

Ecology

Decreased movements of adult female mule deer during winter in arid southwestern North America

Disminución de los movimientos de las hembras adultas de venado bura durante el invierno en el árido suroeste de América del Norte

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Abstract

Deer in northern temperate environments show behavioral and physiological adaptations to conserve energy during winter, including decreased movements. Whether these behaviors persist in warmer temperate environments such as the arid Southwest has received little consideration. We compared daily movements as estimated by continuous-time movement models and minimum subdaily (4 h) straight-line movements of adult female mule deer between winter and spring-autumn seasons in south-central New Mexico. Deer moved less during winter daily (2.90 vs. 4.34 km/d) and subdaily (302 vs. 409 m). Similarly, for deer for which movement data for successive seasons were available, movements between successive seasons were less during the winter (daily = -1.05 km/d; subdaily = -91 m) than the following or preceding spring-autumn. Our results support conservation of decreased movements during winter in the less extreme winters of the arid Southwest. Because some proximate stimuli (i.e., deep snow, very cold temperatures) associated with energy conservation behaviors are lacking in the arid Southwest, our results further support low forage quality and availability being the primary drivers of this behavior.

Keywords: Energy conservation; Movements; Mule deer; New Mexico

Resumen

Los ciervos en entornos templados del norte muestran adaptaciones de comportamiento y fisiológicas para conservar energía durante el invierno, incluyendo una disminución en sus movimientos. Se ha explorado poco si estos comportamientos persisten en ambientes templados más cálidos, como el suroeste árido. Comparamos los movimientos diarios, mediante modelos de movimiento continuo y movimientos mínimos en línea recta subdiarios (4 horas) de hembras adultas de venado bura entre las estaciones de invierno y primavera-otoño en el centro-sur de Nuevo México. Los ciervos se movieron menos durante el invierno, tanto diario (2.90 vs. 4.34 km/día) como subdiario (302 vs. 409 m). Además, para ciervos con datos de movimiento en estaciones sucesivas, los movimientos en invierno fueron menores (diarios = -1.05 km/día, subdiarios = -91 m) en comparación con la primavera-otoño previa o siguiente. Nuestros resultados respaldan la disminución de los movimientos durante el invierno en los inviernos menos extremos del suroeste árido. Dado que algunos estímulos inmediatos (por ejemplo, nieve profunda, temperaturas muy frías) asociados con comportamientos de conservación de energía están ausentes en el suroeste árido, es evidente que nuestros resultados apoyan que la baja calidad y disponibilidad de forraje son los principales factores que impulsan este comportamiento.

Palabras clave: Conservación de energía; Movimientos; Venado bura; Nuevo México

Introduction

Deer in northern temperate environments of North America employ a complex energy conservation strategy during winter, incorporating multiple behavioral and physiological adaptations, including reducing activity (i.e., movements) and limiting feeding while relying on endogenous reserves (Alldredge et al., 1974; Short, 1981; Verme & Ullrey, 1984); growing a highly insulative pelage (Jacobsen, 1980); limiting vascular circulation to the extremities (Parker & Robbins, 1984); and lowering metabolic rate to slow the rate of loss of body reserves (Short, 1981; Silver et al., 1971; Verme & Ullrey, 1984). This strategy is considered primarily an adaptation to conserve energy in response to low forage availability and quality, as well as increased costs of movement associated with snow (Short, 1981; Verme & Ullrey, 1984). Conserving energy by minimizing radiant and convective heat loss was also believed to drive other behaviors such as yarding under dense conifer forest canopies (Marchinton & Hirth, 1984). While initially thought to be a response to extreme cold (Marchinton & Hirth, 1984), yarding likely relates to decreased costs of movement because of reduced snow depths as the presumed temperature-moderating influence of forest canopy (i.e., thermal cover) has been shown to have no real effect on deer condition (Cook et al., 1998; Freddy, 1984). Many of the behavioral aspects (at least) of the winter energy conservation strategy are not invariant, however, and can be affected by proximate stimuli. For example, both movements and feeding periods are reduced less if winter conditions are less severe (Bartmann & Bowden, 1984; Verme & Ullrey, 1984).

Whether these energy conservation behaviors persist in warmer temperate ranges such as the arid southwestern

USA and Mexico has received little consideration. In the arid Southwest, deer similarly experience winter seasonality in terms of temperature and precipitation differences (Krausman et al., 1990; McKinney, 2003; Marshal et al., 2008), which affects forage availability and quality (Kemp, 1983; Krausman et al., 1990; McKinney, 2003; Short, 1981). Consequently, mule deer lose most of their endogenous reserves over winter (Bender et al., 2012; Bender & Hoenes, 2017). However, snow is relatively rare and short-lived in much of the arid Southwest, and winter temperatures are higher than in northern environments (Table 1). Therefore, aside from decreased forage availability and quality, many of the potential proximate stimuli (i.e., deep snow, very cold temperatures) associated with energy conservation behaviors are lacking in the arid Southwest. Moreover, because winter is less extreme in terms of minimum temperatures and particularly snowfall, availability of forage may also be less limiting, although forage quality constraints are similarly severe (Bender, 2020; Kemp, 1983; Krausman et al., 1990; McKinney et al., 2003). Consequently, behavioral responses associated with the winter energy conservation strategy may be less pronounced or absent in the arid Southwest.

If energy conservation behaviors are maintained in the arid Southwest, mule deer (*Odocoileus hemionus*) should move less during the winter, conserving body reserves in the face of lower quality and less abundant forage even if the impacts of winter weather are less severe on forage availability and costs of movement. Thus, our goal was to contrast short-term movements between winter and spring-autumn seasons for adult female mule deer in a Chihuahuan desert-short grass prairie habitat in New Mexico, USA to determine whether deer reduce movements during winter as predicted by the winter

Table 1

Long-term range of monthly mean high and low temperatures (°C) and monthly snowfall (cm) during Dec.-Feb. and Mar.-Nov. at the Corona Range and Livestock Research Center (CRLRC), Corona, New Mexico USA, and the Cusino Wildlife Research Station, Shingleton, Michigan USA. Cusino was selected as a comparison because of the volume and depth of deer nutritional, physiological, and behavioral research conducted there (Verme & Ullrey, 1984). Also presented are the range of conditions on the CRLRC study area for 2005-2008 study period.

Months	Climatic variable	CRLRC	Cusino	Study
Dec.-Feb.	Mean high temperatures	6.7-8.9	-2.8- -1.7	6.4-13.0
	Mean low temperatures	-5.6- -4.4	-11.7- -8.3	-6.3- -1.9
	Mean snow accumulations	13-23	69-109	7.3-17.1
Mar.-Nov.	Mean high temperatures	11.7-28.3	1.7-22.8	14.2-29.1
	Mean low temperatures	-1.1-13.3	-6.7-13.3	-0.5-13.8
	Mean snow accumulations	0-13	0-48	0-5.1

energy conservation strategy. Specifically, we compared minimum daily and subdaily movement distances of adult female mule deer between winter and spring-autumn.

Materials and methods

Our study was conducted on the Corona Range and Livestock Research Center (CRLRC; 34°15'36" N, 105°24'36" W), an 11,290-ha ranch owned and operated by New Mexico State University and located approximately 22.5 km east of Corona, New Mexico (Fig. 1). CRLRC has an average elevation of 1,900 m asl; mean annual precipitation is 40 cm, 87% of which occurs in the Mar.-Nov. period. Snowfall totals < 74 cm annually. Climate of the CRLRC shows distinct seasonality, although the magnitude of seasonal differences in winter is less than seen in northern temperate deer habitats (Table 1).

Topography of the CRLRC is mostly rolling. Vegetation includes perennial grassland, with scattered sparse to dense pinyon (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) woodlands and a few shrublands. Free water was abundant and comparably available in both winter and spring-autumn seasons because of numerous permanent water developments, ≥ 1 of which were present within or adjacent to annual home ranges of study deer (Fig. 1). Deer on the CRLRC do not migrate between distinct summer and winter ranges.

We captured and collared ≥ 2.5 -year-old female mule deer with GPS/VHF radio-collars (Advanced Telemetry Solution, Asanti, Minnesota, USA) programmed to record a position fix every 4 h, early-December 2005-2007, and April, 2006-2007, as part of a larger study of mule deer ecology including other VHF-only radio-collared individuals (Bender et al., 2011, 2013). Deer were captured using a helicopter by aerial net-gunning or darting with

1.5-1.8 mg of carfentanil citrate and 50-75 mg of xylazine hydrochloride per deer. We aged deer as yearling or adult by tooth wear and replacement (Robinette et al., 1957), determined lactation status (Bender et al., 2011), and treated deer with antibiotics, vitamin E/selenium, vitamin B, and an 8-way *Clostridium* bacterin to help alleviate capture stress. Following processing, immobilants were antagonized with naltrexone and tolazoline.

We defined seasons as winter = Dec-Feb and spring-autumn = Mar-Nov. These seasons corresponded with both typical seasonal and phenological patterns on the CRLRC and the Chihuahuan desert-short grass prairie habitats of the arid Southwest in general, as well as important periods in the annual cycle of female mule deer in the arid Southwest (Bender et al., 2011, 2012). We estimated daily movements using continuous-time movement modeling (see Fleming et al., 2014, 2016), using the Speed/Distance analysis in ctmweb (<https://ctmm.shinyapps.io/ctmmweb/>) (Calabrese et al., 2016, 2021). We used only locations with 3D fixes and DOP < 2, as these had an accuracy of < 3 m in our study area. We also determined minimum subdaily movements, defined as the straight-line distance moved between successive 4 h locations, and calculated seasonal means for each deer.

We compared movement distances (km from continuous-time movement models [ctmms]; m between successive subdaily locations) between seasons using PROC GLIMMIX in SAS 9.4 (SAS, 1988), using individual deer as a random effect. We also compared mean daily and subdaily movements between successive seasons for individual deer for which we had both winter and subsequent spring-autumn data, or spring-autumn and subsequent winter data, available. We determined mean seasonal differences in movement distances for each successive time period for each individual,

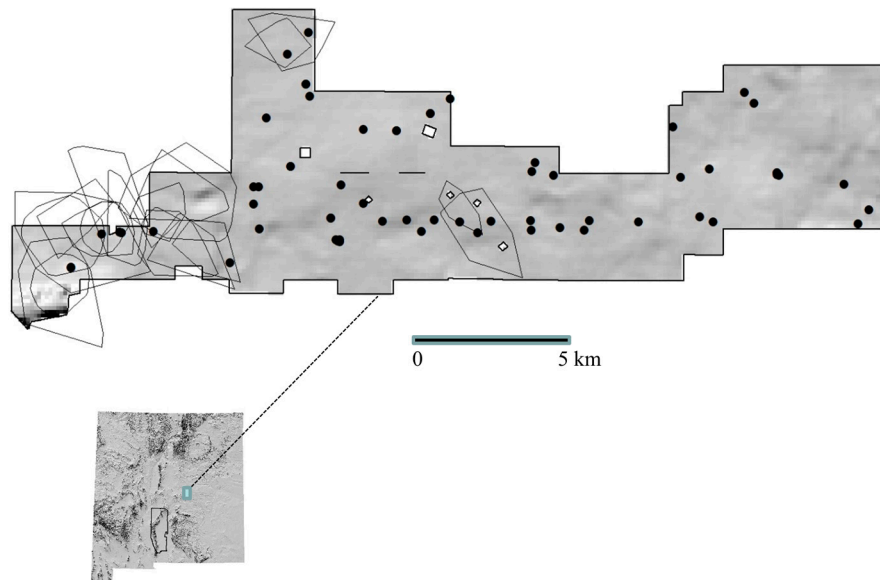


Figure 1. Topographic hillshade showing locations of annual home ranges of adult female mule deer (Bender et al., 2013), and locations of permanent water sources on the Corona Range and Livestock Research Center (CRLRC), east-central New Mexico, USA.

and used bootstrapping with $N = 1,000$ iterations to determine the probability that mean movement distances differed seasonally for this subset of data (see Efron & Tibshirani, 1993).

Additionally, because lactating females enter winter in poorer condition than do dry females and condition subsequently converges between the 2 classes over winter (including on the CRLRC; Bender & Hoenes, 2017), lactation status might affect desire or need to forage and thus movements of deer. However, because deer condition was very low on CRLRC during our study (i.e., lactating females were able to accrue only $\leq 5.7\%$ percent body fat annually at the annual peak in late autumn; Bender et al., 2011, 2013), our GPS/VHF collared sample contained ≤ 2 lactating females each year, and thus we were unable to meaningfully include lactation status in our analyses. Consequently, we explored any potential effect of lactation status on movements by determining the percentile movement distances of lactating females relative to the frequency distribution of dry female movement distances to determine whether lactating females were closer to the mean or extremes of the range of dry females.

Lastly, because our GPS collared sample comprised a limited proportion of the overall radio-collared sample, we compared annual, spring-autumn, and winter home range sizes (Bender et al. 2013; $N = 18$ -27 collared females annually) to see whether movements of our GPS sample were representative of radio-collared deer

in general, comprised of $N = 18$ -27 VHF-only collared adult females for each season (Bender et al., 2011, 2013). For this we compared annual and seasonal home range sizes of the 2 classes (GPS/VHF and VHF-only) using PROC GLM (SAS, 1988), specifically testing the year \times class interaction. We visually located all deer (i.e., both GPS/VHF and VHF-only) via ground tracking of VHF signals a minimum of once per week with additional location emphasis on spring-autumn locations, and mapped locations using the Geographic Information System software package ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, California, USA) (Bender et al., 2011, 2013). We constructed 95% minimum convex polygon (MCP) annual and seasonal home ranges after determining the minimum number of locations to adequately estimate seasonal home range size by plotting size as a function of number of locations (Bender et al. 2013; Kie et al. 1996). For this comparison we used only VHF visual locations of GPS/VHF collared deer so that both GPS/VHF and VHF-only samples were comprised of comparable data.

Results

We collected GPS movement data for 37 seasonal ranges (Table 2), winter 2005-6 through winter 2007-8, from 6-10 GPS/VHF collared adult females annually (mean = 336 and 472 locations per deer for winter and

Table 2

Mean distance moved by adult female mule deer during winter (Dec.-Feb.) and spring-autumn (Mar.-Nov.) seasons as estimated by continuous-time movement modeling (daily) and subdaily straight line movements between successive 4 h locations (subdaily) on the Corona Range and Livestock Research Center, east-central New Mexico, 2005-2007.

Season	Daily (km)			Subdaily (m)		
	Distance	SE	N	Distance	SE	N
Winter	2.90	0.24	24	302	19	24
Spring-Autumn	4.34	0.43	13	409	44	13

spring-autumn ranges, respectively). For all deer, the OUF-anisotropic movement model provided the best fit (i.e., AICc < 2 vs. all other models) of deer movements. The OUF-anisotropic movement model is the most general of ctmm, and includes a home range, correlated positions, correlated velocities, and movements varying by direction (Calabrese et al., 2021; Fleming et al., 2014).

Deer moved less during the winter (Table 2) for both daily ctmm ($F_{1,20} = 6.0$; $p = 0.024$) and minimum subdaily straight-line distances ($F_{1,20} = 4.8$; $p = 0.041$); in both cases the magnitude of differences varied among individual deer ($t_{15} < -2.72$; $p < 0.016$). Similarly, for deer for which movement data for successive seasons were available, movements between successive seasons were always less during the winter season (p (winter < spring-autumn) = 1.000) than the following or preceding spring-autumn season (Table 3).

Additionally, movement distances of lactating females (mean = 42nd percentile; range = 34-55th percentile) were always closer to the average than the extremes of the frequency distribution of movement distances of dry females for each period. Last, neither annual, spring-autumn, or winter home MCP range sizes ($N = 7$ -16 per period) differed between GPS/VHF and VHF-only collared deer ($F_{5,39} \leq 0.94$; $p \geq 0.599$).

Discussion

Despite much less snow and warmer winter temperatures, mule deer females moved less during winter regardless of movement period (i.e., daily, subdaily), supporting the maintenance of this energy conservation behavior in mule deer in the arid Southwest (Verme & Ullrey, 1984). Because deep snow cover and very cold temperatures are typically lacking in the arid Southwest, our results further support low forage quality and availability being the primary drivers of this behavior in deer (Verme & Ullrey, 1984; see below). This latter was reflected by the poor nutritional condition of lactating adult females in the study area (i.e., <5.7% body fat annually at the annual peak in late autumn; Bender et al., 2011, 2013), and in the arid Southwest in general (Bender et al., 2007, 2011, 2012; Bender, 2020), as well as the significant losses in condition seen over winter (Bender & Hoenes, 2017; Hoenes, 2008), despite mule deer likely requiring lower quality forage than white-tailed deer (*O. virginianus*) (Staudenmaier et al., 2022).

While lack of deep snow cover may result in relative forage availability being less impacted during winter in the arid Southwest, senesced forages are still of very low quality, similar to northern environments (Kemp, 1983; Krausman et al., 1990; McKinney, 2003). Low forage quality in winter was reflected in the condition dynamics of deer on the CRLRC; for example, dry females lost on average 32% of body fat reserves and 38% of rump body condition score over winter (L. Bender, unpublished data), even though their condition in late autumn-early winter was already low relative to other southwestern populations (Bender et al., 2007, 2011, 2012). The nutritional condition of deer is driven primarily by forage quality (Bender, 2020; National Research Council, 2007; Tollefson et al., 2010; Verme & Ullrey, 1984; Wakeling & Bender, 2003), illustrating that deer in the arid Southwest face similar constraints in terms of limited nutrient gains from forage intake as do deer in northern environments during winter.

Table 3

Mean movement distances (\bar{x}) and mean differences (D) in mean distance moved daily as predicted by continuous-time movement modeling (daily) and subdaily straight line movements between successive 4 h locations (subdaily) of adult female mule deer for which movement data for successive seasons were available between winter (Dec.-Feb.) and spring-autumn (Mar.-Nov.) on the Corona Range and Livestock Research Center, east-central New Mexico, 2005-2007. p = Probability that seasonal differences differ from 0; N = number of seasonal comparisons.

Period	\bar{x} Summer	\bar{x} Winter	D	90% CI	p	N
Subdaily	400.2	309.6	-90.6 m	-123- -63	1.000	20
Daily	4.21	3.16	-1.05 km	-1.53- -0.63	1.000	20

Deer in northern environments do face additional energetic challenges associated with persistent snow cover, which can limit forage availability (by making location and acquisition of food more difficult; Hovey & Harstad, 1992), diet quality (due to reduced forage quality and availability; McKinney, 2003; Osborn & Jenks, 1998), and increase loss of endogenous reserves (because of increased costs of moving through snow; Bunnell et al., 1990; Mattfeld, 1973). However, while deer in the arid Southwest are less influenced by snow-depth related challenges, northern deer do not face the lack of free water experienced by most deer populations in arid environments because of persistent snow cover in northern environments. Lack of water can present an energetic cost to deer in the arid Southwest, as mule deer may increase movement distances to access water (Heffelfinger, 2006), and winter is much drier than spring-autumn in Chihuahuan desert and short-grass prairie habitats of the arid Southwest (e.g., 87% of precipitation occurs during spring-autumn on the CRLRC).

Because of permanent water developments, water was comparably available seasonally on the CRLRC; water developments were accessible from all deer home ranges, so mule deer did not need to alter their movements in response to seasonal changes in availability of water. Hence, need or preference for free water likely had a negligible effect on deer movements on the CRLRC, unless presence of temporary sources (ephemeral pools, etc.) during the summer monsoon reduce deer movements during spring-autumn because of increased availability. Thus, despite water being effectively controlled in our study, deer still showed less movements during winter. This again supports decreased movements during winter being most influenced by the lack of energetic benefit from seeking and foraging on low quality senesced forage.

Cold temperatures are often thought to influence the winter conservation strategy, despite demonstrated lack of benefit of thermal cover in winter to deer (Cook et al., 1998; Freddy, 1984), the pronounced effect of solar radiation on warming deer (Cook et al., 1998; Parker & Gillingham, 1990; Parker & Robbins, 1984), and deer movements and tolerance of exposure to cold (including bedding in the open) except during the most extreme conditions when high quality forage is available (Moen, 1968; Verme & Ullrey, 1984). Mule deer possess a low thermal critical zone (ca. -20 °C) and show greater tolerance of cold than do white-tailed deer, including a lower metabolic rate response to decreasing temperatures (Mautz et al., 1985; Parker & Robbins, 1984). Hence, they are less affected by even extreme cold, which is seldom the case in the arid Southwest where mean low temperatures

seldom approach their lower thermal tolerance (Table 1). Conversely, the upper thermal critical level of mule deer in winter pelage (5 °C; Mautz et al., 1985) is lower than average high temperatures during winter on our study area (6.7-8.9 °C; Table 1) and much of the arid Southwest. This would require active metabolic activity or behaviors (e.g., panting, etc.) by mule deer to cool themselves, or possibly limiting movements and bedding under shade (although the energetic benefits of the latter are questionable; Cook et al., 1998). Consequently, if temperature affected movements during the winter in our study area, deer would be more likely to decrease movements because of heat stress, not cold stress.

Lastly, while at least one behavioral aspect of the winter energy conservation strategy is seen in mule deer in the arid Southwest, to what degree other adaptations are conserved is unknown. Mule deer in the arid Southwest do develop a highly insulative pelage in winter (Heffelfinger, 2006), but the extent that they may decrease metabolic rate or regulate vascular circulation to the extremities (or need to, in light of the more moderate temperatures) is unknown. Additionally, while lactating females showed a tendency to move less relative to dry females on the CRLRC, whether this is typical is unknown because of our small sample of lactating females. However, given that most females on CRLRC were in poorer condition than females elsewhere in the arid Southwest (Bender et al., 2007, 2011, 2012; Bender & Hoenes, 2017), if very low condition (such as results from lactation) increases movements during winter, this increase would likely have been seen in all CRLRC females regardless of lactation status. Moreover, GPS/VHF and VHF-only collared females showed similar movements (as indexed by home range sizes) seasonally and annually on CRLRC, indicating that movements of GPS/VHF collared females reflected females in general. Although small sample sizes (3-4) precluded including lactation status as an interactive term in the contrast of GPS/VHF and VHF-only collared females, for all females lactation status had no effect on annual or seasonal home range sizes ($p \geq 0.599$).

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