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Forage and Weather Influence Day versus Nighttime Cow Behavior and Calf Weaning Weights on Rangeland☆

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ABSTRACT

We determined the effects of two forage allowance levels (LOW vs. HIGH) and weather conditions on daytime and nighttime movement patterns of young rangeland-raised cows. We also investigated whether calf weaning weights ($n = 42$) were significantly related to postcalving movement patterns of the dam. Global positioning system data were collected over 4 years by recording 5-min interval locations of 52 crossbred cows grazing a 146-ha woodland/grassland pasture for approximately 20 days. The pasture was stocked moderately in 2004 (73 AUMs) and 2005 (78 AUMs) and lightly in 2006 (34 AUMs) and 2007 (32 AUMs). Estimated forage allowance was low in 2004 and 2005 (347 and 438 kg herbage · cow^{-1}, respectively) and high in 2006 and 2007 (1104 and 1884 kg herbage · cow^{-1}, respectively). We calculated distance traveled, path sinuosity, woodland preference, and area explored for each cow during 24 h (D + N), daytime (DAY), and nighttime (PRE dawn and POST sunset) periods. Cows in LOW traveled farther than counterparts in HIGH during D + N and DAY ($P < 0.01$) periods but traveled shorter or similar distances during POST ($P = 0.05$) and PRE ($P = 0.29$) nighttime periods, respectively. Cows in LOW exhibited more sinuous movement paths than cows in HIGH during DAY, PRE, and POST periods ($P \leq 0.01$). Cows in LOW explored larger areas and spent more time in woodlands than counterparts in HIGH ($P < 0.01$). Weather factors associated with thermal comfort affected daily variation in both daytime and nighttime movement patterns of cows. A dam's movement patterns in the weeks immediately following calving were correlated ($P \leq 0.01$) with steer but not heifer calf WW. Moderate stocking rates (LOW treatment) induced behaviors that resulted in higher woodland preference and heavier steer calf WW.

Introduction

Development of grazing management strategies that consistently achieve desired conservation and production goals on western rangelands requires understanding how livestock adjust their behavior in response to environment-specific cues (Launchbaugh and Howery, 2005). In extensive seasonally grazed pastures, granular foraging choices about *where* and *what* to graze (Newman, 2007) aggregate into complex nonrandom spatial patterns of livestock distribution. Foraging choices are influenced by multiple interacting animal-, environment-, and management-related drivers that operate at different scales of time and space (Bailey et al., 1996; Coughenour, 1991; Launchbaugh and Howery, 2005; Senft et al., 1987). The intricacies of the foraging process are being deciphered with increasingly sophisticated tools and analytical approaches designed to discriminate livestock activities (Augustine and Derner, 2013; Ungar et al., 2005, 2011), model animal movement (Ares and Bertiller, 2010; Guo et al., 2009), and determine the relative roles of biotic versus abiotic factors in shaping observed patterns of livestock distribution (Allred et al., 2011; Cooper et al., 2008; Díaz Falú et al., 2014; Peinetti et al., 2011; Sawalhah et al., 2014; Walburger et al., 2009).

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Improved understanding of livestock foraging behavior has allowed the development of management practices designed to modify undesirable patterns of cattle distribution (Bailey and Brown, 2011). Implementation of these techniques, however, has not always produced the desired results (e.g., Cibils et al., 2008) due in part to the highly context-specific nature of livestock-environment interactions. Refining current management tactics will require more reliable predictions of site-specific outcomes of such interactions (as in Stafford Smith, 1988), a task that will be difficult to achieve without advancing current understanding of the foraging process.

Forage availability, often expressed on a per-capita basis as *forage allowance* (kg forage per head) (Allen et al., 2011; Sollenberger et al., 2005), is inversely related to stocking rate (sensu Holechek et al., 2011), which, not surprisingly, has been shown to alter movement patterns and feeding site selection of cattle on rangeland (Hart et al., 1991; Hepworth et al., 1991; Peterson and Woolfolk, 1955; Wagnon, 1963). Stocking rate effects on night versus daytime grazing patterns are less clear, however. Hepworth et al. (1991) reported no stocking rate effects on time spent grazing by steers during daytime versus nighttime hours, whereas Peterson and Woolfolk (1955) observed higher levels of nighttime grazing of cows in light- versus heavy-grazed pastures.

Nighttime grazing has been well documented in cattle (Kilgour, 2012) and can vary from less than 1% (Parsons et al., 2003; Sneva, 1970) to almost 50% (Linnane et al., 2001; Wagnon, 1963) of an individual's grazing time recorded over a 24-h period. Factors associated with the forage and feeding environment (Dwyer, 1961; Wagnon, 1963), the animal (Herbel and Nelson, 1966), and weather/climate conditions (Arnold, 1981; Arnold and Dudzinski, 1978; Linnane et al., 2001; Wagnon, 1963) are apparently responsible for this broad variation in daytime versus nighttime activity. Despite remarkable advances in automated livestock telemetry, which allows 24-h animal movement monitoring (Anderson et al., 2014; Swain et al., 2011), recent studies addressing spatial behaviors of rangeland-raised livestock have rarely partitioned movement patterns into daytime versus nighttime periods (but see Dolev et al., 2014). Our main objective was to determine the effects of forage allowance and daily variation in weather conditions on daytime versus nighttime movement patterns of young nursing cows.

To date, most studies that have used global positioning system (GPS) telemetry to track cattle movement patterns on rangelands have not investigated the relationship between spatial distribution patterns and animal performance indicators (Allred et al., 2011; Bailey et al., 2010; Cooper et al., 2008; Díaz Falú et al., 2014; Peinetti et al., 2011; Russell et al., 2012; Walburger et al., 2009). An earlier study that relied on less frequent visual observations of cattle locations reported no effects of terrain use on animal performance (Bailey et al., 2001; VanWagoner et al., 2006). Our secondary objective was to determine whether movement patterns and feeding site selection of rangeland cows monitored at frequent time intervals via GPS telemetry during the weeks immediately following calving were correlated with calf weaning weights (WWs).

We reanalyzed GPS data collected in two previous studies conducted in the same rangeland pasture applying either moderate (Black Rubio et al., 2008) or light (Wesley et al., 2012) stocking rates (low- and high-forage allowance) for two consecutive seasons each. We hypothesized that as per-capita forage allowance increased (lower stocking rate), cattle would travel shorter distances, explore smaller areas, travel straighter paths, and use woodland areas less often during both day and night. We also hypothesized that regardless of forage allowance conditions, weather would influence day-to-day activity patterns of cows during both daytime and nighttime periods. Finally, because a beef cow's milk production is influenced by pasture forage allowance (Gutiérrez et al., 2013) and given that the dam's milk production influences preweaning calf weight gains (Beal et al., 1990; Liu et al., 2015), we predicted that a calf's WW would be associated with its dam's grazing behavior patterns in the weeks immediately following calving.

Materials and Methods

Study Area Description

Our data were collected at New Mexico State University Corona Range and Livestock Research Center (CRLRC) approximately 22.5 km east of Corona, New Mexico, United States. The CRLRC covers an area of 11 285 ha with elevations ranging from 1743 m to 2042 m. The climate is semiarid, with warm summers and cold winters, and an average of 188 frost-free days. Mean annual precipitation is about 400 mm. Soils of the CRLRC area range from sandy loams to clays overlying caliche hardpan. Vegetation is composed of perennial short grasses with an overstory of sparse to dense piñon pine (*Pinus edulis* Engelm.) and one-seed juniper (*Juniperus monosperma* Engelm) woodland. The predominant understory grasses are blue grama (*Bouteloua gracilis* Willd.), wolftail (*Lycurus sphleoides* Kunth), threeawns (*Aristida* spp.), sideoats grama (*Bouteloua curtipendula* Torr.), and sand dropseed (*Sporobolus cryptandrus* Torr.) (Black Rubio et al., 2008). Data used in this study were collected in a 146-ha pasture with 55% of the area covered by open shortgrass steppe and 45% by piñon-juniper woodlands. A single drinking water source was available on the far west end of the pasture.

Animals and Stocking Rates

All animal handling and experimental procedures were approved by the New Mexico State University Institutional Animal Care and Use Committee. A total of 52 Angus × Hereford crossbred 3-yr-old cows weighing approximately 450 kg were monitored over a 4-year period. Different cows were monitored in each year. Each cow was fitted with a GPS collar (Lotek 2200 or 3300, Lotek Wireless, New Market Ontario, Canada) configured to record and store an animal's position at 5-min intervals in late winter/early spring. In the first 2 years (2004 and 2005), 77 and 88 cows grazed the pasture, respectively, and 8 cows (4 pregnant or lactating and 4 nonpregnant, nonlactating) were tracked in each year for 24 and 25 days, respectively (Black Rubio et al., 2008). In last 2 years (2006 and 2007), the pasture was grazed by 18 pregnant or lactating cows in each year and all the cows were tracked for 24 and 22 days, respectively (Wesley et al., 2012). Thus our study pasture was stocked moderately (1.94 ± 0.04 ha · AUM $^{-1}$) in the first 2 years and lightly (4.45 ± 0.10 ha · AUM^{-1}) in the last 2 years. Recommended stocking rate for the study area averages 1.6 ha · AUM^{-1} (USDA-NRCS, 2011).

Forty-two calves were weighed within 3 days of birth and at weaning, and calf weaning body weight was adjusted for a 205-d weaning body weight (205-d WW). A multiplicative sex adjustment factor of 1.07 (Nelsen and Kress, 1981) was applied to the 205-d WW of female calves. Data from 42 calves (23 heifer calves and 19 steer calves) were obtained over the 4-year period (Endecott, 2006; Mulliniks et al., 2011).

Data Processing

GPS data from two previous studies (Black Rubio et al., 2008; Wesley et al., 2012) (Table 1) were used to calculate distance traveled, path sinuosity, woodland preference index, and daily area explored by each cow. The first three response variables were calculated for each of four daily time periods (see later) using a Java program developed for this study that used the 15-d median sunrise and sunset times during our study period to define daytime and nighttime hours. Daily area explored during each 24-h period (see later) was calculated in ArcGIS 10 (ESRI, Redlands, CA).

Thus four daily time periods were considered for all analyses except for daily area explored. The time periods were 24 h (D + N); presunrise night hours (PRE, from midnight to sunrise); daytime hours (DAY); and postsunset night hours (POST, from sunset to midnight). Daily area explored was calculated for each cow by using the "Minimum Bounding

Table 1
Forage allowance, seasonal precipitation, number of cows, and stocking rate of study pasture during 4 years

Yr	Forage biomass (kg DM · ha^{-1})[1]	Forage allowance (kg DM · $head^{-1}$)	Cumulative precipitation (mm)	Number of cows[2]	AUMs[3]	Ha · AUM^{-1}	Number of tracked cows[4]	Number of sampling days	Number of GPS points
2004	248	347	35	77	73	2.0	8	24	52110
2005	357	438	119	88	78	1.9	8	25	57208
2006	184	1104	30	18	34	4.3	18	24	114581
2007	314	1884	112	18	32	4.6	18	22	97272

[1] Forage allowance for 2004−2006 was calculated using field-derived herbaceous biomass data; in 2007 forage allowance was calculated using the average of NDVI (318 kg DM · ha^{-1}) and precipitation-derived (310 kg DM · ha^{-1}) herbaceous biomass estimates. Regression equations used to estimate NDVI- and rainfall-derived values were: $y = 6181.3 * NDVI - 974.5$ ($R^2 = 0.95$; $SE = 26.53$; $P = 0.13$) and *forage biomass* $= 151.6 + 39.3 *$ *Cumulative Precipitation* ($R^2 = 0.96$, $SE = 24.25$; $P = 0.12$).
[2] Total number of cows in the pasture.
[3] Animal Unit Month.
[4] In 2004−2005 we tracked 4 pregnant or nursing cows and 4 nonpregnant, non-nursing cows while all cows in 2006−2007 were pregnant or nursing.

Geometry, Convex Hull" tool in ArcGIS 10 (ESRI) that delineated the smallest convex polygon containing all GPS location points for an animal during a 24-h period (Black Rubio et al., 2008). To avoid violating spatial autocorrelation assumptions, GPS data were subsampled into 2-h intervals (Perotto-Baldivieso et al., 2012) to calculate the daily area explored. To determine the number of GPS points located within the woodland area, GPS data were extracted to points in ArcGIS 10 (ESRI) and overlaid on a woodland raster layer of the pasture. Woodland preference index was calculated by computing the ratio between percent time spent in the woodland versus percent of our study area covered by woodlands (45%).

The Java program developed for this study was used to calculate distance traveled, path sinuosity, and woodland preference index for each daily time period. The Pythagorean Theorem was used to calculate the distance traveled between consecutive GPS fixes. In this study, the straightness index (Batschelet, 1981) was used to infer path sinuosity and was calculated as the ratio between the distance from the first to the final GPS point during a given time period and the cumulative distances between consecutive points during each period (where *0* indicates most sinuous path and *1* indicates a straight path). The straightness index is a reliable indicator of the tortuosity of travel path in situations where animals engage in oriented (nonrandom) movement (Benhamou, 2004) and in environments where movements are not tightly constrained by physical boundaries as occurs in pens and other intensive animal-raising facilities (Miller et al., 2011). Other authors have calculated path sinuosity as the inverse of the straightness index used in this study (Russell et al., 2012).

Weather data were retrieved from an automatic weather station (USDA NRCS SCAN, Site 2015) located less than 1 mile away from our research site (elevation 1882 m, lat 34°15′N, long 105°25′W). Weather variables considered in this study included actual precipitation (precipitation on any given day during the grazing season, mm), cumulative precipitation (precipitation accumulated between 1/1 and 3/31, mm), wind direction (north = 0°, east = 90°, south = 180°, and west = 270°), wind speed (m · s^{-1}), and daily average, maximum, and minimum air temperatures (°C). Lunar phase (%) was retrieved from the online moon phase calendar and expressed as a percent of full moon for each day (http://www.almanac.com/moon). Cumulative precipitation was used as a proxy for vegetation green-up and was therefore considered a forage-related variable.

Per-capita forage allowance was calculated using herbaceous biomass data collected in open grassland and open woodland areas of the pasture using the comparative yield method. Four 50-m transects were randomly located in an open shortgrass area and another four in open woodland area (8 transects total). Twenty-five quadrats (0.25 m^2) at 2-m intervals were used to estimate herbaceous biomass along each transect, and at 10-m intervals herbaceous biomass was clipped (5 quadrats total along each transect). A forced-air oven at 60°C for 24 −48 h was used to dry the clipped samples; these samples were weighed and used to develop regression equations to estimate herbaceous biomass (Black Rubio et al., 2008). Herbaceous biomass was only measured in the first three sampling seasons; therefore for the last season this variable was estimated using two predictors: 1) Moderate-resolution Imaging Spectroradiometer (MODIS)-derived Normalized Difference Vegetation Index (NDVI) of grassland area pixels and 2) cumulative late winter/early spring precipitation. MODIS images for all four sampling seasons were ordered and downloaded from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL-DAAC, 2011). Each image was overlaid on our study area map in ArcGIS 10 (ESRI), and the average NDVI of 10 pixels covering open grassland area was used to develop a model to predict biomass availability ($yr = 6181.3x - 974.5$; $R^2 = 0.95$; $SE = 26.53$; $P = 0.13$). A second model using cumulative precipitation for each season was developed to predict biomass availability ($yr = 39.3x + 151.6$; $R^2 = 0.96$; $SE = 24.25$; $P = 0.12$). Thus forage allowance (kg · $head^{-1}$) for the fourth year was estimated using the average of predicted biomass availability obtained with the NDVI and cumulative precipitation regression models.

Data Analysis

The influence of forage allowance on cattle movement patterns (distance traveled, path sinuosity, and daily area explored) and habitat use (woodland preference index) was modeled using PROC MIXED in SAS 9.2 (SAS Institute, Cary, NC). Each daily period (D + N, PRE, DAY, and POST) was analyzed separately. Forage allowance (low and high) was used as a fixed effect in the model statement. The random effect was the individual cow nested within forage allowance level by year. The *ddfm = kr* option was selected to provide a better estimate of denominator degrees of freedom and adjust the standard error estimated for each test statistic (Littell et al., 2006). The *pdiff* option in *lsmeans* was used to detect significant differences ($P < 0.05$) among forage allowance levels. Years were the experimental units for comparing forage allowance levels. Years 2004 and 2005 were replicates for low forage allowance, and years 2006 and 2007 were replicates for the high forage allowance level.

To further explore the influence of forage allowance on activity patterns and habitat selection of cows in our study, discriminant analysis was used to determine if animals could be classified into significantly different groups (low vs. high forage allowance conditions) based on the entire suite of behaviors analyzed (movement patterns and habitat selection during each of the four daily periods). PROC DISCRIM in SAS 9.2 (SAS Institute) was used for this analysis. Variable means for each cow ($n = 52$) were computed and included in a single analysis. The predictors included in this analysis were distance traveled, path sinuosity, and woodland preference index for each period (D + N, PRE, DAY, and POST) and daily area explored for D + N period. The discriminant analysis included the following options in SAS 9.2 (SAS Institute); *"pcov method = normal pool = yes manova crossvalidate list"* and *"priors proportional."* Wilks' λ test statistic was used to determine whether differences between groups were statistically detectable at $P \le 0.05$. The stepwise discriminant procedure using PROC STEPDISC in SAS 9.2 (SAS Institute) was also conducted to remove redundant predictors from the discriminant function using the $P = 0.05$ level to include predictors in the model.

We used the corrected Akaike Information Criterion (AIC_c) to determine whether models that best fit the structure of our data documenting day-to-day variation in cattle behaviors included weather variables (actual precipitation, wind direction, wind speed, average daily air temperatures, and lunar phase) in addition to forage allowance and green-up (cumulative precipitation). Model selection was conducted using the ALLMIXED2.SAS (Fernandez, 2007) macro application in SAS 9.2 (SAS Institute). Models with the smallest AIC_c were selected. Thus one model per response variable for each of the four time periods considered was selected. Each best model was then examined to determine the relationship between the dependent and independent variables using a PROC MIXED model with repeated measures in SAS 9.2 (SAS Institute). The subject was individual cow nested within treatment, and the Julian day was treated as the replication unit. The random effect was individual cow nested within forage allowance level and day nested within year. The *ddfm = kr* option was selected to provide a better estimate of denominator degrees of freedom and adjust the standard error estimated for each test statistic (Littell et al., 2006). A spatial power covariance structure that best fit our data was used via the *SP(POW)* option with Julian day as a continuous variable (Littell et al., 2006). Each candidate model was analyzed separately.

Linear regression in SAS 9.2 (SAS Institute) was used to determine if variation in WWs of steer and heifer calves (separate analyses were conducted for each) could be explained by their dams' movement patterns (distance traveled and path sinuosity) during three periods (PRE, DAY, and POST) in the weeks immediately following calving. Quadratic regression in SAS 9.2 (SAS Institute) was used to describe the relationship between habitat selection (woodland preference) and calf WWs when warranted.

Results

Forage Allowance, Cumulative Precipitation, and Other Weather Variables

Average grassland and open woodland forage allowance was 392.5 ± 45.5 and $1\,494 \pm 390$ kg DM · head^{-1} for the low (2004–2005) and high (2006–2007) forage allowance treatments, respectively (see Table 1). Cumulative winter/early spring precipitation was low in 2004 and 2006 (32.5 ± 2.5 mm) and high in 2005 and 2007 (115.5 ± 3.5 mm). Air temperatures during the first 2 yr (2004—2005) were similar and tended to be colder than temperatures recorded in 2006 and 2007, which also exhibited high year-to-year similarity (Table 2). However, lowest air temperatures recorded for all time periods considered (D + N, PRE, DAY, and POST) were similar across all 4 yr of the study. Wind direction during the study was discontinuous and most of the time came out the SW–NW (221°–310°; 60% of days) and NE–SE (100°–150°; 25% of days). We only recorded 2 d with winds out of the WNW–ENE (between 320° and 30°) during the entire study period. Winds out of the SW–NW tended to be stronger than those out of the NE–SE (mean ± SE: 15.8 ± 0.7 km · h^{-1} vs. 11.4 ± 0.8 km · h^{-1}). However, days with winds out of NE–SE tended to be colder than days with SW–NW winds (mean ± SE: 6.9 ± 1.6 vs. 8.3 ± 0.6°C Max. Temp.; 5.7 ± 1.5 vs. 6.8 ± 0.6°C Min. Temp.; 6.3 ± 1.5 vs. 7.6 ± 0.6°C Mean Temp.). Average cumulative and actual precipitation, as well as wind direction and speed, were similar for the first and last 2 yr of this study (low vs. high forage allowance).

Influence of Forage Allowance on Movement Patterns and Habitat Use of Cows

Cows traveled significantly farther during D + N ($P < 0.01$) and DAY ($P < 0.01$) periods when forage allowance was low (6.0 and 4.4 km, respectively) compared with years when forage allowance was high (5.0 and 3.1 km, respectively; Table 3). Conversely, cows that experienced low forage allowance conditions traveled shorter distances (0.95 km) at night during POST hours compared to their high forage allowance counterparts (1.2 km; $P = 0.05$). No differences in distance traveled between forage allowance levels during PRE nighttime hours were detected. Night:Day ratios of distance traveled were significantly higher (i.e. more distance traveled during night vs. daytime) for animals subjected to high vs. low forage allowance levels ($P < 0.01$).

No differences in path sinuosity were detected among cows in low vs. high forage allowance treatments when 24-h periods (D + N) were analyzed (see Table 3). However, when PRE, DAY, and POST periods were analyzed separately, cows that experienced low forage

Table 2
Mean and ranges of daily weather variables at the Corona Range and Livestock Research Center recorded at a weather station located close to the study pasture. Lunar phase data were retrieved from http://www.almanac.com/moon

	2004—Low forage allowance		2005—Low forage allowance		2006—High forage allowance		2007—High forage allowance	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Lunar phase (%)	60.1	2.0-100	51.2	0.0-100	53.5	0.0-100	55.5	0.0-100
Cumulative PPT[1] (mm)	35	30.5-50.8	119.4	109.2-129.5	30.4	27.9-30.5	111.8	78.7-154.9
Actual PPT[2] (mm)	0.8	0.0-12.7	0.8	0.0-7.6	0.5	0.0-2.5	2.5	0.0-27.9
Wind direction (azimuth°)	190.6	14.0-303.0	231.9	82.0-319.0	218.7	127.0-299.0	249.9	42.0-336.0
Wind speed (m · s^{-1})	8.3	3.5-14.8	7.4	3.4-12.5	10	5.8-15.7	8.6	5.3-15.9
Air temperatures								
(Day + night)								
Maximum (°C)	5.4	−1.0 to 13.8	5.9	−5.2 to 14.2	10.4	−3.8 to 19.3	10.3	0.0-17.2
Minimum (°C)	4.2	−1.4 to 12.4	4.6	−5.7 to 13.0	8.9	−4.6 to 17.3	8.9	−1.0 to 15.8
Average (°C)	4.8	−1.2 to 13.2	5.3	−5.4 to 13.6	9.6	−4.2 to 18.3	9.6	−0.5 to 16.5
(Night $_{predawn}$)								
Maximum (°C)	2.6	−3.2 to 9.3	2.8	−5.1 to 11.3	5.9	−5.8 to 15.3	6.7	0.0-13.7
Minimum (°C)	1.8	−4.0 to 8.3	1.9	−5.4 to 10.5	4.6	−7.5 to 14.3	5.3	−0.9 to 12.2
Average (°C)	2.2	−3.5 to 8.8	2.4	−5.2 to 10.9	5.3	−6.4 to 14.9	6.1	−0.4 to 13.0
(Day)								
Maximum (°C)	7	−0.9 to 16.8	8.1	−4.8 to 16.4	12.4	−3.7 to 22.5	13.9	0.7-19.5
Minimum (°C)	5.8	−1.4 to 15.5	6.5	−5.2 to 15.0	10.8	−4.3 to 20.5	12.3	−0.2 to 17.7
Average (°C)	6.4	−1.1 to 16.2	7.3	−5.0 to 15.6	11.5	−4.1 to 21.4	13.0	0.2-18.6
(Night $_{postsunset}$)								
Maximum (°C)	4.6	−2.2 to 11.5	4.3	−6.2 to 14.7	10.1	−4.8 to 18.9	10.1	−1.5 to16.4
Minimum (°C)	3.4	−2.4 to 9.2	3.1	−7.4 to 13.1	8.6	−6.2 to 17.1	8.5	−3.1 to 14.8
Average (°C)	4.1	−2.3 to 10.5	3.8	−6.7 to 14.1	9.5	−5.5 to 18.2	9.4	−2.5 to 15.8

[1] Cumulative PPT: cumulative precipitation from the beginning of each year to the end of each grazing season.
[2] Actual PPT: actual precipitation on any given day during the grazing season.

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Table 3
Movement patterns and habitat use variables (least square means) of cows exposed to 2 levels of forage allowance (kg · head^{-1}) while grazing a rangeland site in central New Mexico during late winter and early spring

Variables	Forage allowance		SE	*P* Value
	High	Low		
Distance walked (km)				
Day + night[1]	5.015	6.036	175.680	<0.001
Night $_{predawn}$	0.793	0.689	96.629	0.286
Day	3.069	4.393	259.360	<0.001
Night $_{postsunset}$	1.152	0.954	98.459	0.049
Night-to-day ratio	0.77	0.37	0.119	0.002
Sinuosity[2]				
Day + night	0.091	0.091	0.004	0.960
Night $_{predawn}$	0.279	0.185	0.025	<0.001
Day	0.160	0.122	0.015	0.013
Night $_{post\ sunset}$	0.414	0.285	0.034	<0.001
Woodland Preference [3]				
Day + night	0.114	0.461	0.057	<0.001
Night $_{predawn}$	0.063	0.497	0.056	<0.001
Day	0.136	0.459	0.060	<0.001
Night $_{post\ sunset}$	0.116	0.418	0.049	<0.001
Area Explored (ha)				
Day + night	13.215	31.304	1.457	<0.001

[1] Periods were: 24 h (day + night), predawn night hours (from midnight to sunrise), daytime hours, and postsunset night hours (from sunset to midnight).
[2] Straightness index values range between 0 (sinuous path) and 1 (straight path).
[3] Preference index: % time spent in woodland/% woodland cover.

allowance consistently exhibited more sinuous movement trajectories than their high forage allowance counterparts ($P \leq 0.01$).

Forage allowance levels significantly ($P < 0.01$) affected woodland preference during all four daily periods analyzed; when forage allowance was high, cows exhibited higher avoidance of woodland areas (lower preference index; Table 3). Cows explored significantly larger daily areas when forage allowance was low compared with counterparts that experienced high forage allowance ($P < 0.01$).

Cows that experienced low versus high forage allowance conditions were discriminated into significantly different groups on the basis of the entire suite of movement and habitat selection responses measured (Wilks' $\lambda = 0.07$, $F_{5,46} = 128.49$; $P < 0.01$). All cows were classified correctly by the discriminant function in the cross-validation procedure. Five out of 13 predictors (distance traveled during nighttime periods, sinuosity during nighttime POST sunset period, woodland preference index during nighttime PRE dawn period, and area explored during D + N period) were selected in the stepwise discriminant procedure.

All models explaining day-to-day variation in activity and habitat selection, except for two (sinuosity after sunset and daily area explored), included at least one weather variable in addition to forage green-up dynamics (cumulative winter + spring precipitation) and forage allowance level (Table 4). Forage allowance effects at the daily time scale were consistent with the seasonal analyses results reported earlier.

Winds from the NE-SE were associated with longer distances traveled during D + N, DAY, and nighttime POST sunset periods (see Table 4). Increasing moonlight was associated with longer distances traveled during nighttime PRE dawn hours. Decreasing mean air temperatures were associated with longer distances walked during POST sunset nighttime hours. In years with more vigorous spring green-up (as inferred by cumulative winter + spring precipitation), animals traveled shorter distances during nighttime hours but traveled farther during the day. Overall, weather factors known to reduce thermal comfort resulted in less sinuous travel trajectories of cows. Straighter movement paths were associated with rainy weather or decreasing air temperatures for D + N periods, winds from the W–NW for PRE dawn nighttime hours, and stronger winds for daytime hours.

Daily preference for woodland areas during all time periods decreased in years with high forage allowance (see Tables 3 and 4) or during seasons with vigorous spring green-up as inferred by winter + spring cumulative precipitation. Weather factors expected to reduce thermal comfort (low air temperatures and rainfall after sunset) were again associated with higher preference for woodlands in all periods analyzed. Cows also exhibited higher preference for woodland sites during all four periods considered on days with winds out of the NE–SE.

Calf Weaning Weights in Relation to Cow Movement Patterns and Habitat Use

In the first 2 yr (low forage allowance), 205-d adjusted calf WWs averaged 248.9 ± 12.9 kg ($n = 8$), while in the last 2 yr (high forage allowance) WWs averaged 202.0 ± 5.4 kg ($n = 34$). Steer calf (SC) WWs (205-d WW) increased significantly with increasing 24-h distances traveled ($R^2 = 0.53$; $P < 0.01$) and 24-h area explored ($R^2 = 0.43$; $P < 0.01$) by their dams in the weeks immediately following calving (Fig. 1). There was no relationship between SC 205-d WW and the 24-h path sinuosity of the dam during the first weeks after calving. Dams

Table 4
Forage (FA level and PPT $_{cumulative}$) and weather predictors that best described the movement patterns and habitat use of cows grazing a grassland/woodland mosaic in late winter/early spring. Models with smallest corrected Akaike Information Criterion (AIC*c*) were selected as final candidate models

Response variable	Best models[1]	AIC$_C$	Delta AIC$_C$
Distance (km)			
Day + night[2]	−FA level − wind direction	19744.4	0.0
Night $_{Predawn}$	+Lunar phase − PPT $_{cumulative}$	17080.1	0.0
Day	− FA level + PPT $_{cumulative}$ − wind direction	19041.8	0.0
Night $_{Postsunset}$	+FA level − PPT $_{cumulative}$ − wind speed − temp $_{mean}$	18168.2	0.0
Sinuosity[3]			
Day + night	+PPT $_{actual}$ − PPT $_{cumulative}$ − temp $_{min}$	−3132.8	0.7
Night $_{Predawn}$	+FA level − PPT $_{cumulative}$ + wind direction	278.1	0.0
Day	+FA level − PPT $_{cumulative}$ + wind speed	−2039.9	0.0
Night $_{Postsunset}$	+FA level + PPT $_{cumulative}$	482.7	0.0
Woodland preference[4]			
Day + night	− FA level − PPT $_{cumulative}$ − temp $_{max}$ − wind direction	1020.8	2.1
Night $_{Predawn}$	− FA level − PPT $_{cumulative}$ − temp $_{max}$ − wind direction	1491.2	0.2
Day	− FA level − PPT $_{cumulative}$ − temp $_{max}$ − wind direction	1259.0	0.0
Night $_{Postsunset}$	− FA level − PPT $_{cumulative}$ − wind direction − temp $_{max}$ + PPT $_{actual}$	1621.9	16.6
Area explored (ha)			
Day + night	− FA level − PPT $_{cumulative}$	9300.9	0.0

[1] FA indicates forage allowance (kg · Head^{-1}); lunar phase (% full moon); PPT $_{actual}$, actual precipitation (mm); PPT $_{cumulative}$, winter-spring precipitation (mm) used as a proxy for early green-up; Temp, air temperature (°C); Wind direction (azimuth °); Wind speed, wind velocity (m · s^{-1}). Temperature variables were computed separately for each time period. Lunar phase was only used in night models.
[2] Periods: 24 hr (day + night), predawn night hours (from midnight to sunrise), daytime hours, and postsunset night hours (from sunset to midnight).
[3] Straightness index values range between 0 (sinuous path) and 1 (straight path).
[4] Preference index: % time spent in woodland/% woodland cover.

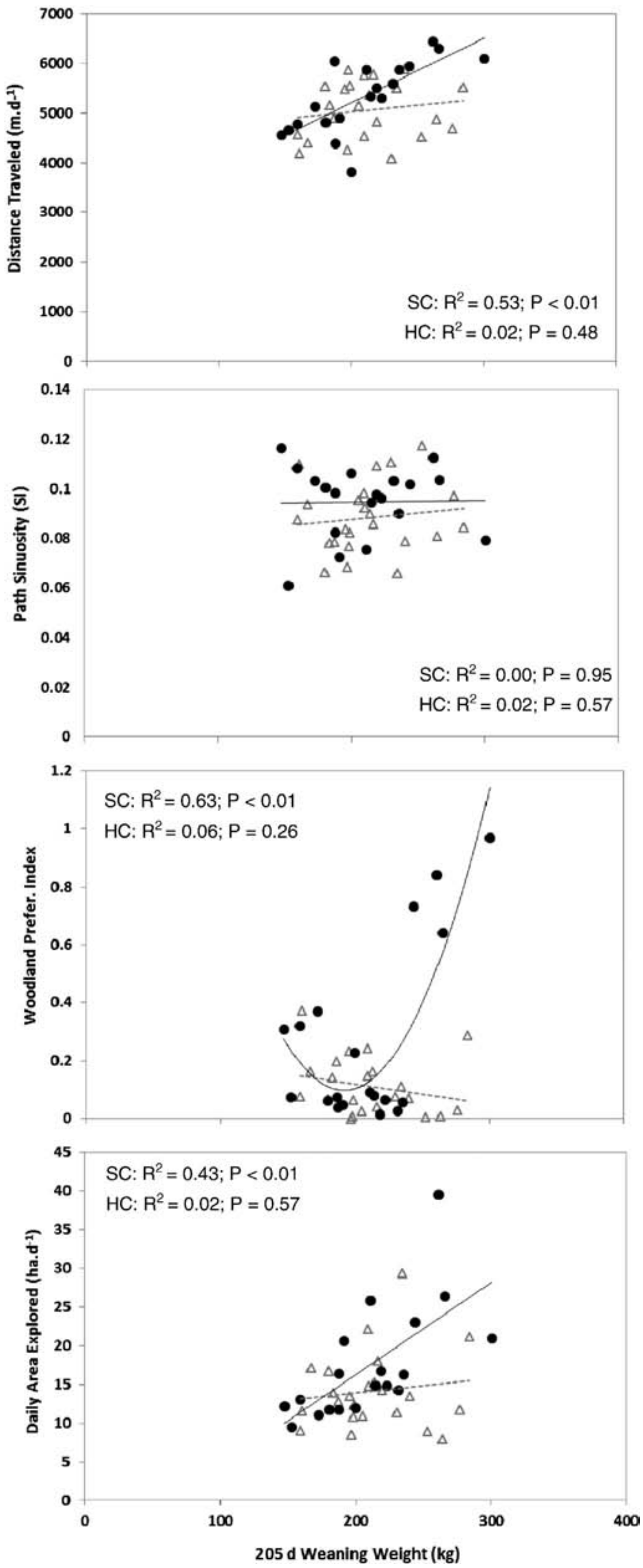

Fig. 1. Relationship between 205 d adjusted weaning weights of steer calves (SC, full circles, solid line) and heifer calves (HC, open triangles, dotted line) and the distance traveled ($km.d^{-1}$), path sinuosity (straightness index, SI; 0 = sinuous, 1 = straight), woodland preference (preference index; <1 = avoidance; 1 = indiference; > 1 = preference), and area explored ($ha.d^{-1}$) by dams during the weeks immediately following calving at a rangeland site in New Mexico.

that weaned lightest and heaviest steer calves showed higher preference for woodland areas ($R^2 = 0.63$; $P < 0.01$) during the weeks following calving. None of the 24-h dam behaviors analyzed (distance traveled, area explored, path sinuosity, or woodland preference) were significant predictors of heifer calf (HC) 205-d WW.

Cows that weaned heavier calves tended to walk longer distances during the daytime hours (SC $R^2 = 0.51$; $P < 0.01$; HC $R^2 = 0.34$; $P < 0.01$) in the weeks immediately following calving (Fig. 2). Increased nighttime distances traveled by the dam were associated with lower 205-d WW in heifer calves (HC $R^2_{\text{predawn}} = 0.31$; $P = 0.01$; HC $R^2_{\text{postsunset}} = 0.29$; $P = 0.01$). In steer calves, however, 205-d WWs were either less tightly associated or unrelated with their dams' nighttime movement patterns in the weeks immediately following calving (SC $R^2_{\text{predawn}} = 0.26$; $P = 0.03$; SC $R^2_{\text{postsunset}} = 0.13$; $P = 0.13$). Cows that followed more sinuous travel pathways during predawn and daytime hours during their offsprings' first weeks of life also tended to wean heavier steer and heifer calves (SC $R^2_{\text{predawn}} = 0.44$; $P < 0.01$; SC $R^2_{\text{daytime}} = 0.25$; $P = 0.03$; HC $R^2_{\text{predawn}} = 0.17$; $P = 0.05$; SC $R^2_{\text{daytime}} = 0.30$; $P = 0.01$). Cows that weaned the heaviest, intermediate, and lightest steer calves showed highest, lowest, and intermediate preference for woodland areas, respectively, during both daytime and nighttime hours in the weeks following calving (SC $R^2_{\text{predawn}} = 0.68$; $P < 0.01$; $R^2_{\text{daytime}} = 0.51$; $P < 0.01$, $R^2_{\text{postsunset}} = 0.67$; $P < 0.01$). However, the same was not true for heifer calves. A dam's daytime and postsunset preferences for woodland areas were not significant predictors of HC 205-d WW. A dam's predawn woodland use was the only significant predictor of HC 205-d WW (HC $R^2_{\text{predawn}} = 0.41$; $P < 0.01$).

Discussion

As predicted, cows that experienced high forage allowance conditions traveled shorter daily (24 h) distances, explored smaller areas of the pasture each day, followed less sinuous pathways during nighttime hours (but not during daytime), and showed higher avoidance of woodland areas compared with their low forage allowance counterparts. Interestingly, the proportion of 24-h distance traveled during nighttime hours (night-to-day ratio) was twice as high for cows that experienced high versus low forage allowance conditions. Perfect classification (0% error rate) of cows into forage allowance level groups on the basis of the entire suite of observed behaviors appeared to be mostly influenced by nighttime movement patterns.

Overall differences in distance traveled among treatment groups in this study agree with a number of earlier experiments (Hart et al., 1991; Hepworth et al., 1991; Quinn and Hervey, 1970) that indicated that as stocking rate increased (lower forage allowance), animals tended to walk longer daily distances (but see Low et al., 1981a). Approximately two-thirds to three-quarters of the distance traveled by cows occurred during daytime hours in agreement with previous studies on cattle ethology (Arnold and Dudzinski, 1978; Dwyer, 1961). Although we did not classify animal movement into activity categories (e.g., grazing, resting, traveling), the night-to-day ratio of distances traveled by cows in this study (0.77 and 0.37 for high and low forage allowance treatments, respectively) falls well within the range of night-to-day ratios of grazing activity (approximately 0.78–0.23) reported in a recent literature review on cattle behavior at pasture (Kilgour, 2012). Cows that experienced low forage allowance showed lower levels of nighttime activity than their high forage allowance counterparts. This finding agrees with Peterson and Woolfolk (1955), who observed higher levels of grazing activity and nighttime travel of cows in light- versus heavy-grazed pastures on shortgrass prairie in Montana. Under conditions of low forage allowance, cows likely expended more energy to harvest forage during daytime hours (they traveled ≈1.3 km farther than their high forage allowance counterparts), which may have constrained their ability to freely engage in nighttime travel.

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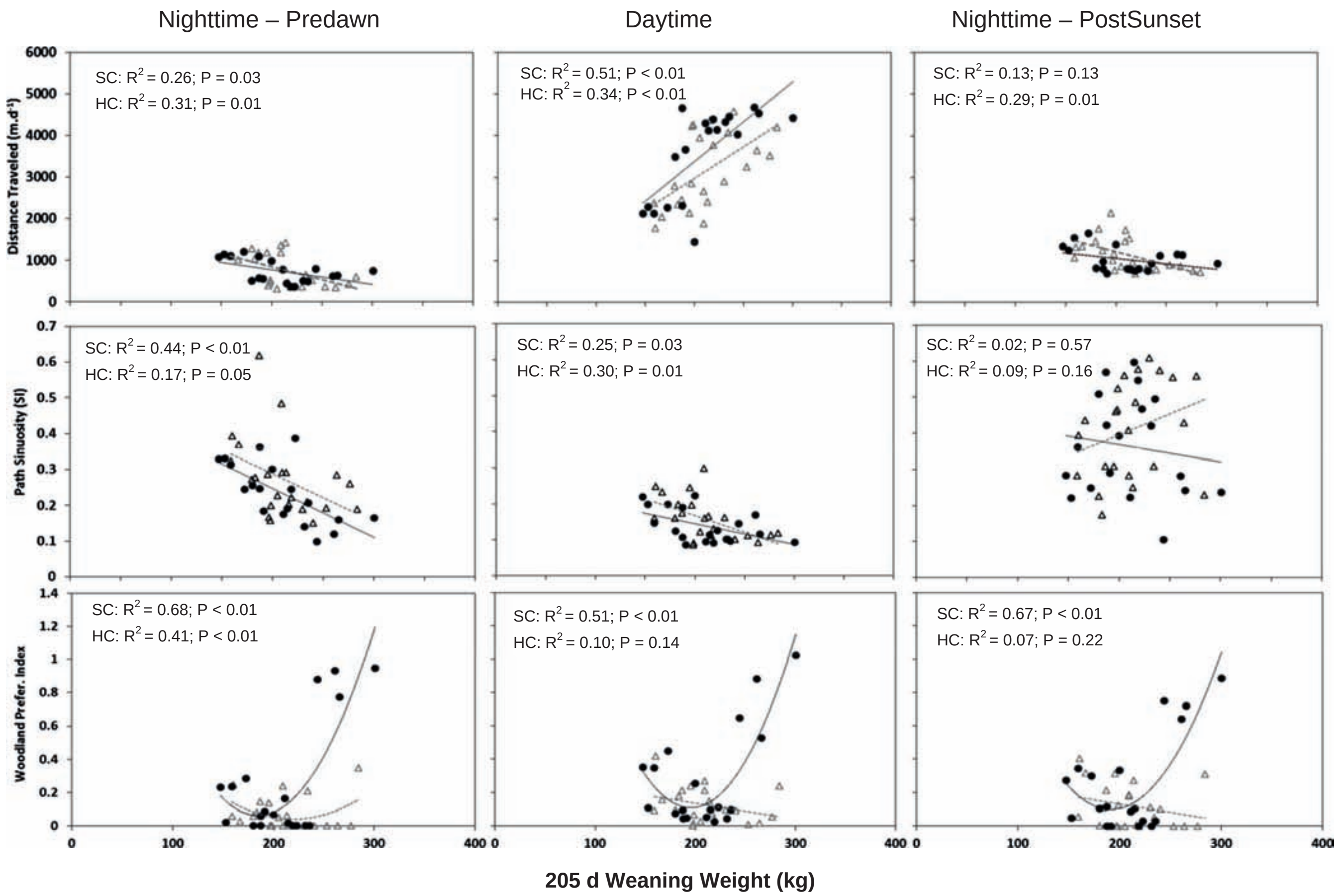

Fig. 2. Relationship between 205 d adjusted weaning weights of steer calves (SC, full circles, solid line) and heifer calves (HC, open triangles, dotted line) and the distance traveled (km.d^{-1}), path sinuosity (straightness index, SI; 0 = sinuous, 1 = straight), woodland preference (preference index; <1 = avoidance; 1 = indiference; > 1 = preference), and area explored (ha.d^{-1}) by dams during pre-dawn (nighttime), daytime, and post-sunset (night-time) hours in the weeks immediately following calving at a rangeland site in New Mexico.

Cattle have been shown to spend more hours grazing when forage is green versus dormant and to spread out (travel farther) during periods of green-up or brown-down presumably "seeking the areas where forage still had green shoots amongst the dry" (Low et al., 1981a). Wagnon (1963) observed that nursing cows on California annual grassland increased nighttime grazing in response to forage green-up, a result that does not appear to be supported by our data. Cumulative precipitation, a surrogate used to infer spring green-up at our site, was inversely related with nighttime travel but positively associated with distances traveled during daytime hours. Sawalhah et al. (2014) found that in years with vigorous spring green-up, cows tended to move among grazing patches (30 × 30 m pixels) more frequently compared with years when vegetation remained dormant. This study suggests that most of this movement occurred during daytime hours when cows were presumably better able to respond to visual cues (greenness) associated with patches of increased forage quality (Howery et al., 2013, and references therein). Again, it is likely that increased energy expenditure invested in daytime search activity may have resulted in reduced motivation to travel during nighttime hours.

Cows that experienced low forage allowance conditions explored a daily area (24-h period) that was more than double the area explored by cows in high forage allowance years. These results are consistent with those reported by Díaz Falú et al. (2014), who found that GPS-collared cattle and sheep expanded or contracted the daily area explored in response to year-to-year variation in the availability of preferred forages. In our study, daily area explored was one of only two response variables whose variation was best explained with a model that only included forage attributes (forage allowance and spring green-up). The fact that weather covariates were unable to account for day-to-day variation of daily areas explored suggests that this variable was possibly mostly controlled by forage attributes.

No differences in path sinuosity among treatments were observed during daytime hours. During nighttime hours, however, cows that experienced low forage allowance followed more sinuous paths than their high forage allowance counterparts. Russell et al. (2012) reported breed differences in path sinuosity of Brahman (highest), Brangus (intermediate), and Angus (lowest) cows grazing Chihuahuan Desert rangeland, which they attributed to more concentrated search patterns observed in Brahman cows. Bison and other wild ungulates are known to adjust movement sinuosity during concentrated searches in response to higher patch forage quality (Fortin, 2003 and references therein). It is possible that night movements of cows that experienced low forage allowance in our study were associated with more concentrated search for forage. However, because the straightness index we used is sensitive to the physical structure (e.g., trees) of the foraging environment (Benhamou, 2004), we speculate that increased time navigating in woodland versus open grassland during predawn hours (time period when treatment differences in woodland use were highest) was the more likely cause of nighttime sinuosity differences between treatments.

Per-capita forage allowance appeared to exert a large influence on plant community (open grassland vs. woodland) selection patterns of cows in our study. Woodland preference of cows that experienced low forage allowance was significantly higher than that of their high forage allowance counterparts. These results confirm the preliminary function proposed by Black Rubio et al. (2008), which suggested that higher forage availability in open grassland decreased the need for shelter on cold winter days, consequently increasing woodland avoidance by cows. Our results also agree with Díaz Falú et al. (2014), who reported that both sheep and cattle spent more time in less preferred vegetation types in years with low forage production.

Weather covariates improved most of the models (11 out of 13) describing day-to-day variation in cattle movement patterns and plant community selection, supporting our second hypothesis. In agreement with previous studies (Allred et al., 2011; Harris et al., 2002) and confirming patterns observed by Black Rubio et al. (2008), our analysis found that weather variables known to affect animal thermal comfort influenced cattle movement patterns at the scale of days (Day + Night) and within-day periods (Night $_{predawn}$, Day, and Night $_{postsunset}$). Decreasing air temperatures were associated with 1) higher woodland preference during both daytime and nighttime periods; 2) longer postsunset distances traveled (possibly searching warmer bedding sites); and 3) straighter 24-h period search patterns. Interestingly, ambient temperatures during all data collection periods were well within the theoretical thermoneutral zone of cattle (Yousef, 1985), suggesting that behavioral responses to thermal cues occur well before the theoretical minimum critical temperature (−20°C; Yousef, 1985) is reached. On rainy days cows appeared to seek shelter in the trees after dusk, which was likely a thermal comfort response that is consistent with cattle behaviors observed by Low et al. (1981b) on Australian rangelands. On days when winds came out of the northeast, cows traveled farther and exhibited higher preference for areas of the pasture covered by piñon juniper woodland. Cows are known to seek shelter on windy or cold days (Low et al., 1981b) and to graze facing into the wind until they reach a fence (Arnold and Dudzinski, 1978) and may have therefore traveled from water (W side of our pasture) into the woodland (E side of our pasture) traversing all the length of our study pasture.

Increasing lunar phase was associated with longer distances traveled by cows during predawn nighttime hours, a result that appears to contrast with earlier studies that reported either no influence (Dwyer, 1961; Wagnon, 1963) or limited influence (Low et al., 1981b) of moonlight on nighttime grazing by cattle. Wagnon (1963) stated that "the presence or absence of moonlight appeared to have no effect [on livestock nighttime activities]" (p.24). Research from the Sahel, where night herding of cattle during the hot dry season is a common practice (Ayantunde et al., 2000), has shown that cattle compose similar diets when grazing at night or during the day (Ayantunde et al., 2002). Cattle possibly rely mostly on the sense of smell during both daytime (Dwyer, 1961) and nighttime grazing, whereas the sense of sight might be more important while traveling. This distinction may explain the apparent discrepancy between our results (we measured distance traveled) and earlier studies that computed the number of times that cows were observed grazing.

Cow movement patterns during the weeks immediately following calving explained more than half of the variation in steer calf WWs but were mostly unrelated to heifer calf 205-d WW, partially supporting our third hypothesis. Sex-related differences in birth weights and growth rates (males > females; Nelsen and Kress, 1976), as well as sex-specific mother-offspring proximity patterns (females > males, Lidfors and Jensen, 1988) may have been responsible for the sex-dependent correlations we observed (see later).

Postcalving distance traveled and area explored by cows over a 24-h period were positively correlated with steer (but not heifer) calf WWs. Dams that traveled farther and covered larger pasture areas may have had access to better and/or more abundant forage resources, which possibly resulted in higher milk yields. This may have favored the relatively heavier and faster-growing male versus female calves that presumably had higher nutritional requirements. Stronger positive correlation between daytime distance traveled by the dam and 205-d WW of steer versus heifer calves, as well as weaker or nonsignificant negative correlation between nighttime movement patterns of mother cows and 205-d WW of steer versus heifer calves may also explain the overall sex dependence of the dam behavior—calf performance relationship. Wesley (2008) tracked young cows and their calves and found that at an early age, calves remain in the proximity of a guard cow during daytime hours but follow their dam more closely during nighttime. Newborn beef heifer calves on pasture have been shown to remain closer to their dams compared with male counterparts (Lidfors and Jensen, 1988) and may have been more prone to follow their mothers during nighttime hours expending more energy in locomotion and gaining less weight. Sex-dependent nighttime movement patterns of calves (females > males) could partially account for the nonsignificant dam behavior–heifer calf 205-d WW correlations.

Interestingly, postcalving cow behaviors associated with high forage allowance treatment (light stocking rates) such as shorter daytime and longer nighttime distances traveled, as well as straighter nighttime travel paths, were all associated with lighter calf WWs. Cows in this treatment weaned calves that were almost 50 kg lighter than calves weaned from low forage allowance treatment (moderate stocking rate). These results were unexpected because cows that experienced high forage allowance were presumably not subject to higher nutritional restrictions compared with their low forage allowance counterparts. Cows that experienced high forage allowance traveled farther at night and may have induced higher levels of nighttime activity in their calves (particularly in heifer calves), a phenomenon that could have caused calves to expend more energy and gain less weight. Alternatively, if greater levels of nighttime movement observed in high forage allowance cows were associated with nighttime grazing, it is possible that the dams' feeding choices were more constrained by calf mobility (particularly in the case of heifer calves) compared with daytime grazing, and cows were therefore composing less nutritious diets, which may have translated in to lower levels of milk production and lighter calves.

Although 24-h path sinuosity of cows during weeks following calving was not correlated with calf 205-d WW, increased path sinuosity during predawn nighttime and daytime hours was associated with higher 205-d WW in both steer and heifer calves. This was the only movement variable we measured that yielded consistent correlations across sexes. It is unclear whether increasing sinuosity in the cows' paths was due to more concentrated forage search (as in Russell et al., 2012) or if cows were just navigating woodland sites. More time allocated to grazing and/or selection of sheltered woodland sites, particularly during the cold predawn hours, could have had favorable indirect impacts on calf 205-d WW.

Correlations between a cow's woodland preference during the weeks immediately following calving and its calf's 205-d WW were also sex-dependent. The dam's woodland preference was a significant predictor of steer but not heifer calf 205-d WW with the exception of predawn woodland preference (time of the day with lowest ambient temperatures), which was positively correlated with 205-d WW of both male and female calves. Cows that weaned the heaviest steer calves exhibited the highest preference for woodlands in the weeks immediately following calving. The combined effect of untapped forage resources in the woodland understory (most cows avoided woodland areas) and higher levels of shelter for both the dam and its calf (particularly during predawn hours) may have resulted in better early growing conditions for calves. Interestingly, dams that weaned the lightest steer calves showed intermediate levels of preference for woodlands. These dams were classified by Wesley et al. (2012) as belonging to a behavioral type characterized by a lower drive to seek forage, having a higher propensity to loaf close to water or in sheltered areas, and exhibiting lower body weight and poorer reproductive parameters that may have been associated with an overall lower nutritional condition.

Management Implications

Levels of forage allowance associated with moderate stocking rates increased the use of woodland understory forage in this study. Woodlands appear to play an important role in generating livestock habitat by providing shelter and emergency forage. Excess forage availability in our light stocking rate treatment (high forage allowance) was associated with increased nighttime activity levels of cows, which appeared to

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have detrimental effects on calf WWs. Our results suggest that in rangeland environments, a dam's spatial behaviors are of consequence to its steer calf's WW and therefore could affect the economics of rangeland-based cow-calf operations. Light stocking rates at this site appear to have promoted less desirable foraging behavior patterns in dams, which apparently resulted in decreased productivity.

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