



Research Article

Sympatric Cattle Grazing and Desert Bighorn Sheep Foraging

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ABSTRACT Foraging behavior affects animal fitness and is largely dictated by the resources available to an animal. Understanding factors that affect forage resources is important for conservation and management of wildlife. Cattle sympatry is proposed to limit desert bighorn population performance, but few studies have quantified the effect of cattle foraging on bighorn forage resources or foraging behavior by desert bighorn. We estimated forage biomass for desert bighorn sheep in 2 mountain ranges: the cattle-grazed Caballo Mountains and the ungrazed San Andres Mountains, New Mexico. We recorded foraging bout efficiency of adult females by recording feeding time/step while foraging, and activity budgets of 3 age-sex classes (i.e., adult males, adult females, yearlings). We also estimated forage biomass at sites where bighorn were observed foraging. We expected lower forage biomass in the cattle-grazed Caballo range than in the ungrazed San Andres range and lower biomass at cattle-accessible versus inaccessible areas within the Caballo range. We predicted bighorn would be less efficient foragers in the Caballo range. Groundcover forage biomass was low in both ranges throughout the study (Jun 2012–Nov 2013). Browse biomass, however, was 4.7 times lower in the Caballo range versus the San Andres range. Bighorn in the Caballo range exhibited greater overall daily travel time, presumably to locate areas of higher forage abundance. By selecting areas with greater forage abundance, adult females in the Caballo range exhibited foraging bout efficiency similar to their San Andres counterparts but lower overall daily browsing time. We did not find a significant reduction in forage biomass at cattle-accessible areas in the Caballo range. Only the most rugged areas in the Caballo range had abundant forage, potentially a result of intensive historical livestock use in less rugged areas. Forage conditions in the Caballo range apparently force bighorn to increase foraging effort by feeding only in areas where adequate forage remains. © 2015 The Wildlife Society.

KEY WORDS activity budget, behavior, bighorn sheep, competition, foraging efficiency, livestock, New Mexico, *Ovis canadensis nelsoni*.

Foraging behavior links individual fitness and population dynamics (Owen-Smith 1979, 1994; Owen-Smith and Novellie 1982; Newman 2007). Although herbivores are often surrounded by an apparent abundance of food, forage varies in quality and quantity spatially and temporally (Owen-Smith 1979, Owen-Smith and Novellie 1982, Senft et al. 1987). Consequently, herbivores must decide where to forage, which plants to consume, and how much time to devote to foraging based on dynamic environmental conditions (Owen-Smith 1979, Bunnell and Gillingham 1985, Newman 2007). These foraging decisions influence an animal's food intake and subsequent nutritional condition,

which can greatly influence survival and reproduction (Cook et al. 2004, Parker et al. 2009, Monteith et al. 2014). Therefore, understanding how animals acquire food and factors that influence their food supply is essential for understanding herbivore ecology and conservation of wild herbivore populations, particularly when forage resources are affected by human activities.

Desert bighorn sheep (*Ovis canadensis nelsoni*; hereafter bighorn) were historically widespread in the southwestern United States and northern Mexico but were substantially reduced after European settlement through impacts of livestock diseases, over-harvest, and habitat degradation (Buechner 1960, Krausman et al. 1999). Intensive recovery efforts (e.g., translocations) by state and federal agencies have resulted in increased population sizes and extant herds in previously extirpated ranges (Valdez and Krausman 1999). Bighorn populations, however, often remain small

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(<100 animals), isolated, and continually threatened by habitat degradation, disease, predation, and loss of genetic diversity (Douglas and Leslie 1999, Valdez and Krausman 1999, Epps et al. 2005). Desert bighorn are important to consumptive and non-consumptive wildlife users, and the sale of hunting tags provide substantial funding to many state wildlife agencies in the western United States. Although many populations have recovered to varying degrees from historical lows, many populations have yet to fully recover. To manage for continued recovery of bighorn, there is a need for information on factors that may limit population growth.

Forage reduction by cattle is hypothesized to limit bighorn populations in areas of sympatry (Buechner 1960, Gallizioli 1977, Krausman 2000). Though bighorn typically inhabit steep, rugged terrain, gentler terrain is also used and spatial overlap with cattle is common (Lauer and Peek 1976, Ganskopp and Vavra 1987, Dodd and Brady 1988, Bissonette and Steinkamp 1996, Brown et al. 2010). Additionally, cattle can acclimate to rugged terrain (Ganskopp and Vavra 1987, Bailey et al. 2004) and increase use during cooler seasons (Holechek et al. 1995) or when forage resources on gentler slopes are depleted (Elenowitz 1983, Goodson et al. 1999).

Spatial overlap between cattle and bighorn can potentially result in forage competition. Desert bighorn diets are typically dominated by shrubs (i.e., browsing), with grasses and forbs (i.e., grazing) seasonally important (Krausman et al. 1999). Cattle are primarily grazers with diets of mostly grasses, with forbs and shrubs seasonally important in some areas (Rosiere et al. 1975, Hakkila et al. 1987, Daniel et al. 1993). Cattle do forage on shrubs (e.g., >20% daily intake; King and Workman 1984, Daniel et al. 1993, Martinez et al. 1997) with consumption increasing as preferred forage (i.e., grasses) declines (Chaikina and Ruckstuhl 2006, Fulbright and Ortega-Santos 2006), during dry periods (Daniel et al. 1993, Stewart et al. 2002) or when grazing intensity is high (Willms et al. 1980, Kie et al. 1991).

Given variable diet composition and space use of cattle and bighorn, diet overlap is likely in areas of sympatric use, particularly during periods of reduced forage abundance. Where spatial overlap does exist, cattle may reduce forage as documented for mule deer (*Odocoileus hemionus*; Loft et al. 1991, Wagoner et al. 2013), elk (*Cervus elaphus*; Stewart et al. 2002), and bighorn (Goodson et al. 1999). Livestock grazing effects may be particularly severe in deserts, where primary productivity is low, especially with year-round grazing. Foraging efficiency may decline because animals must spend more time acquiring food (e.g., increase search time; Owen-Smith 1979, 1994; Bunnell and Gillingham 1985; Robbins 1993). Intake rates can also be reduced (Wagoner et al. 2013), negatively affecting individual fitness (Parker et al. 1996, Cook et al. 2004, Taillon et al. 2006, Monteith et al. 2014).

Activity patterns should represent the cost and efficiencies of food gathering, where an efficient animal minimizes time spent foraging while maximizing intake (Robbins 1993). Our goal was to assess potential influences of sympatric cattle foraging on bighorn forage and determine how forage

characteristics affect bighorn foraging. We assessed bighorn forage composition and biomass and foraging behavior in 1 mountain range used by cattle and other mountain range not used by cattle to investigate influences on bighorn activity budgets and foraging efficiency. We predicted that forage species diversity and biomass for bighorn would be lower under sympatric livestock use. Because foraging efficiency is positively associated with forage biomass (Owen-Smith 1979, Robbins 1993), we predicted that bighorn would be less efficient foragers in the range shared with cattle.

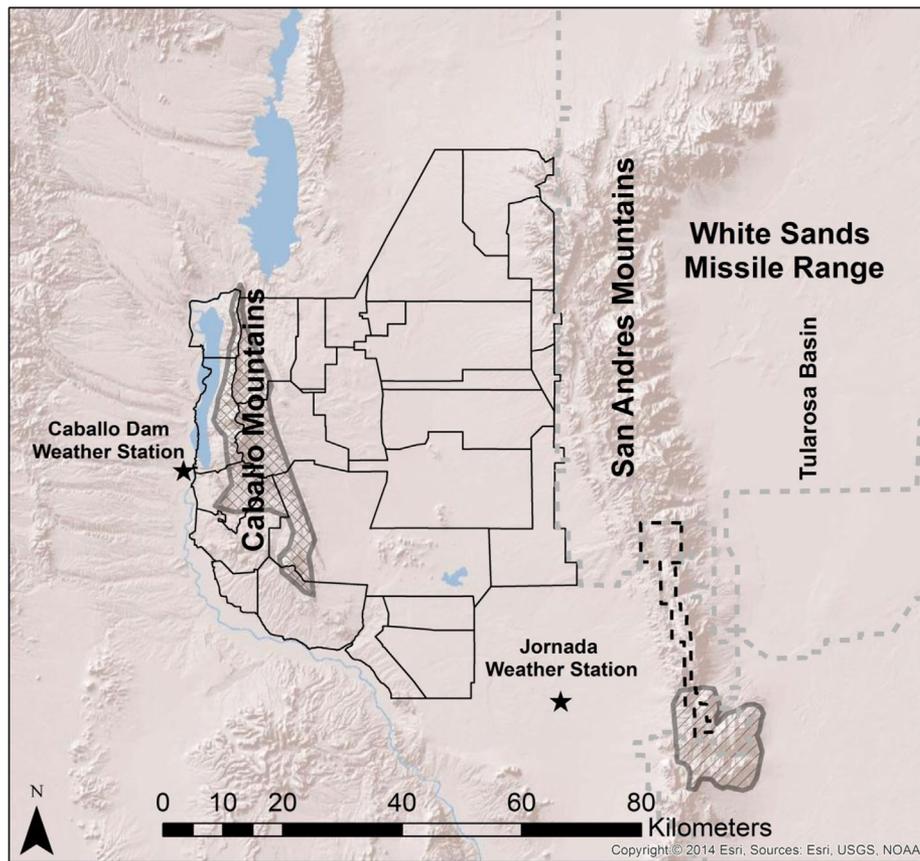
STUDY AREA

The Caballo and San Andres mountain ranges are located in southern New Mexico, USA. The Caballo range is approximately 50 km in length and elevations range from 1,463 m to 2,306 m (Fig. 1). Long-term (1992–2012) average daily maximum temperatures range from 36.1°C in June to 12.9°C in December and average annual precipitation (1992–2012) is 26.4 cm ± 7.2 cm (Caballo Dam, NM, approx. 6 km west of the Caballo range, 1,292 m elevation; Western Regional Climate Center [WRCC] 2012).

The San Andres range, approximately 50 km east of the Caballo range, is approximately 137 km in length and includes portions of the White Sands Missile Range (WSMR) and San Andres National Wildlife Refuge (SANWR); elevation ranges from 1,280 m to 2,377 m. Average daily maximum temperatures range from 34.4°C in June and 13.3°C in December and average annual precipitation is 25.8 cm ± 10.2 cm (Jornada Experimental Range, approx. 17 km west of the San Andres range, 1,316 m elevation, 1992–2012; WRCC 2014).

Soils on both ranges are shallow and well drained, with a coarse gravel to stony composition interspersed with a fine to coarse loamy sand mix (Bullock and Neher 1980, Neher 1984). Limestone bedrock and thinly bedded shale layers are often exposed on steep slopes (Silver 1952, Kottlowski 1955). Foot slopes are shallow gravelly alluvial and colluvial soils dissected with deep gullies and arroyos (Bullock and Neher 1980, Neher 1984). Both ranges have a steep escarpment on one side with the other side more gently sloping; the escarpment in the Caballo range faces west, whereas it faces east in the San Andres.

The Caballo and lower elevation San Andres ranges are characterized by Chihuahuan desert scrublands, creosote bush (*Larrea tridentata*) desert, and desert grasslands. Common shrubs include creosote bush, ephedra (*Ephedra* spp.), four-wing saltbush (*Atriplex canescens*), mariola (*Parthenium incanum*), mesquite (*Prosopis glandulosa*), mountain mahogany (*Cercocarpus montanus*), ocotillo (*Fouquieria splendens*), sotol (*Dasyllirion wheeleri*), and tarbush (*Flourensia cernua*). Common grasses include grama grasses (*Bouteloua* spp.) and tobosa grass (*Hilaria mutica*). Other species include Parry's agave (*Agave parryi*), cane cholla (*Cylindropuntia imbricata*), one-seed juniper (*Juniperus monosperma*), and prickly pear (*Opuntia* spp.). The Caballo and San Andres ranges share a similar suite of ungulates including mule deer (*Odocoileus hemionus*) and javelina (*Pecari tajacu*), and predators including coyote



- ★ Weather Stations
-  San Andres Mountains Study Area
-  Caballo Mountains Study Area
-  Caballo and Jornada Grazing Allotments
- - - San Andres National Wildlife Refuge
- - - White Sands Missile Range

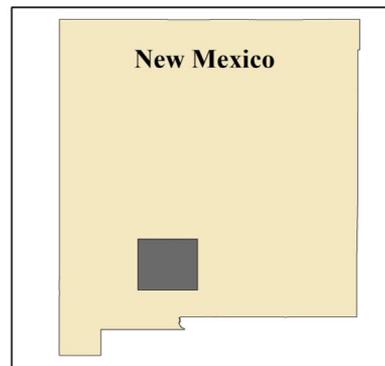


Figure 1. Location of study areas in the Caballo and San Andres mountain ranges, New Mexico, USA.

(*Canis latrans*), mountain lion (*Puma concolor*), and bobcat (*Lynx rufus*). Oryx (*Oryx gazella*), an African antelope species, is present on WSMR on low elevation footslopes of the San Andres range (Hoenes and Bender 2010). Mule deer densities are similarly low in both ranges.

In 2012, there were an estimated 95–100 bighorn in the Caballo range and 115–135 in the San Andres range (New Mexico Department of Game and Fish 2013). In May 2012, there were a combined 32 bighorn with very high frequency (VHF) radio collars in the Caballo (11 F, 3 M) and San Andres ranges (13 F, 5 M). The Bureau of Land Management (BLM) manages the majority of the Caballo range, with 8 livestock grazing (i.e., cattle and horses) allotments that border or contain all available desert bighorn habitat.

These allotments permit year-round use with animal unit months (AUMs) ranging from 605 to 6,790 AUMs during the study period (BLM, unpublished data), with AUMs generally increasing with the size of the allotment. The San Andres range is contained entirely within WSMR, and public access is not permitted. Other than occasional stray cattle, there have been no livestock in the San Andres range since at least 1951 (Sandoval 1979). Radio-collared bighorn were concentrated in the southern portion of the San Andres range >3 decades ago (Sandoval 1979) and continue to use the same areas today (New Mexico Department of Game and Fish [NMDGF], personal communication); we accordingly restricted our study area to the Black, Bennett, Black Brushy, and Goat Mountain complex (approx. 150–200 km²; Fig. 1).

METHODS

Forage Resources

We collected forage composition and biomass data seasonally from May 2012 to November 2013. Based on long-term (1992–2012) climate data on average daily high temperatures and mean monthly precipitation, we defined April–June as hot-dry (30.1°C, 4.0 cm ± 0.6 cm average seasonal precipitation), July–October as hot-wet (31.2°C, 16.0 cm ± 1.5 cm), and November–March as cool-dry (16.9°C, 3.0 cm ± 0.4 cm; WRCC 2014). We were logistically unable to sample additional mountain ranges during this study; therefore, we could not replicate the effect of cattle use at multiple bighorn-occupied ranges that included those both used and unused by cattle. Instead, we stratified each range into cattle-accessible and cattle-inaccessible areas. By doing so, we were able to investigate effects of cattle foraging within the Caballo range and compare it to the San Andres range, where cattle are not present and should therefore reflect natural forage conditions. We created 32 permanently marked 200-m forage biomass transects in each range (hereafter range-wide transects) by randomly selecting points created using ArcGIS (ESRI, Inc., Redlands, CA). We determined cattle accessibility to transects by looking for cattle sign (e.g., droppings, tracks, visual observation) and considering slopes usable by cattle being ≤30% (Mueggler 1965, Ganskopp and Vavra 1987) estimated using a clinometer. Each transect was oriented in a random direction and was composed of 10 equally spaced 1-m² plots. We stratified transects based on elevation (low <2,000 m; high >2,000 m), aspect (north [northwest, north, and northeast]; south [southwest, south, and southeast]), and accessibility to cattle (i.e., accessible or inaccessible). Because the San Andres range is higher, we limited transects in that range to the maximum elevation in the Caballo range to avoid confounding influences of increasing elevation on forage. We sampled 4 replicate transects in each unique combination of strata (i.e., elevation, aspect, cattle accessibility).

At each range-wide transect, we used a modification of the comparative yield method (Haydock and Shaw 1975, Sandoval 1979, Krausman et al. 1999, Marshal et al. 2005) to estimate edible forage biomass for species known to be in bighorn diets in southern New Mexico (Sandoval 1979, Krausman et al. 1999). We assessed each 1-m² plot for browse (i.e., woody shrubs and trees) biomass of only the edible portions of the plant (i.e., leaves, inflorescences, and twigs <5 mm in diameter) up to 1 m high, with each plot assigned a rank from 0 to 4 in 0.5 increments, where a rank of 0 represents a plot with no edible biomass, 1 = 25%, 2 = 50%, 3 = 75%, 4 = 100% full of edible biomass (Marshal et al. 2005). We estimated groundcover biomass (i.e., non-dormant, green portions of grasses and forbs) similarly but with a height of 0.5 m (Marshal et al. 2005). For both browse and groundcover, we clipped edible biomass from ≥10 plots/rank and dried them to a constant mass at 60°C.

Additionally, we recorded forage characteristics at locations where foraging efficiency observations were collected for bighorn. We recorded data on foraging site transects

similarly to range-wide transects, except with a 100-m equally spaced 10-plot transect. Transect direction followed the foraging group's path. Bighorn typically foraged linearly where individuals followed the path of a dominant adult female. So, foraging site transects typically represent forage assessments for >1 efficiency observation. We determined location of foraging site transects based on detailed recording of the foraging animal's location. We used a global positioning system unit with a topographical map, landmarks noted during foraging observations (e.g., large shrubs among mostly grasses, large boulders, unique cracks in cliff walls), and the presence of fresh fecal pellets, tracks, and evidence of recent herbivory to ensure the correct location of foraging site transects. We completed foraging site transects within 3 days of observations of foraging bouts. Because we visited foraging transects after an observed foraging event, they do not account for biomass removed by foraging and may underestimate forage cues bighorn used to select foraging sites. We recorded percent slope for all range-wide and foraging site transects. All methods and procedures were approved by New Mexico State University's Institutional Animal Care and Use Committee (IACUC protocol #2011-039).

Foraging Observations

Bighorn groups were typically small (i.e., <8 animals) and widely dispersed over large and remote areas. We collected activity budget and foraging efficiency data during daylight hours year-round by locating bighorn through visual scanning and use of telemetry in a quadrant system in each range; however, if we observed desert bighorn opportunistically while moving between quadrants, we also recorded activity budget and foraging efficiency data. Once located, we observed behavior through a spotting scope (Swarovski AT65, Absam, Austria) at distances of 500–1,500 m. We used instantaneous scan sampling at 5-minute intervals (Altmann 1974). We separated observations into 4 daily time periods: early morning (sunrise to 0900 hours) late morning (0901–1200 hours), early afternoon (1201–1500 hours), and late afternoon (1501 hours to sunset; no night observations). We categorized activities as grazing (i.e., feeding on grass and forb species), browsing (i.e., feeding on woody species), standing, traveling, bedded, and miscellaneous social behavior (i.e., nursing, combat; Wilson et al. 2009). We classified animals as adult males, adult females, yearlings (13–24 months old; not distinguished by sex), and lambs (≤12 months old).

We used focal animal sampling (Altmann 1974) to assess foraging efficiency via feeding time using accepted food abundance (AFA; Owen-Smith 1979). We collected data only for adult females for foraging efficiency because of their dominant influence on population growth (Gaillard et al. 1998, 2000). Although bite rate and bite size are direct measures of intake, collecting these data is often impracticable with wild animals (Bunnell and Gillingham 1985). Therefore, we used AFA, defined as feeding seconds/50 steps, to index foraging efficiency (Owen-Smith 1979, Dunham 1982, Smith and Cain 2009). We observed animals

for >2 minutes before data collection to ensure they were intent on feeding (i.e., intermittently feeding while taking steps). For AFA observations, we selected the first adult female that commenced feeding as the focal animal and recorded her behaviors into a digital voice recorder until she had taken 50 front leg steps. We recorded subsequent observations identically until all adult females were observed or the group moved out of sight. Group sizes were typically small (i.e., <8 animals) and rarely contained >3 adult females, therefore a randomization protocol for focal animal selection was unnecessary. We omitted foraging interruptions of <4 seconds from the activity sequence (e.g., head up and visually scanning <4 seconds; Wronski 2002). If the animal engaged in non-feeding activities (e.g., standing vigilant) for >2 minutes, we terminated the observation when non-feeding activity began (Owen-Smith 1979). Sampling bighorns rarely provided observation periods >2 hours. Based on group proximity, marked individuals, and group composition, we seldom resighted the same group during the same day, which reduced multiple observations of the same uncollared individuals during the same day. We generally avoided repeated sampling of the same individuals on the same day for foraging efficiency. Efficiency observations that were taken on the same day, although infrequent, only occurred if the animal had moved into a different area (i.e., >500 m away from original observation).

Statistical Analysis

We used linear regression to estimate the relationship between rank value and dry biomass of browse and groundcover forage types from the clipped plots, and then we estimated biomass for unclipped plots using the linear model. We averaged biomass among plots for each transect for all forage types. We used the average value/transect as the sampling unit for analysis. To assess differences in edible biomass between ranges and among seasons, we used repeated measures analysis of variance (ANOVA) in SAS 9.4 (PROC MIXED, SAS institute, Cary, NC) with range, season, and cattle accessibility as fixed factors and transects as repeated measures using an unstructured covariance structure. We tested for differences in edible biomass of foraging site transects between ranges and among seasons using ANOVA. We used independent sample *t*-tests to assess differences between slopes of range-wide and foraging site transects and between cattle-accessible and inaccessible foraging site characteristics in the Caballo range; we tested for equal variance using Levene's test and if rejected, we used Welch's *t*-test.

To include all efficiency observations, we converted AFA to foraging seconds/step to standardize across all observations for analysis. We used ANOVA in SPSS version 22 (SPSS IBM, Armonk, NY) to investigate differences in AFA between ranges and among seasons. We calculated and analyzed activity budgets similarly to Wilson et al. (2009), where we estimated activity averages for each age and sex class per time period for each observation. We used the average activity value for each day period as the sampling unit to compare activity budgets between ranges, among day

periods, and among seasons for each age and sex class using ANOVA in SPSS version 22. We transformed data using the natural logarithm for biomass and AFA and used the arcsine-square root for proportional data. We used residual diagnostics to check for normality and variance assumptions (Zar 1999). We used $P < 0.10$ as our statistical significance criterion.

RESULTS

Range-Wide Forage Resources

We recorded 36 browse and 33 groundcover forage species on range-wide forage transects (Supplementary Table S1). There were 31.3% fewer forage species recorded in the Caballo range ($n=44$) than in the San Andres range ($n=64$). The Caballo range had 29.4% fewer browse ($n=24$) and 33.4% fewer groundcover ($n=20$) forage species than did the San Andres range (34 browse species, 30 groundcover species). Plot rank and biomass were linearly related for browse (Caballo: $r^2 = 0.90$; San Andres; $r^2 = 0.86$) and groundcover (Caballo: $r^2 = 0.90$; San Andres; $r^2 = 0.84$) in both the Caballo and San Andres ranges (Supplementary Table S2).

Edible browse biomass was on average 4.7 times higher in the San Andres ($\bar{x} = 56.5 \text{ g/m}^2$, $SE = 7.1$) than in the Caballo range ($\bar{x} = 9.9 \text{ g/m}^2$, $SE = 2.2$; $F_{1, 58} = 108.85$, $P < 0.001$). Biomass measured in each range depended on season (i.e., range \times season interaction; $F_{4, 58} = 3.01$, $P = 0.025$). The influence of cattle accessibility on browse biomass depended on range (i.e., range \times cattle interaction; $F_{1, 58} = 4.06$, $P = 0.049$; Fig. 2). Within the Caballo range, cattle-inaccessible areas had an average of 10.9 g/m^2 ($SE = 2.4 \text{ g/m}^2$) edible browse biomass compared to 8.9 g/m^2 ($SE = 3.7 \text{ g/m}^2$) in areas accessible to cattle (Tukey HSD, $P = 0.139$). Conversely, areas in the San Andres range that would be inaccessible to cattle had lower browse biomass (43.7 vs. 69.3 g/m^2) than areas that would be accessible to cattle (Tukey HSD, $P = 0.909$).

Edible groundcover biomass was low in all seasons during the study period, averaging 0.9 g/m^2 in the Caballo range ($SE = 0.1 \text{ g/m}^2$) and 2.6 g/m^2 in the San Andres range

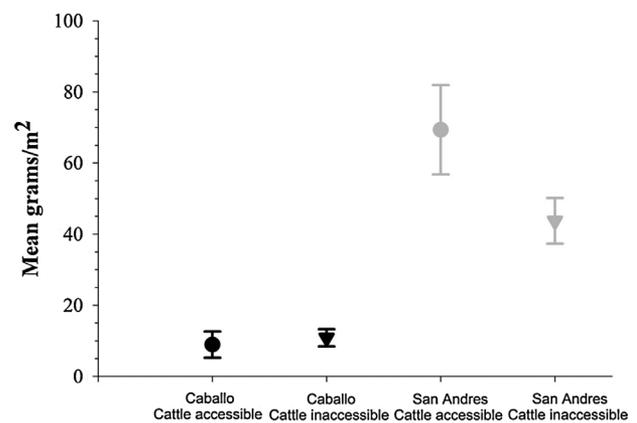


Figure 2. Mean range-wide edible browse biomass in cattle accessible (circles) and inaccessible (triangles) areas in the Caballo (black) and San Andres (gray) mountains ($\pm SE$), New Mexico, USA, 2012–2013.

Table 1. Foraging site and range-wide mean edible browse and groundcover biomass (g/m²) of cattle accessible (Yes), inaccessible (No), and all (Overall) transects, Caballo and San Andres ranges, New Mexico, USA, 2012–2013.

Forage type	Transect type	Cattle access	\bar{x}	Caballo			San Andres		
				SE	<i>n</i>	\bar{x}	SE	<i>n</i>	
Browse	Foraging site	No	36.8	12.8	29	31.0	5.2	17	
		Yes	18.2	7.7	14	0.0	0.0	0	
		Overall	30.8	9.0	43	31.0	5.2	17	
	Range-wide	No	10.9	2.4	80	43.7	6.4	80	
		Yes	8.9	3.7	80	69.3	12.6	80	
		Overall	9.9	2.2	160	56.5	7.1	160	
Groundcover	Foraging site	No	1.5	0.4	29	2.1	0.8	17	
		Yes	2.3	0.6	14	0.0	0.0	0	
		Overall	1.8	0.4	43	2.1	0.8	17	
	Range-wide	No	0.9	0.2	80	1.9	0.3	80	
		Yes	0.8	0.2	80	3.3	0.5	80	
		Overall	0.9	0.1	160	2.6	0.3	160	

(SE = 0.3 g/m²; Supplementary Table S3); therefore, we did not test for differences among ranges, seasons, or cattle accessibility.

Foraging Site Forage Resources

We collected data on forage resources at 43 and 17 foraging site transects in the Caballo and San Andres ranges, representing 79% (Caballo) and 43% (San Andres) of recorded foraging observations, respectively; the unsampled foraging sites were inaccessible to humans. Foraging sites had an average slope of 42% in the Caballo ($n = 34$, SE = 2.0) and 56% in the San Andres ($n = 15$, SE = 2.4). Foraging site slopes in the Caballo and San Andres ranges were steeper than the slopes of range-wide transects (Caballo: 42.3% vs. 27.8%; $t_{52.9} = 4.01$, $P < 0.001$; San Andres: 56.1% vs. 41.9%; $t_{43.3} = 3.063$, $P = 0.001$). In the Caballo range, cattle-accessible foraging sites were steeper than were the range-wide transects (30.7% vs. 16.4%; $t_{23} = 4.961$, $P < 0.001$), but the slope of cattle-inaccessible foraging sites were similar (46.5% vs. 39.1%, $t_{22.2} = 1.636$, $P = 0.116$). Slopes of cattle-inaccessible transects in the San Andres range were similar between foraging sites and range-wide transects (56.1% vs. 54.3%; $t_{29} = 0.449$, $P = 0.656$).

Edible browse biomass was similar between foraging site transects in the Caballo and San Andres ranges ($F_{1, 53} = 0.108$, $P = 0.744$; Table 1) and did not differ seasonally ($F_{3, 53} = 1.054$, $P = 0.376$). Edible groundcover biomass was similar between ranges at foraging site transects (Table 1). In the Caballo range, foraging site transects had >2 times greater browse biomass than did range-wide transects (Fig. 3), and browse biomass was >2.3 times greater in cattle-inaccessible and >100% greater in cattle-accessible foraging-site transects versus range-wide transects (Table 1). Browse biomass estimates were similar ($t_{41} = 0.956$, $P = 0.345$) between cattle-accessible ($\bar{x} = 18.2$ g/m², SE = 7.7) and cattle-inaccessible ($\bar{x} = 36.8$ g/m², SE = 12.8) foraging site transects (Table 1). Edible groundcover biomass was similar among transects at foraging sites that were cattle-accessible and cattle-inaccessible (Table 1). Contrary to the pattern observed in the Caballo range, browse biomass in the San Andres range was 45% less at foraging site versus

range-wide transects (Fig. 3); groundcover biomass was similar at foraging site and range-wide transects (Table 1).

Activity Budgets

We restricted adult male activity budget analysis to seasons corresponding with rut (i.e., hot-wet 2012, hot-dry 2013, hot-wet 2013) because we did not have enough samples in other seasons (i.e., cool-dry 2013; <10% of M observations occurred outside rut). Adult males spent more time traveling in the Caballo (18%; $n = 73$) than in the San Andres range (9%, $F_{1, 124} = 7.969$, $P = 0.006$; $n = 58$; Fig. 4), but grazing (12% vs. 8%), browsing (14% vs. 16%), standing (28% vs. 27%), and bedding (27% vs. 37%) behaviors did not differ by range ($P > 0.10$; Table 2).

We included all available seasonal data for adult female activity budget analysis (i.e., hot-wet 2012, cool-dry 2013,

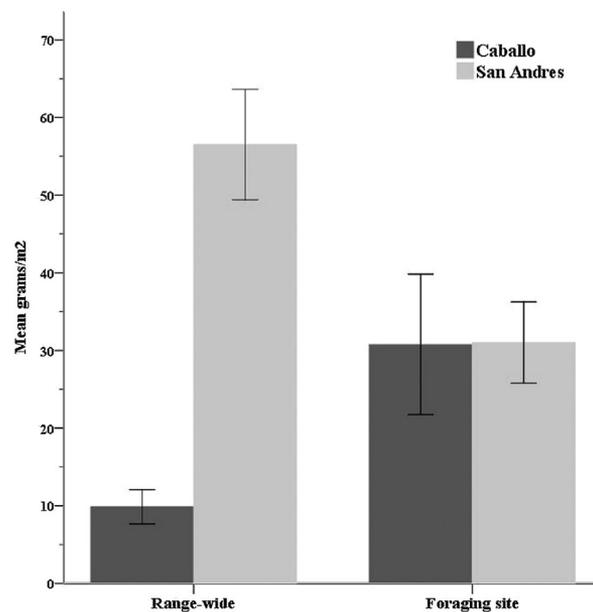


Figure 3. Mean edible browse biomass at range-wide and foraging site transects (\pm SE), Caballo and San Andres mountains, New Mexico, 2012–2013.

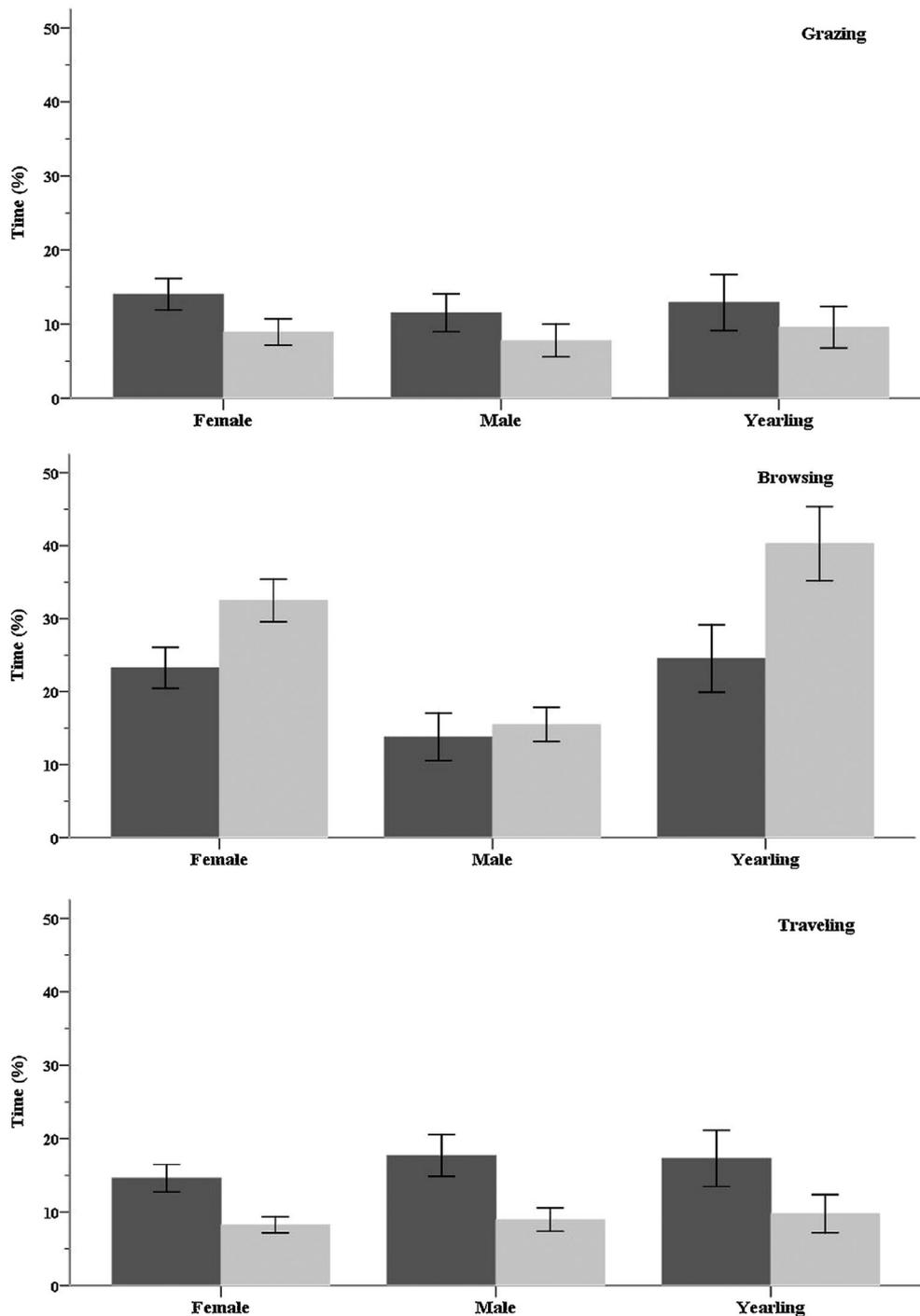


Figure 4. Grazing, browsing, and traveling times of desert bighorn sheep adult males, adult females, and yearlings by season in the Caballo (dark gray bars) and San Andres ranges (light gray bars), New Mexico, 2012–2013. Error bars are 1 standard error of the mean.

hot-dry 2013, hot-wet 2013). Adult females in the Caballo range ($n = 90$) spent less time browsing (23%) than those in the San Andres range (32%, $F_{1, 161} = 6.075$, $P = 0.015$; $n = 79$; Fig. 4) but more time traveling (15% vs. 8%) in the Caballo than in the San Andres range ($F_{1, 153} = 6.220$, $P = 0.014$; Fig. 4). Season and period affected traveling (i.e., season \times period interaction; $F_{3, 153} = 2.724$, $P = 0.008$). Time spent grazing (14% vs. 9%), standing (18% both ranges), and bedding (30% vs. 32%) were similar

($P > 0.10$) between the Caballo and San Andres ranges (Table 2). Range and season affected grazing activity (i.e., range \times season interaction; $F_{3, 158} = 7.515$, $P < 0.001$).

We included all available seasonal data for yearling activity (i.e., hot-wet 2012, cool-dry 2013, hot-dry 2013, hot-wet 2013). Yearlings spent less time browsing in the Caballo range (25%; $n = 46$) compared to the San Andres range (40%, $F_{1, 74} = 9.226$, $P = 0.003$; $n = 36$; Fig. 4) but more time traveling in the Caballo versus San Andres range

Table 2. Analysis of variance results for the main effect of range, season, and day period on averaged (pooled) daily time spent grazing, browsing, traveling, standing, and bedded for adult male, adult female, and yearling (both sexes) desert bighorn sheep, Caballo and San Andres ranges, New Mexico, USA, 2012–2013.

Sex/age class	Behavior	Mountain range		Range		Season		Day period	
		Caballo	San Andres	F	P	F	P	F	P
Adult male ^a	Grazing	12	8	1.509	0.222	4.594	0.012	0.468	0.705
	Browsing	14	16	1.403	0.238	3.161	0.046	1.302	0.277
	Traveling	18	9	7.969	0.006	0.902	0.409	1.053	0.372
	Standing	28	27	0.086	0.770	4.229	0.017	2.285	0.082
	Bedded	27	37	2.141	0.146	0.508	0.603	0.785	0.505
Adult female ^b	Grazing	14	9	0.013	0.911	6.860	<0.001	0.681	0.565
	Browsing	23	32	6.075	0.015	4.447	0.005	0.351	0.788
	Traveling	15	8	6.220	0.014	2.668	0.050	0.532	0.661
	Standing	18	18	0.001	0.973	3.361	0.020	1.339	0.264
	Bedded	30	32	0.016	0.898	2.355	0.074	0.732	0.534
Yearling ^c	Grazing	13	10	0.555	0.459	3.551	0.018	0.529	0.664
	Browsing	25	40	9.226	0.003	5.581	0.002	0.493	0.688
	Traveling	17	10	2.947	0.090	1.574	0.203	0.765	0.517
	Standing	15	16	0.097	0.756	1.393	0.252	2.613	0.058
	Bedded	30	24	1.440	0.234	2.230	0.092	0.355	0.786

^a Caballo: $n = 58$, San Andres: $n = 73$; range: $F_{1, 124}$, season: $F_{2, 124}$, day period: $F_{3, 124}$.

^b Caballo: $n = 79$, San Andres: $n = 90$; F distribution degrees of freedom for range: grazing 1,158; traveling 1,153; browsing, standing, and bedding 1,161. F distribution degrees of freedom for season and day period: grazing 3,158; traveling 3,153; browsing, standing and bedding 3,161.

^c Caballo: $n = 36$, San Andres: $n = 46$; range: $F_{1, 74}$, season: $F_{3, 74}$, day period: $F_{3, 74}$.

(17% vs. 10%; $F_{1, 74} = 2.947$, $P = 0.090$; Fig. 4). Grazing (13% vs. 10%), standing (15% vs. 16%), and bedding (30% vs. 24%) activity were similar ($P > 0.10$) between ranges (Table 2).

Foraging Efficiency

Foraging bout lengths were similar in the 2 ranges and averaged 356.7 seconds ($n = 92$; $SE = 25.8$) in the Caballo range and 337.5 seconds ($n = 94$; $SE = 21.2$) in the San Andres range. Feeding seconds/step (i.e., AFA) did not differ between the 2 ranges, and averaged 6.5 seconds ($SE = 0.6$) and 5.2 seconds ($SE = 0.3$) in the Caballo and San Andres ranges, respectively ($F_{1, 176} = 0.096$, $P = 0.757$).

DISCUSSION

Despite major differences in browse abundance between the 2 ranges, adult female bighorn in these populations had similar levels of foraging efficiency, contrary to our original prediction. Bighorn in the Caballo range apparently adjusted their foraging behavior by increasing travel time in search of areas where forage is adequate to increase feeding efficiency. We found no effect of cattle accessibility on bighorn forage in the Caballo range, possibly a result of our conservative designation of cattle accessibility and historically intensive livestock use greatly reducing forage abundance except in the most rugged areas. The effect of sympatric cattle use in the Caballo range appeared to perpetuate depleted forage on lower slopes, restricting bighorn foraging to limited areas of suitable forage abundance.

Southern New Mexico supported domestic sheep and cattle grazing since at least the 1850s (Grover and Musick 1990). By the early 20th century, there were approximately one million domestic cattle and between $3\text{--}5 \times 10^6$ domestic sheep in New Mexico (Dick-Peddie 1993, Fredrickson et al. 1998). Extensive livestock use has contributed to the

conversion of southern New Mexico from grasslands to creosote and mesquite (typically not bighorn forage species) dominated scrubland (Grover and Musick 1990). Although stocking levels were reduced in the mid- to late-20th century (Grover and Musick 1990), historical intensive livestock use negatively affected rangeland soils and vegetation (Grover and Musick 1990, Holechek et al. 1995, Gibbens et al. 2005, Krausman et al. 2009).

We documented that areas (i.e., foraging sites visited) in the Caballo range with slopes averaging $>40\%$ had 2 times greater forage abundance than the surrounding environment. This may indicate that historically intensive livestock use, particularly by domestic sheep that forage extensively on steep slopes (e.g., 30–45%) and ridge tops (McDaniel and Tiedeman 1981), depleted forage, and altered soils in all but the most rugged areas. Typically, steep slopes, high water runoff, and low water infiltration into shallow soils result in lower vegetative biomass compared to flatter areas (e.g., cattle-accessible areas; Herbel and Gile 1973, Hillel 2004, Monger and Bestelmeyer 2006, Duniway et al. 2010), as was apparent in the San Andres range 6 decades after livestock removal. In the Caballo range, reduced biomass and depleted or compacted organic soil layers, potentially from historical overgrazing, may have increased water runoff and limited availability of water to plants (Fleischner 1994).

We conducted our study in one of the driest and warmest periods on record for New Mexico (National Oceanic and Atmospheric Administration 2015), and we documented very limited groundcover (i.e., grass and forb) biomass in the cattle-grazed range. Cattle can increase their use of rugged terrain during periods of drought and when preferred forage is scarce (Elenowitz 1983, Goodson et al. 1999). Cattle in the Caballo range are grazed year-round (BLM, unpublished data) and are likely acclimated to more rugged conditions (Ganskopp and Vavra 1987, Bailey et al. 2004). Higher than

expected cattle foraging on steep slopes (i.e., >30%) in the Caballo range would not only reduce our ability to detect a cattle-induced reduction of bighorn forage but also perpetuate the poor forage conditions we observed.

Activity patterns of an herbivore are largely dictated by abundance and distribution of forage resources (Bunnell and Gillingham 1985) and activity patterns should reflect the cost and efficiency in which animals can acquire food (Robbins 1993). In areas with reduced food availability, foraging effort is necessarily increased (Robbins 1993). Bighorn in the Caballo range traveled more, apparently searching for adequate forage. Increased search effort appears to be at the cost of overall daily browsing time. Similar results were found in studies of greater kudu (*Tragelaphus strepsiceros*; Owen-Smith 1979) and elk and mule deer (Wickstrom et al. 1984). Our activity data were collected only during daylight hours, and information on nocturnal activity is needed for a more complete assessment of the efficiency of food acquisition in both ranges.

Owen-Smith (1979) reported that AFA increased for greater kudu as forage availability increased in the wet season. Likewise, Dunham (1982) reported that AFA of impala (*Aepyceros melampus*) was highest in the wet season and declined as forage abundance decreased into the dry season. Thus, we expected that bighorn in the San Andres range would forage more efficiently compared to bighorn in the Caballo range because of higher biomass. This prediction was not supported, at least not as foraging efficiency is traditionally defined. Foraging efficiency was similar between adult females in the Caballo and San Andres ranges because foraging site characteristics were consistently similar between ranges. Wronski (2002) reported that adult female impala maintained consistent AFA throughout the wet and dry seasons by adjusting their diet based on available food types, with browsing dominating the dry seasons and grazing the wet seasons. Rather than seasonally switching between predominantly grazing or browsing, bighorn in our study were predominantly browsers but selected palatable browse species as they were seasonally available.

The index of efficiency we used was based on feeding time during a foraging bout. As such, we could not detect differences in bite rate or bite size, nor account for nutritional differences of diet items across seasons, which affect food and nutrient intake (Bunnell and Gillingham 1985, Parker et al. 1996). Because our observations were at distances greater than >750 m, we could neither discriminate among consumed plants in forage bouts, nor were we able to quantify forage items for nutritional content. Therefore, our measurements of efficiency cannot describe nutritional intake of bighorn sheep, and is possible that forage conditions in the Caballo range result in nutritional deficiencies for bighorn despite observed foraging efficiency (i.e., AFA).

The relationship between an herbivore's forage resources and food acquisition may ultimately affect population growth (Wilmshurst et al. 1995). We documented that relatively limited forage forced bighorn to increase foraging effort to find high-quality forage. Increases in travel time can increase energy costs (Parker et al. 1984, Robbins 1993). As animals

increase investments in searching for food, their overall foraging efficiency typically declines (Robbins 1993), and unless otherwise compensated for (e.g., nocturnal feeding, bite rate and size), it will negatively influence animal condition (Bunnell and Gillingham 1985).

MANAGEMENT IMPLICATIONS

If managing bighorns is a priority on ranges with historical livestock grazing and where cattle still graze, particularly in arid ranges, managers should assess bighorn habitat for cattle-induced forage reduction and consequent impacts on bighorn foraging ecology. Poor forage conditions can substantially increase bighorn foraging effort. In heavily grazed ranges, managers can mitigate immediate impacts of cattle sympatry on bighorn by identifying and conserving areas where adequate forage exists and take steps toward promoting the regeneration of forage by removing cattle. Where absent, locally informed livestock grazing systems should be implemented and rangeland response carefully monitored. We suggest that bighorn carrying capacity and population goals be estimated in context of available forage rather than on the basis of range size and animal densities. Translocation is a common conservation tool for bighorn and target ranges should be chosen where cattle sympatry is minimized.

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