



## Original Research

# Relationships Between Landscape Greenness and Condition of Elk, Mule Deer, and Pronghorn in New Mexico<sup>☆</sup>



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## ABSTRACT

Nutritional condition drives large herbivore population performance and is related to precipitation and forage quality in the arid Southwest. Because precipitation is difficult to measure at home-range scales, we tested whether satellite-derived vegetation indices of landscape greenness (i.e., indices of vegetation phenology or photosynthetic activity including normalized difference vegetation index [NDVI], soil-adjusted vegetation index [SAVI], and enhanced vegetation index [EVI]) were correlated to the condition of three species of large herbivores (elk, mule deer, pronghorn). We used canonical correlation analysis to relate seasonal landscape greenness with several measures of large herbivore condition. We also used linear mixed models to relate each measure of condition to seasonal landscape greenness separately for each herbivore population-year to see if any patterns were masked by multivariate analysis. Landscape greenness indices were only weakly related to condition of large herbivores, and the effect of landscape greenness on condition was always weaker than lactation status with the exception of pronghorn, an income breeder. Different indices also frequently gave highly variable and conflicting relationships between seasonal landscape greenness and condition of large herbivores. Overall, expected positive relationships between herbivore condition and landscape greenness indices were seen in only 8% of 2 988 possible outcomes. Because indices of landscape greenness are increasingly being used to relate wildlife population demographics to precipitation through a presumed effect on forage quality and resultant nutritional condition, we caution this use in arid environments unless a direct landscape greenness-forage quality or greenness-condition link is demonstrated.

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## Introduction

Nutritional condition is the driver of large herbivore population performance in the arid Southwest (Bender et al., 2007a, 2012a, 2013a; Hoenes, 2008; Bender and Piasecke, 2010; Halbritter and Bender, 2011a) and is related to precipitation and forage quality (McKinney, 2003; O'Gara, 2004a; Halbritter and Bender, 2015). Precipitation affects large herbivore condition but is problematic to measure within smaller areas like the individual home range. Consequently, precipitation data are usually taken from a limited number of sites scattered throughout a study area, which may be near, but seldom within, home ranges (e.g., Bender et al., 2011; Halbritter and Bender, 2011a). However,

precipitation patterns at different points on a landscape may not accurately reflect the precipitation that occurs within individual home ranges (Stubblefield et al., 2006; Caltrider, 2012). This is especially true in arid landscapes, where precipitation is highly variable both spatially and temporally (Pennington and Collins, 2007; Caltrider, 2012).

Satellite-derived vegetation indices, including the normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), and enhanced vegetation index (EVI), measure vegetation reflectance as an index of photosynthetic activity or plant phenology (hereafter, landscape greenness; Tucker, 1979; Huete, 1988; Huete et al., 1997, 2002). For example, photosynthetically active vegetation reflects much of the near-infrared light that strikes it, while absorbing much of the red light. In contrast, senesced vegetation reflects more red light and less near infrared light. Thus, landscape greenness indices are able to index photosynthetic activity by measuring the fraction of photosynthetically active solar radiation absorbed (Tucker, 1979; Huete, 1988; Huete et al., 1997, 2002; <http://www.landscapetoolbox.org/>). Although many vegetation greenness indices have been developed, NDVI, SAVI, and EVI have been the most commonly available preprocessed data (although red and near-infrared imagery is readily

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available for processing into any vegetation index). Consequently, they, especially NDVI, have been mostly commonly used in natural resources management (Pettorelli et al., 2011).

By indexing photosynthetic activity or plant phenology, these indices may allow inferences between precipitation and large herbivore condition because they may correlate with forage quality (Kerr and Ostrovsky, 2003; Pettorelli et al., 2005a; Ryan et al., 2012). Landscape greenness indices thus may provide a tool to indirectly measure the effects of precipitation on large herbivore condition at spatial scales such as the home range (Pettorelli et al., 2005a, 2005b; Ryan et al., 2012). To test this hypothesis, we related landscape greenness indices to multiple indices of condition of elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) from several populations covering an array of habitat conditions in arid and semiarid New Mexico. Our objective was to determine whether landscape greenness indices were correlated to nutritional condition of large herbivores, as well as to assess the generality of results among species differing significantly in dietary quality requirements.

## Study Areas

Our study populations occurred in five locations within New Mexico (Table 1). The San Andres Mountains (SAM) site covered approximately 11,000 km<sup>2</sup> in south-central New Mexico, approximately 40 km east of Las Cruces. Chihuahuan desert scrub is the major vegetation type, with pinyon (*Pinus edulis* Engelm.)–juniper (*Juniperus* spp.) associations at higher elevations (Hoenes and Bender, 2012). The Chaco Culture National Historical Park (CCNHP) site covered 308 km<sup>2</sup> in northwestern New Mexico approximately 30 km southwest of Nageezi. This site is desert grassland with scattered juniper woodlands (Bender et al., 2012b). The Sacramento Mountains (LNF) site encompassed approximately 1 800 km<sup>2</sup> in the southern Sacramento Mountains of southcentral New Mexico west of Alamogordo. The vegetation communities in the Sacramento Mountains are extremely diverse due to differences in elevation and precipitation and included pinyon-juniper and Gambel oak (*Quercus gambelii* Nutt.) woodland; ponderosa pine (*P. ponderosa* Doug. ex Laws.) typically mixed with pinyon-juniper or Douglas fir (*Pseudotsuga menziesii* [Mirb] Franco); mixed conifer forest with pockets of aspen (*Populus tremuloides* Michx.); and numerous mountain meadows (Halbritter and Bender, 2011b). The Corona Range and Livestock Research Center (CRLRC) site encompassed 113 km<sup>2</sup> approximately 23 km northeast of Corona, New Mexico. Vegetation was composed of perennial short grasses with an overstory of sparse to dense pinyon-juniper woodland (Bender et al., 2013b). The pronghorn on CRLRC were bounded by impassible fences that did not allow them to actively select different areas of the ranch for foraging; thus they utilize the entire pasture in which they occur. Consequently, we evaluated pronghorn by pastures rather than within home ranges. The north-central New Mexico (NC) site encompassed approximately 4 860 km<sup>2</sup> in Colfax County, New Mexico. Vegetation types are varied in the area, although most of the mule deer in this study site were associated with lower elevation short grassland, oakbrush shrubland, and pinyon-juniper woodlands (Bender et al., 2007b).

**Table 1**  
Mean annual precipitation (cm), mean high temperature in July (°C), mean low temperature in January (°C), number of years of data for a species at a site (population-years), annual sample sizes, and total sample size of individuals used in analyses for elk, mule deer, and pronghorn populations.

Site	Species	Precipitation	Mean temperature		Population-yr	Annual N	Total N
		Annual	July high	January low			
San Andres	Deer	20–35	35	–3	4	10–26	72
CCNHP	Elk	23	32	–11	3	14–23	52
LNF	Elk	67	22	–7	1	25	25
CRLRC	Pronghorn	40	29	–6	3	14–25	47
CRLRC	Deer	40	29	–6	1	17	17
Northcentral	Deer	44	28	–8	1	13	13

CCNHP, Chaco Culture National Historical Park; LNF, Sacramento Mountains; CRLRC, Corona Range and Livestock Research Center.

## Methods

### Nutritional Condition

Methods for animal capture and condition assessment were identical among populations (see Bender et al., 2007a, 2012a, 2013a; Bender and Piasecke, 2010; Halbritter and Bender, 2011a for additional details). Briefly, we captured adult (age 1.5 or older) females by darting or net gun from a helicopter. Dated individuals were immobilized with a mixture of carfentanil citarate and xylazine hydrochloride. All individuals were treated with vitamin E/selenium, vitamin B, an 8-way *Clostridium* bacterin, and penicillin G procaine to alleviate capture stress.

We measured condition at the local seasonal peak at the end of the spring–autumn season (SSA) in late November–early December. We measured rump fat thickness at its thickest point immediately posterior to the cranial process of the tuber ischium (pin bone; MAXFAT) using a SonoVet 2000 (Medison, Seoul, South Korea) portable ultrasound with a 5-mHz probe. For mule deer, we estimated body fat (BF) using  $BF = 5.68 + 5.93 \times \text{MAXFAT (cm)}$  (Stephenson et al., 2002). If no subcutaneous fat was present, we used a rump body condition score (rBCS) to determine BF, where  $BF = 4.014 \times \text{rBCS} - 2.021$  for female desert mule deer (*O. h. eremicus*; Bender et al., 2012a) and  $BF = 3.444 \times \text{rBCS} - 0.746$  for female Rocky Mountain mule deer (*O. h. hemionus*; Bender et al., 2007a). We estimated rBCS by palpating the sacral ridge and soft tissue along the sacroscopic ligament and scored on a scale of 1–5 in intervals of 0.25, where 1 = emaciated and 5 = obese (Bender et al., 2007a).

We estimated body fat of elk similarly except that we combined MAXFAT and rBCS measures into a combined measure (rLIVINDEX), where  $\text{rLIVINDEX} = \text{rBCS}$  when  $\text{MAXFAT} < 0.3 \text{ cm}$  and  $\text{rLIVINDEX} = (\text{MAXFAT} - 0.3) + \text{rBCS}$  when  $\text{MAXFAT} > 0.3 \text{ cm}$  (Cook et al., 2001). We then estimated BF from rLIVINDEX using the following:  $BF = -7.15 + 7.32 \times L - 0.99 \times L^2 + 0.06 \times L^3$ , where  $L = \text{rLIVINDEX}$  (Cook et al., 2001). If MAXFAT was not measured, we calculated BF from rBCS using the following:  $BF = 4.478 \times \text{rBCS} - 4.618$  (Cook et al., 2001).

For pronghorn, we measured MAXFAT and rBCS identically to mule deer. However, we did not estimate BF for pronghorn because no predictive models have been developed for pronghorn.

For each species, we also estimated a withers body condition score (wBCS) by palpating the top of the withers posterior to the shoulder hump and scoring the amount of sacral ridge discernable on a scale of 1.0–5.0 (Cook, 2000; Bender et al., 2007a). We used an ultrasound to measure the thickest point of the longissimus dorsi (loin) near the spine between the 12th and 13th ribs (Cook, 2000; Cook et al., 2001). We also measured heart girth as the circumference of the chest cavity immediately behind the legs and ventral to the peak of the shoulder hump (Bender et al., 2007a) and body mass by using a spring scale or estimated mass from girth regression models (Cook, 2000).

### Home Ranges

We located radio-collared individuals  $\geq 1$  time per week (see Bender et al., 2007b, 2012b, 2013a; Halbritter and Bender, 2011b). We used locations from April to November to create a SSA seasonal home range

for the season before capture and condition assessment in late November or early December. For each individual, we delineated a 95% minimum convex polygon SSA home range after the minimum number of locations to adequately estimate seasonal home range size was determined by plotting size as a function of locations (Bender et al., 2007b). Mule deer home range size varied from 8 to 125 km<sup>2</sup>; elk home range size from 52 to 83 km<sup>2</sup>; and pronghorn from 9 to 30 km<sup>2</sup> (Bender et al., 2007a, 2012a, 2013a; Hoenes, 2008; Bender and Piasecke, 2010; Halbritter and Bender, 2011a).

#### Vegetation Landscape Greenness

We obtained 250-m resolution NDVI, EVI, and SAVI raster datasets, or unprocessed near-infrared (NIR), red (RED), and blue (BLUE) reflectance band rasters, for processing (Huete, 1988) from MODIS imagery (<https://lpdaac.usgs.gov/>). NDVI is the base vegetation index, and  $NDVI = (NIR - RED) / (NIR + RED)$  (Tucker, 1979). SAVI adds a correction factor to the red and near-infrared values to minimize the effect of soil reflection on the index (Huete, 1988); that is,  $SAVI = (NIR - RED) / (NIR + RED + L) \times (1 + L)$ , where L is a soil brightness correction factor, which approaches 1 in areas with low vegetation cover, and 0 in areas with high vegetation cover. We used a constant of 0.5, which has been shown to effectively minimize the effect of soil reflectance under a variety of conditions (Huete, 1988; Huete et al., 1997). EVI incorporates further modifications to NDVI to be more sensitive to changes in areas of high vegetation biomass, reduce the influence of atmospheric conditions, and correct for canopy background (Huete et al., 2002).  $EVI = G \times [(NIR - RED) / (NIR + C_1 \times RED - C_2 \times BLUE - L)]$ , where  $L = 1$ ,  $C_1 = 6$ ,  $C_2 = 7.5$ , and  $G = 2.5$  with MODIS imagery (Huete et al., 2002; Jiang et al., 2008). Because NDVI and EVI datasets come in 16-d intervals and SAVI datasets come in 8-d intervals, we created mean monthly rasters for the months of April–November by averaging each 16- or 8-d interval within the month the images were taken. The resulting raster image provided a mean of landscape greenness for each month.

We clipped monthly NDVI, SAVI, and EVI rasters using SSA home range polygons and calculated the mean of each index for each SSA home range for the April–November period and for key biological seasons corresponding to the life history of the species. We based biological seasons on critical life processes of adult females, which included late-gestation–parturition (Apr–Jun), primary lactation (Jul–Sep), and postlactation (Oct–Nov) (Bender et al., 2011, 2013a; Bender and Piasecke, 2010). We similarly determined average landscape greenness for the SSA and each biological season for grassland and shrubland habitat types separately (see later) to account for dissimilar effects that habitat has on body condition (Bender et al., 2007b, 2012b; Halbritter and Bender, 2011b) and the greater responsiveness of open (i.e., forage producing; grasslands and shrublands in our habitat types) habitat types to precipitation-induced growth.

We used SSA home range polygons to clip vegetation land cover raster layers and delineated three cover classes: grass, shrub, and forest/woodland. We used the US Geological Survey Southwest Regional Gap Analysis (SWReGAP; <http://swregap.nmsu.edu>) digital vegetation maps for the CRLRC, CCNHP, and NC study areas. For the SAM, we used a vegetation association map of nine major habitat types (Hoenes and Bender, 2012). For the LNF study area, we used a raster created from the SWReGAP vegetation classifications and US Forest Service operations maps, which condensed the original 48 SWReGAP habitat types into 17 cover types that reflected the major vegetative communities present in the study area (Halbritter and Bender, 2011b).

#### Condition Modeling

We used canonical correlation analysis (CCA; Morrison, 1990) to determine interset and intraset relations between indices of landscape greenness for the SSA and each biological season with indices of

condition (BF, rBCS, wBCS, MAXFAT, and LOIN; we excluded girth and mass from CCA analyses because of frequent missing values). Indices of landscape greenness included NDVI, EVI, SAVI, and ln NDVI, an adjustment commonly used to correct NDVI for plateauing at low leaf area index (Ryan et al., 2012). Because of high correlations within predictor and outcome variable sets, we interpreted canonical structure (variable/ivariate weights) rather than canonical weights (Campbell, 1982). Moreover, because of the negative effects of lactation on the condition of adult females (Piasecke and Bender 2011; Bender and Hoenes, 2017), we included lactation status as a predictor of condition (coded 0 = not lactating, 1 = lactating) in all analyses. We used a likelihood ratio test in SAS 9.2 (SAS Institute Inc., Cary, NC) to test for overall significance and a canonical redundancy analysis (Stewart and Love, 1968) to determine the proportion of variance in the condition variables accounted for by the landscape greenness indices and lactation status. For all CCA analyses, we pooled data among years within a species and site to increase sample size and maximize the range of variation among predictor variables. We conducted similar analyses for grasslands and shrublands separately for all study areas and populations except for pronghorn on CRLRC because this study area was composed of 98% grassland. We did not include mule deer on CRLRC or the NC site in canonical analysis because of small sample sizes.

Last, to clarify relationships among individual landscape greenness indices and condition of each species at each site, we modeled each measure of condition separately as a function of seasonal NDVI, EVI, and SAVI metrics for each population-year (i.e., species-site-year combination) using a mixed model with lactation as a random effect (PROC MIXED; SAS Institute Inc.). As with the CCA, we also tested grasslands and shrublands separately for all study areas and populations except for pronghorn on CRLRC. We summarized significant results between landscape greenness and animal condition and tested whether proportion of positive results differed among landscape greenness indices using paired contingency tables (Zar, 1996).

#### Results

Only the first canonical variate showed statistical significance for all analyses. Conditions of elk in LNF ( $F_{20,47} > 1.9$ ,  $P < 0.040$ ) and CCNHP ( $F_{15,119} > 3.2$ ,  $P < 0.001$ ) and mule deer in the SAM ( $F_{20,170} > 1.7$ ,  $P < 0.036$ ) were associated with landscape greenness, but lactation always had a stronger effect on condition and no models accounted for > 46% of the variation in condition (Table 2). Relationships were similar when landscape greenness was determined from grassland and shrubland habitat types only for elk in CCNHP ( $F_{15,119} > 3.4$ ,  $P < 0.001$ ) and mule deer in the SAM ( $F_{20,170} > 1.7$ ,  $P < 0.044$ ), but not elk in LNF ( $P > 0.125$ ) (see Table 2). Use of ln NDVI did not significantly improve model results above those of uncorrected NDVI (see Table 2), so we interpret only NDVI, SAVI, and EVI results. Similarly, normalizing NDVI, SAVI, and EVI within years at each site did not improve fit or result in different interpretations of models (L. Bender, unpublished data).

Relationships with condition were highly variable among landscape greenness indices. For example, NDVI and EVI indicated that summer landscape greenness was most positively associated with condition of elk on LNF, whereas SAVI indicated that condition was most weakly associated with landscape greenness in summer (see Table 2). Similarly, the entire SSA period was comparably strong as any individual season for EVI and SAVI but much weaker using NDVI.

Similar variability was seen with elk in CCNHP. Landscape greenness during spring and SSA was most strongly positively related to condition with NDVI and EVI but was most strongly negatively related to elk condition with SAVI. Similarly, SAVI indicated that summer and autumn landscape greenness were most strongly positively related to elk condition; in contrast, these seasons were both negatively related to condition by NDVI. Assessing grasslands and shrublands alone showed comparable inconsistencies among landscape greenness indices and

**Table 2**  
Variable/variante weights and model coefficient of determination ( $R^2$ ) for the canonical correlations among indices of landscape greenness and indices of condition of mule deer, elk, and pronghorn in arid New Mexico by lactation status (Lac) and season (SSA = spring, summer, and autumn; Sp = spring; Su = summer; Au = autumn). Results are included for the entire landscape and for grassland and shrubland only.

Species	Index	Landscape						Grassland						Shrubland					
		Lac	SSA	Sp	Su	Au	$R^2$	Lac	SSA	Sp	Su	Au	$R^2$	Lac	SSA	Sp	Su	Au	$R^2$
Mule deer	NDVI	-0.57	0.21	0.12	0.32	0.39	0.29	-0.54	0.16	0.01	0.19	0.28	0.25	-0.56	0.19	0.08	0.31	0.36	0.29
	lnNDVI	-0.58	0.18	0.07	0.30	0.37	0.27	-0.52	0.14	-0.08	0.13	0.25	0.29	-0.56	0.17	0.03	0.29	0.36	0.23
	EVI	-0.57	0.25	0.31	0.22	0.22	0.34	-0.58	0.19	-0.06	0.21	0.24	0.26	-0.59	0.27	0.04	0.27	0.29	0.29
	SAVI	-0.58	0.20	0.04	0.26	0.33	0.27	-0.58	0.12	-0.02	0.20	0.28	0.27	-0.58	0.26	0.08	0.30	0.35	0.27
Elk (CCNHP)	NDVI	-0.66	0.38	0.30	-0.12	-0.31	0.36	-0.68	0.46	0.36	0.10	-0.07	0.31	-0.70	0.40	0.31	-0.22	0.12	0.33
	lnNDVI	-0.65	0.41	0.16	-0.09	-0.31	0.37	-0.68	0.46	0.37	0.08	-0.08	0.31	-0.69	0.43	0.48	-0.03	-0.17	0.33
	EVI	-0.71	0.30	0.49	-0.05	-0.09	0.28	-0.67	0.16	-0.50	0.44	0.32	0.31	-0.70	-0.11	0.52	-0.39	-0.31	0.29
	SAVI	-0.70	-0.11	-0.47	0.29	0.22	0.31	-0.69	-0.01	-0.47	0.33	0.21	0.33	-0.70	-0.11	-0.47	0.29	0.22	0.31
Elk (LNF)	NDVI	-0.71	0.24	0.31	0.47	0.21	0.42	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
	lnNDVI	-0.75	0.41	0.43	0.48	0.37	0.32	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
	EVI	-0.62	0.43	0.31	0.45	0.39	0.36	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
	SAVI	-0.62	0.20	0.20	0.14	0.23	0.46	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
Pronghorn	NDVI	-0.31	0.35	0.24	0.23	-0.39	0.24	–	–	–	–	–	–	–	–	–	–	–	–
	lnNDVI	-0.28	0.17	0.19	0.19	-0.50	0.21	–	–	–	–	–	–	–	–	–	–	–	–
	EVI	-0.30	-0.37	-0.57	0.59	0.57	0.26	–	–	–	–	–	–	–	–	–	–	–	–
	SAVI	-0.31	-0.08	-0.55	0.63	0.50	0.24	–	–	–	–	–	–	–	–	–	–	–	–

NDVI, normalized difference vegetation index; lnNDVI, natural log of NDVI; EVI, enhanced vegetation index; SAVI, soil-adjusted vegetation index; CCNHP, Chaco Culture National Historical Park; LNF, Sacramento Mountains.

did not increase model strength based on redundancy analysis for either elk population.

Results for mule deer were somewhat more consistent. Landscape greenness during the summer and autumn had the strongest positive effect on deer condition regardless of index or habitat component assessed, with the exception that EVI indicated the strongest positive effect from spring greenness. Assessing grasslands and shrublands alone did not increase strength of models (see Table 2).

Landscape greenness was also related to condition of pronghorn ( $F_{12,140} = 38.1, P < 0.001$ ). Unlike elk and mule deer, however, indices of landscape greenness had a greater effect on pronghorn condition than did lactation status, although strengths of relationships were weak ( $R^2 < 0.26$ ). Similar to elk and mule deer, indices differed on effects of seasonal landscape greenness on condition. For example, EVI and SAVI showed a strong positive effect of summer and autumn landscape greenness and a strong negative effect of spring landscape greenness on pronghorn condition; NDVI, in contrast, indicated a strong negative effect of autumn landscape greenness and a positive but weaker effect of spring landscape greenness on pronghorn condition (see Table 2). NDVI also indicated that SSA landscape greenness was positively associated with pronghorn condition, whereas EVI indicated a negative effect and SAVI showed little effect of SSA landscape greenness on pronghorn condition.

Among linear mixed models of individual condition indices, few significant positive associations were seen;  $\leq 23\%$ ,  $\leq 12\%$ , and  $\leq 20\%$  of seasonal landscape greenness relationships were positively associated with mule deer, elk, and pronghorn condition, respectively (Table 3). For all results in total, only 8% of possible relationships were positively associated with any condition index (see Table 3). Among landscape greenness indices, EVI showed the greatest number of expected positive associations for mule deer (EVI = 77; SAVI = 53; NDVI = 41), elk (EVI = 34; SAVI = 19; NDVI = 10), and pronghorn (EVI and SAVI = 8; NDVI = 2) and accounted for 119 of 252 (47%) positive associations, which was more than SAVI (32%;  $P = 0.004$ ) and NDVI (21%;  $P < 0.001$ ).

**Discussion**

Landscape greenness indices have previously been related to diet quality and condition of large herbivores (e.g., Ryan et al., 2012). In contrast, we found that landscape greenness indices were at best weakly related to condition, showed variable and inconsistent relationships with condition, and were more weakly related to condition than was lactation status (with the exception of pronghorn; see Table 2).

This was the case whether the entire landscape was assessed or canopy structure was simplified by evaluating only grassland or shrubland. Our results likely primarily reflected the differences between what landscape greenness indices actually measure and the nutritional needs of

**Table 3**  
Proportion of positive and negative relationships ( $P < 0.10$ ) between indices of landscape greenness, species, and seasons among all study population-years.

Index	Species	Season	Positive relationships	Negative relationships	Total possible
NDVI	Mule deer	SSA	0.06	0.14	124
		Spring	0.01	0.08	124
		Summer	0.14	0.10	124
		Autumn	0.13	0.12	124
	Elk	SSA	0.02	0.00	105
		Spring	0.03	0.08	105
		Summer	0.04	0.03	105
		Autumn	0.01	0.02	105
	Pronghorn	SSA	0.00	0.00	20
		Spring	0.05	0.00	20
		Summer	0.05	0.05	20
		Autumn	0.00	0.20	20
EVI	Mule deer	SSA	0.14	0.09	124
		Spring	0.08	0.09	124
		Summer	0.23	0.03	124
		Autumn	0.17	0.04	124
	Elk	SSA	0.03	0.00	105
		Spring	0.06	0.05	105
		Summer	0.11	0.00	105
		Autumn	0.12	0.03	105
	Pronghorn	SSA	0.00	0.00	20
		Spring	0.00	0.20	20
		Summer	0.20	0.00	20
		Autumn	0.20	0.00	20
SAVI	Mule deer	SSA	0.09	0.11	124
		Spring	0.05	0.08	124
		Summer	0.14	0.06	124
		Autumn	0.15	0.03	124
	Elk	SSA	0.01	0.02	105
		Spring	0.02	0.07	105
		Summer	0.09	0.02	105
		Autumn	0.07	0.05	105
	Pronghorn	SSA	0.00	0.00	20
		Spring	0.00	0.20	20
		Summer	0.20	0.00	20
		Autumn	0.20	0.00	20
Total			0.08	0.06	2988

SSA, spring, summer, and autumn; NDVI, normalized difference vegetation index; EVI, enhanced vegetation index; SAVI, soil-adjusted vegetation index.

large herbivores. Landscape greenness indices measure plant phenology or photosynthetic activity, not plant species composition or forage quality; thus, landscape greenness and forage or diet quality are not synonymous. This may be particularly true in arid and semiarid environments where plant species composition can be dominated by species of low nutritive value, unpalatable species, or late-successional growth forms (e.g., Hoenes and Bender, 2012). For example, locoweeds (*Astragalus* spp.) are among the first species to green up in spring on our arid study areas, which would result in enhanced landscape greenness but no positive effect on herbivore nutrition.

Diets of large herbivores become increasingly dependent on plant species composition as forage quality requirements increase. Previously, NDVI was positively associated with body condition in the African buffalo (*Syncerus caffer*; Ryan et al., 2012), an extreme bulk feeder (Hofmann, 1985). Our study species included elk, an intermediate feeder, and two concentrate selectors, mule deer and pronghorn. Forage quality needs are highest in concentrate selectors and lowest in bulk feeders, so plant species composition is of greater importance to concentrate selectors (Hofmann, 1985; O'Gara, 2004a). For example, African buffalo primarily forage on grasses, whereas mule deer and pronghorn are more dependent on higher-quality forages such as forbs and browse (Short, 1981; O'Gara, 2004a; Yoakum, 2004), which represent much rarer components of the foraging landscape (Hoenes and Bender, 2012; Halbritter and Bender, 2015). Thus, species with more selective diets are less likely to have their dietary requirements reflected solely by increasing landscape greenness, regardless of index used. This was evident in our study populations, where the relative strength of canonical redundancy results reflected decreasing dietary quality requirements, from elk ( $R^2 < 0.46$ ) to mule deer ( $R^2 < 0.34$ ) to pronghorn ( $R^2 < 0.26$ ; see Table 2).

However, while elk showed stronger relationships between landscape greenness and condition than did mule deer or pronghorn, elk were also affected by aridity effects on plant composition. Model fits for all landscape greenness indices were weaker for elk in the more arid CCNHP habitat, where quality forages were rarer than in the more mesic LNF site (Halbritter and Bender, 2011b, 2015; Bender et al., 2012b). Thus, although concentrate selectors like mule deer and pronghorn are particularly impacted by the relative scarcity of high-quality forage characteristic of arid environments (Bender et al., 2007a, 2012a, 2013a), even elk, intermediate feeders that can subsist on lower-quality forage (Hofmann, 1985; Cook, 2002; O'Gara, 2004a; Sandoval et al., 2005), were also impacted.

Reproduction likely exacerbates any disconnect between increasing landscape greenness and diet quality. Diet quality, and hence plant species composition, is key for successful reproduction (i.e., Cook, 2002; Wakeling and Bender, 2003; O'Gara, 2004a, 2004b). Lactating females were consistently in much poorer condition than dry females in each of our study populations (Bender et al., 2007a, 2011, 2012a, 2013a; Halbritter and Bender, 2011a), indicative of relatively low diet quality (Cook, 2002; Wakeling and Bender, 2003). Among our study species, pronghorn have the highest reproductive investment, followed by mule deer and then elk (Geist, 1998; O'Gara, 2004b). The relative strength of the lactation effect on condition (see Table 2) reflected the continuum among our species from the most capital breeder (elk) to the least capital breeder (pronghorn) (Stephens et al., 2009). Only with pronghorn was the relative strength of landscape greenness comparable with the lactation effect on condition (see Table 2), likely because pronghorn have the highest per capita investment in reproduction and their high metabolism makes them increasingly dependent on available forage (i.e., income) rather than stored reserves for successful reproduction (O'Gara, 2004a, 2004b).

In populations like ours that are in relatively poor condition (Bender et al., 2007a, 2012a, 2013a; Bender and Piasecke, 2010; Halbritter and Bender, 2011a), nutritional demands of late gestation and lactation may preclude responses in condition to landscape greenness. Following winter, large herbivores face increased nutritional demands to regain

reserves lost during winter, and if pregnant, for fetal growth (Cook, 2002; Wakeling and Bender, 2003; O'Gara, 2004a, 2004b). As nutritional needs for reproduction increase, nutritional gains from increased forage quality may be allocated to meet daily energy requirements and the increasing requirements of late gestation. Consequently, little increase in nutritional condition may occur in response to increasing landscape greenness in spring. Moreover, no change in condition may occur throughout the entire SSA period for lactating females because of the energetic demands of lactation (Cook, 2002; Wakeling and Bender, 2003; O'Gara, 2004a, 2004b). In many cases in our study populations, lactating females showed little or no gain in condition over the entire SSA period (Piasecke and Bender, 2011; Bender and Hoenes, 2017). The strength of the lactation effect relative to landscape greenness may be magnified in Southwestern monsoonal environments, where summer monsoonal rainfall and hence plant phenology are often poorly timed to late gestation and lactation needs, especially for pronghorn and elk (O'Gara, 2004a; Bender and Piasecke, 2010; Bender et al., 2013a). Monsoonal rains typically arrive well after parturition in many areas of the Southwest, exacerbating the consequences of quality forage being rare and frequent seasonal drought on herbivore condition during late gestation and lactation (O'Gara, 2004a; Hoenes and Bender, 2012; Halbritter and Bender, 2015).

Among landscape greenness indices, NDVI has been the index most often used to relate wildlife population demographics and habitat quality (e.g., Boone et al., 2006; Pettolelli et al., 2007, 2011; Ryan et al., 2012), although we are aware of no data indicating that NDVI is superior to SAVI or EVI in assessing habitat quality for wildlife. This is significant because these three indices often indicated contradictory relationships for the effects of landscape greenness on condition (see Table 2). Further, none were consistently and predictably related to individual condition (see Tables 2 and 3). For example, positive relationships between condition and landscape greenness indices were present only approximately 8% of the time, or barely more than expected by random chance alone (i.e., 5% expected to be positive and 5% negative at  $\alpha = 0.10$ ). We anticipated that EVI or SAVI would be more strongly correlated with condition than NDVI because these indices attempt to account for more landscape and atmospheric distortions that affect landscape greenness indices. However, none of the indices performed well (see Table 3), although EVI accounted for most (47%) of the few positive relationships between landscape greenness and condition.

The limitations of the indices we used may also have affected our results, although such an effect was likely secondary to the influence of plant species composition. For example, NDVI is highly susceptible to "saturation," meaning large expanses appear to be vegetation when reflected material is actually soil (Huete, 1988). Soils can strongly affect reflectance based on the interaction of plant cover, soil color, and soil moisture, so different soil types reflect different amounts of light in the red and near-infrared wavelengths (Huete, 1988; Huete et al., 1997). Consequently, SAVI was developed to compensate for soil reflectance, particularly in environments where vegetation cover is low (i.e., < 40%; Huete, 1988). However, adjusting for the influence of soils may decrease the sensitivity of the vegetation index. SAVI is generally less sensitive to changes in vegetation and more sensitive to atmospheric differences than is NDVI (Huete, 1988; Huete et al., 1997; <http://www.landscapetoolbox.org/>). While SAVI thus may have been expected to perform better than NDVI or EVI in our more arid sites (i.e., SAM, CCNHP, CRLRC), SAVI results were neither stronger nor more consistent than the other indices in these areas (see Tables 2 and 3).

Similarly, differing canopy backgrounds can affect NDVI as well. For example, NDVI loses sensitivity in areas with higher vegetation biomass; consequently, very small changes in NDVI potentially reflect very large changes in photosynthetically active vegetation. EVI was developed to be more sensitive to changes in areas of high vegetation biomass, as well as to reduce the influence of atmospheric conditions and correct for canopy background (Huete et al., 2002; <http://www.landscapetoolbox.org/>). EVI thus tends to be more sensitive to

characteristics of the vegetation canopy such as total vegetative cover and plant phenology as compared with NDVI, which responds primarily to the amount of chlorophyll present. However, EVI requires a blue band, which typically has a low signal-to-noise ratio (Huete et al., 2002; Jiang et al., 2008), which may decrease sensitivity. Despite this, EVI accounted for most (47%) of the few positive relationships between landscape greenness and condition we observed. This result was consistent for both areas of higher vegetation biomass (i.e., LNF, NC), as well as more arid sites.

### Management Implications

Indices of landscape greenness, especially NDVI, are increasingly being used to relate precipitation or plant phenology to wildlife population demographics. Often, the assumed or implied mechanism for this is a link among landscape greenness, forage quality, and nutritional condition (Boone et al., 2006; Pettorelli et al., 2007; Ryan et al., 2012). We caution against this use in arid environments unless this link is directly demonstrated, as we were unable to document this relationship among three large herbivores in several arid and semiarid Southwestern habitats. Moreover, many of the interpretations linking NDVI and demographics involve seasonal associations, yet we found different landscape greenness indices often predicted contradictory seasonal relationships between landscape greenness and condition. Despite modifications in SAVI and EVI to address known limitations of NDVI, there are no good criteria to assume that any index is more reliable in terms of relating habitat conditions to individual or population performance of large herbivores. While indexing phenology or photosynthetic activity, landscape greenness indices do not directly measure forage or forage quality, and this likely accounted for our results as indices tended to perform better (albeit still poorly) as diet quality requirements of herbivores declined. Where quality forage is rare, as in arid environments, the energetic demands of reproduction have far more influence on herbivore condition than does landscape greenness, with the possible exception of extreme income breeders like pronghorn. Consequently, without demonstrating a direct link between indices and nutritional condition, results that suggest links between any index such as NDVI and population demographics risk being spurious in arid environments.

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