

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

The Prairie Naturalist

Great Plains Natural Science Society

---

6-2017

## Diel and Monthly Movement Rates by Migratory and Resident Female Pronghorn

Paul F. Jones

T. Andrew Hurly

Chelsea Jensen

Karl Zimmer

Andrew Jakes

Follow this and additional works at: <https://digitalcommons.unl.edu/tpn>



Part of the [Biodiversity Commons](#), [Botany Commons](#), [Ecology and Evolutionary Biology Commons](#), [Natural Resources and Conservation Commons](#), [Systems Biology Commons](#), and the [Weed Science Commons](#)

---

This Article is brought to you for free and open access by the Great Plains Natural Science Society at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in The Prairie Naturalist by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

## Diel and Monthly Movement Rates by Migratory and Resident Female Pronghorn

PAUL F. JONES, T. ANDREW HURLY, CHELSEA JENSEN,  
KARL ZIMMER, AND ANDREW JAKES

Alberta Conservation Association, #400, 817 – 4th Avenue S., Lethbridge, Alberta, Canada, T1J 0P3 (PFJ)

University of Lethbridge, Lethbridge, Alberta, Canada, T1K 3M4 (TAH, CJ)

Alberta Conservation Association, 101 – 9 Chippewa Road, Sherwood Park, Alberta, Canada, T8A 6J7 (KZ)

University of Calgary, 2500 University Drive N.W., Calgary, Alberta, Canada, T2N 1N4 (AJ)

**ABSTRACT** Animal movement patterns are variable, with certain species primarily being diurnal and others nocturnal. Pronghorn (*Antilocapra americana*) are regarded as diurnal animals moving predominately during daylight hours. Anecdotal accounts, however, suggest that pronghorn move during the night but the extent, frequency, and importance of these nocturnal movement behaviors are unknown. To evaluate movements, we combined global positioning system relocation data from collared female pronghorn in the Northern Sagebrush Steppe between 2003 and 2007 with sunrise/sunset data within a geographical information system platform. We assessed whether mean and maximum movement rates were influenced by diel period (dawn, day, dusk, and night), month (January through December), movement strategy (migrant or resident), and year individuals were captured (2003, 2005, or 2006). Diel period and month greatly influenced mean and maximum movement rates. Pronghorn were indeed primarily diurnal in activity but significant movement did occur at night. Our results indicate pronghorn primarily move during the daytime, a period when humans also are most active on the landscape. This movement cycle has important implications for management and conservation of pronghorn at the northern periphery of its range.

**KEY WORDS** *Antilocapra americana*, diel, migrator, month, movement rates, northern sagebrush steppe, pronghorn.

Most understanding of pronghorn (*Antilocapra americana*) movement patterns is based on coarse scale assessments and have focused on migration. Pronghorn are known to make long-distance migrations between seasonal ranges (Berger 2004). In the northern hemisphere, migration typically occurs in the fall, following the rut, when they travel from summer ranges to winter ranges, and then in the spring, prior to fawning, when they reverse their route and return to fawning/summer ranges. Environmental factors (e.g., winter severity), nutritional requirements, and anthropogenic modification of the landscape heavily influence pronghorn migrations and distances travelled (Bruns 1977, O’Gara 2004, Seidler et al. 2015). Conservation efforts strive to maintain migration routes for pronghorn (Dodd et al. 2011, Sawyer et al. 2016). However, conservation and management of the species often does not examine fine scale movement patterns that might affect successful migration or survival. More specifically, relatively little is known about fine scale daily and monthly movement patterns of pronghorn. Fine scale information on pronghorn movement behavior is currently limited to behavioral assessments of time spent in various activities (e.g., feeding, resting) (Amstrup 1978, Reynolds 1984, Dodd et al. 2011), but these behavioral assessments indicate little about actual distances moved. Further, most activity budgets are based on visual observations made during the day and do not provide any indication of nocturnal activity (Hayes and Krausman 1993). Information on daily and seasonal diurnal

and nocturnal activity is needed to recognize how animals interact with their environment and in particular how peak activity periods may overlap with anthropogenic disturbances that can affect species management or conservation recommendations.

Ungulates respond behaviorally to human disturbance in various manners (Kilgo et al. 1998, Beckmann et al. 2012, Brown et al. 2012). When examining effects on wildlife, the presence of roads and the varying traffic volume associated with them can be considered proxies for human activity on the landscape. Peak traffic volume on roads typically occurs during daylight hours. For example, peak traffic volume on US Highway 89 in Arizona was highest during daytime hours (1000 to 1700; Dodd et al. 2011). Both elk (*Cervus elaphus*) and pronghorn may be highly responsive to human disturbance and noise on roads during the day, with pronghorn being more responsive to the disturbance (Brown et al. 2012). Traffic volume on roads activated threat responses causing pronghorn to behave as they would towards a natural threat (Gavin and Komers 2006). In addition, roads hinder the natural movement patterns of pronghorn by altering resource distributions and availability through habitat loss and fragmentation (Beckmann et al. 2012, Seidler et al. 2015) and can cause direct and indirect mortality, especially when coupled with fences (Harrington and Conover 2006, Jones 2014). This higher sensitivity to human disturbance is likely because pronghorn are generally described as diurnal animals

(Amstrup 1978, Reynolds 1984, Dodd et al. 2011) that do not usually exhibit nocturnal movement. We are unaware of any conclusive studies that indicate pronghorn switch movement patterns within diel periods (i.e., from diurnal to nocturnal) in response to human disturbance, as seen in other species (Kilgo et al. 1998, Webb et al. 2010, Northrup et al. 2012). However, anecdotal accounts suggest that pronghorn are capable of nocturnal movement. Data from global positioning system (GPS) collars can provide additional insights into the movement patterns of pronghorn.

The objective of our study was to assess fine scale movement rates for female pronghorn. Our appraisal critically examines the belief that pronghorn are solely diurnal and assesses which diel periods contain peak activity and how these activity periods vary by month, movement strategy, and year. Specifically, through geospatial analysis of GPS collars and sunrise/sunset data, we assessed if movement rates differed between four diel periods (dawn, day, dusk, and night) within a 24 hour (hr) day. Further, we examined whether pronghorn movement rates varied monthly (January through December) and whether the movement strategy of individuals (migrant versus resident) influenced their movement rates. Lastly, we examined whether there were variations in these rates based on year of capture (2003, 2005, or 2006). We predicted that movements would occur predominately during the day as previously noted (Amstrup 1978, Reynolds 1984, Dodd et al. 2011) and movement rates would be lower during May and June, when female pronghorn are restricted in their

movements by the presence of fawns (Byers 1997). Certain pronghorn migrate in both the fall and spring (Sawyer et al. 2005, White et al. 2007, Jakes 2015), and we predicted that movement rates during March/April (spring migration) and October/November (fall migration) would be the highest and may include nocturnal activity as pronghorn adjust their movement patterns in response to daily human activity. In addition we predicted that migrant pronghorn would have greater movement rates compared to resident animals during migration months but should exhibit similar movement patterns during the other months of the year. Lastly, we predicted that movement rates would not vary based on year of capture, given that yearly variation in environmental conditions was minimal during the study period. Evaluation of these predictions will improve our understanding of fine scale temporal movement patterns of pronghorn; thus, knowing when pronghorn exhibit the greatest activity, both daily and monthly, will aid in developing strategies that reduce potential conflicts between pronghorn and human activity or disturbance (Webb et al. 2013).

## STUDY AREA

Our study area falls within the Northern Sagebrush Steppe, covering southern Alberta, parts of southwestern Saskatchewan, and parts of north-central Montana (Fig. 1). It is contained within the broader Mixedgrass and Dry Mixedgrass Natural Subregions within the Grassland Bi-

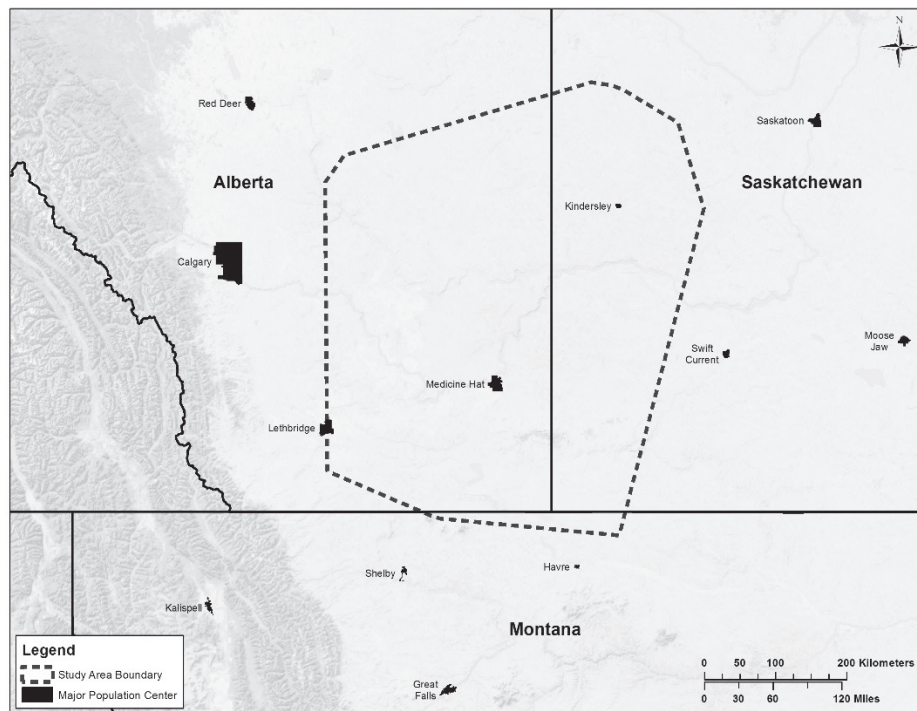


Figure 1. Map of study area within the Northern Sagebrush Steppe in Alberta, Saskatchewan, and Montana where pronghorn (*Antilocapra americana*) moved between 2003 and 2007 (Data sources: AltaLIS 2015, ISC 2015, MBMSC 2009, ESRI World Terrain Base 2009).

ome (Coupland 1961). The study area was predominately a patchwork of native prairie, annual, and perennial cropland with the exception of two large regions of native prairie: 1) southeastern Alberta / southwestern Saskatchewan (south of the Trans-Canada Highway and the Cypress Hills); and 2) Canadian Forces Base Suffield in the central portion of the study area. Predominant land use activities include commercial livestock grazing, energy development, agricultural crop production, wind energy development, transportation network, rural acreage development, and urban expansion (Alberta Environmental Protection 1997). Urban centers include Lethbridge on the west side and Medicine Hat in the center of the study area.

## METHODS

### Pronghorn Capture

We captured female pronghorn using a net fired from a helicopter (Jacques et al. 2009a), and then hobbled, blindfolded, and fitted individuals with Lotek GPS 3300 collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) and an Allflex ear tag. We completed 3 rounds of collaring: December 2003 ( $n = 24$ ), March 2005 ( $n = 25$ ), and March 2006 ( $n = 25$ ). Only one member of a group or herd of pronghorn were collared. In addition, captures occurred within 3 geographical units (south, central, and north) of the study area, with captures occurring in each unit in successive years starting in the south (see Jones et al. 2015 for description of capture locations) to alleviate any concerns of independence between study animals. Collars recorded a location every 4 hrs and dropped off after 46–52 weeks. We recaptured 4 females in July 2014 to replace failed collars and 17 females in March 2007 to remove collars due to faulty drop-off mechanisms. The Alberta Wildlife Animal Care Committee reviewed and approved the capture and handling protocol prior to issuance of agency wildlife capture and handling permits (Alberta Sustainable Resource Development, Fish and Wildlife Research Permits 11861, 16707, and 20394). We did not consider fix success to be a likely source of bias in our analysis (Frair et al. 2010) because our GPS collars had a 98% fix-success rate.

### Movement Rates

We calculated movement rates (km/h) for each individual using the UTM coordinate relocation data within Microsoft Excel (2010) to determine the distance between relocations and then dividing the distance by the total elapsed time between relocations. We discarded the first and last relocation for each individual, as we did not have a previous or successive relocation with which to calculate a movement rate. We used movement rate as opposed to distance to ensure consistency between relocations and differences in time between relocation acquisition as well as the length of time for each

diel period (see below). We considered movement rates as minimum rates because the true distance moved between relocations is likely larger than the Euclidean distance between relocations.

### Diel Period Determination

We classified each relocation into 1 of 4 diel periods (dawn, day, dusk, and night). We first assigned each successive relocation as either day or night, based on the daily sunrise/sunset times (obtained from [www.timeanddate.com/sun/canada/medicine-hat?month=3&year=2012](http://www.timeanddate.com/sun/canada/medicine-hat?month=3&year=2012)) using a custom tool built in ArcGIS (K. Zimmer, Alberta Conservation Association, unpublished data). We partitioned the year into 10-day intervals (i.e., interval 1 = January 1 to 10, interval 2 = January 11 to 20, etc.). We used the sunrise and sunset times of the midpoint of that 10-day period to assign relocations to diel periods, resulting in GPS relocations time-stamped before sunrise classified as night, after sunset classified as night, or after sunrise but before sunset classified as day. This resulted in calculated movement rates that followed the sequence below (where  $n =$  night and  $d =$  day):

Location #:	1—2—3—4—5—6—7—8—9—10
Period:	n—n—d—d—n—n—n—n—d—d

We then broke each day into 4 periods using the sequential day and night periods as the starting point. Using the above sequence, if we classified the first relocation as  $n1$  (night relocation #1), then between  $n1$  and the next night relocation ( $n2$ ), we assigned the movement rate to the night period. Between the last night relocation ( $n2$ ) and the first day relocation ( $d3$ ), we assigned the movement rate to the dawn period. Between the initial day relocation ( $d3$ ) and the last day relocation ( $d4$ ) we assigned the movement rate to the day period, and between the last day relocation ( $d4$ ) and the next night relocation ( $n5$ ) we assigned the movement rate to the dusk period. During certain times of the year there were more than 2 relocations falling within the initial classifications of day (e.g., summer) or night (e.g., winter) periods. Again using the sequence above, after the initial nighttime relocation for each pronghorn, there are 4 relocation points during the night ( $n5 - n8$ ) for a 12-hr night. We then calculated a single movement rate for each diel period for each day, accounting for the extended period (i.e., night period for the example above) by adding up the total distance moved between successive relocations and dividing by the total elapsed time. We repeated this diel series throughout the year for each animal, with diel period times adjusted in accordance with sunrise and sunset times for each 10-day calendar interval. Thus, as summer days have earlier sunrises and later sunsets, the longer summer days would have more relocations than shorter winter days and conversely the shorter summer nights would have fewer relocations included in the movement rate cal-



ulation than longer winter nights. Using this approach we have a rough assessment of pronghorn movements during the crepuscular periods, where our dawn period corresponds to the transition from night to day and our dusk period is the transition period from day to night. In addition, due to the limitation of having 4-hr relocations and varying sunrise/sunset times throughout the year, our calculation of a movement rate for the dawn and dusk period will not evenly overlap sunrise/sunset times (i.e., 2 hr on either side of sunrise/sunset). We acknowledge that additional finer scale movements would have been detected if our relocation fix rate was at a finer scale (e.g., hourly or every half-hour), which in turn would provide greater insight into movement rates during the crepuscular time periods.

### Movement Rate Analysis

To assess the difference in diel and monthly movement rates, we first calculated a mean movement rate per diel period per month for each individual pronghorn. We then assigned each individual pronghorn a movement strategy (migrator or resident) and a year of capture value (2003, 2005, or 2006). We classified movement strategy for pronghorn, following Jakes (2015), by measuring net squared displacement (the Euclidean distance between a starting location and each subsequent location along a movement pathway) throughout a given year (Bunnefeld et al. 2011). Pronghorn with discrete seasonal ranges were considered migrant while individuals with overlapping seasonal ranges were considered resident (Berger 2004). We assessed if movement rates varied based on year of capture (2003, 2005, and 2006) to account for any potential yearly variation in environmental conditions (e.g., forage quality, snow cover). We log-transformed the data (movement rate and maximum movement rate) as they were not normally distributed. We then used a multivariable mixed-effect ANOVA to assess for difference in mean movement rates with the log of the movement rates as the response variable and diel period, month, movement strategy, and year of capture as the fixed effects; also, we included the interactions of diel period and month and month and movement strategy. To account for repeated measures on the same individual, we included pronghorn identification number as a random effect in the analysis. Whereas these values represent the greatest generality in describing movement, they obscure what pronghorn are capable of doing. Thus, for each individual we also determined the maximum movement rate per diel period on a monthly basis. This maximum rate reveals, for example, significant movements during the migratory periods that otherwise would have been diluted by many days of non-migratory movements. We first assessed the differences between mean maximum movement rates and mean movement rates using a paired t-test. Then we used a multivariable mixed-effect ANOVA to assess for difference in mean maximum movement rates with the log of the maxi-

um movement rates as the response variable and diel period, month, movement strategy, and year of capture as the fixed effects; also, we included the interactions of diel period and month and month and movement strategy. Again, we included pronghorn identification number as a random effect in the analysis. We reported means ( $\pm$  SE) based on the raw data where individual pronghorn were the sample unit, while we reported the statistical test values using the log-transformed data based on the least squared means used by the ANOVA. All analyses were performed in JMP v12.2.0 (SAS, Cary, NC, USA) at a significance level of  $\alpha = 0.05$ .

### RESULTS

We captured 74 pronghorn between December 2003 and March 2006, but mortalities, collar failure, or lost collars resulted in insufficient data for analysis from 16 individuals. Consequently, we analyzed data from 58 pronghorn, of which 18 were captured in 2003, 22 were captured in 2005, and 18 were captured in 2006. Of the 58, 25 were migratory and 33 were residents.

Examination of mean movement rates of all pronghorn combined indicated that movement rates were highest during the day, followed by dawn and dusk periods, with the least movement at night ( $F_{3,2252} = 36.95$ ,  $P < 0.001$ ; Table 1). However, our data showed that female pronghorn did indeed move at night (13.3% of mean movement rates). There was variation in monthly movement rates ( $F_{11,2255} = 62.61$ ,  $P < 0.001$ ) with the highest movement rates occurring during April, October, and November, and lowest rates during February and the summer months (June through September; Table 1). There was a significant interaction between diel period and month ( $F_{33,2255} = 20.99$ ,  $P < 0.001$ ; Fig. 2a). There was not a difference in movement rates based on movement strategy ( $F_{1,510} = 2.14$ ,  $P = 0.145$ ; Table 1) or year of capture ( $F_{2,53} = 0.92$ ,  $P = 0.407$ ; Table 1). However, there was a significant interaction between month and movement strategy ( $F_{11,2266} = 3.35$ ,  $P < 0.001$ ; Fig. 3a).

Mean maximum movement rates were five times greater than mean rates across all individuals. The daytime mean maximum rate was  $0.76 (\pm 0.024)$  km/hr compared with  $0.21 (\pm 0.008)$  km/hr mean daytime movement rate; the nighttime mean maximum rate was  $0.30 (\pm 0.008)$  km/h compared with  $0.08 (\pm 0.002)$  km/hr mean nighttime movement rate. The greatest maximum movement rate was exhibited by a migrant pronghorn (#39) at dusk during September when she moved at a rate of 5.26 km/hr. Overall the mean maximum movement rates differed significantly from the mean movement rates ( $t_{57} = 90.81$ ,  $P < 0.001$ ). Although the mean maximum movement rates were consistently much higher than mean movement rates, the overall patterns paralleled those of the mean rates with strong effects of diel period ( $F_{3,2306} = 30.78$ ,  $P < 0.001$ ; Table 1), month ( $F_{11,2306} = 26.20$ ,  $P < 0.001$ ; Table 1), and the interaction between diel period and

Table 1. Mean and mean maximum movement rates (km/hr) by diel period, month, year, and movement strategy by female pronghorn (*Antilocapra americana*) in the Northern Sage Steppe between 2003 and 2007. Note that mean  $\pm$  SE values reported used the raw data and thus do not perfectly reflect the Least Squared Means used by the ANOVA in the analysis.

Variable	Category	N Pronghorn	Mean Movement Rate (km/hr)	Mean Movement Rate SE (km/hr)	Mean Maximum Movement Rate (km/hr)	Mean Maximum Movement Rate SE (km/hr)
Diel Period	Dawn	58	0.13	0.004	0.55	0.017
	Day	58	0.21	0.008	0.76	0.024
	Dusk	58	0.18	0.005	0.74	0.020
	Night	58	0.08	0.002	0.30	0.008
Month	January	42	0.16	0.006	0.64	0.033
	February	42	0.11	0.006	0.39	0.022
	March	58	0.15	0.006	0.67	0.036
	April	57	0.20	0.011	0.75	0.036
	May	57	0.16	0.007	0.64	0.030
	June	56	0.12	0.006	0.47	0.025
	July	47	0.13	0.006	0.46	0.022
	August	47	0.12	0.003	0.43	0.013
	September	49	0.12	0.005	0.53	0.037
	October	42	0.18	0.011	0.76	0.053
	November	42	0.18	0.007	0.68	0.042
	December	54	0.16	0.008	0.59	0.034
Movement Strategy	Migrator	25	0.17	0.006	0.72	0.019
	Resident	33	0.13	0.004	0.48	0.009
Year	2003	18	0.14	0.007	0.54	0.017
	2005	22	0.15	0.007	0.61	0.017
	2006	18	0.15	0.007	0.60	0.016

month ( $F_{33,2306} = 9.25, P < 0.001$ ; Fig. 2b). Movement strategy was not significant ( $F_{1,2307} = 2.21, P = 0.14$ ; Table 1), while year of capture ( $F_{2,34} = 5.34, P = 0.01$ ; Table 1) was significant for maximum movement rates. However, the interaction between month and movement strategy was significant ( $F_{11,2306} = 3.27, P < 0.001$ ; Fig. 3b).

## DISCUSSION

Our results demonstrate that movement by pronghorn varies on circadian, circannual and annual bases, some of which clearly corresponds to seasonal migrations. Although most movement was associated with daylight hours, pronghorn did exhibit biologically meaningful nocturnal movement (13.3%

of mean movement rates), but this movement was minor in comparison to movement rates during the dawn, day, and dusk periods. Further, nocturnal movement occurred not only during migration but also during all months. These findings support the idea that pronghorn do move during all times of the diel cycle (Kitchen 1974) but are predominately a diurnal species (Amstrup 1978, Reynolds 1984, O'Gara 2004, Dodd et al. 2011). This consistent pattern of moving predominately during the day across seasons contrasts with those patterns of other ungulates that have shown considerably greater nocturnal movements (white-tailed deer [*Odocoileus virginianus*]; Kammermeyer and Marchinton 1977; reindeer [*Rangifer tarandus tarandus*]; Skarin et al. 2010; Columbia black-tailed deer [*O. hemionus columbianus*]; Long et al. 2013; mule deer

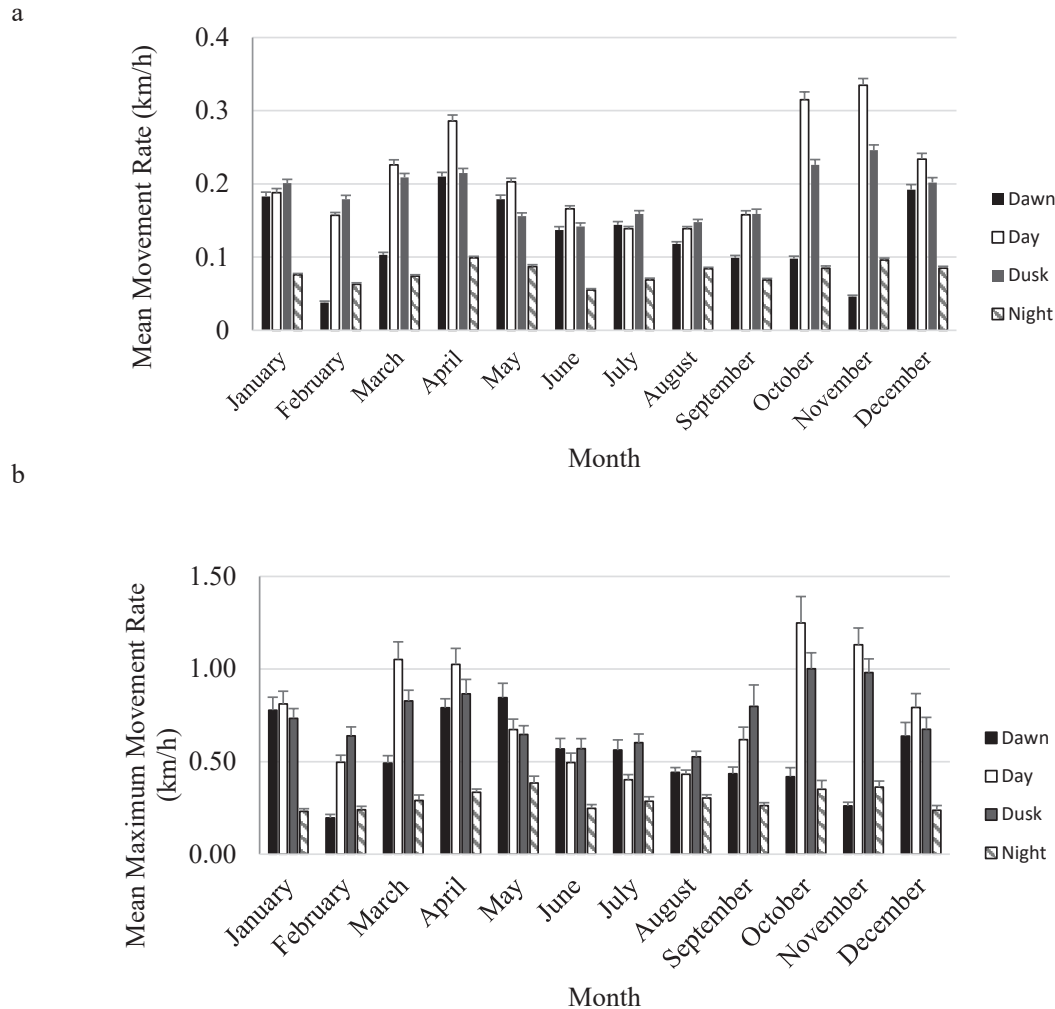


Figure 2. Mean (a) and mean maximum (b) movement rates (km/hr) per month by diel period of female pronghorn (*Antilocapra americana*) in the northern sage steppe between 2003 and 2007. Bars are mean  $\pm$  SE based on the raw data and thus do not perfectly reflect the least squared means used by the ANOVA in the analysis.

[*O. hemionus*]: Webb et al. 2013). Pronghorn inhabit open terrain and evolved keen eyesight and mercurial speed to avoid predators (Yoakum et al. 2014). These strategies make them well-suited to forage and move during daylight hours and helps explain the contrast seen in foraging and movement pattern of other ungulates.

The general daily movement pattern seen in our data consisted of increasing movement rates from dawn through the day and then decreasing from day to dusk and dusk to night. Pronghorn repeated this general pattern across all months except late summer (July and August) and mid-winter (January and February). During these two seasons, there was an increase in movement rate between day and dusk. A similar pattern occurred in peak movement for pronghorn in southeastern Idaho during dusk hours over the summer (Reynolds 1984). Reynolds (1984) noted a second peak in movement

during dawn hours, and attributed both peaks to increased foraging. Both Kitchen (1974) and Amstrup (1978) found peak activity shortly after sunrise and just before sunset, with the greatest peak in activity during these times occurring during the summer. The warmest months of the year in Alberta are July and August; therefore, we attribute the peak in dusk movement during these two months as a behavioral response to avoid the heat of the day. On the other hand, January and February tend to be two of the coldest months in Alberta. Pronghorn in southern Alberta and northern Montana during the winter occupied microhabitats that had more favorable climatic conditions than the surrounding area (Bruns 1977). Bruns (1977) also found that during winter, pronghorn remained bedded well after sunrise, but as conditions improved, bedding duration decreased. White-tailed deer exhibited a similar pattern of activity during the winter with

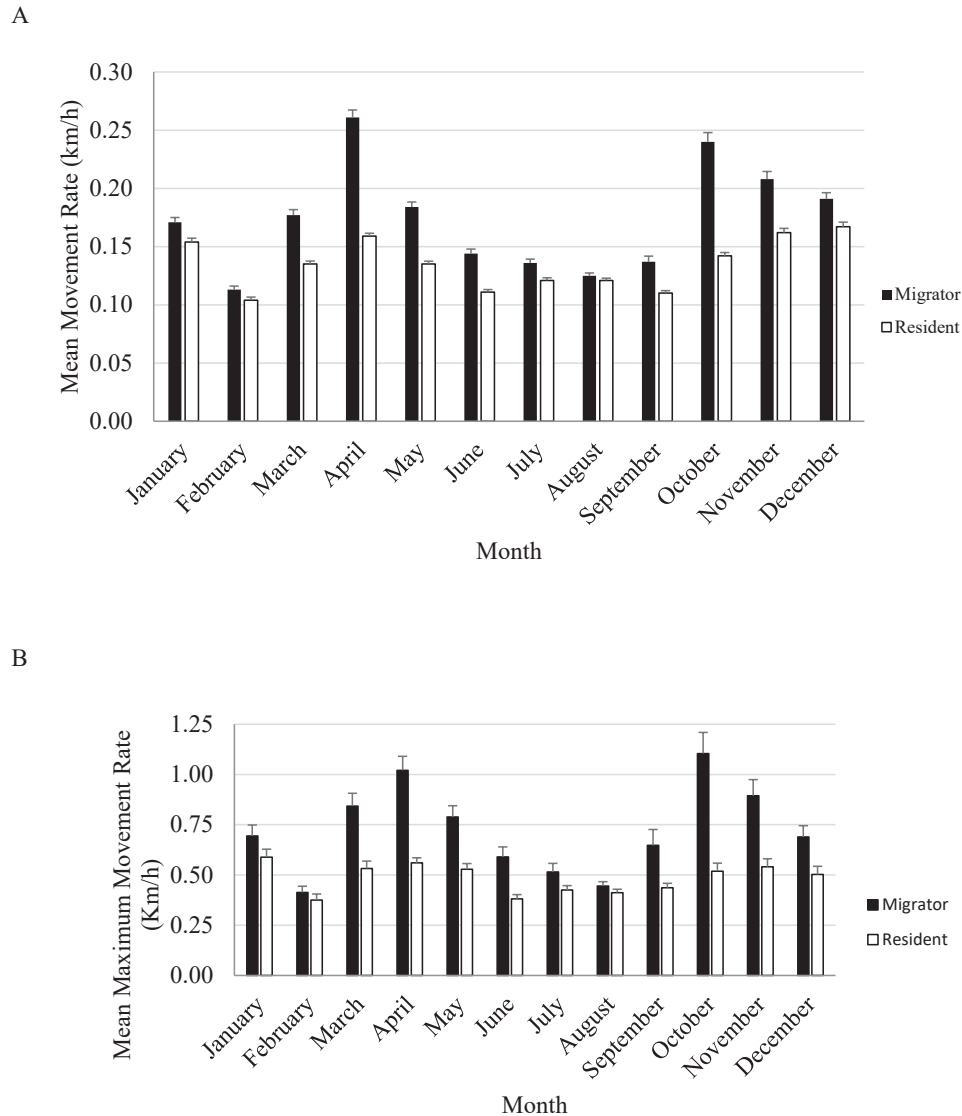


Figure 3. Mean (a) and mean maximum (b) movement rates (km/hr) per month by movement strategy of female pronghorn (*Antilocapra americana*) in the northern sage steppe between 2003 and 2007. Bars are mean  $\pm$  SE based on the raw data and thus do not perfectly reflect the least squared means used by the ANOVA in the analysis.

the reduced activity during the morning (the coldest part of the day) being an adaptive strategy to conserve energy (Beier and McCullough 1990). We believe the peak in movement between day and dusk during January may be in preparation for bedding down for the night where pronghorn showed an increase in foraging during the dusk period (when it is still warmer), prior to the onset of the coldest part of the diel period (i.e., night), where movements were reduced as they settled into a favorable bedding location for the night.

We predicted that movement rates of pronghorn would be the least during May and June compared to the other months due to parturition limitations. June through September tended

to have low movement rates for pronghorn during our study, a period that includes parturition and weaning of fawns. Mule deer in Oregon (Long et al. 2009) and white-tailed deer and elk in southern Manitoba (van Beest et al. 2013) also decreased their movements associated with parturition. Pronghorn typically give birth between mid-May and early June in Alberta (Mitchell 1980, Barrett 1981). During the initial three weeks of life, pronghorn fawns employ a hiding strategy where they remain bedded for extended periods, rising only to feed and defecate (Byers 1997). The fawn's hiding strategy restricts a female's ability to move freely throughout the landscape. Byers (1997) found that most females moved



about 70 m from her fawn and remained at this distance when not nursing. Following the hiding phase, fawns begin to move around with the female and start to group up with other pronghorn. The reduced overall movement rates seen during June through September may be a direct consequence of a female's limited ability to move freely across the landscape with fawns at heel.

The greatest overall daily movement rates occurred during October/November (fall migration) and April (spring migration). These months are when migratory pronghorn move between seasonal ranges and the maximum values likely better reflect migratory movements than do the mean values. During the fall months these movements allow pronghorn to reach intended seasonal ranges before resources become limited and/or weather conditions become extreme (Sawyer et al. 2005, Jacques et al. 2009b, Jakes 2015). During spring, migrations tend to be longer in duration as pronghorn follow 'green-up' to restore condition and prepare for parturition (Dalton 2009, Jakes 2015), a phenomenon seen in other ungulates including mule deer (Monteith et al. 2011), red deer (*Cervus elaphus*; Bischof et al. 2012), and Mongolian gazelle (*Procapra gutturosa*; Mueller et al. 2007). Therefore, migratory pronghorn continue moving during migration interspersed with resting or foraging stopover sites (Jakes 2015, Seidler et al. 2015). The greater movement rates seen in April are likely the result of migratory individuals finishing their spring migration, which typically occurs at the end of March to mid-April for pronghorn in the Northern Sagebrush Steppe (Suitor 2011, Jakes 2015).

A unique pattern emerged when we examined movement rates based on the interaction of individual movement strategy and month. We had predicted that during the months when pronghorn were migrating the movement rates would be greater for migrants, but when both migrants and residents were on seasonal ranges, the movement rates would be similar; however, this was not the case. What was evident is the movement rates during each month were higher for migrants than residents. We hypothesize that one of two factors may cause this disparity in movement rates. The first relates to familiarity to local surroundings and conditions. Resident pronghorn may be more familiar with their surroundings and events (i.e., climatic variation, disturbance) from one month to the next (Beier and McCullough 1990) and spend less time moving around their seasonal ranges resulting in lower movement rates. Migratory pronghorn, on the other hand, may need to reacquaint themselves to seasonal ranges having spent time away from the local area, which is manifested as higher movement rates. For example, individuals that migrated south for the winter, upon returning to their summer range, may need to become familiar with the distribution of succulent forage based on local climatic events (e.g., previous snowfall pattern). Alternatively, we hypothesize migrants may be inclined to move continuously because of individual learned behavior as a strategy to maximize fitness; that is,

the timing and movement patterns are passed down from one generation to the next. Additional research is required to test our hypotheses (or alternatives such as landscape configuration) to understand why the differences in movement patterns between the two movement strategies occurs. Either way, individuals are making trade-offs when selecting a movement strategy, and these differences and plasticity in strategy provide further evidence for the need to conserve individuals from both behavioral groups (Barnowe-Meyer et al. 2013).

Our study examined the temporal movement patterns of pronghorn on a diel basis. Further refinement and understanding of these movement patterns could occur with a more intense relocation schedule that is now achievable with advancements in GPS collar technology. In addition, further research is required to understand how these temporal movement patterns for pronghorn translate into spatial patterns on the landscape, particularly in relation to roads and fences. For example, Seidler et al. (2015) demonstrated the use of stopover sites for pronghorn along their migration routes in the Greater Yellowstone Ecosystem. They attributed the use of these stopover sites to impediments (roads and fencing) and not the quality of resources in the area (Seidler et al. 2015). Understanding timing associated with the use of stopover sites in relation to impediments will provide greater insight to pronghorn stopover ecology. For example, one could examine if there is an interaction between road characteristics (e.g., traffic volume) and the innate pronghorn diel movement behavior (i.e., daytime movement) that makes crossing roads difficult. Resource managers can effectively conserve pronghorn if they account for both the temporal and spatial movement processes and patterns.

## MANAGEMENT IMPLICATIONS

Our results indicate pronghorn accomplish their activity cycle primarily during the daytime. Though we did document nighttime movements during every month, we did not observe a significant increase in nocturnal movements during the migration months when individual pronghorn may move long distances between seasonal ranges. In our study area, pronghorn migrations are occurring across a fragmented and developed landscape primarily during the day, which is the period when humans are most active on the landscape. Managers need to account for daytime movements to ensure migration routes are not lost or jeopardized by human activity. Loss of migration routes will play a significant role in the conservation of pronghorn at the northern periphery of their range.

## ACKNOWLEDGMENTS

This project was an extension of a larger program delivered as a joint effort between the Alberta Conservation Association (ACA), Alberta Fish and Wildlife (ABF&W) and the

University of Calgary (UofC). We acknowledge the efforts of M. Grue and J. Landry-Deboer (ACA), D. Eslinger and K. Morton (ABF&W), M. Sutor, C. Gates and D. Bender (UofC) in the delivery of the larger program examining movement, migration, and resource use by pronghorn in Alberta. We thank the following for their assistance with the pronghorn captures: C. Wilson, T. Vandenbrink, and B. Lithgow of Bighorn Helicopters, Inc. and M. Shelton and J. Row of Pathfinder Helicopter Wildlife Management. K. Paul and S. Judge of Allison Air Service were instrumental in the aerial relocation of collared pronghorn during the larger study. We gratefully acknowledge the assistance and guidance on the analysis of the data provided by C. Schwarz. Funding was provided by the Alberta Antelope Guides, Alberta Conservation Association, Alberta Fish and Game Association (Zone 1), Alberta Parks and Recreation, Alberta Professional Outfitters Society (Legacy Fund and Wildlife Management Fund), Canadian Forces Base Suffield, Foundation for North American Wild Sheep – Eastern Chapter, Safari Club International, Safari Club International Alberta Chapter, and Safari Club International Northern Alberta Chapter (Hunting Heritage Fund).

## LITERATURE CITED

- Alberta Environmental Protection. 1997. The Grassland Natural Region of Alberta. Alberta Environmental Protection, Lethbridge, Alberta, Canada.
- AltaLIS. 2015. Alberta Base Features [shapefiles]. Calgary, Alberta, Canada. <[http://www.altalis.com/products/base/20k\\_base\\_features.html](http://www.altalis.com/products/base/20k_base_features.html)>. Accessed 25 July 2015.
- Amstrup, S. C. 1978. Activities and habitat use patterns of pronghorns on Montana-Wyoming coal lands. *Proceedings of Pronghorn Workshop* 8:270–306.
- Barnowe-Meyer, K. K., P. J. White, L. P. Waits, and J. A. Byers. 2013. Social and genetic structure associated with migration in pronghorn. *Biological Conservation* 168:108–115.
- Barrett, M. W. 1981. Environmental characteristics and functional significance of pronghorn fawn bedding sites in Alberta. *Journal of Wildlife Management* 45:120–131.
- Beckmann, J. P., K. Murray, R. G. Seidler, and J. Berger. 2012. Human-mediated shifts in animal habitat use: sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. *Biological Conservation* 147:222–233.
- Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:1–51.
- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *American Naturalist* 180:407–424.
- Bruns, E. H. 1977. Winter behavior of pronghorns in relation to habitat. *Journal of Wildlife Management* 41:560–571.
- Brown, C. L., A. R. Hardy, J. R. Barber, K. M. Fristrup, K. R. Crooks, and L. M. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. *PLoS ONE* (7):e40505.
- Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- Byers, J. A. 1997. *American pronghorn: social adaptations and the ghosts of predators past*. University of Chicago Press, Chicago, Illinois, USA.
- Coupland, R. F. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. *Journal of Ecology* 49:135–167.
- Dalton, K. A. 2009. *Pronghorn: migration triggers and resource selection in southeastern Oregon*. Thesis. Washington State University, Pullman, USA.
- Dodd, N. L., J. W. Gagnon, S. Sprague, S. Boe, and R. E. Schweinsburg. 2011. Assessment of pronghorn movements and strategies to promote highway permeability: US Highway 89. Final Report 619. Arizona Department of Transportation. Phoenix, Arizona, USA.
- ESRI World Terrain Base. 2009. World terrain base. ESRI, Redlands, California, USA. <[http://server.arcgisonline.com/ArcGIS/rest/services/World\\_Terrain\\_Base/MapServer](http://server.arcgisonline.com/ArcGIS/rest/services/World_Terrain_Base/MapServer)>.
- Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions: Biological Sciences* 365:2187–2200.
- Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology* 84:1775–1780.
- Hayes, C. L., and P. R. Krausman. 1993. Nocturnal activity of female desert mule deer. *Journal of Wildlife Management* 57:897–904.
- Harrington, J. L., and M. R. Conover. 2006. Characteristics of ungulate behavior and mortality associated with wire fences. *Wildlife Society Bulletin* 34:1295–1305.
- Information Services Corporation (ISC). 2015. *SaskAdmin\_2015\_URBAN\_MUNICIPALITY* [shapefile]. Regina, Saskatchewan, Canada. <[ftp://portaldata:freedata@ftp.isc.ca/PackagedData/SaskAdmin2015/SaskAdmin\\_2015\\_URBAN\\_MUNICIPALITY.zip](ftp://portaldata:freedata@ftp.isc.ca/PackagedData/SaskAdmin2015/SaskAdmin_2015_URBAN_MUNICIPALITY.zip)>. Accessed 25 July 2015.
- Jacques, C. N., J. A. Jenks, C. S. Deperno, J. D. Sievers, T. W. Grovenburg, T. J. Brinkman, C. C. Swanson, and B. A. Stillings. 2009a. Evaluating ungulate mortality associated with helicopter net-gun captures in the Northern Great Plains. *Journal of Wildlife Management* 73:1282–1291.

- Jacques, C. N., J. A. Jenks, and R. W. Klaver. 2009b. Seasonal movements and home-range use by female pronghorns in Sagebrush-Steppe Communities of western South Dakota. *Journal of Mammalogy* 90:433–441.
- Jakes, A. F. 2015. Factors influencing seasonal migrations of pronghorn across the Northern Sagebrush Steppe. Dissertation. University of Calgary, Calgary, Alberta, Canada.
- Jones, P. F. 2014. Scarred for life: the other side of the fence debate. *Human-Wildlife Interactions* 8:150–154.
- Jones, P. F., M. Grue, M. Suitor, D. J. Bender, C. Gates, D. Eslinger, and J. Landry-DeBoer. 2015. Variability in the selection patterns of pronghorn: are they really native prairie obligates? *The Prairie Naturalist* 47:94–109.
- Kammermeyer, K. E., and R. L. Marchinton. 1977. Seasonal change in circadian activity of radio-monitored deer. *Journal of Wildlife Management* 41:315–317.
- Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12:1359–1364.
- Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. *Wildlife Monographs* 38:1–96.
- Long, E. S., T. C. Jacobsen, B. J. Nelson, and K. M. M. Steensma. 2013. Conditional daily and seasonal movement strategies of male Columbia black-tailed deer (*Odocoileus hemionus columbianus*). *Canadian Journal of Zoology* 91:679–688.
- Long, R. A., J. G. Kie, R. T. Bowyer, and, M. A. Hurley. 2009. Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. *Wildlife Biology* 15:288–298.
- Mitchell, G. J. 1980. The pronghorn antelope in Alberta. University of Regina. Regina, Saskatchewan, Canada.
- Montana Base Map Service Center (MBMSC). 2009. Montana Incorporated Cities and Towns [shapefiles]. Department of Administration, Information Technology Services Division. Helena, Montana, United States of America. <<http://giscoordination.mt.gov/default.asp>>. Accessed 28 May 2011.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2:1–34.
- Mueller, T., K. A. Olson, T. K. Fuller, G. B. Schaller, M. G. Murray, and P. Leimgruber. 2007. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology* 45:649–658.
- Northrup, J. M., J. Pitt, T. B. Muhly, G. B. Stenhouse, M. Musiani, and M. S. Boyce. 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *Journal of Applied Ecology* 49:1159–1167.
- O’Gara, B. W. 2004. Behavior. Pages 145–194 in B. W. O’Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. University Press Colorado, Boulder, Colorado, USA.
- Reynolds, T. D. 1984. Daily summer movements, activity patterns, and home range of pronghorn. *Northwest Science* 58:300–311.
- Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.
- Sawyer, H., P. A. Rodgers, and T. Hart. 2016. Pronghorn and mule deer use of underpasses and overpasses along U.S. Highway 191. *Wildlife Society Bulletin* 40:211–216.
- Seidler, R. G., R. A. Long, J. Berger, S. Bergen, and J. P. Beckmann. 2015. Identifying impediments to long-distance mammal migrations. *Conservation Biology* 29:99–109.
- Skarin, A., Ö. Danell, R. Bergström, and J. Moen. 2010. Reindeer movement patterns in alpine summer ranges. *Polar Biology* 33:1263–1275.
- Suitor, M. J. 2011. Factors influencing pronghorn movements in the Northern Mixed Grasslands Ecoregion. Thesis. University of Calgary, Calgary, Alberta, Canada.
- Van Beest, F. M., E. Vander Wal, A. V. Stronen, and R. K. Brook. 2013. Factors driving variation in movement rate and seasonality of sympatric ungulates. *Journal of Mammalogy* 94:691–701.
- Webb, S. L., K. L. Gee, B. K. Strickland, S. Demarais, and R. W. DeYoung. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. *International Journal of Ecology*, vol. 2010, Article ID 459610, 12 pages, 2010. doi:10.1155/2010/459610.
- Webb, S. L., M. R. Dzialak, D. Houchen, K. L. Kosciuch, and J. B. Winstead. 2013. Spatial ecology of female mule deer in an area proposed for wind energy development. *Western North American Naturalist* 73:347–356.
- White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation* 135:502–510.
- Yoakum, J. D., P. F. Jones, J. Cancino, R. J. Guenzel, R. Seidler, A. Munguia-Vega, I. Cassaigne, and M. Culver. 2014. Pronghorn management guides. Fifth edition. Western Association of Fish and Wildlife Agencies’ Pronghorn Workshop and New Mexico Department of Game and Fish, Santa Ana Pueblo, New Mexico, USA.

Submitted 9 Dec 2016. Accepted 18 Mar 2017. Associate Editor was M. Colter Chitwood.