




Research Article

Classifying the Migration Behaviors of Pronghorn on Their Northern Range

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ABSTRACT Migration functions as an adaptive strategy to improve fitness by allowing individuals to exploit spatiotemporal gradients of resources. Yet migration, especially among large ungulates, is increasingly threatened by human activities, making it necessary to understand variation in migratory behavior. We identified different movement strategies for pronghorn (*Antilocapra americana*) at the northern limit of the species' range, and tested hypotheses for variation between migratory behaviors. From 2003–2010, we captured 185 female pronghorn across Alberta and Saskatchewan, Canada, and Montana, USA. We identified discrete migratory behaviors, including seasonal migration, facultative winter migration, potential post-fawning migration, and the use of stopover sites. Fifty-five percent of individuals undertook seasonal migrations, and we recorded the longest reported round-trip migration for the species at 888 km. Some (22%) seasonal migrations included ≥ 1 stopover sites, with significantly greater use of stopovers during spring than fall. Migrants (34%) and residents (20%) undertook facultative winter migrations, with the majority (68%) undertaken by migrants. Additionally, 12% of individuals exhibited potential post-fawning migrations. For each season, we estimated a suite of movement metrics and used multivariate statistics to compare movement similarities across migration behaviors. Correspondence analyses revealed 3 groupings of migration behavior. Spring migration was its own grouping, characterized by more sinuous and slower movements, consistent with the forage maturation hypothesis. Fall migration, facultative winter migration, and potential post-fawning migration clustered in a single group that displayed linear, fast movements, consistent with being influenced by ecologically limited resources such as severe winters or predation avoidance. Lastly, spring and fall stopover sites were grouped together as a means to use high-quality forage during migration, also consistent with the forage maturation hypothesis. At the northern periphery of pronghorn range, differences between migratory behaviors are influenced by various ecological factors, merit increased attention, and contribute to overall persistence. © 2018 The Wildlife Society.

KEY WORDS *Antilocapra americana*, facultative winter migration, net squared displacement, Northern Sagebrush Steppe, post-fawning migration, pronghorn, seasonal migration, stopover sites.

Migration is a large-scale movement strategy common across taxa caused by complex interactions between exogenous (i.e.,

ecological requirements and environmental cues) and endogenous (i.e., learned traits and demography) factors that animals undertake to improve fitness across spatiotemporal gradients (Dingle and Drake 2007). Migration in ungulates can generally be defined as a seasonal round-trip movement between discrete areas (Berger 2004). Migratory movements generally consist of 2 major components: the migratory pathway and stopover sites along this pathway (Sawyer and Kauffman 2011). Most ungulate populations are partially migratory, defined as a population with a percentage of individuals that migrate and others that remain residents (Dingle and Drake 2007). Yet in partially migratory populations, it is unclear why individuals within a population

Received: 9 December 2016; Accepted: 9 March 2018

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use various movement strategies. Theory suggests that individuals balance trade-offs between costs (e.g., predation, parasites) and benefits (forage, reduced snow) that regulate the proportion of the population migrating (Fryxell and Sinclair 1988, Bolger et al. 2007, Hebblewhite and Merrill 2011). Regardless of the mechanism(s) maintaining partial migration, migratory movements are plastic in ungulates (Cagnacci et al. 2011). Identifying and quantifying varying migratory behaviors is important for facilitating a more holistic approach to conserving ungulates (Bolger et al. 2007).

Ungulate migrations occur worldwide and respond specifically to forage productivity gradients in space and time in Africa (Wilmschurst et al. 1999), Asia (Singh et al. 2010), and North America (Hebblewhite et al. 2008). In the Northern Hemisphere, spring migrations allow ungulates to take advantage of improving forage quality for 2 main purposes. First, migrating adults meet nutritional requirements and restore depleted energetic reserves lost during winter. Second, spring migration allows adults to invest in reproduction (Parker et al. 2009). Termed the forage maturation hypothesis (FMH) because of the trade-off between plant growth and forage quality at intermediate forage biomass levels, or by following the green wave, theory predicts that ungulates will migrate following green up of high-quality forage in seasonal environments to meet these requirements (Fryxell and Sinclair 1988, Myrsetrud 2013).

Migration in search of high-quality forage during spring can also benefit ungulates by reducing predation risk and density-dependent competition (Fryxell and Sinclair 1988, Myrsetrud et al. 2011). Ungulates may use stopovers sites along migration pathways to increase foraging events at high-quality sites (Sawyer and Kauffman 2011). During spring, migratory ungulates temporally match movements with increasing forage quality; thus, under the FMH we expect that spring migratory movements should be more sinuous and slower to move through the green wave than fall migratory movements (Sawyer and Kauffman 2011). Some ungulates display post-birthing migration after parturition, where offspring follow females to areas that provide essential resources and to rejoin larger groups to decrease predation risk (DeMars et al. 2016), whereas others migrate before parturition (Milner-Gulland et al. 2011). Ungulates may also have distinct movement patterns that can be altered based on changes in reproductive status (Singh and Ericsson 2014).

In fall, forage senesces and environmental conditions change, prompting ungulates to move to seek improved forage conditions (Hoskinson and Tester 1980, Albon and Langvatn 1992). Ungulate migration during fall is also likely affected by winter conditions, such as snow depth, that limit winter range (Mautz 1978, Fieberg et al. 2008). Likewise, the combination of limiting winter conditions and the brown wave of senescence will influence ungulates to initiate fall-winter migrations more rapidly than spring, and thus migratory movements should be faster, more linear, and of shorter duration. Especially for smaller ungulates that are more sensitive to snow depth (Telfer and Kelsall 1984), individuals may display low fidelity to specific winter ranges, undertaking facultative migratory movements (facultative

winter migration hereafter). Facultative winter migrations are defined as migrations from one winter range to another in response to extreme environmental conditions (winter severity and extreme snowfall); they are presumed to enhance body condition and chances of survival (Bruns 1977, Dingle and Drake 2007). Discriminating between typical seasonal migrations and these facultative winter migrations could provide insights into limiting conditions for ungulates, especially at northern regions (Barrett 1982, Poole and Mowat 2005).

Pronghorn (*Antilocapra americana*) are a highly vagile species, the fastest land mammal in North America, and occur across the prairies, intermountain valleys, and sagebrush steppes of western North America. We compared characteristics of seasonal migration (e.g., spring, fall) for adult female pronghorn migration at the northern periphery of their range in Alberta, Saskatchewan, and Montana in the Northern Sagebrush Steppe ecoregion (hereafter NSS; Fig. 1). Despite a growing conservation focus on pronghorn long-distance movement (Berger 2004), little is known about the migratory ecology for this species. Pronghorn populations are often partially migratory (Berger 2004, White et al. 2007, Kolar et al. 2011), and we anticipated that populations at the northern range periphery would show the longest migrations and display the highest prevalence of migration because of spatiotemporal variability in resource abundance. For example, Teitelbaum et al. (2015) and Mueller et al. (2011) reported that animal migration distance increased at northern latitudes with increasing spatiotemporal variation in normalized difference vegetation index (NDVI) for migratory ungulates. Consequently, we anticipated that pronghorn use stopover sites (Seidler et al. 2015) more frequently during spring than fall migration to match temporal latitudinal gradients of forage quality. Thus, we expected pronghorn to follow the forage productivity pulse during spring migration, displaying slower, more tortuous migratory paths with more stopovers to reach summer range than during fall migration (Sawyer et al. 2009). In contrast to spring, we projected that like many other ungulates, fall migration would be influenced by forage senescence (Hoskinson and Tester 1980) or forage senescence and snowfall (Fieberg et al. 2008). Therefore, we expected that fall migrations would show higher movement rates, have less tortuosity, be shorter in duration and distance, and use fewer stopovers to reach winter range (Fieberg et al. 2008). Although many ungulates show high fidelity to winter ranges, pronghorn show lower fidelity in part because they are susceptible to accumulating snow and are thought to continue to move in search of lower snow depths under severe winter conditions (Bruns 1977). Therefore, we also anticipated that facultative winter migrations could be identified after the classic fall migration period.

Our objectives were to examine broad predictions of the FMH based on comparing movement metrics during different migratory behaviors of pronghorn. First, we predicted that pronghorn at their northern range would undertake longer seasonal migrations and have a higher proportion of migratory individuals compared to other areas across pronghorn range

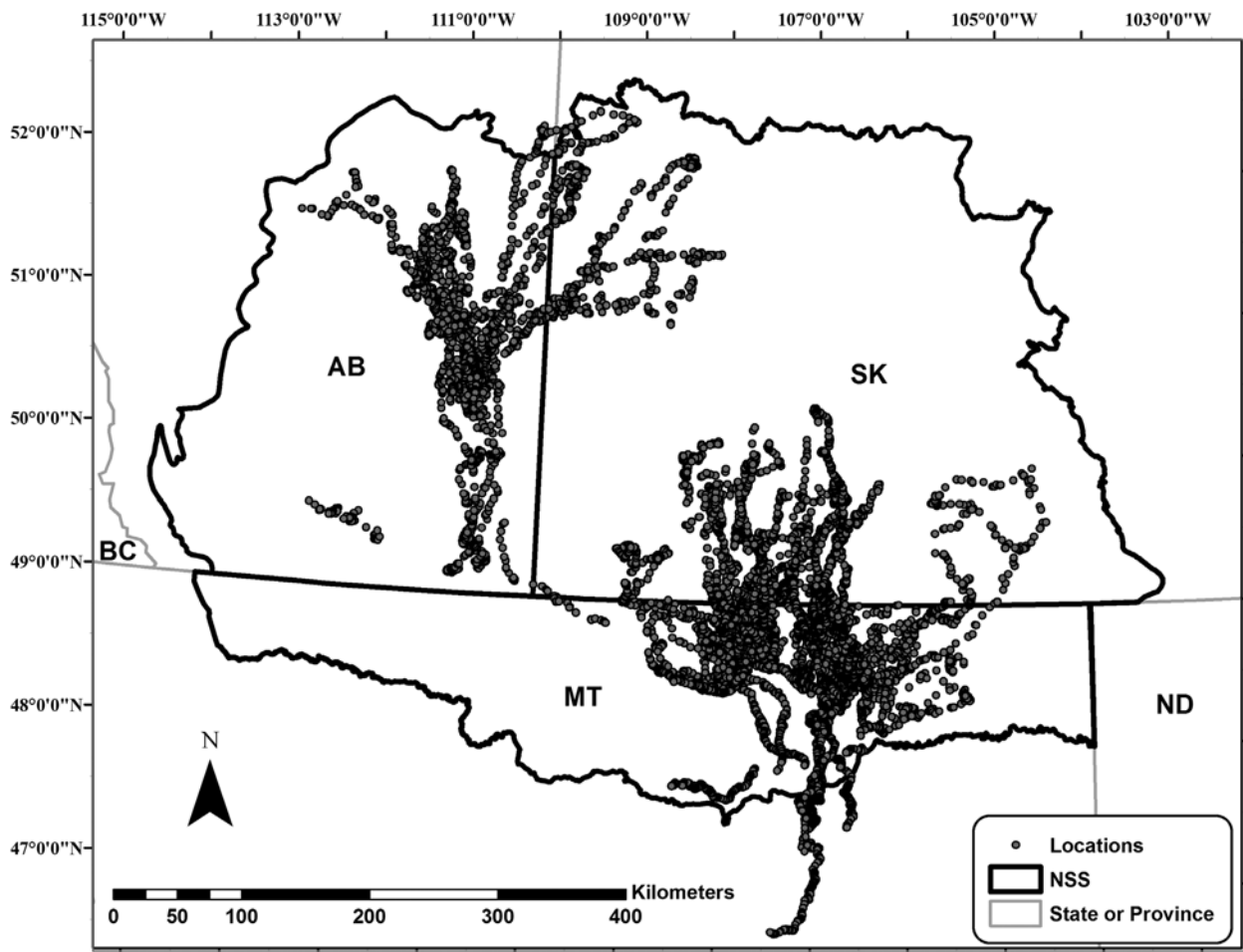


Figure 1. The Northern Sagebrush Steppe (NSS) with pronghorn migration relocations, 2003–2011.

(Mueller et al. 2011, Teitelbaum et al. 2015). Second, we predicted a greater proportion of stopover sites identified during spring compared to fall migration (Sawyer and Kauffman 2011, Seidler et al. 2015). Third, we predicted that pronghorn would undertake slower, longer in duration, and more sinuous migrations compared to fall which would be faster, shorter in duration, and more linear migrations. Fourth, we predicted that pronghorn would engage in fast and direct facultative winter migrations on their northern range to escape limiting conditions and locate suitable winter ranges (Bruns 1977, Fieberg et al. 2008). Lastly, we predicted multivariate analysis would indicate that spring migrations would be dissimilar to all other movements because they are influenced by forage phenology gradients (Bischof et al. 2012, Myserud 2013). In contrast, we expected fall migration, facultative winter migrations, and potential post-fawning migration behaviors to be more similar in characteristics because of their faster nature. We expected stopover sites to yield dissimilar metrics from different migration periods (Sawyer and Kauffman 2011).

STUDY AREA

We studied pronghorn migratory movements across the NSS from 2003–2011. The study area encompassed 315,876 km²

of the prairie regions of Alberta, Saskatchewan, and northern Montana. The landscape is characterized as flat with open plains and rolling hills as a result of glacial recession and deposits. Rivers and other waterways have exposed badlands, creating deep coulees throughout the region (Mitchell 1980). The region is considered semi-arid, receiving an annual mean of 392 mm of precipitation, with approximately 70% as rainfall (Environment Canada 2010). Approximate seasonal start dates for winter, spring, summer, and fall are 21 December, 20 March, 21 June, and 22 September, respectfully. The study area experienced severe winter conditions from 2008–2011, especially during the winter of 2010–2011 when mean temperatures were below average and snow accumulation broke regional records (Appendix A). Habitat across the region is a mosaic of native prairie, pastures, and irrigated and dryland agricultural fields. In general, native grassland species include needle and thread grass (*Stipa comata*), June grass (*Koeleria cristata*), and blue grama (*Bouteloua gracilis*). Evergreen shrubs include silver sagebrush (*Artemisia cana*), big sagebrush (*Artemisia tridentata*), and horizontal juniper (*Juniperus horizontalis*). Forbs and other native vegetation include American silverberry (*Elaeagnus commutate*), western snowberry (*Symphoricarpos occidentalis*), and prickly pear cactus (*Opuntia polyacantha*).

Major cultivated crops include alfalfa, peas, canola, wheat, mustard, and hay (Mitchell 1980). Dominant fauna include elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), and greater sage-grouse (*Centrocercus urophasianus*).

Land administration and development varied across the NSS with a mix of 50:50 private to public (e.g., Bureau of Land Management, Crown Land in Canada) land ownership, and a mix of land use throughout the region. Cattle ranches dominate in Alberta and Montana, whereas farming is generally more prevalent in Saskatchewan. Oil and natural gas wells occur at high densities in Alberta and continue to be developed in Montana and Saskatchewan. Relative to other regions in the United States and southern Canada, there are low densities of paved roads; however, the resurgence of natural gas and oil production in the previous 30 years has led to increased unpaved service roads. Human population is relatively sparse with highest densities in Lethbridge and Medicine Hat, Alberta, Regina and Swift Current, Saskatchewan, and Havre and Glasgow, Montana.

METHODS

We conducted our exploration of migratory behavior on 185 adult female pronghorn with global positioning system (GPS) collars by first classifying individual movements as migratory, mixed-migratory, or resident and identifying potential post-fawning and facultative winter migrations at the northern periphery of pronghorn range. Second, we identified stopover sites during spring and fall migratory pathways. Third, we estimated movement metrics (e.g., duration, distance) for each migratory behavior identified in our first step above. Finally, we used multivariate analysis to compare quantitative movement parameters during each of these migratory behaviors and examined potential spatial variability in migratory metrics and behaviors.

We captured adult female pronghorn during the winter across the NSS from 2003–2010 via net gun fired from a helicopter (Jacques et al. 2009a). We captured pronghorn across cultivated and native prairie habitats from 2003–2006 in Alberta and primarily native habitat from 2008–2010 in Montana and Saskatchewan. We fit captured individuals with GPS telemetry-collars (Lotek GPS 3300 and ARGOS 7000SA models; Lotek Wireless, Newmarket, Ontario, Canada). We captured 185 individuals and obtained relocations every 2 ($n = 64$) or 4 ($n = 121$) hours; we successfully retrieved data from 173 individuals. After accounting for mortalities during the study ($n = 54$) and the collection of multiple years of data for certain individuals ($n = 13$), we analyzed 170 unique animal-years (our sample unit). We obtained wildlife capture and handling permits from the Alberta Wildlife Animal Care Committee, from the Montana Fish, Wildlife & Parks approved by the Institutional Animal Care and Use Committee (IACUC), and from the Saskatchewan Ministry of Environment, which conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Classifying Pronghorn Migrations

We first classified migratory periods using non-linear models of net squared displacement (NSD; Bunnefeld et al. 2011). Net squared displacement measures the Euclidean distance between a starting location and each subsequent location along a movement pathway. Similar to others (Mysterud et al. 2011, Eggeman et al. 2016), we adapted NSD for pronghorn migration, developing species-specific criteria (Singh et al. 2016). We used NSD data and graphical outputs to classify individuals as migratory, mixed-migratory, or resident using each daily noon relocation for each pronghorn (Fig. 2). We classified migrants as those that moved between 2 distinct seasonal ranges in a biological year, whereas a mixed-migratory strategy meant that an individual used 3 geographic areas in a year (the location of the winter range changed; Bunnefeld et al. 2011). A resident showed no movements between distinct seasonal ranges during a calendar year. For each individual, we identified transition dates between residence and migration based upon variation in NSD from locations on winter range, beginning 2 days after capture to account for post-capture related movements. We classified individuals as a migrant when they had an NSD between 1% greater than the average winter range (in terms of NSD) and <95% of the average summer range to include possible discrete fawning range and summer range areas during late spring and early summer versus specific winter range areas (Suitor 2011). Thus, an individual began spring migration (or ended fall migration) when NSD exceeded (returned to within) 1% of the average winter NSD and ended spring migration (or began fall migration) when NSD reached (dropped below) 95% of the average summer NSD. An individual was considered a mixed-migrant when NSD did not return to within 1% of the preceding average winter NSD. An individual was classified as a resident where these specifications were not met.

We identified whether individuals displayed potential post-fawning or facultative winter migrations regardless of strategy within this framework. We defined potential post-fawning migrations as movement from an initial distinct fawning range during the known parturition dates for pronghorn in our region (White et al. 2007, Suitor 2011, Singh and Ericsson 2014) to a separate summer range; these were special cases that we identified at the end of spring migration. We used the maximum (rather than the average) NSD for the summer range to help separate potential post-fawning migration by discriminating the fawning range from the later summer range (S1, available online in Supporting Information). We noted a weakness of our approach was the lack of information about parturition status; hence, we label it potential post-fawning migration but included the behavior because of its relatively high prevalence and potential significance. To identify potential facultative winter migrations, we used the same process as for calculating spring migration dates but applied the algorithm after the end of fall migration (Fig. 2). An important biological consideration was the differentiation between fall and facultative winter migrations in individuals using a mixed-migratory strategy. We assumed that fall migrations

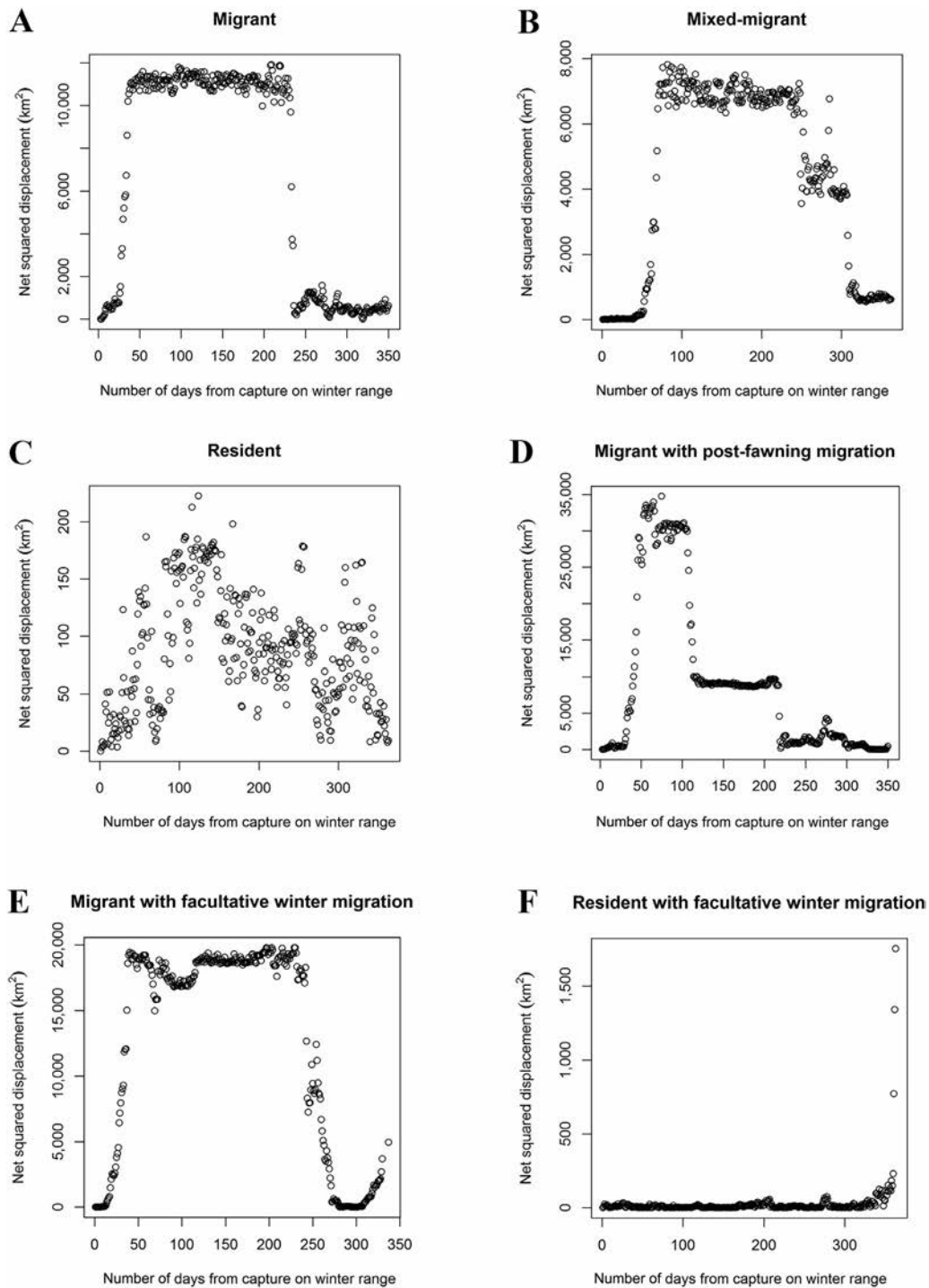


Figure 2. Graphical examples of pronghorn movement strategies across the Northern Sagebrush Steppe, 2003–2011 for migration behaviors defined as migrant (A), mixed-migrant (B), resident (C), migrant with potential post-fawning migration (D), migrant with facultative winter migration (E), or resident with facultative winter migration (F) based on daily net squared displacement. Note that we captured all pronghorn in Alberta or Saskatchewan, Canada, or Montana, USA, during winter (Dec–Mar) of the respective capture year. Axis scales vary for each graph and open circles depict daily relocations for each individual.

had been completed once relocations had clustered for >30 days (i.e., had reached a winter range), and therefore were not considered as a stopover. Subsequent direct movements from an initial winter range to the next suitable winter range were considered facultative winter migrations. We presumed that facultative winter migrations did not include stopover sites

because they were rapid movements to escape extreme local conditions (Dingle and Drake 2007). Accordingly, an individual could make only 1 fall migration but afterwards could partake in multiple facultative winter migrations to find suitable conditions. For each individual, we identified start and stop locations to extract identified migration

periods from each set of GPS relocations, using an R (R Development Core Team 2012) script and set of standardized rules (S1 and S2, available online in Supporting Information). We estimated NSS mean seasonal migration start and stop dates, mean migratory durations, and dates and durations of potential post-fawning migrations and facultative winter migrations across the region. We considered the NSS a single pronghorn population from a genetic (Lee et al. 1994) and movement perspective, but we tested for proportional differences of movement strategies between our 2 main groups of captured animals in Alberta and Montana-Saskatchewan using chi-square tests because of environmental variation between the 2 areas during the years animals were collared (Appendix A).

We discriminated movement states within spring and fall migratory pathways for each individual animal-year to identify stopover sites and calculate subsequent metrics. We used the *adehabitatLT* package (Calenge 2011) in R 2.15.2 (R Development Core Team 2012) following the methods of Guéguen (2001) to extract stopover sites from the migratory pathway. Similar to the migration classification, this method used the step lengths along the overall pathway and partitioned sequential observations into segments corresponding to active migration and stopover sites.

Analysis

We estimated movement metrics for spring, fall, potential post-fawning, facultative winter migrations, and stopover sites. For each migratory behavior, we estimated 1) Euclidean distance (i.e., the straight-line distance between start-stop relocations); 2) measured pathway distance (i.e., the summed distance between each relocation along the overall pathway vector); 3) ratio of displacement (measure of tortuosity between 0–1) where the closer the ratio is to 1, the more direct the movement (Benhamou 2004); 4) movement rates in km/hour for the Euclidean distance and measured pathway distance; and 5) mean bearing. We determined movement rates by first dividing either the Euclidean distance or measured pathway distance by the duration of each movement (i.e., 2 hr or 4 hr) and further standardized to an hourly rate. Finally, we compared the tendency for facultative winter migrations among resident versus migratory animals. We used Student *t*-tests to test differences between movement metrics for strategy types and used

sequential Bonferroni methods to account for experiment-wise error rates in multiple comparisons of movement metrics (Rice 1989). We confirmed that movement metrics were approximately normally distributed using graphical plots and normal q–q plots. To account for environmental variation, we tested for differences between our 2 main groups of captured animals in Alberta and Montana-Saskatchewan in movement metrics using Student *t*-tests to test for differences corrected for multiple comparisons as above.

We used multivariate analyses to group migration behaviors based on calculated metrics and to detect factors influencing metric results. We used correspondence analysis and subsequent between-class analysis (BCA) to assess if migration behaviors could be grouped based on calculated metrics of individuals using duration, Euclidian distance, displacement ratio, and movement rate factors (Dolédec and Chessel 1987). We used Monte Carlo permutation tests to assess the statistical significance of the BCA grouping (999 permutations, $\alpha = 0.05$; Dray and Dufour 2007). We used analysis of variance (ANOVA) for each migration behavior to test for environmental factor influences on annual variation amongst pronghorn movement metrics.

RESULTS

Classifying Pronghorn Migrations

Global positioning system collars had a 98% fix-success rate and so we did not consider fix success to be a likely source of bias (Frair et al. 2010). Of the 170 animal-years (185 GPS-collared individuals), 94 (55%) exhibited seasonal migrations (either migratory or mixed-migratory) and 76 (45%) were classified as resident. Of the 94 migratory animal-years, 11 (12%) included potential post-fawning migrations and we identified 36 facultative winter migrations (68% of facultative winter migrations were made by migratory animals). Of the 76 animal-years classified as residents, we identified 17 facultative migrations (32% of facultative winter migrations were made by residents; Table 1). We identified 164 spring ($n = 94$) and fall migrations ($n = 70$) of varying distances (Fig. 3). Collar attrition and mortality of some individuals during spring and summer seasons factored into the decreased sample of fall migratory pathways. Of the 70 individuals for whom we recorded spring and fall migrations,

Table 1. Movement strategy animal-year totals and percentages for each migration behavior in a partially migratory population of pronghorn across the Northern Sagebrush Steppe transboundary region of the United States and Canada, 2003–2011. We provide the number of individuals that make up animal-year totals and percentages for each migratory behavior. Facultative winter migration totals and percentages include 6 individuals (4 migrants and 2 residents) that undertook 2 facultative winter migrations during a given animal-year.

Movement strategy (n^a)	Spring migration ($n^b = 88$)	Fall migration ($n^b = 69$)	Post-fawn migration ($n^b = 11$)	Facultative migration ($n^b = 46$)	Spring stopover ($n^b = 26$)	Fall stopover ($n^b = 9$)
Migratory (58)	58 (62%)	34 (49%)	5 (45%)	21 (40%)	13 (48%)	5 (56%)
Mixed-migratory (36)	36 (38%)	36 (51%)	6 (55%)	15 (28%)	14 (52%)	4 (44%)
Resident (76)				17 (32%)		
Total (170)	94 (100%)	70 (100%)	11 (100%)	53 (100%)	27 (100%)	9 (100%)

^a Animal-years.

^b Individual pronghorn.

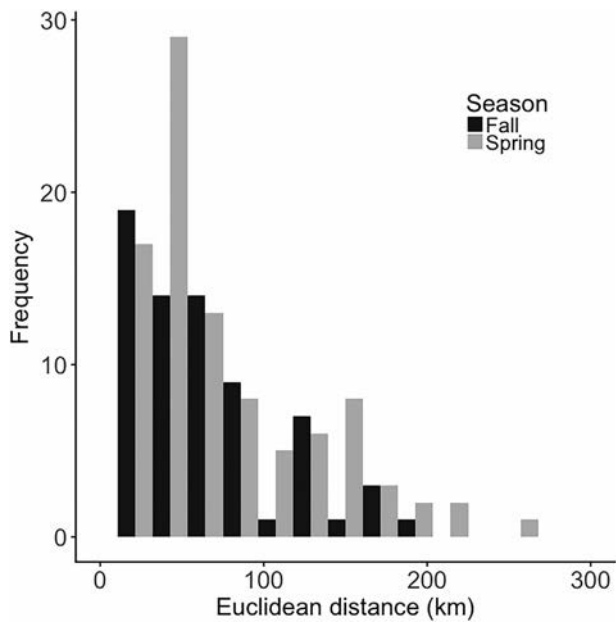


Figure 3. Histogram illustrating the distribution of spring ($n = 94$) and fall ($n = 70$) pronghorn migrations based on Euclidean distance (km; i.e., the straight-line distance between start and stop relocations) from collared female pronghorn across the Northern Sagebrush Steppe, in pronghorn captured in Alberta or Saskatchewan, Canada, or Montana, USA, 2003–2011.

36 (51%) used the mixed-migratory strategy and did not return to the same winter range (Table 1). We found significant proportional differences in movement strategies between Alberta and Montana-Saskatchewan. In Alberta, 27 (40%) collared individuals migrated and 40 (60%) were residents ($\chi^2_1 = 6.04$, $P = 0.014$), whereas in Montana-Saskatchewan, 67 (65%) collared individuals migrated and 36 (35%) were residents ($\chi^2_1 = 3.93$, $P = 0.048$).

We identified 45 stopover sites among 36 migrations that included ≥ 1 stopover (22% of all migrations). These included 34 identified during spring (76% of all stopover sites) and 11 identified during fall (24% of all stopover sites). There was greater use of stopovers during spring than fall ($t_{162} = 2.57$, $P = 0.011$). Finally, 9 of the 36 migrations (25%) where we identified stopover sites included 2 stopover sites (7 during spring, 2 during fall; Table 1).

Migratory Metrics

For the 94 spring migrations, the mean start and stop dates were 22 March and 10 April, lasting on average 20 days. Pronghorn migrated a mean Euclidean distance of 77.1 km in spring, over a moderately tortuous path (ratio = 0.55) at an average speed of 0.22 km/hour in a northerly direction (356.6° ; Table 2). The only aspect of spring migration that differed between Alberta ($n = 27$) and Montana-Saskatchewan ($n = 67$) capture groups was the distance ($P = 0.013$, $SE = 14.3$), with Alberta animals migrating a mean Euclidean distance of 37.5 km farther than Montana-Saskatchewan animals (Tables 3 and 4; Table S3, available online in Supporting Information). For the 70 fall migrations, the mean start and stop dates were 31 October

and 10 November, lasting on average 11 days. Pronghorn migrated a mean Euclidean distance of 64.6 km in fall, over a linear path (ratio = 0.67) at an average speed of 0.35 km/hour in a southerly direction (176.2° ; Table 2). Fall migration parameters differed more between Alberta ($n = 17$) and Montana-Saskatchewan ($n = 53$), with Alberta migration on average beginning earlier (33 ± 7.0 [SE] days, $P = 0.001$), ending earlier (25 ± 5.9 days, $P = 0.001$), having longer duration (8 ± 3.7 days, $P = 0.038$), and longer distances (52.5 ± 14.9 km, $P = 0.002$) than Montana-Saskatchewan migration (Tables 3, 4, and S3). For the 70 round-trip migrations recorded, pronghorn migrated a mean Euclidean distance of 146.1 km and mean measured pathway distance of 283.6 km. The longest annual migration in our study was by an individual migrating a Euclidean distance of 435 km (888 km measured pathway distance).

For the 11 potential post-fawning migrations, the mean start and stop dates were 10 June and 16 June, lasting, on average, 7 days. Pronghorn moved a mean distance of 43.3 km during this period, over a modestly linear path (ratio = 0.61) at an average speed of 0.44 km/hour in an easterly direction (86.3° ; Table 2). Only the mean start and stop dates during potential post-fawning migration differed between Alberta ($n = 5$) and Montana-Saskatchewan ($n = 6$) capture groups. In Alberta, potential post-fawning migration on average began later (28 ± 5.1 days, $P = 0.001$) and ended later (31 ± 4.4 days, $P = 0.001$) than Montana and Saskatchewan migration (Tables 3, 4, and S3).

For the 53 facultative winter migrations, the mean start and stop dates were 23 December and 1 January, lasting on average 10 days. We identified almost all facultative winter migrations in Montana and Saskatchewan ($n = 52$) compared to Alberta ($n = 1$; Tables 3 and 4). Pronghorn moved a mean distance of 41.2 km during this period over a highly linear path (ratio = 0.71) at an average speed of 0.26 km/hour in a southerly direction (175.8°). Migratory individuals started facultative winter migrations an average of 8 days earlier than residents, beginning 21 December and ending 30 December, whereas resident individuals started 29 December and ended 7 January, both lasting on average 10 days ($P = 0.169$, $SE = 5.7$ for start dates, $P = 0.222$, $SE = 6.6$ for end dates). We did not detect significant differences between migratory and resident individual mean distance ($P = 0.298$, $SE = 9.1$), path tortuosity ($P = 0.218$, $SE = 0.06$), or movement rates using Euclidean distance ($P = 0.068$, $SE = 0.04$). We detected a significant difference in movement rates between migratory and resident individuals using measured pathway distance ($P = 0.046$, $SE = 0.04$). We used chi-square analysis to test the expected and observed frequency of facultative winter migration initiated by migratory and resident individuals and found migrants tended to display facultative winter migrations more frequently than residents ($\chi^2_1 = 3.73$, $P = 0.05$).

Spring stopover sites started 5 April and ended 14 April, lasting on average 10 days and occurred in Alberta ($n = 8$) and Montana-Saskatchewan ($n = 26$; Tables 3 and 4). Pronghorn moved a mean distance of 3.5 km during the approximate 10-day stopover, following an overly tortuous

Table 2. Summary of pronghorn movement metrics for each migration behavior in animal-years across the Northern Sagebrush Steppe transboundary region of the United States and Canada, 2003–2011.

Metric	Migration behavior (<i>n</i>)							
	Spring (94)	Fall (70)	Post-fawn (11)	Facultative-migrant (36) ^a	Facultative-resident (17) ^a	Spring stopover (34)	Fall stopover (11)	
Mean start date	22 Mar	31 Oct	10 Jun	21 Dec	29 Dec	05 Apr	06 Oct	
SE	1.5	4.2	4.9	3.7	4.4	2.3	4.6	
Mean stop date	10 Apr	10 Nov	16 Jun	30 Dec	07 Jan	14 Apr	15 Oct	
SE	1.9	3.8	5.2	4.3	5	2.5	4.3	
Mean duration (days)	20	11	7	10	10	10	10	
Median	15	7	6	6	6	8	8	
SE	1.7	1.3	1.6	2	2.5	0.97	2.1	
Mean Euclidean distance (km)	77.1	64.6	43.2	44.2	34.7	3.5	2.8	
Median	56.7	54.6	45.2	30.8	25.9	2.7	2.4	
SE	5.6	5.5	5.1	6.5	6.3	0.46	0.61	
Mean measured distance (km)	162.4	108.6	97.7	68.4	60.4	40.6	38.2	
Median	111.9	86	78.6	42.5	45.6	26.7	33.9	
SE	13.9	10.6	24.7	11.3	12	6.2	11	
Mean displacement ratio	0.55	0.67	0.61	0.74	0.66	0.12	0.12	
Median	0.51	0.67	0.57	0.76	0.76	0.07	0.09	
SE	0.02	0.03	0.09	0.03	0.05	0.02	0.03	
Mean Euclidean distance rate (km/hr)	0.22	0.35	0.44	0.28	0.20	0.02	0.01	
Median	0.18	0.28	0.38	0.25	0.16	0.02	0.01	
SE	0.01	0.03	0.11	0.03	0.03	0.002	0.003	
Mean measured distance rate (km/hr)	0.37	0.50	0.66	0.38	0.29	0.16	0.14	
Median	0.35	0.46	0.61	0.34	0.27	0.15	0.13	
SE	0.01	0.03	0.09	0.03	0.03	0.01	0.02	
Mean bearing ^o	356.6	176.2	86.8	171	185.7	28.8	166.2	
SE	4.2	4.5	18.9	8	14.2	7.7	9.9	
Mean general direction	North	South	East	South	South	Northeast	South	

^a Metrics may not be complete due to animal death or collar falling off during migration.

path (ratio = 0.12) at an average speed of 0.02 km/hour (Table 2). Fall stopover sites started 6 October and ended 15 October, lasting on average 10 days and occurring in Alberta ($n = 6$) and Montana-Saskatchewan ($n = 5$; Tables 3 and 4). Pronghorn moved a mean distance of 2.8 km during fall stopovers, following an overly tortuous path (ratio = 0.12) at an average speed of 0.01 km/hour (Table 2). For spring and fall stopover sites, we did not find significant differences for any calculated metrics between the pronghorn in Alberta or Montana-Saskatchewan (Table S3).

Multivariate Analysis

We found annual variation in metrics of some migration behaviors using ANOVA and confirmed through subsequent analysis of deviance tests. We identified variation in movement dates and Euclidian distances, whereas displacement ratio, Euclidean distance rates, and measured distance rates typically did not differ annually (Table 5). Fall migration and potential post-fawning migrations exhibited significant ($P < 0.001$) annual variation (Table 5).

Using BCA, we found 3 general groupings of migratory behavior based on similarities in individual movement metrics (Fig. 4). Fall migration, potential post-fawning migrations, and facultative winter migrations were associated as 1 general group. Spring migration formed a second distinct group, and spring and fall stopovers were classified as a third group. Between-class variance was 31.5%, whereas 68.5% of variance was explained by observations within

groups ($P = 0.001$), indicating that based on individual movement metrics, these 3 groups are significantly different.

DISCUSSION

Our objectives were to record and compare movement metrics and migratory behaviors of pronghorn at the northern periphery of their range within the context of the FMH hypothesis. Our results indicated that pronghorn seasonal (i.e., spring and fall) migrations in the NSS are consistent with the FMH. We predicted that pronghorn in the NSS would undertake longer seasonal migrations compared to other areas inhabited by pronghorn, and we observed the longest migration of pronghorn reported to date in the literature, consistent with the FMH that populations at their northern range extent should display longer migrations to exploit greater spatiotemporal variability in forage (Hebblewhite et al. 2008, Peters 2015, Teitelbaum et al. 2015). In addition, 30 individuals made round-trip migrations of ≥ 200 km, which exceed distances reported in previous pronghorn studies (Berger 2004). Comparatively, in Wyoming, pronghorn made spring migrations between 82 km and 177 km (Sawyer et al. 2005, Sheldon 2005); in North Dakota, mean spring migration was 75 km and fall migration was 63 km (Kolar et al. 2011), whereas in Idaho, pronghorn migrated a mean distance of 44 km (Hoskinson and Tester 1980). Our mean migration distances exceed

Table 3. Summary of pronghorn movement metrics for each migration behavior in animal-years for individuals captured in Alberta, Canada, portion of the Northern Sagebrush Steppe transboundary region, 2003–2007. No facultative winter migrations were completed by resident individuals.

Metric	Migration behavior (<i>n</i>)						
	Spring (27)	Fall (17)	Post-fawn (5)	Facultative-migrant (1) ^a	Spring stopover (8)	Fall stopover (6)	
Mean start date	21 Mar	07 Oct	25 Jun	26 Nov	09 Apr	02 Oct	
SE	3.2	5	3.4	NA	5.6	2.3	
Mean stop date	14 Apr	23 Oct	03 Jul	02 Dec	18 Apr	14 Oct	
SE	4.3	3.7	3.3	NA	5.6	3.8	
Mean duration (days)	25	17	9	7	11	13	
Median	20	15	8		10	9	
SE	3.1	3.4	1.8	NA	2.1	3.4	
Mean Euclidean distance (km)	103.9	104.3	47.8	51.1	3.0	3.4	
Median	89.4	123.1	45.2		2.7	2.5	
SE	13.2	14.2	8.7	NA	0.81	1.1	
Mean measured distance (km)	215.4	162.9	100.3	86.5	44.7	49.2	
Median	186.4	170.1	94.2		34.3	28.6	
SE	33.0	26.3	10.9	NA	14.9	18.9	
Mean displacement ratio	0.53	0.68	0.51	0.59	0.10	0.11	
Median	0.49	0.68	0.57		0.05	0.10	
SE	0.04	0.03	0.10	NA	0.04	0.03	
Mean Euclidean distance rate (km/hr)	0.22	0.32	0.27	0.3	0.01	0.01	
Median	0.16	0.26	0.30		0.01	0.01	
SE	0.03	0.04	0.06	NA	0.004	0.003	
Mean measured distance rate (km/hr)	0.38	0.44	0.51	0.52	0.16	0.14	
Median	0.38	0.40	0.52		0.14	0.14	
SE	0.03	0.04	0.05	NA	0.03	0.02	
Mean bearing ^o	355.5	176	201.1	160.5	15.2	175	
SE	7.5	8.5	27.5	NA	19.5	14.4	
Mean general direction	North	South	South	South	North	South	

^a Metrics may not be complete due to animal death or collar falling off during migration.

Table 4. Summary of pronghorn movement metrics for each migration behavior in animal-years for individuals captured in Montana, USA, or Saskatchewan, Canada, portion of the Northern Sagebrush Steppe transboundary region, 2008–2011.

Metric	Migration behavior (<i>n</i>)						
	Spring (67)	Fall (53)	Post-fawn (6)	Facultative-migrant (35) ^a	Facultative-resident (17) ^a	Spring stopover (26)	Fall stopover (5)
Mean start date	22 Mar	09 Nov	28 May	21 Dec	29 Dec	04 Apr	10 Oct
SE	1.7	4.9	3.8	3.7	4.4	2.6	9.9
Mean stop date	08 Apr	17 Nov	02 Jun	31 Dec	07 Jan	12 Apr	17 Oct
SE	2.0	4.6	2.9	4.3	5.0	2.9	8.9
Mean duration (days)	19	9	6	10	10	9	7
Median	12	5	3	6	6	8	7
SE	2.0	1.2	2.6	2.0	2.5	1.1	1.8
Mean Euclidean distance (km)	66.4	51.8	39.4	44.0	34.7	3.7	2.1
Median	49.9	49.2	37.0	30.6	25.9	2.7	2.3
SE	5.4	4.1	6.3	6.7	6.3	0.6	0.4
Mean measured distance (km)	141.1	91.2	95.5	67.9	60.4	39.3	25.1
Median	98.7	69.6	58.6	41.2	45.6	26.3	33.9
SE	13.5	9.9	46.4	11.6	12.0	6.8	7.1
Mean displacement ratio	0.56	0.66	0.69	0.74	0.66	0.13	0.15
Median	0.52	0.67	0.84	0.76	0.76	0.12	0.07
SE	0.02	0.03	0.14	0.03	0.05	0.02	0.06
Mean Euclidean distance rate (km/hr)	0.22	0.36	0.57	0.28	0.20	0.02	0.02
Median	0.18	0.28	0.44	0.23	0.16	0.02	0.01
SE	0.02	0.04	0.19	0.03	0.03	0.003	0.005
Mean measured distance rate (km/hr)	0.36	0.52	0.78	0.37	0.29	0.16	0.15
Median	0.34	0.46	0.69	0.33	0.27	0.16	0.13
SE	0.02	0.03	0.15	0.03	0.03	0.01	0.04
Mean bearing ^o	357.0	176.2	70.2	171.6	185.7	32.3	157.3
SE	5.0	5.7	27.2	8.0	14.2	8.3	14.7
Mean general direction	North	South	East	South	South	Northeast	Southeast

^a Metrics may not be complete due to animal death or collar falling off during migration.

Table 5. Analysis of variance test *P*-values from comparisons of annual variation in movement metrics for pronghorn migration behaviors across the Northern Sagebrush Steppe transboundary region of the United States and Canada, 2003–2011. We adjusted the overall alpha level ($\alpha = 0.05$) for experiment-wise error. A $P < 0.001$ indicates a significant difference between years for each metric.

Season	Start date	Stop date	Duration	Euclidean distance	Measured distance	Displacement ratio	Euclidean distance rate	Measured distance rate
Spring migration	0.008	0.030	0.481	0.048	0.128	0.765	0.866	0.744
Fall migration	0.004	0.033	0.024	<0.001 ^a	0.040	0.742	0.893	0.886
Post-fawn migrant	0.009	<0.001 ^a	0.692	0.275	0.994	0.618	0.619	0.538
Facultative migrant	0.252	0.584	0.016	0.006	0.005	0.050	0.204	0.110
Spring stopover	0.348	0.096	0.160	0.573	0.196	0.313	0.384	0.624
Fall stopover	0.089	0.259	0.260	0.311	0.235	0.698	0.906	0.091

^a Indicates a significant difference between years.

those of Sonoran pronghorn (*A. a. sonoriensis*) at the southern periphery of the species range that moved 42 km when traveling to and from summer ranges and as much as 130 km within home ranges from cool-season to hot-season habitats (O’Gara 2004, Hervert et al. 2005).

We predicted that pronghorn in the NSS should have the highest proportions of migratory individuals compared to other areas across pronghorn range (Mueller et al. 2011, Teitelbaum et al. 2015), but our results do not support this prediction. Across the NSS, 55% of collared pronghorn undertook seasonal migrations, which is lower than proportions reported in Wyoming (70%, White et al. 2007; 81%, Beckmann and Seidler 2009) but is above the proportion of pronghorn from North Dakota (45%, albeit migrations were defined as >15 km between seasonal range; Kolar et al. 2011) and South Dakota (10%, Jacques et al. 2009b). Both Wyoming studies described individuals within intermountain valley systems, whereas the North Dakota and South Dakota studies reported on individuals in similar grassland or sagebrush steppe systems to the NSS. Differences could be due to localized climatic variation during the years of the study, altitudinal and latitudinal migration differences between sites, or for unknown reasons. We collected multi-year data on 13 individuals that confirmed migratory flexibility at the individual level. Of these, 3 individuals (23%) switched movement strategies (i.e., switched from mixed-migratory to resident) from one year to the next, which suggests pronghorn exhibit annual plasticity in spatiotemporal variant systems and may learn movement strategies through social interactions, and that migration is therefore not a fixed behavior (Barnowe-Meyer et al. 2013, Gaillard 2013).

We predicted a greater use and proportion of stopover sites used during the spring migration compared to the fall migration. Our results showed that 75% of stopover sites occurred during spring compared to 25% in fall. Engaging in slow, steady movements during spring, interspersed with stopovers likely provides pronghorn an opportunity to track forage green-up, allowing individuals to select high-quality forage to recover from the previous winter and prepare for fawning (Myysterud 2013, Seidler et al. 2015). In contrast, during fall, only 13% of identified migrations included at

least 1 stopover site, consistent with more directed movements and the FMH. We noted that specifically during fall, individuals that initiate migration earlier may also be more likely to stopover. We did not explicitly test whether pronghorn follow the green wave of vegetation during the spring or conversely jumping the brown wave during the fall; however, our results are consistent with slower spring movements predicted by the FMH. Future studies could explicitly test this mechanism using our quantitative analysis of pronghorn migratory behavior, time-to-event models, and dynamic measures of forage availability (e.g., NDVI).

We predicted that spring migrations would be slower, longer in duration, and more sinuous compared to fall, which would be faster, shorter in duration, and more linear migrations. Following the FMH, our results support this prediction where spring migrations were 9 days longer, 12.5 km farther, and 13% more sinuous than fall migrations. Fall migration was more directed, with rapid movements and fewer stopovers, which are in general agreement with other pronghorn migratory studies (Sawyer et al. 2005, Sheldon 2005, Kolar et al. 2011).

Though most of our results provide support that pronghorn seasonal migrations in the NSS are consistent with the FMH, we did identify 2 migration behaviors (i.e., facultative winter and potential post-fawn migrations) during other seasons that suggest factors other than forage quality influence migration. We collected only 1 year of data on most individuals; therefore, we were unable to track an individual’s return migratory path to a former winter or summer range. Thus, we cannot truly test whether the same individual displayed facultative movements from 1 year to the next. However, facultative winter migrations are defined as migrations from one winter range to another in response to extreme environmental conditions. We identified 47 individuals that undertook a total of 53 facultative winter migrations, seemingly in response to snow depth. Pronghorn morphology renders them highly sensitive to snow accumulation because they have the lowest mean chest height and highest foot-loading index of any North American ungulate (Telfer and Kelsall 1984). Like previous studies (Bruns 1977), we observed facultative winter migrations during severe winter conditions initiated by hundreds of individuals

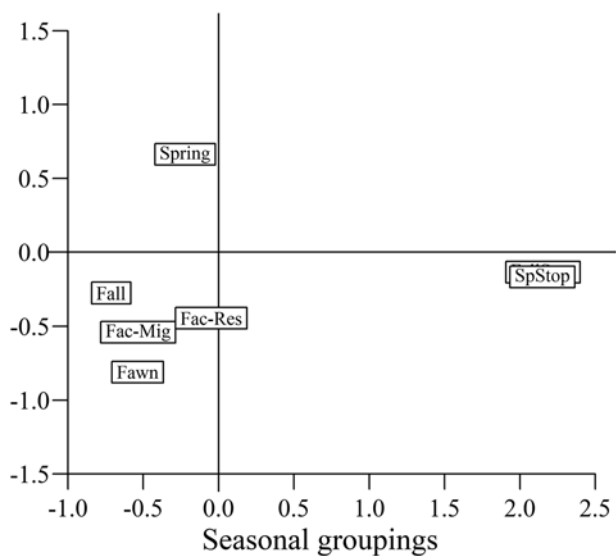


Figure 4. Between-class analysis results of migration behaviors from collared female pronghorn captured in Alberta or Saskatchewan, Canada, or Montana, USA, across the Northern Sagebrush Steppe, 2003–2011. Results indicated 3 distinct groupings of migration classification based on individual movement metrics. Spring and fall stopovers are tightly grouped and as a result, overlap in this graphical output. Grouping metrics include duration (days), Euclidean distance (km), displacement ratio, and movement rate (km/hr). Figure labels are Spring = spring migration, Fall = fall migration, Fawn = potential post-fawning migration, Fac-Mig = facultative winter migration of migrant pronghorn, Fac-Res = facultative winter migration of resident pronghorn, SpStop = spring stopover, and FallStop = fall stopover.

that were almost due south in direction (away from higher snow accumulation) and were the most linear of all migration behaviors investigated. For example, pronghorn captured in Alberta between 2003 and 2006 experienced typical winter conditions based on long-term climatic data (Environment Canada 2010; Appendix A), and only accounted for 1 of 47 individuals that undertook a facultative winter migration. Individuals captured in Montana and Saskatchewan from 2008–2010 experienced colder temperatures and extreme snow accumulations (Environment Canada 2010, National Oceanic and Atmospheric Administration [NOAA] 2014; Appendix A), and as a result, 46 of the 47 individuals that undertook facultative winter migrations occurred during this time. We also found that 68% of facultative winter migrations were undertaken by migrants and 32% were undertaken by residents, suggesting that migration may be a behavioral syndrome across a boldness spectrum (Chapman et al. 2011, Found and St. Clair 2016). Further time-to-event analyses of migration timing could specifically test drivers of facultative winter migration in future studies (Fieberg et al. 2008).

Secondly, we identified and characterized potential post-fawning migrations made by females after parturition, not previously documented for pronghorn, which suggests further study is warranted to understand potential fitness consequences of these movements (Singh and Ericsson 2014). Fawning occurs synchronously across pronghorn populations where individuals fawn in isolation and neonates are considered hidlers (Gregg et al. 2001). After pronghorn

give birth, females and fawns aggregate into nursery herds during the late spring and summer (Kitchen 1974). Potential post-fawning migrations were more rapid than spring migrations. However, such directed movements could also be consistent with avoidance of predation risk, but we were unable to test hypotheses regarding predation. In part, this was because we cannot determine if identified potential post-fawning migrations were made by females with fawn-at-heel or by females whose neonates were lost because we did not collect data on fawning success during the study.

Finally, we observed distinct groupings of movement behaviors based on multivariate analysis. Spring migration had dissimilar movement metrics from all other movement behaviors and is a method to return to important fawning locations and summer range in good condition to prepare for parturition. Fall migrations, facultative winter migrations, and potential post-fawning migrations were grouped in a second category, characterized by faster movement rates and low tortuosity. We suggest that these long-distance movements are in response to ecologically limiting conditions (i.e., lack of productive or available forage, predation risk on fawn-at-heel, or weakened female), and are undertaken to increase individual survivorship. Spring and fall stopovers sites were grouped together, suggesting that both are undertaken to take advantage of high-quality forage or as resting locations along the migratory pathway (Sawyer and Kauffmann 2011).

MANAGEMENT IMPLICATIONS

We suggest that managing for pronghorn migration is essential for population maintenance. We identified migration metrics including timing, duration, and distance traveled to provide managers insights to conserve or enhance pronghorn migratory paths. Annual spring migrations typically occur in a predictable and synchronous manner, which could be managed during the same annual timeframe, following forage maturation. Similarly, facultative winter migrations occur in response to recognizable, extreme winter conditions that can be managed annually as weather conditions dictate. For example, during spring and fall migratory periods, or severe winters, cost-effective practices such as opening gates, fence modifications, and creating opportunities to cross roads and railroads could facilitate pronghorn movement. In addition, migration could be facilitated through the use of management tools and policies, such as barrier modifications, migration enabling structures, habitat enhancements, land easements, multi-jurisdictional agreements and data sharing, and community education. These actions allow individual pronghorn and their offspring to move in response to fluctuating environments and stochastic events and facilitate continued movement across increasingly human-modified landscapes.

ACKNOWLEDGMENTS

We thank D. J. Bender, J. P. N. Landry-Deboer, D. H. Eslinger, M. G. Grue, K. Morton, and M. J. Sutor in Alberta; J. C. Carlson, J. A. Gude, P. T. Gunderson, J. T. Herbert, K. R. Johnson, D. Jørgensen, M. G. Sullivan, and S.

Thompson in Montana; C. Lees and J. Pogorzelec in Saskatchewan for field assistance and logistical support. We thank P. M. Lukacs for providing analytical assistance, and comments from K. L. Montieth and 2 anonymous reviewers on previous versions of the manuscript. We also thank Allison Air Service, Bighorn Helicopters, Inc., Hitch Aviation, Pathfinder Helicopter Wildlife Management, and Quicksilver Air for excellent capture and surveillance of pronghorn during the study. This study was funded by the Alberta Antelope Guides, Alberta Fish and Game Association (Zone 1), Alberta Professional Outfitters Society, Canadian Forces Base Suffield, Foundation for Northern American Wild Sheep – Eastern Chapter, Safari Club International, Safari Club International Alberta Chapter & Northern Alberta Chapter, Alberta Conservation Association (ACA), Petro-Canada, Sustainable Grasslands Applied Research program, Montana Fish, Wildlife & Parks (FWP), U.S. Bureau of Land Management (BLM), World Wildlife Fund (WWF), University of ACS–Accelerate Program, Alberta Sport Recreation Parks and Wildlife Foundation, Montana Chapter of The Wildlife Society, and Counter Assault. In-kind support was provided by The Miistakis Institute, FWP, ACA, BLM, and WWF.

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Associate Editor: Kathryn Schoenecker.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s website.

APPENDIX A

Winter climatic conditions for pronghorn capture years (2003–2011) and long-term (1981–2010) trend that indicate temperature and snowfall at 2 weather stations across the Northern Sagebrush Steppe transboundary region of the United States and Canada.

Location	Winter (Nov–Mar)	\bar{x} °C	\bar{x} °C max.	\bar{x} °C min.	Snowfall (cm)
Medicine Hat, AB	2003–2004	-5.0	0.1	-10.1	87.2
Medicine Hat, AB	2004–2005	-3.1	3.4	-9.6	82.4
Medicine Hat, AB	2005–2006	-2.0	3.5	-7.5	89.5
Medicine Hat, AB	2006–2007	-3.2	3.1	-9.5	0.0
Medicine Hat, AB ^a	1981–2010	-4.5	1.2	-10.3	67.3
Glasgow, MT	2007–2008	4.7	16.3	-6.7	58.4
Glasgow, MT	2008–2009	0.4	10.7	-9.9	93.5
Glasgow, MT	2009–2010	1.0	10.9	-8.8	73.2
Glasgow, MT	2010–2011	-3.2	5.8	-12.1	264.4
Glasgow, MT ^a	1981–2010	4.3	14.3	-5.8	76.7

^a 30-year mean.