0	0	0	7	8	-1	15
229	-106.949	41.751	Span Bridge	0	0	0	0	23	23	0	46
241	-106.725	41.733	Box Culvert	0	0	0	0	31	37	-6	68
242	-106.695	41.730	Box Culvert	0	0	0	0	18	26	-8	44
243 - 244	-106.666	41.731	Machinery Underpass	0	0	0	0	86	302	-216	388
246	-106.627	41.739	Machinery Underpass	0	0	0	0	9	15	-6	24
259	-106.402	41.704	Span Bridge	0	0	0	0	7	4	3	11
259	-106.402	41.704	Span Bridge	0	0	0	0	20	28	-8	48

Subfigure A. Pronghorn movements in the autumn.

Source: Benjamin Robb

Subfigure B. Pronghorn movements in the spring.

Figure 11. Maps. Pronghorn use of underpasses.

Subfigure A. Mule deer movements in the autumn.

Source: Benjamin Robb

Subfigure B. Mule deer movements in the spring.

Figure 12. Maps. Mule deer use of underpasses.

CHAPTER 6. MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Our study was able to document the movements and seasonal ranges of 89 GPS-collared pronghorn in southwest Wyoming. These data, in collaboration with studies led by Fred Lindzey, Hall Sawyer, and Jeffrey Beck, provide a total sample of 476 pronghorn and their seasonal ranges along the I80 corridor in southern Wyoming. Of this dataset, only six pronghorn have ever successfully crossed I80. These data confirm that I80 is a substantial barrier to movement of pronghorn, which makes any potential pronghorn migrations effectively impossible. Pronghorn do continue to cross I80 in some underpass structures that we monitored, but in low numbers. Additionally, carcass data collected by WYDOT provided evidence that pronghorn attempt to cross the interstate in other locations. The locations of these attempted crossings align with our predictions of where we would expect pronghorn to move, which adds to our confidence that our connectivity maps broadly predict the most likely locations of historical movements prior to the development of I80.

The maps and analyses we produced in our study can be used by managers to locate potential crossing structures to facilitate movements across I80. Such efforts may also enable the reestablishment of historical migrations if and where they once occurred. In the case of pronghorn, overpasses would be most effective at facilitating movement. However, because an overpass to restore pronghorn movements would be a major investment in pronghorn conservation, future work will need to locate at a more fine scale the most productive and feasible locations where crossing structures would succeed. Nonetheless, the input from our study will provide a valuable first step at generalizing the overall areas where crossing structures, and associated game-proof fencing, could restore movements across this nearly impermeable barrier.

We placed cameras on 24 underpass structures crossing under I80. Structures varied in size and design from box like structures to span bridges over water courses. Pronghorn and mule deer used these underpasses, although deer use was much higher than pronghorn use. Pronghorn are generally averse to using underpasses, but fences likely contributed to the low use of some of these underpasses. Many span bridges over rivers, such as the one at mile marker 47.8, are partially fenced so that during spring runoff the area is impassable.

Recommendations

We identified four general areas that were potentially seasonal movement networks that could be ideal locations to restore connectivity using crossing structures:

- East of Lyman: mile posts 59, 68, 71, 72, 74, 76, 114, 116, and 118.
- East and West of Wamsutter: mile posts 147–159, 165 – 178, 181 –186, 188, 191 –200, 202 –203, 205, and 208–210.
- East of Rawlins: mile posts 223 –230, 234, and 237.
- West of Laramie: mile posts 253 –255, 262, 264, 295, 297, 315, and 316.

More fine-scale work will need to identify where the most economically and logistically feasible locations would be for crossing structures. Nonetheless, our analyses indicate that these areas would connect pronghorn habitats in areas where pronghorn are seemingly already attempting to cross, and where they likely moved in the past.

- Pronghorn use of underpasses tended to be highest at the Table Rock area (mile markers 135 – 148) as well as span bridges along rivers. For the purposes of pronghorn habitat connectivity, these areas can be prioritized to better promote connectivity.
- Mule deer use of underpasses was highest at Dana Ridge, as well as the underpasses from mile markers 12 –18 east of Evanston, Wyoming. These underpasses east of Evanston did not have game-proof fencing following their sides (see Image 1 for an example of game-proof fencing), and some had ROW damage. We believe that improving the fencing along the sides, similar to the Dana Ridge area, could be a valuable management tool to promote mule deer habitat connectivity and minimize any chance of vehicle collisions.
- High deer use of structures in the areas east of Evanston warrant further evaluation to better understand how seasonally moving deer are using these structures and what potential impact I80 is having on mule deer in this area.
- We noted that adjacent fencing to underpass structures varies greatly in design, condition, and type. In many cases, fences could be more wildlife friendly. A simple modification in fences could lead to improved wildlife passage at some structures. For example, the fenced entrances to underpasses between mile markers 241 – 246 need to be manually opened to permit wildlife passage aside from jumping over the fence. We believe the bottom wire of these fenced entrances can be modified so that more pronghorn can move under throughout the year.
- It was encouraging to see that many structures received some wildlife use, although low at times. A more detailed evaluation of structure dimensions, fencing, and juxtaposition to landscape features should be conducted and then compared to observed deer and pronghorn use. This may provide a better understanding of how to improve existing and future structures to facilitate wildlife movement.

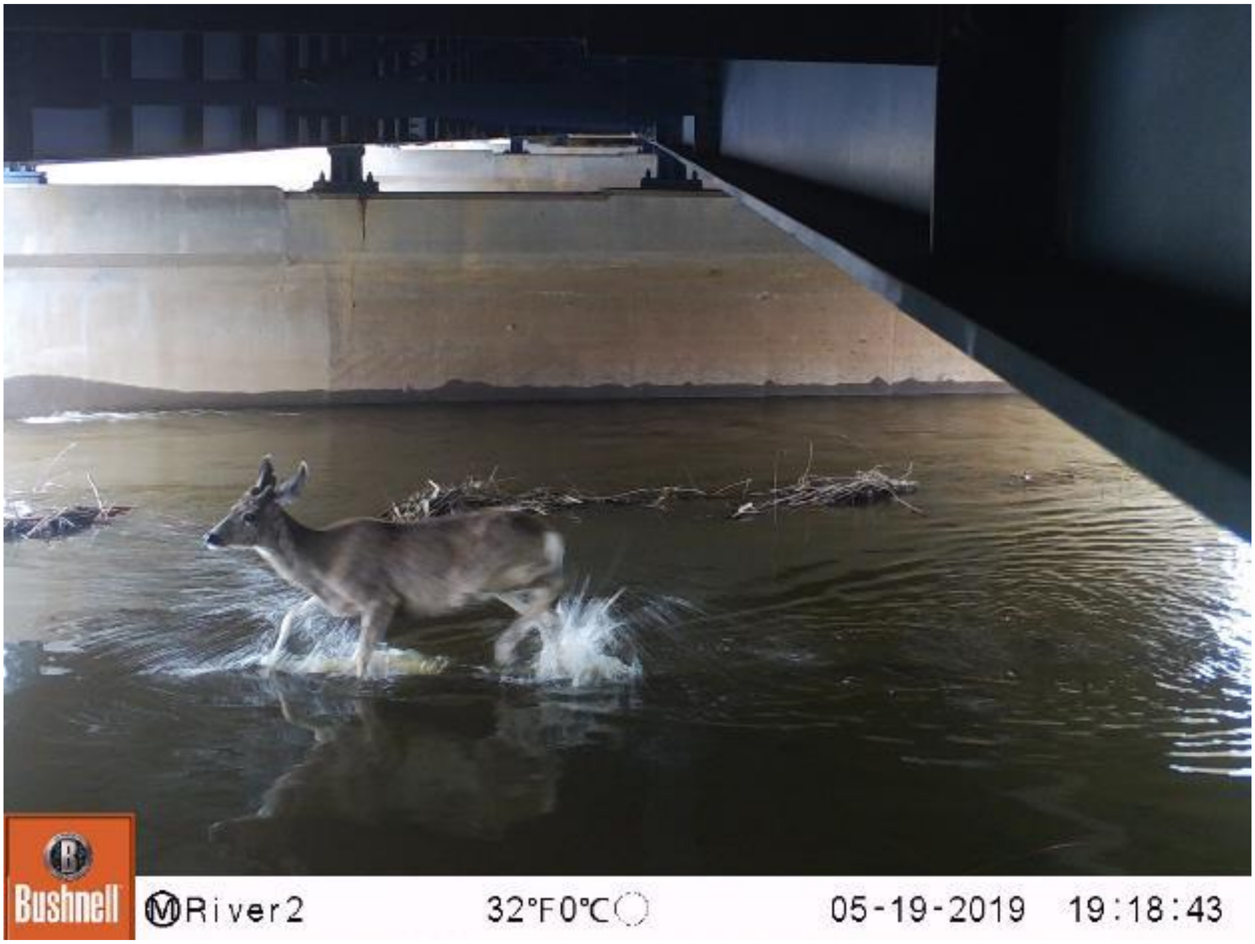
APPENDIX A. IMAGES

Source: Benjamin Robb

Image 1. Machinery underpass at mile marker 243.9 just west of Dana Ridge.

Source: Benjamin Robb

Image 2. The two mule deer using this machinery underpass at Dana Ridge illustrate the high seasonal use of this underpass for migrating mule deer.



Source: Benjamin Robb

Image 3. This span bridge over the Platte River (eastern side, mile marker 229) was primarily used by mule deer, despite the relativley high number of humans within this area.

Source: Benjamin Robb

Image 4. The western side of the Platte River span bridge (mile marker 229) was used by both mule deer and pronghorn, even when seasonal flooding made movement a challenge.

Source: Benjamin Robb

Image 5. The two machinery underpasses we monitored in the Table Rock area (mile markers 145 and 148) were primarily used by pronghorn (and feral horses).

Source: Benjamin Robb

Image 6. This span bridge (mile marker 47.8) had pronghorn use on the western side of the Blacks Fork River despite a fence at the opening.

Source: Benjamin Robb

Image 7. This machinery underpass (mile marker 208) was just west of Rawlins and was moderately used by mule deer and pronghorn.

ACKNOWLEDGEMENTS

We thank Corinna Riginos for her assistance with compiling the pronghorn carcass data. We are extremely appreciative of Enid White (WYDOT) for all of her help assisting us in this project. Hall Sawyer and Jeffrey Beck were data contributors and their help was invaluable to this project. M. Zornes, P. Burke, J. Short, A. Deru, E. Hall, T. Cufaude, L. Knox, H. O'Brien, W. Schultz, and S. Stephens from the Wyoming Game and Fish Department all helped with the planning and implementation of pronghorn captures as well as collar retrieval, along with M. Valdez and P. Lionberger of the BLM Rock Springs Field Office. We thank the graduate students that helped lead the GPS collar projects that contributed to this dataset: D. Sheldon, K. Taylor, A. Reinking, C. Kyle, E. Gelzer, and C. Wallace. Native Range Capture Services provided the aerial support for the safe collaring of pronghorn. Finally, we thank Knobloch Family Foundation, Wyoming Game and Fish Department, Wyoming Department of Transportation, and Wyoming Governor's Big Game License Coalition for additional funding and support throughout this project.

REFERENCES

1. Dingle, H. and Drake, V. A. ‘‘What Is Migration?’’ *BioScience* (2007) doi:10.1641/B570206.
2. Fryxell, J. M. and Sinclair, A. R. E. ‘‘Causes and consequences of migration by large herbivores’’. *Trends in Ecology and Evolution* 3, 237–241 (1988).
3. Mysterud, A., Loe, L. and Zimmermann, B. ‘‘Partial migration in expanding red deer populations at northern latitudes–a role for density dependence?’’ *Oikos* 1817–1825 (2011) doi:10.1111/j.1600-0706.2010.19439.x.
4. Cagnacci, F. *et al.* ‘‘Partial migration in roe deer: Migratory and resident tactics are end points of a behavioural gradient determined by ecological factors’’. *Oikos* 120, 1790–1802 (2011).
5. Sawyer, H. and Kauffman, M. J. ‘‘Stopover ecology of a migratory ungulate’’. *Journal of Animal Ecology* 80, 1078–1087 (2011).
6. Biebach, H., Friedrich, W. and Heine, G. ‘‘Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds’’. *Oecologia* 69, 370–379 (1986).
7. Chapman, B. B., Brönmark, C., Nilsson, J. Å. and Hansson, L. A. ‘‘The ecology and evolution of partial migration’’. *Oikos* 120, 1764–1775 (2011).
8. Grayson, K. L. and Wilbur, H. M. ‘‘Sex- and context-dependent migration in a pond-breeding amphibian’’. *Ecology* 90, 306–312 (2009).
9. Mueller, T. *et al.* ‘‘How landscape dynamics link individual-to population-level movement patterns: a multispecies comparison of ungulate relocation data’’. *Global Ecology and Biogeography* 20, 683–684 (2011).
10. Fryxell, J. M., Greever, J. and Sinclair, A. R. E. ‘‘Why are migratory ungulates so abundant?’’ *The American Naturalist* 131, 781–798 (1988).
11. Barrett, M. W. ‘‘Distribution , behavior, and mortality of pronghorns during a severe winter in Alberta’’. *The Journal of Wildlife Management* 46, 991–1002 (1982).
12. Jakes, A. F., Gates, C. C., DeCesare, N. J., Jones, P. F., Goldberg, J. F., Kunkel, K. E. and Hebblewhite, M. ‘‘Classifying the migration behaviors of pronghorn on their northern range’’. *Journal of Wildlife Management* 82, 1229–1242 (2018).
13. Hoskinson, R. L. and Tester, J. R. ‘‘Migration behavior of pronghorn in southeastern Idaho’’. *The Journal of Wildlife Management* 44, 132–144 (1980).
14. Telfer, E. S. and Kelsall, J. P. ‘‘Adaptation of some large North American mammals for survival in snow’’. *Ecology* 65, 1828–1834 (1984).
15. Kauffman, M. J., Meacham, J. E., Sawyer, H., Steingisser, A. Y., Rudd, W. J. and Ostlind, E. ‘*Wild migrations: Atlas of Wyoming's ungulates*’. (2018).
16. Martinka, C. J. ‘‘Mortality of northern Montana pronghorns in a severe winter’’. *The Journal of Wildlife Management* 31, 159–164 (1967).
17. Oakley, C. and Riddle, P. ‘‘The impact of a severe winter and fences on antelope mortality in southcentral Wyoming’’. in *Proceedings of the Sixth Antelope States Workshop* 155–173 (1974).
18. Ryder, T. J., Irwin, L. L. and Moody, D. S. ‘‘Wyoming's Red Rim pronghorn controversy: History and current status’’. in *Proceedings of the Eleventh Biennial Pronghorn Antelope Workshop* 195–206 (1984).

19. Byers, J. A. '*American pronghorn: Social adaptations and the ghosts of predators past*'. (University of Chicago Press, 1997).
20. O'Gara, B. and Yoakum, J. '*Pronghorn: Ecology and management*'. (University Press of Colorado, 2004).
21. Harrington, J. L. and Conover, M. R. ''Characteristics of ungulate behavior and mortality associated with wire fences''. *Wildlife Society Bulletin* 34, 1295–1305 (2006).
22. Yoakum, J. D., Jones, P. F., Cancino, J., Guenzel, R. J., Seidler, R., Munguia-Vega, A., Cassaigne, I. and Culver, M. ''Pronghorn management guides fifth edition''. in *Twenty-Fifth Biennial Pronghorn Workshop* 159 (2014).
23. Sheldon, D. P. ''Pronghorn movement and distribution patterns in relation to roads and fences in southwestern Wyoming''. (University of Wyoming, 2005).
24. Seidler, R. G., Green, D. S. and Beckmann, J. P. ''Highways, crossing structures and risk: Behaviors of Greater Yellowstone pronghorn elucidate efficacy of road mitigation''. *Global Ecology and Conservation* 15, e00416 (2018).
25. Goodwin, G. A. and Ward, A. L. '*Mule deer mortality on Interstate 80 in Wyoming: Causes, patterns, and recommendations*'. (1976).
26. Sawyer, H., Lebeau, C. and Hart, T. ''Mitigating roadway impacts to migratory mule deer-a case study with underpasses and continuous fencing''. *Wildlife Society Bulletin* 36, 492–498 (2012).
27. Robb, B. S. ''Pronghorn migrations and barriers: Predicting corridors across Wyoming's Interstate 80 to restore movement''. (University of Wyoming, 2020).
28. Sundstrom, C. '*Some factors influencing pronghorn antelope distribution in the Red Desert of Wyoming*'. (1969).
29. Lacava, M. E. F., Gagne, R. B., Stowell, S. M. L., Gustafson, K. D., Buerkle, C. A., Knox, L. and Ernest, H. B. ''Pronghorn population genomics show connectivity in the core of their range''. *Journal of Mammalogy* 1–11 (2020) doi:10.1093/jmammal/gyaa054.
30. Ward, L. A. '*Mule deer behavior in relation to fencing and underpasses on Interstate 80 in Wyoming*'. (1982).
31. Plumb, R. E., Gordon, K. M. and Anderson, S. H. ''Pronghorn use of a wildlife underpass''. *Wildlife Society Bulletin* 31, 1244–1245 (2003).
32. Sawyer, H., Rodgers, P. A. and Hart, T. ''Pronghorn and mule deer use of underpasses and overpasses along U.S. Highway 191''. *Wildlife Society Bulletin* 40, 211–216 (2016).
33. Deblinger, R. D. and Alldredge, A. W. ''Migratory patterns of pronghorn in the Red Desert, Wyoming''. in *Proceedings of the Eleventh Biennial Pronghorn Antelope Workshop* 90–91 (1984).
34. Reinking, A. K., Smith, K. T., Monteith, K. L., Mong, T. W., Read, M. J. and Beck, J. L. ''Intrinsic, environmental, and anthropogenic factors related to pronghorn summer mortality''. *Journal of Wildlife Management* 82, 608–617 (2018).
35. Taylor, K. L., Beck, J. L. and Huzurbazar, S. V. ''Factors influencing winter mortality risk for pronghorn exposed to wind energy development''. *Rangeland Ecology and Management* 69, 108–116 (2016).
36. Bjørneraas, K., Van Moorter, B., Rolandsen, C. M. and Herfindal, I. ''Screening global positioning system location data for errors using animal movement characteristics''. *Journal of Wildlife Management* 74, 1361–1366 (2010).
37. Gavin, S. D. and Komers, P. E. ''Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk?'' *Canadian Journal of Zoology* 84, 1775–1780 (2006).

38. Dodd, N. L., Gagnon, J. W., Sprague, S., Boe, S. and Schweinsburg, R. E. '*Assessment of pronghorn movements and strategies to promote highway permeability: US Highway 89*'. http://trid.trb.org/view.aspx?id=1118656 (2011).
39. Gates, C. C., Jones, P., Suitor, M., Jakes, A., Boyce, M. S., Kunkel, K. and Wilson, K. ''The influence of land use and fences on habitat effectiveness, movements and distribution of pronghorn in the grasslands of North America''. in *Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes?* (eds. Somers, M. J. & Hayward, M. W.) 227–290 (2012). doi:10.1007/978-1-4614-0902-1.
40. Clevenger, A. P. and Waltho, N. ''Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals''. *Biological Conservation* 121, 453–464 (2005).
41. Sawyer, H., Lindzey, F. and McWhirter, D. ''Mule deer and pronghorn migration in western Wyoming''. *Wildlife Society Bulletin* 33, 1266–1273 (2005).
42. Berger, J., Cain, S. L. and Berger, K. M. ''Connecting the dots: an invariant migration corridor links the Holocene to the present.'' *Biology Letters* 2, 528–531 (2006).
43. Soanes, K., Taylor, A. C., Sunnucks, P., Vesk, P. A., Cesarini, S. and van der Ree, R. ''Evaluating the success of wildlife crossing structures using genetic approaches and an experimental design: Lessons from a gliding mammal''. *Journal of Applied Ecology* 55, 129–138 (2018).
44. Huijser, M. P., McGowen, P., Fuller, J., Hardy, A., Kociolek, A., Clevenger, A. P., Smith, D. and Ament, R. '*Wildlife-vehicle collision reduction study: report to Congress*'. https://www.fhwa.dot.gov/publications/research/safety/08034/08034.pdf (2008).
45. Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M. and Berger, J. ''Global decline in aggregated migrations of large terrestrial mammals''. *Endangered Species Research* 7, 55–76 (2009).
46. Sawyer, H., Kauffman, M. J., Nielson, R. M. and Horne, J. S. ''Identifying and prioritizing ungulate migration routes for landscape-level conservation''. *Ecological Applications* 19, 2016–2025 (2009).
47. Bastille-Rousseau, G., Wall, J., Douglas-Hamilton, I. and Wittemyer, G. ''Optimising the positioning of wildlife crossing structures using GPS telemetry''. *Journal of Applied Ecology* 0–1 (2018) doi:10.1111/1365-2664.13117.
48. Ng, S. J., Dole, J. W., Sauvajot, R. M., Riley, S. P. D. and Valone, T. J. ''Use of highway undercrossings by wildlife in southern California''. *Biological Conservation* 115, 499–507 (2004).
49. Evink, G. '*Interaction between roadways and wildlife ecology: a synthesis of highway practice. National Cooperative Highway Research Program, Synthesis 305. Transportation*'. (2002).
50. Noss, R. F. ''Landscape connectivity: Different functions at different scales''. in *Landscape linkages and biodiversity* vol. 2 27–39 (1991).
51. Chetkiewicz, C.-L. B., St. Clair, C. C. and Boyce, M. S. ''Corridors for conservation: Integrating pattern and process''. *Annual Review of Ecology, Evolution, and Systematics* 37, 317–342 (2006).
52. McCune, B. and Keon, D. ''Equations for potential annual direct incident radiation and heat load stable''. *Journal of Vegetation Science* 13, 603–606 (2002).
53. Weiss, A. D. ''Topographic position and landform analysis''. in *Poster Presentation,*

ESRI Users Conference (2001).
54. U.S.G.S. ‘‘National Hydrography Dataset’’. (2015).
55. Rigge, M., Shi, H., Homer, C., Danielson, P. and Granneman, B. ‘‘Long-term trajectories of fractional component change in the Northern Great Basin, USA’’. *Ecosphere* 10, (2019).
56. Xian, G., Homer, C., Rigge, M., Shi, H. and Meyer, D. ‘‘Characterization of shrubland ecosystem components as continuous fields in the northwest United States’’. *Remote Sensing of Environment* 168, 286–300 (2015).
57. Rigge, M., Homer, C., Cleeves, L., Meyer, D. K., Bunde, B., Shi, H., Xian, G., Schell, S. and Bobo, M. ‘‘Quantifying western U.S. rangelands as fractional components with multi-resolution remote sensing and in situ data’’. *Remote Sensing* 12, 1–26 (2020).
58. Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. and Kausrud, K. ‘‘The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology’’. *Climate Research* 46, 15–27 (2011).
59. Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J. and Stenseth, N. C. ‘‘Using the satellite-derived NDVI to assess ecological responses to environmental change’’. *Trends in Ecology and Evolution* 20, 503–510 (2005).
60. Zeller, K. A., Vickers, T. W., Ernest, H. B. and Boyce, W. M. ‘‘Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study’’. *Plos One* 12, e0179570 (2017).
61. Pitman, R. T. *et al.* ‘‘Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management’’. *Journal of Applied Ecology* 54, 1687–1698 (2017).
62. Muff, S., Signer, J. and Fieberg, J. ‘‘Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation’’. *Journal of Animal Ecology* 89, 80–92 (2020).
63. Johnson, C. J., Nielsen, S. E., Merrill, E. H., Trent, L. and Boyce, M. S. ‘‘Resource selection functions based on use – availability data: Theoretical motivation and evaluation methods’’. *Journal of Wildlife Management* 70, 347–357 (2006).
64. Boyce, M. S., Vernier, P. R., Nielsen, S. E. and Schmiegelow, F. K. A. ‘‘Evaluating resource selection functions’’. *Ecological Modelling* 157, 281–300 (2002).
65. Whittington, J., Hebblewhite, M., Decesare, N. J., Neufeld, L., Bradley, M., Wilmshurst, J. and Musiani, M. ‘‘Caribou encounters with wolves increase near roads and trails: A time-to-event approach’’. *Journal of Applied Ecology* 48, 1535–1542 (2011).
66. Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H. and Matthysen, E. ‘‘The application of “least-cost” modelling as a functional landscape model’’. *Landscape and Urban Planning* 64, 233–247 (2003).
67. McClure, M. L., Hansen, A. J. and Inman, R. M. ‘‘Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data’’. *Landscape Ecology* 31, 1419–1432 (2016).
68. Cushman, S. A., Chase, M. and Griffin, C. ‘‘Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa’’. in *Spatial Complexity, Informatics, and Wildlife Conservation* 1–458 (2010). doi:10.1007/978-4-431-87771-4.
69. McRae, B., Popper, K., Jones, A., Schindel, M., Buttrick, S., Hall, K., Unnasch, B. and Platt, J. ‘*Conserving nature’s stage: Mapping omnidirectional connectivity for resilient terrestrial landscapes in the pacific northwest*’. (2016).

70. Jayadevan, A., Nayak, R., Karanth, K. K., Krishnaswamy, J., Defries, R., Karanth, K. U. and Vaidyanathan, S. ‘‘Navigating paved paradise: Evaluating landscape permeability to movement for large mammals in two conservation priority landscapes in India’’. *Biological Conservation* 247, 108613 (2020).
71. Brennan, A. *et al.* ‘‘Characterizing multispecies connectivity across a transfrontier conservation landscape’’. *Journal of Applied Ecology* 1700–1710 (2020) doi:10.1111/1365-2664.13716.
72. Collingridge, D. S. ‘‘A Primer on quantitized data analysis and permutation testing’’. *Journal of Mixed Methods Research* 7, 81–97 (2013).
73. R Core Team. ‘‘R: A language and environment for statistical computing’’. (2016).
74. Calenge, C. ‘‘The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals’’. *Ecological Modeling* 197, 516–519 (2006).
75. Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. ‘‘glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling’’. *R Journal* 9, 378–400 (2017).
76. van Etten, J. ‘‘gdistance: Distances and routes on geographical grids’’. (2018).
77. Bhardwaj, M., Olsson, M. and Seiler, A. ‘‘Ungulate use of non-wildlife underpasses’’. *Journal of Environmental Management* 273, 111095 (2020).
78. Gordon, K. M. and Anderson, S. H. ‘‘Mule deer use of underpasses in Western and Southeastern Wyoming’’. in *ICOET 2003 Proceedings* (2003).
79. Jones, P. F., Jakes, A. F., Eacker, D. R., Seward, B. C., Hebblewhite, M. and Martin, B. H. ‘‘Evaluating responses by pronghorn to fence modifications across the northern Great Plains’’. *Wildlife Society Bulletin* 42, 225–236 (2018).