

# Are bison movements dependent on season and time of day? Investigating movement across two complex grasslands

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**Abstract.** The American plains bison (*Bison bison*) is an iconic herbivore on North American grasslands, yet many questions surrounding their basic biology remain unanswered. We analyzed fine-resolution movement data (12 minute) from two of the largest remaining prairie tracts in the Great Plains of North America to address whether bison movement and distance travelled are affected by seasonal or diurnal rhythms. We fit binomial movement and movement distance data to generalized linear mixed models to test whether site, season, or time of day affected movement. Our top models included season-site and season-time of day interactions as fixed effects. Overall, bison were more likely to move during the day than at night regardless of season or site. There was considerable overlap between our sites across most seasons, with the strongest divergence occurring in autumn for movement probability and distance. During the summer, daytime bison movement declined in favor of nighttime movement, potentially in response to high temperatures. Day and nighttime movement distance and probability both were lowest in the winter. That site alone was not a significant predictor of bison movement or movement distance may suggest that their response to seasonal and diurnal rhythms is biologically innate. Therefore, we conclude that season and time of day should be considered in future bison movement analyses. Here, we present the first replicated analysis of fine-resolution, seasonal, and diurnal bison movements across two large complex landscapes using a long-term dataset. As ungulate behavior changes in response to the Anthropocene, filling the knowledge gaps in their basic biology is critical to their continued conservation.

**Key words:** American plains bison; conservation; diurnal rhythms; ecology; landscape; prairie; seasonality; ungulate movement.

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## INTRODUCTION

Since their decline in the 19th century, American bison (*Bison bison* L.) have become an icon for many grassland restoration and conservation

organizations in North America. Many of these groups cite hypothesized keystone effects that bison may have on grassland ecosystems as a rationale for some of the reintroduction projects

that are ongoing (Fuhlendorf et al. 2018, McMillan et al. 2019). However, there is evidence that these effects are often confounded with management actions and may not be due to bison reintroduction alone (Allred et al. 2011b, Fuhlendorf et al. 2018). Rather, research suggests that the interaction between bison (and other grazers) and disturbance processes (e.g., fire) may have a more significant influence on grassland ecosystems than grazer species alone (Allred et al. 2011b). The feedback between grazing behaviors and fire disturbance, in particular, increases landscape complexity, which is critical to maintaining grassland biodiversity (Fuhlendorf et al. 2009). While we know a great deal about where bison move, we know very little about the mechanisms influencing their movement decisions.

Animal movement and behavioral studies, including those of bison, have historically been limited to visual or high frequency radio-tracking studies because of the high costs, or practical difficulties associated with using fine-resolution (<3 m accuracy), high fix-rate (<1 h per fix) global-positioning system (GPS) tracking technology (Tomkiewicz et al. 2010). These limitations have kept nighttime movements and fine-resolution behavioral patterns unknown for many species, including some charismatic megafauna (Tomkiewicz et al. 2010, Owen-Smith and Goodall 2014). Recently, however, researchers have shown that some ungulates alter their non-migratory movement patterns in response to seasonal (Owen-Smith and Goodall 2014, Schmidt et al. 2016) and diurnal (Hazlerigg and Tyler 2019) rhythms. Unlike many ungulates that track seasonal shifts in forage quality (Merkle et al. 2016), there is currently no conclusive evidence suggesting that bison movement shifts seasonally (Geremia et al. 2019). To date, much of our bison ecology knowledge is based on studies of small, homogeneously managed landscapes, and single or small herds (Towne et al. 2005, Fuhlendorf et al. 2010, Allred et al. 2011b). Historically, bison would have roamed large, complex, and unfragmented landscapes (Hornaday 1889, Fuhlendorf et al. 2009). Therefore, while previous studies have provided valuable insights into bison behavior, they may not reflect behavioral responses to complex landscapes critical to grassland biodiversity (Fuhlendorf et al. 2009). Additionally, almost all of what we know about bison

behavior on complex landscapes is skewed toward habitat or resource selection models (i.e., point pattern analyses; Edelhoff et al. 2016) based primarily on the spatial distribution of somewhat temporally fixed landscape features such as topography or the distribution of water bodies (e.g., Allred et al. 2011b, Kohl et al. 2013). Thus, there is a distinct knowledge gap surrounding how bison move in general, let alone how they move with seasonal and diurnal rhythms.

We had the opportunity to use a robust bison movement dataset from two well-known herds in the Southern Great Plains to address these fundamental gaps in our knowledge about bison movement. Seasonal and diurnal rhythms are known to affect ungulate movement broadly (Johnson et al. 2002, Owen-Smith et al. 2012, Owen-Smith and Goodall 2014), but the importance of these basic and critical factors has been mostly overlooked for American bison. Therefore, as many bison reintroduction projects are ongoing across the Great Plains (Fuhlendorf et al. 2018, McMillan et al. 2019), addressing gaps in our fundamental understanding of bison movement has significant management and conservation value. We conducted this descriptive study asking: (1) Does bison movement probability and (2) distance change between seasons and times of day; or are they better explained by differences between the two independent herds and landscapes alone? Overall, we hoped to determine whether movement patterns across seasons and times of day were consistent across two independent sites.

## METHODS

### Study areas

The data we used in our study were collected across two sites in Oklahoma that vary considerably in their management, topography, vegetation, and climate: The Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve (TPP) and the United States Fish and Wildlife Service's Wichita Mountains Wildlife Refuge (WMWR). The TPP, located in Osage County, Oklahoma, is an approximately 16,000-ha tract located at the southern end of the Flint Hills ecoregion of North America. The TPP is dominated by vegetation typical of a productive tallgrass prairie ecosystem (e.g., *Andropogon gerardii*

Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, *Dalea candida* Michx. ex Willd., *Echinacea pallida* (Nutt.) Nutt., *Liatris* spp., *Asclepias* spp., etc.; Table 1). Temperature and precipitation are highly variable across the TPP, which is typical for grassland ecosystems globally, but averages range from 13° to 16°C and 100–200 cm annually (Brock et al. 1994, McPherson et al. 2007, Table 1). The TPP is divided into two distinct units based on the dominant grazer (cattle or bison), and our study focused on data collected in the 9,400-ha bison unit (~72% of the total preserve area) where approximately 2,500 bison are allowed to freely graze year-long. Most of the TPP is managed with fire under the patch-burning management paradigm that is focused on restoring structural heterogeneity on the landscape (Hamilton 2007). Fire in the TPP bison unit is randomly applied across the unit, with time-since-fire ranging from 0 to 6 years across all of the patches. Bison at the TPP focally graze recently burned patches disproportionately more than those that were burned previous years, creating a temporally and spatially shifting mosaic of grassland structure across the area (Hamilton 2007, Allred et al. 2011a). Fire is applied at various times throughout the year in the TPP bison unit to mimic historic fire regimes (Hamilton 2007).

The WMWR is a 23,884-ha refuge managed by the U.S. Fish and Wildlife Service in Comanche county, Oklahoma. The WMWR is made up of several ecosystems that vary with elevation (range 422–755 m above sea level; Table 1), but

the grasslands occurring throughout the refuge are characterized as mixed-grass prairie (e.g., *Schizachyrium scoparium* (Michx.) Nash, *Bouteloua gracilis* (Kunth) Lag. ex Griffiths, *Comandra pallida* (A. DC.) Piehl, *Penstemon albidus* Nutt., *Agrostis elliottiana* Schult., *Aristida purpurea* Nutt., etc.; Table 1). Precipitation and temperatures are variable at the refuge. Precipitation is much lower on average (27–66 cm; Table 1) than at the TPP, but temperatures were similar to TPP (10°–16°C; (Brock et al. 1994, McPherson et al. 2007; Table 1). WMWR is actively managed with prescribed fire and grazing, although unlike the TPP, the approximately 650 bison and 220 long-horn cattle at the WMWR are free to graze jointly across the majority of the refuge.

#### Data collection

For this study, we utilized GPS-telemetry data from the TPP and WMWR bison herds, collected across multiple temporal resolutions (Allred et al. 2011a). GPS collars were deployed on seven female individuals from the TPP, and six female individuals from WMWR from November 2008 to November 2010 and November 2010–July 2012, respectively. Collar location data were recorded at 12-minute temporal intervals for all individuals. When recorded across long-temporal intervals, ungulate movement data (particularly those of bison) may be confounded by fence-effects, or other restrictions to movement correlated to restrictive, manmade landscape features. Therefore, our use of 12-minute data collection allowed us to reduce the effect of fences

Table 1. The total area (ha), elevation (m), range of slope (%), fire management, dominant plant community, average forage productivity (kg/ha), forage productivity range (kg/ha), and average annual rainfall (cm) between the Tallgrass Prairie Preserve (TPP) and Wichita Mountains Wildlife Refuge (WMWR).

Site	Total area (ha)	Elevation min-max (m)	Slope min-max (%)	Fire management	Dominant plant community	Average forage productivity (kg/ha)	Forage productivity min-max (kg/ha)	Average annual rainfall (cm)
TPP	9,400	244–335	0–45	Patch-burn	Tallgrass prairie	4,231	1,267–9,021	95
WMWR	23,885	422–755	0–50	Large Rx fire	Mixed-grass prairie	2,874	336–6,888	62

*Notes:* We define large prescribed (Rx) fire as single fires that cover the majority (or sometimes all) of the landscape. We refer to patch-burns as being small (far less than half the area of a landscape) fires that are heterogeneously applied across a landscape through time (see Fuhlendorf et al. 2009). Average annual rainfall was procured from the Foraker and Medicine Park Mesonet stations (<https://www.mesonet.org>) at the TPP and WMWR, respectively, and represents the conditions during the years 2008–2012. Forage productivity and plant community metrics were obtained from the United States Department of Agriculture's Web Soil Survey (<https://websoilsurvey.nrcs.usda.gov>) and represent total available dry forage under normal conditions.

and other barriers on our movement analyses. From 2008 to 2010, patches within the TPP bison unit were annually burned and the unit was moderately stocked ( $2.1 \text{ AUM/ha}^{-1}$ ; One animal unit month [AUM] is equal to the forage required to feed one 454 kg cow and calf for one month) across a 9,400-ha unit. From 2010 to 2012, the WMWR did not have a fixed burn schedule and was lightly stocked with bison ( $0.32 \text{ AUM} \cdot \text{ha}^{-1}$ ) and longhorn cattle ( $0.11 \text{ AUM/ha}^{-1}$ ). The location data we acquired were differentially corrected using GPS base stations located on TPP and WMWR (Allred et al. 2011a).

### Data analysis

To investigate how diurnal, seasonal, and site affect bison movement patterns, we calculated movement metrics from our GPS data and stratified them by season and time of day. We used the package *amt* in R (R Core Team 2019, Signer et al. 2019) to clean and process all of our GPS data prior to analysis. We resampled the entire dataset using our fix-rate to ensure that each movement track represented an uninterrupted series of 12-minute movements for each individual in our dataset (Barnett and Moorcroft 2008, Signer et al. 2017). Next, we calculated the distance travelled for each 12-minute movement in our grouped and processed dataset using the function *step\_length* (Signer et al. 2019). Using movement distance, as opposed to other primary movement measures, allowed us to most simply and effectively detect state-changes typical in non-migratory ungulates through time (Edelhoff et al. 2016). We used the function *time\_of\_day* (Signer et al. 2019) to determine whether a movement occurred during the day or night (factor with two levels), which were determined following official sunrise and sunset times for the specific date that a movement occurred. We also assigned a season (i.e., spring, summer, autumn, or winter; a factor with four levels) to each movement based on its calendar date using the *time-stamp* for each GPS-fix.

We use generalized linear mixed models with binomial link functions to form alternative models of the probability of movement being affected by site, season, and/or time of day. We quantified the support the data provided for those models using Akaike information criterion. We classified all movements  $<3 \text{ m}$  as

non-movements (recorded as 0), as this distance was within the error rate for the collars, and all movements  $>3 \text{ m}$  as a movement (recorded as 1). We then used the R package *lme4* (Bates et al. 2015) to develop multiple generalized linear mixed models using all pairwise combinations of site, season, and time of day as fixed effects with individual used as the random intercept.

We used gamma distributed generalized linear mixed models with log link functions to investigate whether bison movement distances were affected by site, season, and/or time of day. We quantified the support the data provided for those models using Akaike information criterion. We included individual ID number as the random intercept parameter for each model. We developed mixed-effects models for all pairwise combinations of site, season, and time of day as fixed effects.

Table 2. Model comparison tables where delta-AIC values and degrees of freedom are reported for each combination of model parameters we tested.

Model parameters	$\Delta\text{AIC}$	df
<b>Binomial</b>		
Site $\times$ Season + Season $\times$ TOD	0.0	13
Site $\times$ Time of Day + Season $\times$ TOD	197.2	11
Season $\times$ TOD	247.8	9
Site $\times$ TOD	2508.9	5
Season + TOD	2619.0	6
TOD	2682.8	3
Site + TOD	2684.5	4
Site $\times$ Season	27052.8	9
Season	27353.5	5
Site + Season	27355.0	6
Null	28086.8	2
Site	28087.9	3
<b>Movement distance</b>		
Site $\times$ Season + Season $\times$ TOD	0.0	14
Site $\times$ TOD + Season $\times$ TOD	1194.1	12
Season $\times$ TOD	1335.9	10
Season + TOD	5934.5	7
Site $\times$ TOD	21712.3	6
Site + TOD	22439.0	5
Time of Day	22452.0	4
Site $\times$ Season	31630.0	10
Site + Season	32733.8	7
Season	32735.4	6
Site	49013.9	4
Null	49024.5	3

Notes: Models were fit to predict movement (Binomial) or movement distances. We set Individual as the random intercept effect for all of our models.

## RESULTS

We analyzed 554,971 total data points in this study, with nearly 70% of those coming from the TPP ( $n = 391,195$ ) and the remaining 30% from the WMWR ( $n = 163,776$ ). The mean 12-minute step length across all of our sites was 55.3 m, with a standard deviation of 107 m ( $SE = 0.1$  m), and mean step lengths at TPP and WMWR were 57.5 m ( $SD = 112.5$  m) and 49.8 m ( $SD = 92.4$  m), respectively.

### Movement probability

Season-site and season-time of day pairwise interactions best described the probability of bison movement compared to our other models (Table 2). Although observed relative movement frequencies between our sites were not clear across all seasons, the most divergence occurred in the autumn (TPP  $\bar{x} = 0.79$ ,  $SD = 0.02$ ; WMWR  $\bar{x} = 0.74$ ,  $SD = 0.04$ ; Fig. 1). Overall, we found that bison were more likely to move during the

day than at night across all seasons (Fig. 2). Following predictions from our top model, our observed bison movement frequencies changed seasonally where bison moved most often during the day in the winter than any other time and season ( $\bar{x} = 0.89$ ,  $SD = 0.02$ ; Fig. 2). Our observed nighttime relative movement frequencies rose to their peak from spring ( $\bar{x} = 0.68$ ,  $SD = 0.03$ ) to summer ( $\bar{x} = 0.72$ ,  $SD = 0.06$ ) and were lowest in the winter ( $\bar{x} = 0.65$ ,  $SD = 0.05$ ; Fig. 2). Conversely, our observed daytime relative movement frequencies declined to their lowest from spring ( $\bar{x} = 0.87$ ,  $SD = 0.01$ ) to summer ( $\bar{x} = 0.83$ ,  $SD = 0.03$ ) and then steadily rose to their peak from autumn ( $\bar{x} = 0.87$ ,  $SD = 0.02$ ) to winter ( $\bar{x} = 0.89$ ,  $SD = 0.02$ ; Fig. 2).

### Movement distance

The distance that bison move during a single movement event is best described by season-site and season-time of day pairwise interactions compared to all of our other models (Table 2).

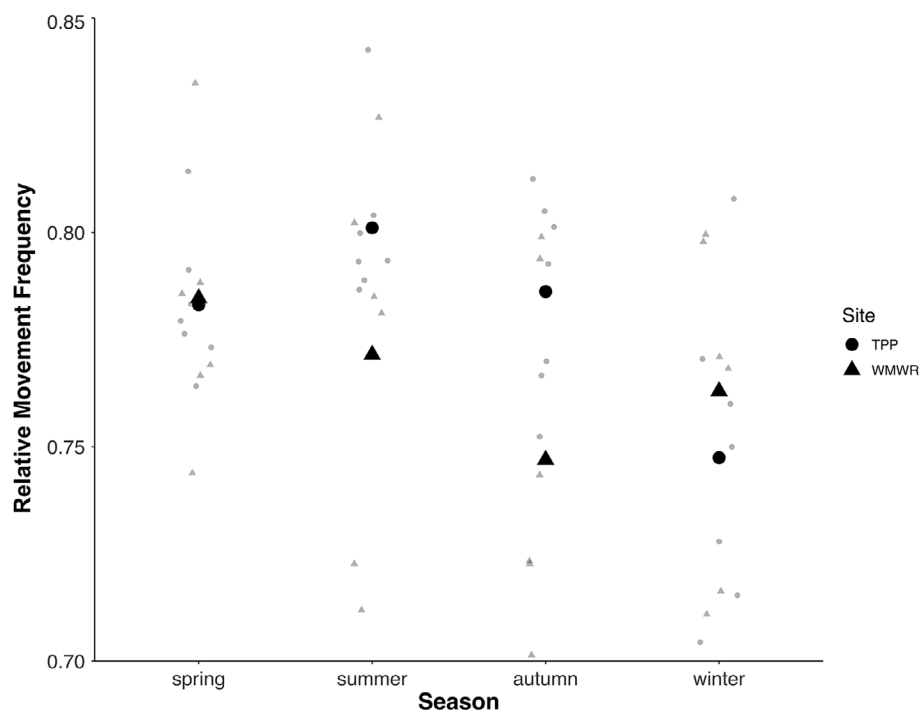


Fig. 1. Relative movement frequencies across all four seasons (spring, summer, autumn, and winter) and our two sites (TPP and WMWR). Small points represent mean movement frequency for each individual, and large points represent the mean movement frequency across all individuals. Data are from the two bison herds we used in this study.



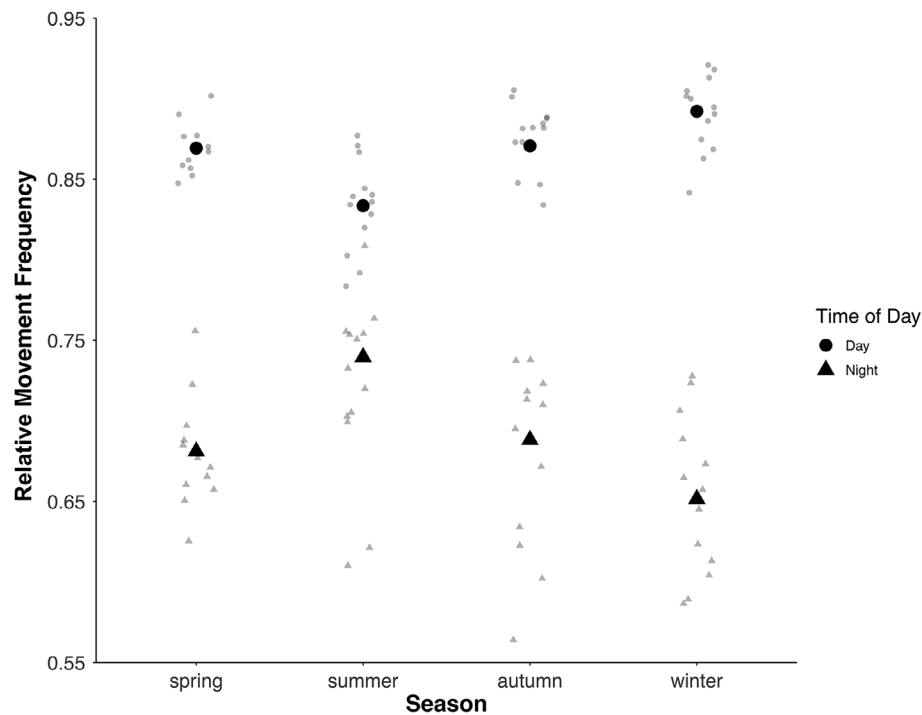


Fig. 2. Observed movement frequencies across all four seasons (spring, summer, autumn, and winter) and two times of day (day and night). Data are from two bison herds in the Great Plains, and were collected 2008–2010 and 2010–2012, respectively. Smaller points represent the mean movement frequency for each individual, and larger points represent the mean movement frequency across all individuals.

For most of the year, bison movements were similar between our two sites (Fig. 3). However, the clearest difference between the two sites occurred in autumn (TPP  $\bar{x}$  = 61.1 m, SD = 103.7; WMWR  $\bar{x}$  = 43.6 m, SD = 81.4; Fig. 3). The mean distance travelled for a single movement event for our bison was always higher during the day than at night regardless of season (Fig. 4; Table 3). Our observed mean distance travelled during the day was relatively constant during the spring ( $\bar{x}$  = 73.2 m, SD = 114.3,  $n$  = 95,710), summer ( $\bar{x}$  = 77.2 m, SD = 140.2,  $n$  = 89,016), and autumn ( $\bar{x}$  = 76.7 m, SD = 109.7,  $n$  = 39,434), but was lowest in the winter ( $\bar{x}$  = 55.5 m, SD = 103.3,  $n$  = 61,075; Fig. 4). Mean nighttime distances peaked from spring ( $\bar{x}$  = 42.0 m, SD = 96.6,  $n$  = 80,106) to summer ( $\bar{x}$  = 57.9 m, SD = 109.5,  $n$  = 62,412), but then declined from autumn ( $\bar{x}$  = 37.5 m, SD = 82.0,  $n$  = 43,470) to winter ( $\bar{x}$  = 21.0 m, SD = 51.3,  $n$  = 83,748; Fig. 4).

## DISCUSSION

Much of the literature on bison ecology is focused on analyzing single herds that roam small, homogenously managed landscapes (Towne et al. 2005, Fuhlendorf et al. 2010, Allred et al. 2011b). To the best of our knowledge, our study represents the first analysis of seasonal and diurnal bison movements using data from two distinct herds on large complex landscapes. Further, even though our sites differed in size, topography, management, vegetation, forage productivity, and precipitation (Table 1), we found that bison movement probability and distance may be more affected by seasonal and diurnal rhythms than site differences alone. This is especially notable since one of our sites—the Tallgrass Prairie Preserve—is managed primarily to maximize structural heterogeneity (Hamilton 2007). The variability in movement distance between our two sites (Table 3) is likely due to

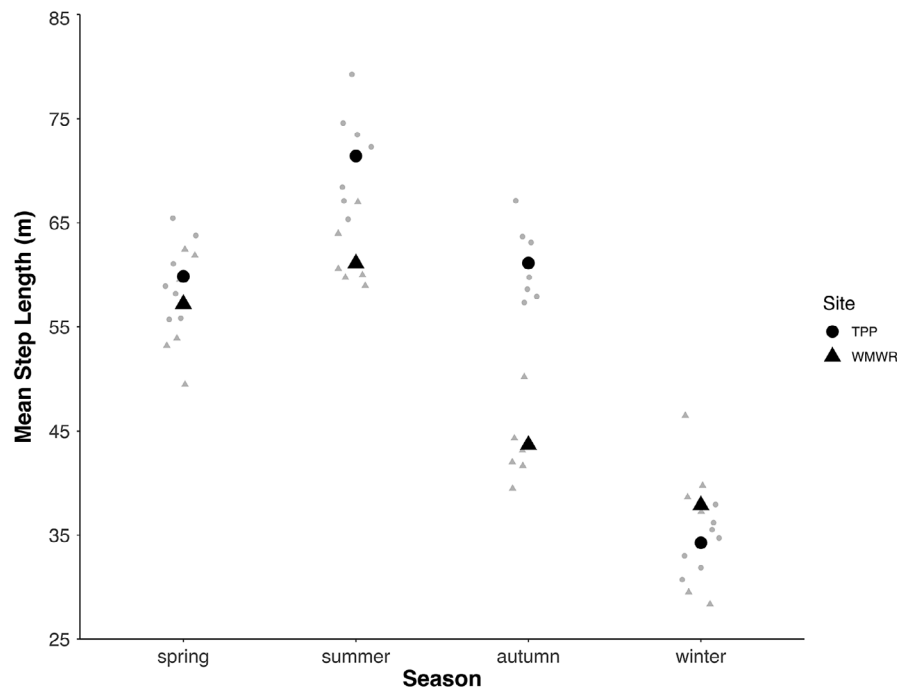


Fig. 3. Mean bison step length distances (m) by season (spring, summer, autumn, and winter) and between our two sites in the Great Plains: the Tallgrass Prairie Preserve (TPP) and the Wichita Mountains Wildlife Refuge (WMWR). Small points represent mean step lengths (m) for each individual, and large points represent the mean step length (m) across all individuals. Step lengths represent the total distance moved during a 12-minute period. Total GPS points we recorded for spring, summer, autumn, and winter were 175,816; 151,428; 82,904; and 144,823, respectively.

the topographical differences between the two sites as bison generally avoid steep slopes (Table 1; Allred et al. 2011b, Kohl et al. 2013), restricting movement at the WMWR more than at the TPP. That movement distances were more variable at the TPP than at the WMWR may also be due in-part to the shifting spatial arrangement of fire at the TPP (i.e., patch-burning; Hamilton 2007), which significantly alters bison resource selection (Allred et al. 2011a). Our results follow recent studies elsewhere showing that seasonal and diurnal rhythms generally have strong effects on ungulate movement decisions (Owen-Smith and Goodall 2014). Therefore, we conclude that season and time of day should be considered as important predictors of bison movement in future studies.

We found that bison movement and distance travelled were partially explained by the interaction between season and time of day, which drive many landscape and life-history patterns that are

known to affect movement. For example, seasonal and diurnal rhythms both work to drive many landscape patterns like vegetation distribution and quality (Geremia et al. 2019). As ungulates, bison movement decisions are significantly affected by forage quantity, quality, and distribution across landscapes (Fortin et al. 2003, Geremia et al. 2019), all of which are partly driven by seasonal and diurnal rhythms in photosynthesis (Pilarski 1999) and weather. For example, that our observed bison movement distances were more variable overall during the day than at night may be partly explained by differences in forage quality, as ungulate movement rates correlate with diurnal changes in photosynthesis (Owen-Smith and Goodall 2014). Furthermore, many important bison life-history events recur in seasonal patterns (e.g., breeding and calving), and may partially explain some of our results (Lott 2002). It is possible that our results represent a species-wide response to season and

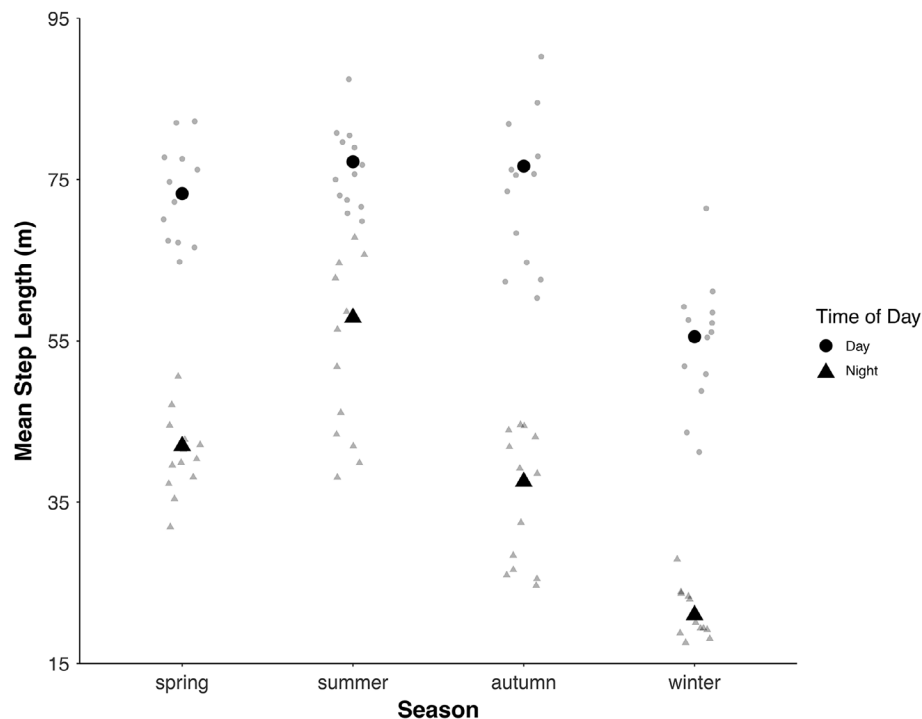


Fig. 4. Mean bison step length distances (m) by season (spring, summer, autumn, and winter) and time of day (day and night). Data are from two bison herds in the Great Plains, and were collected 2008–2010 and 2010–2012, respectively. Smaller points represent the mean movement frequency for each individual, and larger points represent the mean movement frequency across all individuals. Total GPS points we recorded for spring, summer, autumn, and winter were 175,816; 151,428; 82,904; and 144,823, respectively.

time of day, but more data from the broader North American population are needed to confirm that hypothesis.

Differences between daytime and nighttime movement probability and distances may represent a response to temperature fluctuations during those seasons. Specifically, we observed that the differences between daytime and nighttime movement distances and probabilities were the lowest during the summer than any other season. To regulate their internal temperature during particularly warm times of the year, bison may seek out thermal refugia where operative temperatures are lower than the surrounding environment (Allred et al. 2013). However, some ungulates also may move at different times throughout the diurnal cycle to offset the effects of thermal stress (Owen-Smith 1998, Owen-Smith and Goodall 2014), electing to move in the cooler parts of the diurnal cycle rather than the heat of the day. Therefore, our observed

movements may be partially explained by bison moving at times that minimize their exposure to unfavorable weather patterns, and should be considered directly in future studies.

Bison movements, as with all ungulates, are undoubtedly influenced by plant phenology (Merkle et al. 2016). Plant phenology changes heterogeneously across space and time, being significantly affected by precipitation, elevation, temperature, light, and also by various land management actions (e.g., fire, grazing, etc.; Bischof et al. 2012, Aikens et al. 2017, Geremia et al. 2019). Therefore, the relationship between ungulate movement and plant phenology is nearly infinitely complex and is often highly variable between individuals within a non-migratory ungulate population (Mueller et al. 2011, van Beest et al. 2013). Due to the complex, and data-intensive nature of time-series phenological analyses of ungulate movement, our study helps put into focus points in time when phenology may



Table 3. Summary table showing the total GPS observations collected, mean movement distance (Mean step length), and standard deviation in movement distances (SD) across each season (spring, summer, autumn, and winter) and time of day (day and night) for our bison movement dataset.

Season	Time of day	Total GPS observations	Mean step length (m)	SD
Tallgrass Prairie Preserve (TPP)				
Spring	Day	65,530	72.8	116.2
Spring	Night	54,224	44.1	102.8
Summer	Day	68,985	78.0	146.3
Summer	Night	48,634	61.9	114.7
Autumn	Day	27,638	80.4	114.9
Autumn	Night	27,545	42.1	87.2
Winter	Day	37,374	54.4	109.5
Winter	Night	51,708	19.6	43.2
Wichita Mountains Wildlife Refuge (WMWR)				
Spring	Day	30,146	74.1	110.1
Spring	Night	25,816	37.4	82.0
Summer	Day	18,795	74.0	114.6
Summer	Night	13,032	42.5	85.4
Autumn	Day	10,014	65.7	92.0
Autumn	Night	13,525	27.3	68.1
Winter	Day	17,789	57.4	91.3
Winter	Night	24,493	23.4	63.1

be driving seasonal differences in bison movements. For example, we show that bison move less often and shorter distances in the winter compared to other seasons. Future research pairing each 12-minute movement with daily Normalized Difference Vegetation Index (NDVI) values during the autumn and winter would offer insight into how any seasonal changes in greenness might be driving those movements.

Our study represents the first assessment of seasonal and diurnal bison movement using fine-resolution GPS data from multiple herds on multiple large complex landscapes. The bulk of bison movement studies are focused on how landscape patterns influence where bison are likely to move (e.g., Kohl et al. 2013, Geremia et al. 2019). We know of no other studies analyzing bison movement through time, irrespective of landscape (e.g., slope and elevation) or resource selection patterns (e.g., foraging area,

home-ranges, etc.). Therefore, our study is intended to be a starting point in addressing why seasonal and diurnal rhythms affect the frequency and magnitude of bison movements. Future studies should use more complex methods of landscape analysis (including plant phenology metrics matched with each movement) to zero-in on the mechanisms that might be driving the seasonal and diurnal bison movements we describe here. The results of movement studies are likely to change with scale (Rivrud et al. 2010, Northrup et al. 2016) and landscape complexity (Crone et al. 2019). Ungulate movement is also significantly affected by weather (Rivrud et al. 2010, Schmidt et al. 2016) and is predicted to change drastically in response to climate shifts resulting from the Anthropocene (Dirzo et al. 2014, Craine et al. 2015). Therefore, future studies should also continue to uncover the interactions between scale, landscape complexity, and weather on ungulate movement patterns. If we are to conserve iconic species like bison into the future, it is essential that researchers continue to close gaps in our basic understanding of ungulate movement to buffer against future change.

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