

Foraging behavior of heritage versus recently introduced herbivores on desert landscapes of the American Southwest

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Abstract. Since the 1800s managed grasslands and shrublands of the arid American Southwest have been grazed predominantly by cattle originally bred for temperate climates in northern Europe. A heritage breed, the criollo cattle, has survived in northern Mexico for more than 400 years under desert-like conditions of low and variable rainfall, hot temperatures in the growing season, and both spatially and temporally scarce levels of primary production. We tested the hypothesis that the heritage breed has a broader spatial foraging distribution under harsh environmental conditions, and that its distribution is driven by environmental variables which differ from those that control the distribution of the introduced European breed. Movements of individual criollo and Angus breed animals were monitored autonomously in the northern Chihuahuan desert of southern New Mexico, USA. Georeferenced foraging locations acquired at 5-minute intervals for each animal were fit to a logistic regression using environmental factors as predictors. In the spring, when forage availability was high and more uniformly distributed across the landscape, animal foraging patterns were similar for both breeds. In the fall when forage availability was low and non-uniformly distributed, the two breeds exhibited very different foraging patterns: heritage animals foraged across a much larger spatial extent whereas their domestic counterparts remained in close proximity to the permanent source of water. These differences in foraging behavior driven by environmental variables have important implications for sustainability of rangelands in spatially and temporally variable environments. Heritage breeds of animals that are generalist foragers during unfavorable conditions can reduce environmental impacts compared to more recently introduced breeds.

Key words: Chihuahuan desert; criollo cattle; GPS monitoring; herbivory; landscape foraging patterns; resource selection functions.

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INTRODUCTION

Domestication of plants and animals over the past 10,000 years of agricultural development has

generated a high diversity of heritage varieties of crop plants and livestock breeds (Mignon-Grasteau et al. 2005, Diamond 2002, Gupta 2004, Caramelli 2006). In the last century, many

heritage plants and animals have been lost or have become endangered with the advent of modern agriculture (Harlan 1975, Oldfield and Alcorn 1987, FAO 1998*a, b*). Heritage organisms are recognized as a valuable source of biodiversity (Wood and Lenne 1997) and are presently viewed as an ecological alternative to reduce environmental impacts and to increase human adaptation to changing climate (Altieri 1999, and 2004, Letourneau and Bothwell 2008, Hajjar et al. 2008). Because of the influence of Europeans on historical agricultural development in the U.S., breeds that originated in Europe are still used as the primary grazing animal (Notter 1999). However, in some ecosystems, heritage animals may provide viable alternatives to minimize environmental impacts as human population densities continue to increase with increasing demands on ecosystem goods and services (MEA 2005). Our goal was to compare foraging behavior of a heritage breed of livestock with a commonly used domestic breed to determine the potential for heritage animals to be used in managed landscapes of the American Southwest.

Domestication is a process in which animals adapt to human-dominated environments through breeding for selected traits (Price 1999, Mignon-Grasteau et al. 2005). Modern selection by humans has increased animal production, and as a consequence, domestic animals are often highly dependent on resources provided by humans (Diamond 2002). In contrast, heritage animals are less modified by artificial selection such that they maintain more similarities with homologous wild animals (Myserud, 2010). For example, in the hot deserts of the American Southwest, heritage animals that thrive in arid environmental conditions have been subjected to an evolutionary process over many generations to adapt to spatial and temporal variations in forage availability and quality. Desert-adapted herbivores should be able to broadly explore the environment in search of forage and water. Thus, it is expected that the foraging behavior of heritage animals differs from domestic counterparts due to this different recent evolutionary history. In this paper, we compare the foraging behavior of heritage animals with those from a domestic breed to test the hypotheses that grazing patterns of heritage animals: (1) result in a broader use of the landscape when resources

are limited, and (2) are affected by different drivers than those that shape the foraging patterns of domestic counterparts.

Hypotheses were tested by comparing foraging behavior of Mexican criollo breed with domestic Angus British breed. The Mexican criollo breed originated in North Africa, and was introduced into the U.S. in 1493 (Rouse 1977). Criollo cattle were distributed across the American Southwest until the introduction of European cattle in the late 1800s (Sponenberg and Olson 1992). At present, criollo animals survive with little human care or intervention primarily in remote areas of Mexico. Beginning in the early 1900s, cattle that originated in temperate climates of Europe have been widely used throughout the U.S. European breeds cannot survive in hot, dry environments without water and food supplementation during periods of low forage availability (Winder et al. 1996, Obeidat et al. 2002). In this study, we used GPS collars to characterize the foraging spatial distribution in a desert landscape, and we used logistic regression to evaluate the relationship between foraging patterns and environmental drivers of each breed.

MATERIAL AND METHODS

Environmental variables were used to characterize biotic and abiotic resources in a landscape where monitoring experiments were conducted. Foraging raster maps were generated from foraging positions of Angus British and Mexican criollo cows determined using GPS collars. Logistic models were generated by fitting foraging raster maps using environmental variables as predictors.

Environmental characterization

The experiments were conducted at the Jornada Experimental Range (32°37' N; 106°40' W) located in the northern Chihuahuan desert in a 2425 ha fenced area. Long-term mean annual precipitation (80 years) at this site is 24.5 cm (Wainwright 2006); on average, more than half of annual rainfall occurs in July through September. Long-term mean monthly temperature for the same period of time varies from 26°C in July to 4°C in January. Vegetation of the study area is a semidesert grassland with sandy soils dominated

by honey mesquite (*Prosopis glandulosa* Torrey) intermixed with perennial grasslands dominated by black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.), and threeawns (*Aristida* spp.). Soap-tree yucca (*Yucca elata*), and broom snake-weed (*Gutierrezia sarothrae*) are common sub-dominants. Lowland grasslands dominated by tobosa (*Pleuraphis mutica*) and burrograss (*Schleropogon brevifolius*) occur on soils with high clay content.

Environmental variables were represented by 20 m resolution raster maps of variables important to livestock distribution: grass cover type, woody density, elevation, distance to nearest road, and distance to drinking water (Coughenour 1991, Bailey et al. 1996). The 20 m pixel was used to match the resolution of the foraging raster maps (see below). The grass cover type map resulted from an object oriented classification of a 4 November 2004 QuickBird image (0.70 m pixel resolution) as either grass dominated or non grass (Laliberte et al. 2007). The grass pixels were further classified into 16 classes by combining four cover types defined by the dominant perennial grass species (tobosa, black grama, other grasses, and forbs) with four classes of percentage cover (0–15, 15–30, 30–60, >60). This map was transformed to 20 m pixel resolution using the resample function in ARCGIS 9.1 (ESRI 2000). The woody density map was derived from a map that resulted from classifying the same QuickBird image as either woody dominant or non woody. First, the woody grid map was transformed to a point map by assigning a point to each pixel classified as woody. Then, a point density function in ARCGIS 9.1 (ESRI 2000) was used to generate a density map which was then transformed to a 20 m resolution grid map. This procedure was used because it was not possible to distinguish individual plants when canopies were overlapping. Woody density values on the map ranged from a minimum of 0 to a maximum of 1300 in each 20 m grid.

A digital elevation map derived from a USGS 7.5 min topographic map was used to represent different topographic locations. Differences in elevation across the landscape were less than 25 m. Maps of distance to nearest roads and to permanent drinking water were created using a distance function in ARCGIS 9.1 (ESRI 2000) from a road map of the area and a map of a

single permanent drinking water source located at the southern edge of the area.

Foraging distribution

Movements of Angus and criollo mature cows were monitored in spring and fall of 2005 to determine foraging patterns and to evaluate the relationship between foraging patterns and environmental variables represented as a raster maps. The same environmental maps were used for both seasons because they were based on physical features and dominant perennial species that do not significantly vary with season. Animals were monitored in two seasons to evaluate foraging behavior during a period of high (spring) and low forage availability (fall). Sampling conducted at the study site in 2005 verified that forage availability and quality were significantly lower in fall than in spring at the time where monitoring experiments were conducted (Roacho-Estrada et al. 2008).

Animals of both breeds foraged within the study area simultaneously to ensure the same environment was experienced by both breeds. It was previously verified that interbreed interactions are unlikely when animals of both breeds are foraging in a large landscape (2400 ha) at very low density (100 ha per animal) (Koppa 2007). Using a density of 100 ha/animal the two breeds were always in different groups with no temporal overlap in distribution (Koppa 2007).

Detailed monitoring of individual animal movement lasted four weeks in each of the two seasons. Each monitoring event (2 breeds, 2 seasons) consisted of 4 blocks, each of which comprised separate sets of six mature cows per breed tracked for one week. The same animals were used in both seasons. Animals were equipped with a GPS (Global Positioning System) collar with left/right motion sensors (Lotek 3000), configured to acquire spatial positions at 5-minute intervals. Collar data were differentially corrected using data from a nearby base station (31°41'29" N; 36°16'17" W) to increase precision to ± 5 m.

Animal position data were classified into foraging or non-foraging activities. Only GPS positions classified as foraging were used in this study. We interpreted consecutive animal locations at ≤ 5 m as resting and those at ≥ 100 m as long distance walking (Ungar et al. 2005). The

subset of consecutive animal locations that were between >5 and <100 m were assumed to include foraging and short distance walking activities. Within this subset of locations, we assigned an animal position to foraging when the left/right motion sensor counts exceeded the 55th percentile based on previous studies (Ganskopp and Bohnert 2006). A 55th percentile was determined for each individual animal and season using all recorded motion sensor data.

Foraging maps of 20 m pixel resolution were created for each breed and season by classifying each pixel as used or not used for foraging. The 20 m pixel was considered to be a large enough size to control for the lack of independence of successive GPS collar observations. A pixel was classified as used if it corresponded with one or more foraging positions. Foraging positions surrounding the permanent water source were excluded to avoid an unrealistic increase of fit of foraging distribution models in areas heavily used by animals (i.e., sacrifice areas, Valentine 2001). The size of the excluded area (~ 21 ha) was inferred using the boundary of the cloud of animal positions around the water source.

Statistical approach

Resource selection functions (RSF) estimated using multiple logistic regressions were used to determine the relationship between environmental variables and foraging distribution. Logistic models are applied when resources (i.e., area of the land) can be classified into two mutually exclusive classes (i.e., used or not used) (Manly et al. 2002, Walburger et al. 2009, Allred et al. 2011). The RSF models generated in this study correspond with the census type of design (Manly et al. 2002) because we were able to determine if each resource unit (20×20 m grid cell) was used for foraging or not in each season by each breed based on the high frequency of the monitoring data (5 minutes) for all animals in the experiments.

All foraging position data for each treatment (6 animals \times 4 weeks) were randomly split into training (80%) and validation (20%) sets within blocks using a SAS (SAS Institute 2003) macro RANSPLIT (Fernandez 2003). Data from each block (6 animals \times 1 week) within treatment were split equally to have all blocks represented in the training and validation sets. Separate foraging

raster maps were constructed from training and validation datasets. Foraging maps of training data were used to generate the models and maps of validation data were used to check model performance. One RSF function for each treatment was generated using multiple logistic models. Each RSF was generated based on a foraging raster map that resulted from the combination of training sets from all blocks within treatment.

Continuous and discrete environmental variables were used as predictors in the multiple logistic models. Continuous variables were: elevation, woody plant density, distance to nearest road, and distance to drinking water. Discrete variables comprised three dummy variables derived from the grass cover map: tobosa, black grama, and other grasses. Grass cover represented an aggregate measure of forage with two levels: high ($>30\%$) or low ($\leq 30\%$).

Logistic models were generated using LOGISTIC (Fernandez 2003), a SAS 9.1 macro application (SAS Institute 2003). Before fitting the model, exploratory analyses were performed using diagnostic partial delta logit plots to check for multicollinearity and nonlinearity between predictor variables. All variables were retained for further analysis because collinearity was not detected. Nonlinearities in woody density, distance to the nearest road, and distance to water were corrected by adding square terms to the model (Boyce et al. 2003). Hosmer and Lemeshow goodness-of-fit tests for overdispersion (Fernandez 2003) were not significant in any of the models.

Model performance was assessed using the foraging raster maps generated with the validation data sets following the k-fold cross validation procedure (Boyce et al. 2002). The following procedure was used in each treatment: (1) run the model to assign a foraging probability value to each 20 m pixel of the map representing the study landscape, (2) rank all pixels according to the foraging probability values assigned by the model, and split them in 10 groups (bins) of equal number of pixels, (3) pair foraging locations from the foraging raster maps with the corresponding pixel of the foraging probability map to match foraging location and bin number; this procedure was performed separately for each of the four validation sets (blocks) within

treatments, (4) perform Spearman-rank correlation (r_s) test between number of foraging positions and bin number, and (5) average all four correlations (r_s) within treatments.

In order to have a different assessment of model performance, we evaluated the models using a Receiver Operating Characteristic (ROC) analysis (Cumming 2000). The ROC curve represents the proportion of correct and incorrect classifications of the model over a continuous range of threshold probabilities (cutoff value). The most common summary statistic for ROC curve is the integral of the area under the curve (AUC) (Hosmer and Lemeshow 2000). When $AUC = 0.5$ then the predictive power of the model is null; conversely the perfect model fit will have an AUC value of 1. Thus, AUC values ranging from 0.7 to 0.9 are considered satisfactory, and an $AUC > 0.9$ indicates high accuracy of the model (Boyce et al. 2002 and references therein).

RSF models were used to specifically address the two research hypotheses. The first hypothesis was evaluated by comparing the foraging pattern of the two breeds in each season. Raster maps of foraging probability of the landscape with a 20 m pixel resolution were generated based on each RSF function. The frequency distribution of foraging probability, derived from the foraging probability maps, was used as an indication of how evenly distributed across the landscape the foraging pattern of each breed is expected to be under different environmental conditions. The second hypothesis was evaluated using:

- the β coefficients from the logistic models to determine animal selection ($\beta > 0$) or avoidance ($\beta < 0$). In addition, in the case of continuous variables (elevation, woody density, distance to nearest road, and distance to water), we determined how foraging probability changed over a continuous range of variation in a single predictor. We converted the logit values to foraging probability (0–1) and then plotted the resulting foraging probability as a function of values of a single predictor.
- a forward stepwise procedure was applied on each logistic model to rank environmental variables based on their predicted value.

Model performance

RSF models constructed with the complete set of predictors were significantly different from the null model in all treatments ($P < 0.001$). Both methods used to check model performance consistently showed that the quality of each model was satisfactory (Tables 1 and 2). The number of observed foraging positions increased with foraging probability values (bin number). Spearman correlation (r_s) values were higher than 0.9 in all treatments except in criollo in fall where r_s was equal to 0.68. The area under the ROC curve (AUC) was equal or higher than 0.8, which is evidence of a good fit of all models (Hosmer and Lemeshow 2000).

RESULTS

Foraging pattern

Both breeds showed a significant spatial overlap in their distribution but animals consistently segregated in the use of the landscape, which indicated low interbreed interactions. Spatial foraging patterns of animals were similar in spring (Fig. 1 a, b); predictions from RSF functions showed similar foraging distribution between breeds in this season (Fig. 2a). A percentage of the area of the landscape with foraging probability lower than or equal to 0.1 was 52% (Angus) and 56% (criollo) during this season. In the fall, foraging area of Angus animals was almost entirely bound to the southern half of the study site where the water point was located (Fig. 1c). In contrast, the criollo animals showed a more even distribution of foraging during this season (Fig. 1d). The predicted spatial distribution of foraging differed between breeds during fall (Fig. 2b); the percentage of area with low foraging probability (≤ 0.1) was 61% for Angus but only 3% for criollo.

Drivers of foraging patterns

Animals of both breeds showed a strong selection for areas dominated by tobosa and black grama, and a weaker selection (smaller β values) for areas labeled as “other grass” (Tables 1 and 2). Grass cover [high ($>30\%$) or low ($\leq 30\%$)] was not important in determining foraging of Angus in spring (nonsignificant P -value). Selection for high grass cover was observed only in criollo in spring. Criollo in fall

Table 1. Resource selection functions for Angus and criollo breeds in spring season.

Variables	Angus in Spring			Criollo in Spring		
	β	SE	<i>P</i>	β	SE	<i>P</i>
Intercept	269.5	12.1	**	317.8	12.1	**
Tobosa	0.8	0.04	**	0.6	0.04	**
Black grama	0.6	0.03	**	0.5	0.03	**
Other grass	0.5	0.03	**	0.4	0.03	**
Grass cover	-3e-3	0.02	ns	0.1	0.02	**
Elevation	-0.2	0.01	**	-0.2	0.01	**
Woody density	-0.01	3e-4	**	-0.01	5e-4	**
Woody density ²	5e-6	5e-7	**	1e-6	1e-6	ns
Distance roads	-1e-3	2e-4	**	3e-4	2e-4	ns
Distance roads ²	1e-6	2e-7	**	-3e-7	3e-7	ns
Distance water	1e-3	8e-5	**	2e-3	8e-5	**
Distance water ²	-5e-7	2e-8	**	-7e-7	2e-8	**
AIC			22500			24460
<i>r_s</i>			0.973			0.904
AUC			0.870			0.887

Notes: Abbreviations are as follows: AIC = Akaike information criterion; *r_s* = Spearman-rank correlation; AUC = Area Under the ROC (Receiver Operating Characteristic) Curve; ** *P* < 0.01; ns: nonsignificant at *P* < 0.10. A square term was added in the variables "woody density," "distance to road," and "distance to water" to correct for nonlinearities.

Table 2. Resource selection functions for Angus and criollo breeds in fall season.

Variables	Angus in Fall			Criollo in Fall		
	β	SE	<i>P</i>	β	SE	<i>P</i>
Intercept	245.1	13.1	**	50.6	7.5	**
Tobosa	0.8	0.04	**	1.3	0.05	**
Black grama	0.8	0.03	**	1.2	0.04	**
Other grass	0.5	0.03	**	0.8	0.04	**
Grass cover	-0.1	0.02	**	-0.1	0.02	**
Elevation	-0.2	0.01	**	-0.04	0.01	**
Woody density	0.01	4e-4	**	0.01	4e-4	**
Woody density ²	-7e-6	6e-7	**	-1e-5	7e-7	**
Distance roads	2e-3	2e-4	**	-0.01	3e-4	**
Distance roads ²	-2e-6	3e-7	**	5e-6	3e-7	**
Distance water	2e-3	1e-4	**	2e-5	7e-5	**
Distance water ²	-1e-6	3e-8	**	-2e-7	1e-8	**
AIC			27048			18494
<i>r_s</i>			0.918			0.678
AUC			0.925			0.794

Note: Symbols are as in Table 1.

had greater probabilities of foraging across a wider range of elevations than criollo in spring (Fig. 3a). Criollo animals avoided sites with high woody density while Angus animals did not avoid these sites (Fig. 3b). Roads did not appear to play an important role in determining preference for foraging under the conditions of these experiments as the probability of use was similar at different distances to roads (Fig. 3c). Conversely, animals showed a clear foraging selection pattern for sites located at different distances from the permanent water source (Tables 1 and 2, Fig. 3d). Criollo were much less dependent on water during the fall than Angus animals;

foraging probability for Angus decreased at sites located >2000 m from the water source. In contrast, foraging probability for criollo animals was higher than 0.9 for sites at a distance \leq 4000 m from the water source. In the spring, both breeds showed similar foraging selection patterns with increasing distance to water.

Water, elevation, and vegetation (areas dominated by tobosa or black grama) were the most important factors determining foraging distribution of both breeds in this landscape. Distance to water was the most important foraging predictor in all treatments (Table 3). The second most important predictor was elevation in the spring

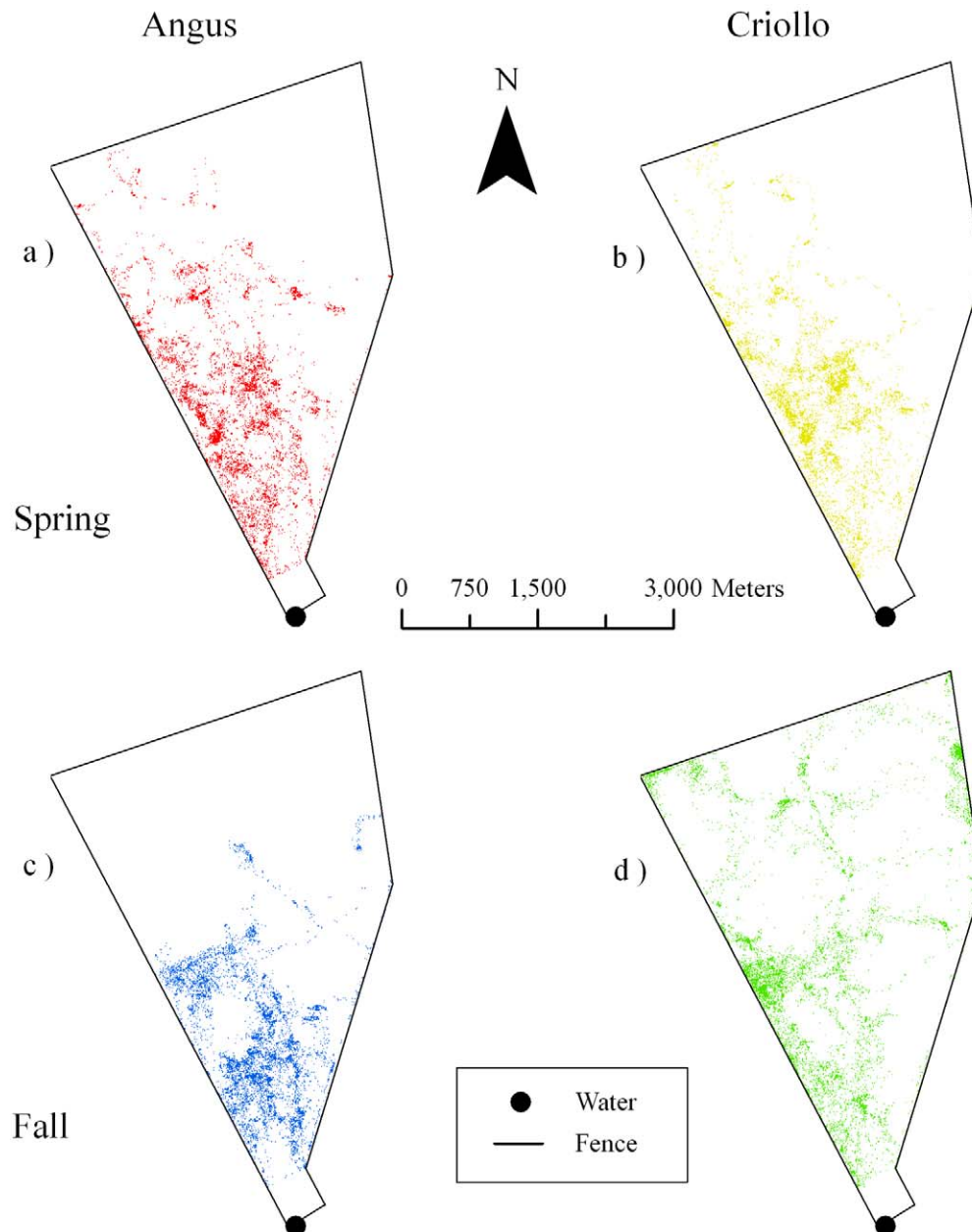


Fig. 1. Observed used (color) and not used (white) pixels for foraging in Angus and criollo breeds during the spring and fall seasons. Note: The size of the pixels is 20×20 m, and the use of the area surrounding the water point is not shown.

which indicated selection for low elevation areas. Frequently, soils of low elevation sites have high clay content and are dominated by tobosa. Black grama was the second most important variable in the fall for both breeds.

DISCUSSION

The foraging selection pattern is the main mechanism by which large herbivores interact with their environment (Rook et al. 2004). Foraging pattern displayed by a large herbivore

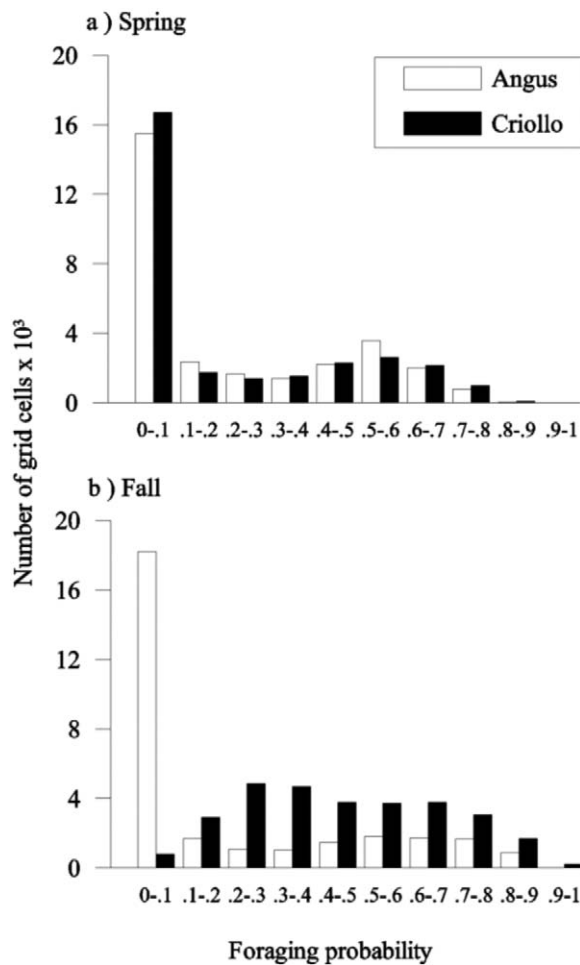


Fig. 2. Foraging probability distribution of 20×20 m pixels predicted by the models for different combination of breeds (Angus and criollo) and seasons (spring and fall).

results from an integration of morphological, physiological, and behavioral traits that arise from natural selection acting over several generations (Owen-Smith and Novellie 1982, Cassini 1994). Artificial selection tends to modify the foraging characteristics of domestic animals (Price 1999, Mignon-Grasteau et al. 2005). In this study, we found that animals of the heritage breed had a broader foraging pattern than Angus animals when environmental conditions were less favorable. Our results suggest that heritage animals may have developed foraging behaviors that match characteristics of desert environments better than domestic Angus animals.

The most important drivers of grazing pattern for both breeds and seasons were distance to water, grass cover type, and elevation. The study pasture was a relatively flat area with elevation differences <25 m which, by themselves, may not significantly affect animal movement. Animals may graze low elevation sites more frequently if they are selecting for tobosa grasslands that are found in lowlands at the Jornada (Peters and Gibbens 2006). Therefore, water and vegetation were likely the main drivers of the foraging patterns; however, the relative importance of these drivers varied with breeds and seasons. In spring, the foraging patterns of both breeds were mostly driven by distance to water. In the fall, criollo animals showed a lower dependence on water and responded more to the spatial distribution of forage than Angus. Low forage availability in fall may have induced criollo animals to explore a larger area of the landscape. Angus animals appeared to consistently select foraging sites as central place foragers around a limited distance to water, similar to other studies (Valentine 1947, Pinchak et al. 1991, Pringle and Landsberg 2004, Van Vuren 2001, Allred et al. 2011). The broad use of the landscape by the heritage breed may be due in part to its body size, which is typically smaller (~ 800 kg/animal) than the European breeds (~ 1200 kg/animal) (Sponenberg and Olson 1992). Domestication almost always results in modifications of body size (Mignon-Grasteau et al. 2005). In addition, body size is one of the most important traits determining differences between large herbivore impacts on grasslands (Bailey et al. 1996, Rook et al. 2004).

Predictive models of foraging distribution patterns

Autocorrelation is a common source of lack of independence encountered in spatial studies in ecology (Carl and Kühn 2007). The use of multiple logistic models requires the statistical assumption of independence. Spatial autocorrelation may affect error and parameter estimates of the statistical model (Legendre 1993, Lennon 2000), but doesn't necessarily invalidate the statistical model (Boyce et al. 2002, Diniz-Filho et al. 2003). Undoubtedly, the spatial dependence of animal tracking datasets tends to decline with distance. However, spatial autocorrelation may still be present at larger scales but is frequently

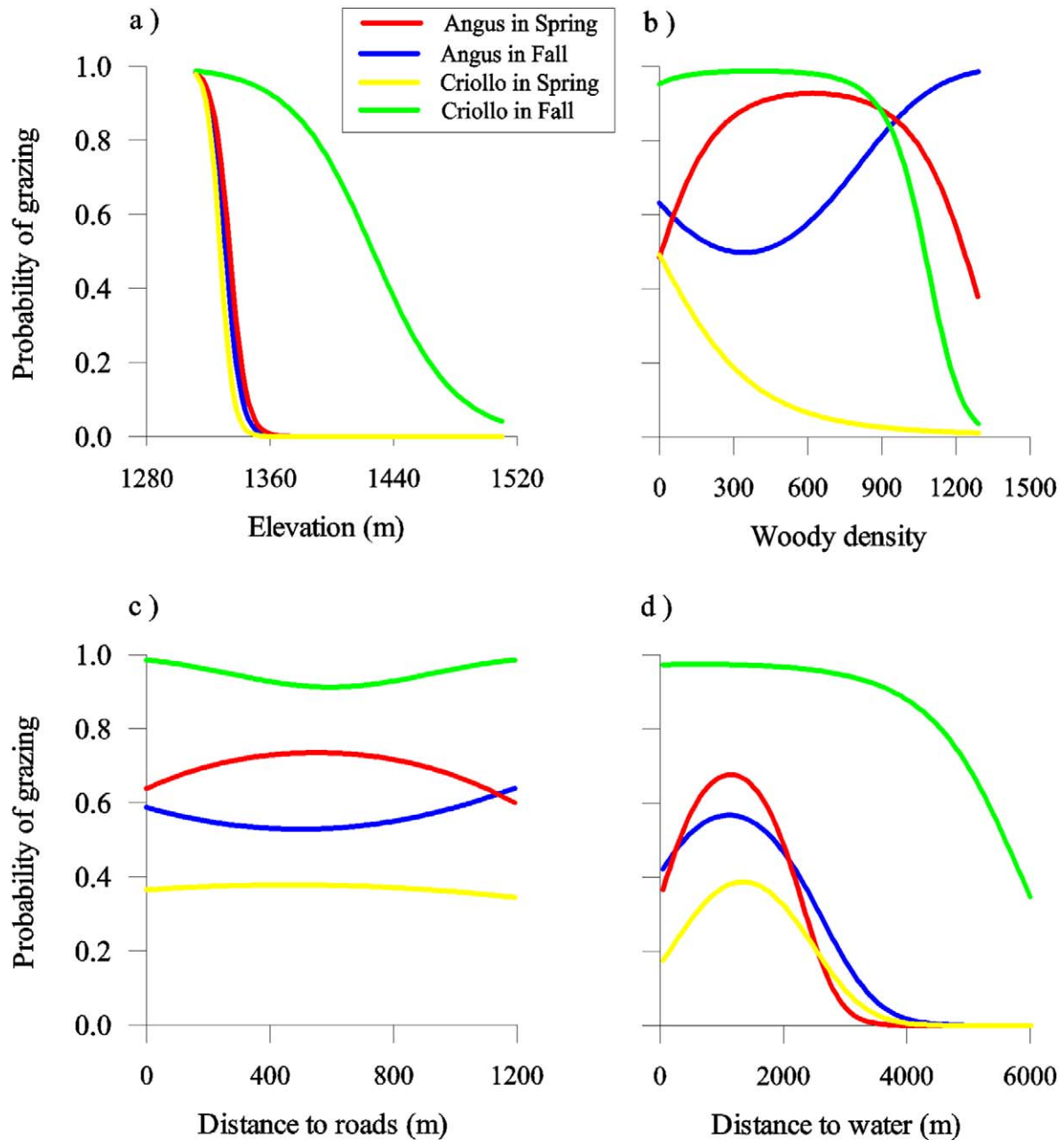


Fig. 3. Probability of use of resource units as a function of different predictors when all other predictors in the RSF function were kept constant. Woody density was measured in relative units from 0 (no woody) to 1300 maximum value of the pasture. Fixed values used to construct figures were: “tobosa” = 1, “black grama” = 1, “other grass” = 1; “vegetation cover” = “high”, “elevation” = 1330, “woody density” = 100, “distance roads” = 100, “distance water” = 1000.

undetected because data is usually insufficient to quantify the spatial structure of the data at this scale (Fortin and Dale 2009.). In our study, RSF

were generated from 20 m pixel maps representing the pasture in which each pixel was classified as grazed or ungrazed based on tracking data.

Table 3. Position and score of predictors for foraging site selection in different treatments according with a forward stepwise model selection procedure.

Treatment	Variable	Position	Score	P†
Angus Spring	Distance to water	1	2786.8	***
	Elevation	2	634.3	***
	Distance to water ² ‡	3	243.8	***
	Tobosa	4	119.3	***
	Black gramma	5	121.8	***
Criollo Spring	Distance to water	1	3198.8	***
	Elevation	2	771.7	***
	Distance to water ²	3	390.8	***
	Woody density	4	287.6	***
	Black gramma	5	85.7	***
Angus Fall	Distance to water	1	4930.5	***
	Black gramma	2	735.3	***
	Distance to water ²	3	526.9	***
	Elevation	4	100.9	***
	Woody density	5	83.3	***
Criollo Fall	Distance to water	1	925.34	***
	Black gramma	2	379.8	***
	Tobosa	3	120.4	***
	Roads	4	112.2	***
	Other grass	5	110.7	***

†*** $P < 0.001$.

‡ Squared term.

Therefore, animal positions that were inside a 20 m grid cell classified as grazed were not considered replications, a procedure which tended to reduce autocorrelation. Rather than controlling spatial autocorrelation, its occurrence can be used to explore the effect of spatial scale of analysis (Diniz-Filho et al. 2003), and needs to be investigated in more detail in animal tracking studies.

We found that landscape distribution patterns of foraging were adequately represented using statistical models constructed from key environmental factors. However, the predictive factors evaluated in this study constituted a partial set of environmental factors that drive foraging decisions. Although main roads are often used as travel corridors, roads were not an important predictor in our experiments. A well established web of cattle trails commonly observed in this arid landscape may be a better predictor of foraging distribution than roads (Pringle and Landsberg 2004). In addition, animal selection of foraging sites often dynamically adjusts to temporal changes in resource availability (Wallace et al. 1995, Weber et al. 1998, Adler and Hall 2005). Animal diets in this desert environment change seasonally with variation in forage availability (Holechek et al. 1994, De Alba Becerra et al. 1998). Thus, it is expected that the

performance of the models would have been significantly improved if a larger number of potential decision factors had been evaluated. Moreover, the RSF models developed in this study corresponded with conditions of very low animal density. Under these conditions, the foraging pattern was likely driven by the environment while interactions between animals were less likely to have a large effect. However, the relationships between foraging pattern and variations in animal density are not well understood.

Ecological consequences of the observed foraging patterns

High levels of herbivory are considered one of the most important causes of desertification in arid ecosystems around the world (Asner et al. 2004). In the Southwestern U.S., historically high stocking rates in the late 1800s combined with periodic drought favored the expansion of woody plants into perennial grasslands, the formation of coppice dunes, and soil erosion (Fredrickson et al. 1998, Peters and Gibbens 2006). Overgrazing occurs when herbivore density is well above carrying capacity but can also occur with low herbivore densities if the spatial pattern of foraging is highly uneven (Coughenour 1991, Pringle and Landsberg 2004). Uneven

distribution of foraging results in an overuse of some areas of the landscape and underuse of others. Heavily used areas can generate erosion processes with local as well as broad impacts (Nasha et al. 2003). A more even distribution of animals tends to minimize undesirable effects of overgrazing by dispersing impacts across a larger part of the landscape. Therefore, improving the spatial and temporal patterns of foraging is one of the major management goals of free ranging domestic ungulates (Pringle and Landsberg 2004, Bailey et al. 2006).

The foraging patterns displayed by large herbivores result from a composite response to variables at different spatiotemporal scales (Gross et al. 1995). Matching the scale of animal behavior with the scale of environmental variability can be an outcome of foraging decisions at the community level (Senft et al. 1987). However, foraging distribution across a landscape most probably results from tradeoffs between dietary and non-dietary factors. Adequate levels of intake are balanced by animals with factors such as site accessibility, distance to water, thermal comfort, or reduced predation risk (Mueggler 1965, Pinchak et al. 1991, Plumb and Dodd 1993, Etzenhouser et al. 1998, Fortin et al. 2003, Frair et al. 2005, Black Rubio et al. 2008). The foraging pattern can be interpreted as a complex adaptation to several environmental factors. Environmental conditions other than dietary factors could act as important constraints on the foraging pattern. These constraints are expected to be more important in animals less adapted to the environment (Price 1999), such as Angus in the arid American southwest compared to criollo, the heritage breed.

The choice of the most adapted domestic herbivores to be used for sustainable management is often unclear or based on partial information (Rook et al. 2004). Our results show that foraging pattern of heritage animals can be better adapted to a dry environment than commonly-used domestic animal breeds from the ecological perspective of reducing environmental impacts and desertification risks. However the hypotheses addressed in this study were evaluated with short-term experiments, and need to be verified under a wider range of environmental conditions. Additionally, differences (if any) in secondary production of heritage vs.

domestic animals are unknown. Undoubtedly, the choice of domestic animals depends more on cultural and economic issues rather than environmental reasons.

CONCLUSIONS

Managed grazing systems are the most extensive human activity on drylands globally (Asner et al. 2004). The introduction of domestic herbivores in the American Southwest has resulted in important environmental impacts (Buffington and Herbel 1965, Bahre and Shelton 1993). Livestock overgrazing in the late 1800s to early 1900s combined with multi-year drought resulted in broad-scale conversion of perennial grasslands to shrublands dominated by xerophytic, unpalatable shrubs (Gibbens et al. 2005, Fredrickson et al. 1998, Havstad et al. 2006). The legacy of this grazing practice remains to present day, as reflected by the dominance of shrubs in these ecosystems and the continued use of European cattle as the breed of choice. A cost-effective way of reducing environmental impacts of large herbivores can be achieved by matching animal foraging characteristics with environmental conditions (Senft et al. 1987, Bailey et al. 1996). These decisions need to be re-evaluated in view of increasing human demands on the environment that lead to the need for lower-impact, better adapted heritage agricultural animals.

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