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Authors: Cain, James W., Avery, Mindi M., Caldwell, Colleen A., Abbott, Laurie B., and Holechek, Jerry L.

Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00296

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Wildlife Biology 2017: wlb.00296
doi: 10.2981/wlb.00296
Published 2017. This article is a US government work
This is an Open Access article
Subject Editor: Simon Chamallié-Jammes. Editor-in-Chief: Ilse Storch. Accepted 29 November 2016

Diet composition, quality and overlap of sympatric American pronghorn and gemsbok

James W. Cain III, Mindi M. Avery, Colleen A. Caldwell, Laurie B. Abbott† and Jerry L. Holechek

J. W. Cain III and C. A. Caldwell (ccaldwel@nmsu.edu), U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, New Mexico State Univ., PO Box 30003, MSC 4901, Las Cruces, NM 88003, USA. – M. M. Avery, Dept of Fish, Wildlife and Conservation Ecology, New Mexico State Univ., Las Cruces, NM, USA. – †L. B. Abbott (posthumous) and J. L. Holechek, Dept of Animal and Range Science, New Mexico State Univ. Las Cruces, NM, USA

Species with a long evolutionary history of sympatry often have mechanisms for resource partitioning that reduce competition. However, introduced non-native ungulates often compete with native ungulates and competitive effects can be exacerbated in arid regions due to low primary productivity. Our objectives were to characterize diet composition, quality, and overlap between American pronghorn *Antilocapra americana* and introduced non-native gemsbok *Oryx gazella* in southcentral New Mexico, USA. Severe drought occurred between 2010 and 2011, which allowed us to evaluate drought impacts on diet composition, quality, and overlap. Using feces collected from each species, we assessed diet composition and overlap with microhistological analysis and diet quality using fecal nitrogen (FN) and fecal 2,6-diaminopimelic acid (FDAPA). Pronghorn diet was primarily composed of shrubs in the cool–dry season (64.5%) then shifted to forbs in the warm–dry (64.7%) and warm–wet (54.1%) seasons. Pronghorn diet also shifted to shrubs during drought (50.7%). Gemsbok diets were evenly distributed across forage types. Fifty-three percent of the species of plants consumed by pronghorn and gemsbok were shared; diet overlap averaged 0.44 ± 0.06 (SE) and 0.49 ± 0.06 during the warm–dry seasons of 2010 and 2011, respectively. During drought, key forage species shared between pronghorn and gemsbok included yucca *Yucca* spp., prickly pear *Opuntia* spp., globemallow *Sphaeralcea coccinea* and horsenettle *Solanum elaeagnifolium*, comprising 50% of the pronghorn and 40% of the gemsbok diets. Fecal nitrogen and FDAPA decreased in pronghorn by 26% and 27% between the warm–dry season of 2010 (non-drought) and the warm–dry season of 2011 (drought), respectively. Drought had little effect on dietary quality for gemsbok. Gemsbok can use forage with lower nutritional content giving them an advantage over pronghorn, particularly during drought periods. Pronghorn are more dependent upon precipitation, which may be important to consider in light of increasing drought frequency associated with climate change.

Dietary distinctions arising from morphological differences (e.g. body size, muzzle width) among ungulate species contributes to resource partitioning and facilitates coexistence of sympatric ungulates that rely on the same basic forage resources (Bell 1970,1971, Jarman 1974). Differential habitat selection further limits dietary overlap and competition between species with similar diets (O'Shaughnessy et al. 2014, Anderwald et al. 2015, 2016). In order for exploitative competition to occur between sympatric ungulates, species must have overlapping space and forage use, and forage resources must be limited. Thus, dietary overlap and the potential for competition between sympatric herbivores should occur during periods of low forage abundance due to seasonal reductions in primary productivity (Jenkins and Wright 1988, Putman 1996), overgrazing (Baldi et al. 2004), or drought-induced declines in forage (Dawson and Ellis 1996).

Species with a long evolutionary history of sympatry have evolved mechanisms for resource partitioning to reduce competition (Putman 1996), whereas introduced non-native ungulates often compete with native ungulates due to a lack of evolved mechanisms for resource partitioning (Voeten and Prins 1999, Acevedo et al. 2007, Marshal et al. 2008a). Furthermore, introduction of non-native ungulates in arid and semi-arid environments may be more likely to lead to increased competition than in temperate areas due to reduced levels of primary productivity resulting in a lower overall forage base (Schwartz and Ellis 1981, Marshal et al. 2008a, Acebes et al. 2012). However, if native and introduced ungulates differ widely in body size and digestive physiology, the potential for competition should be decreased due to diet partitioning based on the allometric relationships among

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forage quality, quantity, and body size (Bell 1971, Jarman 1974).

American pronghorn *Antilocapra americana* (pronghorn) populations throughout the arid southwestern United States experience seasonal variation in forage quantity and quality due to low and spatially patchy precipitation (Gedir et al. 2015). While water availability is the most important physical factor that limits primary production in arid ecosystems (Noy-Meir 1973), the lag time between precipitation and its influence on wild herbivores has a profound impact on ungulate population dynamics in arid systems (McKinney and Smith 2007, Marshal et al. 2009, Gedir et al. 2015). Seasonal variability in precipitation has been correlated with forage nutritional quality and body condition of wild herbivores (Simpson et al. 2007, Marshal et al. 2008b, McKinney et al. 2008). In arid environments, pronghorn diets vary among seasons, and years, with forbs being a critical component when available (Buechner 1950, Stephenson et al. 1985, Smith et al. 1998). However, when forage becomes limiting during dry periods, pronghorn will select whichever available forage that best fulfills nutritional needs.

Following a severe drought from 2001 to 2003, a pronghorn population in southcentral New Mexico declined from 533 individuals to 135 individuals by 2005. While domestic livestock are not grazed in much of this area, non-native South African gemsbok *Oryx gazella* co-occur with pronghorn. Gemsbok were introduced to White Sands Missile Range (WSMR) in the 1960s to produce a population capable of sustaining moderate levels of sport harvest. Since the initial release, the gemsbok population increased to 3000–6000 expanding their range throughout the installation and into the surrounding areas (Burkett et al. 2002, Bender et al. 2003). One reason WSMR was chosen as the introduction site for gemsbok was that it was believed that gemsbok would be less likely to compete with native ungulates (e.g. mule deer *Odocoileus hemionus* and pronghorn) on WSMR than elsewhere in southern New Mexico (Saiz 1975). Previous studies of the potential for competition between non-native gemsbok and native ungulates using microhistological analysis of fecal pellets reported mixed results (Dye 1998, Smith et al. 1998, Fletcher 2000). Some reported that gemsbok are primarily grazers in New Mexico (Dye 1998, Smith et al. 1998), whereas others reported a substantial browse component in gemsbok diets (Reid and Patrick 1983, Marquez and Boecklen 2010). Overall, gemsbok diets in New Mexico are flexible and dependent on precipitation and forage conditions, with increases in browse consumption during drought and cool–dry periods when nutritious grasses are limited in abundance.

Our objectives were to compare seasonal changes in dietary quality using fecal nitrogen (FN) and fecal 2,6-diaminopimelic acid (FDAPA), and diet composition and overlap using fecal microhistology of pellets collected from sympatric pronghorn and gemsbok during periods with average precipitation and drought conditions. We predicted that the potential for competition, and therefore dietary overlap, would increase between pronghorn and gemsbok during dry seasons. During both summer and winter dry periods, production declines for grasses and forbs, which are favoured by gemsbok and pronghorn, respectively. We expected that the decline in availability of preferred forage types would result in both herbivores shifting their diets to include more shrubs, thus increasing dietary overlap.

Study area

The study was conducted within northwest region of White Sands Missile Range in southcentral New Mexico, USA (Fig. 1). The climate is semi-arid with a monsoon precipitation cycle. Mean annual rainfall near the study area is 220.2 mm (SD = 80.8 mm; Bosque del Apache, NM 25 km west-northwest of the center of study area; Western Regional Climate Center [WRCC] 2016) with approximately 61% falling during the monsoon season (July–October). Mean daily high and low temperatures are 34.7°C and 18.8°C during summer and 13.9°C and –5.4°C during winter (WRCC 2016). High temperature during summer commonly exceeds 38.0°C (Western Regional Climate Center 2016). We delineated seasons based on long-term climate data and classified March through June as warm–dry season, July through October as warm–wet season, and November through February as the cool–dry season. Rainfall was approximately 12% below average during the first year of our study in 2010 and near normal during the beginning of the warm–dry season, then progressing to abnormally dry, the least severe drought category in June 2010. Rainfall decreased further in early 2011 leading to exceptional drought, the most severe drought classification which is characterized by a Palmer drought severity index $\leq$ –5.0. Total precipitation from November 2010 through June 2011 was 93% below average (National Drought Mitigation Center 2012, Western Regional Climate Center 2016).

The terrain includes open grasslands, dry lakebeds, lava flows, shrublands and canyons. Common vegetation types include Chihuahuan Desert scrub, closed basin scrub, alkali sink scrub and desert grassland. Common grasses include grama grasses *Bouteloua* spp., dropseeds *Sporobolus* spp., tobosa *Pleuraphis mutica* and fluff grass *Erioneuron pulchellum*. Common shrubs include a variety of yucca *Yucca* spp., prickly pear *Opuntia* spp., mormon tea *Ephedra* spp., tarbush *Flourensia cernua*, snakeweed *Gutierrezia* spp., creosote bush *Larrera tridentata* and honey mesquite *Prosopis glandulosa*; forbs included spiny golden aster *Xanthisma spinulosum*, Tahoka daisy *Machaeranthera tanacetifolia*, field bahia *Bahia absinthifolia*, globemallow *Sphaeralcea* spp. and bristle chinchweed *Pectis papposa*.

Other ungulates on the study area included mule deer *Odocoileus hemonius* and collared peccary *Pecari tajacu*. Livestock grazing does not occur on WSMR. Predators, including mountain lion *Puma concolor*, coyote *Canis latrans* and bobcat *Lynx rufus* occur throughout the area.

Methods

Pronghorn and gemsbok populations

We captured 29 American pronghorn (two fawn males, five adult males, 22 adult females) in April 2007 and December 2008 by chemical immobilization from a helicopter using carfentanil citrate and xylazine hydrochloride (Bender et al.

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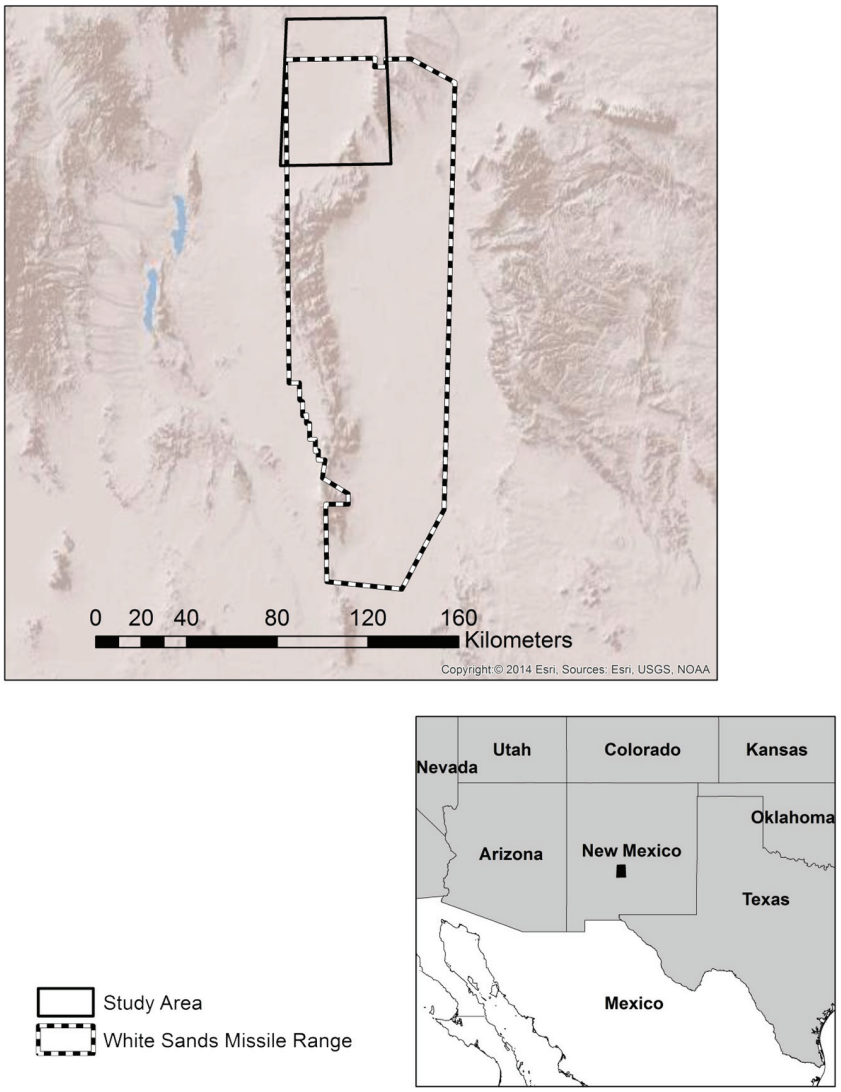


Figure 1. Location of the study area in south central New Mexico, USA where we studied diet composition, quality and overlap of sympatric American pronghorn and non-native gemsbok.

2013). We fitted each animal with a mortality-sensitive very high frequency (VHF) telemetry collar (Advanced Telemetry Systems, Isanti, MN, USA); carfentanil citrate and xylazine hydrochloride were reversed with naltrexone and tolazoline. We relocated radio-collared pronghorn from the ground weekly with a hand-held telemetry receiver from March 2010 through June 2011 (model R-1000, Communications Specialists, Orange, CA, USA) and recorded locations using a hand-held global positioning system (GPS).

Diet composition and diet quality

During our weekly relocation of radio-collared pronghorn, we observed animals and waited to collect fecal samples until the majority of animals in a herd had defecated and moved on. We then collected approximately 2 g of fresh fecal pellets from each pellet group and composited the pellets from each pellet group within each sampling area for each day of sampling. Fresh fecal samples were collected from gemsbok when observed in the same areas and within the same time period as pronghorn using the same collection protocol. For both pronghorn and gemsbok, we made a concerted effort to collect fecal samples only from spatially segregated groups of animals to obtain a more representative sample from the herds and avoid re-sampling the same groups or individuals within a short period of time. Gemsbok were not observed with pronghorn during the warm–wet and cool–dry seasons, thus fresh fecal composites were obtained for gemsbok in the same areas as the pronghorn during the 2010 and 2011 warm–dry seasons. Given the senescence of winter and early spring forbs and the lack of forage growth during the warm–dry season, we expected that the potential for dietary overlap and forage competition between pronghorn and gemsbok would be highest during the warm–dry season.

We oven dried composited fecal samples at 55°C for 48 h, then ground them with a Wiley mill through a 1.0 mm mesh screen. Approximately one-third of each composited fecal sample was evaluated for diet composition using microhistological analysis and the remaining portion of the sample was evaluated for fecal nitrogen (FN) and

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fecal 2,6-diaminopimelic acid (FDAPA). Slides were prepared for microhistological analyses following the methods of Sparks and Malechek (1968) as modified by Holechek (1982) and Alipayo et al. (1992). All microhistological analyses were performed by a single observer (M. M. Avery) to reduce variation inherent in multiple observers. Each slide was systematically examined across 20 microcope fields at 100 × magnification (Holechek and Vavra 1981, Holechek and Valdez 1985). Reference slides were preapared in the same manner as the fecal samples to validate identification of plant fragments in fecal samples. To identify plant particles, diagnostic characteristics included microanatomical epidermal cells including parallel veins, silica, cell size and shape, shape of cell wall, stomata size, stomata shape and orientation, and associated companion cells, shape and number of cells making up the base of the trichome, and the presence of crystals (Metcalfe and Chalk 1950, Metcalfe 1960, Sparks and Malechek 1968). When identifying a grass species in fecal material, two diagnostic microepidermal anatomical characteristics were selected, while one or two microanatomical epidermal features in forbs or shrubs was required for positive confirmation. Percent composition was determined for each plant species in each composite sample (Holechek and Gross 1982). We then averaged the composite samples collected from each samping area within each season for each ungulate species. We assumed that potential biases from differential digestibility of various forage species would either be minimal or would equally affect our diet composition estimates for both pronghorn and gemsbok (Alipayo et al. 1992).

To calculate dietary overlap between pronghorn and gemsbok, we used the Kulcyznski's similarity index (Oosting 1956) with the diet composition data obtained from microhistological analysis:

$$SI = \frac{2\sum_{i=1}^{l} C_i}{\sum_{i=1}^{l} (P_{ij} + P_{ik})} \times 100$$

where C_i is the lesser proportion of plant species i in the diets of both herbivores and P_{ij} and P_{ik} are the proportions of plant species i in the diet of herbivore j and k, respectively. We selected Kulcyznski's similarity index because it provides a direct measure of common proportionality between herbivore diets (Holechek et al. 1984); this index is symmetrical and ranges from 0 to 1, with 1 representing complete dietary overlap. For the purpose of this study, the similarity index represented the percentage overlap of the pronghorn and gemsbok diets during the 2010 and 2011 warm–dry seasons. We considered similarity indices ≥ 0.45 to be biologically meaningful, particularly in the context of the extreme drought observed during our study.

Two commonly used metrics for assessing dietary quality in herbivores include FN and FDAPA (Dennehy 2000, Robinson et al. 2001). Fecal nitrogen is positively related to dietary nitrogen, dietary protein and digestibility (Holechek et al. 1982a, Brown et al. 1995, Osborn and Ginnett 2001) while FDAPA represents rumen bacterial populations and thus the status of digestible energy (Davitt and Nelson 1984). The reliability of FN as an index of dietary quality may be compromised by forages with high tannin content. However, FDAPA passes unabsorbed through the digestive track with no measurable loss (Davitt and Nelson 1984). Together, FN and FDAPA provide an accurate assessment of dietary quality of ruminants in the event consumption of tannins compromises nitrogen absorption.

A portion of the composited fecal sample was evaluated for FN using the combustion method of Verheyden et al. (2011) at New Mexico State Univ. in the Dept of Animal and Range Science Nutrition Laboratory (Las Cruces, NM). The remaining portion of the composited fecal samples were analyzed for FDAPA by the Wildlife Habitat and Nutrition Laboratory at Washington State University (Pullman, WA) using the method of Davitt and Nelson (1984).

Data analyses

Due to issues with heteroscedasticity and non-normal data, we transformed the similarity index data using the logit transformation prior to analyses. We used a general linear model to assess similarity of diet for pronghorn and gemsbok during the warm–dry seasons of 2010 and 2011. Descriptive statistics are presented on the original scale of measurement. In addition, we assessed differences in FN and FDAPA during the warm–dry season between years (warm–dry 2010 versus warm–dry 2011) using the Welch's t-test due to unequal variances. All statistical analyses were conducted in SPSS (ver. 17.0).

Results

Pronghorn consumed 75 identifiable plant species. Pronghorn diet was dominated by shrubs during the cool–dry season (64.5%) then shifted to forbs in the warm–dry (64.7%) and warm–wet (54.1%) seasons (Table 1). Pronghorn diet also shifted to shrubs during the drought in the warm–dry season of 2011 (50.7%; Table 1). During the warm–dry seasons of 2010 and drought of 2011, gemsbok consumed 50 identifiable plant species that were evenly distributed across the three forage types (grasses, shrubs, forbs) throughout both years. Of the 85 species of plants consumed by pronghorn and gemsbok (19 grasses, 26 shrubs, 40 forbs), 53% (13 grasses, 17 shrubs, 15 forbs) were shared (Table 2). Dietary overlap between the two ungulates averaged 0.44 (SE = 0.06) and 0.49 (SE = 0.06) during the warm–dry seasons of 2010 and 2011, respectively. Thus, dietary overlap was similar across both warm–dry seasons ($F_{1,12} = 0.164$, $p = 0.694$). During the drought of 2011, key forage species shared between pronghorn and gemsbok included yucca, prickly pear, globemallow and horsenettle *Solanum elaeagnifolium*. Cumulatively, these four species represented 50% of the pronghorn diet and 40% of the gemsbok diet. Forb consumption by pronghorn deceased 37% between the warm–dry season of 2010 and 2011 (Table 2); pronghorn consumption of prickly pear increased from under 4% of the diet to over 24%, consumption of *Artemisia* spp. (a diverse family of perennial shrubs that include asters and daisies) doubled from approximately 3 to 6%, and horsenettle increased from 2% to almost 10% of the diet. Gemsbok consumption of grasses decreased from 54% to 45% between the warm–dry season of 2010 and 2011 (Table 2). Most noteably, during the drought in 2011, gemsbok consumption of prickly pear

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Table 1. Diet composition (percent) based on microhistological analysis of feces collected from American pronghorn on White Sands Missile Range, New Mexico, USA. Seasons are represented by cool–dry (November–February), warm–dry (March–June), warm–wet (July–October).

	2010			2011
	Cool–dry (n = 9 [26])[1]	Warm–dry (n = 18 [90])	Warm–wet (n = 22 [106])	Warm–dry (n = 5 [49])
Grasses				
Aristida spp.	0.5	0.5	3.0	1.0
Bouteloua spp.	1.5	2.8	2.5	2.0
Setaria leucopila	0.0	0.5	0.1	0.5
Sporobolus spp.	0.5	1.0	1.8	1.7
Unknown grasses	1.0	2.4	3.9	3.5
Total grasses	3.5	7.2	11.3	8.7
Shrubs				
Aloysia wrightii	–	1.4	0.5	–
Artemisia spp.	3.7	2.6	6.5	5.9
Atriplex canescens	5.1	1.8	0.5	1.9
Ephedra spp.	7.2	0.0	0.5	0.5
Fallugia paradoxa	4.1	1.2	1.9	2.9
Juniperus spp.	4.0	0.0	0.5	1.0
Krascheninnikovia lanata	1.6	1.0	0.5	0.5
Opuntia spp.	21.3	3.8	7.4	24.2
Prosopsis glandulosa	0.0	0.5	2.2	0.5
Quercus turbinella	6.1	0.5	0.5	0.5
Rhus ssp.	0.5	1.5	8.6	1.5
Rumex spp.	2.5	0.5	0.0	0.0
Yucca spp.	8.4	11.1	3.7	10.8
Unknown shrubs	–	2.2	1.3	0.5
Total shrubs	64.5	28.1	34.6	50.7
Forbs				
Ambrosia spp.	1.6	1.7	1.0	4.0
Aphanostephus ramosissimus	1.2	5.0	3.6	0.5
Croton spp.	1.8	9.5	8.3	1.0
Garrya spp.	0.0	3.8	2.0	0.0
Gutierrezia sarothrae	1.3	0.5	1.2	1.1
Helianthus petiolaris	1.8	2.0	5.3	0.5
Hoffmannseggia glauca	0.0	5.5	4.1	10.1
Lepidium spp.	0.0	3.3	0.0	0.5
Lesquerella spp.	1.6	6.2	5.1	0.0
Machaeranthera spp.	1.0	5.2	1.0	1.5
Marrubium vulgare	0.0	4.6	0.5	0.5
Mentzelia spp.	1.5	5.4	1.4	0.5
Peganum harmala	0.0	0.5	0.0	1.6
Plantago patagonia	0.0	3.2	0.0	0.0
Sphaeralcea spp.	4.0	3.8	9.9	6.8
Solanum elaeagnifolium	14.2	2.2	3.6	9.8
Tidestromia lanuginosa	0.0	1.3	2.0	0.0
Tiquilia ssp.	1.0	1.0	0.0	0.5
Unknown forbs	1.0	0.0	5.1	1.7
Total forbs	32.0	64.7	54.1	40.6

[1]Sample size represents the number of composite fecal samples. Composite samples were comprised of fecal pellets collected from multiple individuals within observed during a single observation. Number in brackets represents the number of pellet groups from individual animals sampled for the composite samples.

increased from 1.7% to 5.7%, consumption of *Yucca* spp. more than doubled from 10% to 22.5%, and globemallow increased from 2% to 9% of the diet (Table 2).

From the warm–dry season of 2010 (normal precipitation) to the warm–dry season of 2011 (drought), FN and FDAPA decreased in pronghorn by 26% ($t_{2,21} = 2.91$; $p = 0.009$) and 27% ($t_{2,21} = 2.43$; $p = 0.024$), respectively (Table 3). Drought had no effect on dietary quality in gemsbok as measured by FN in 2010 (1.47% ± 0.21) and during the drought of 2011 (1.50% ± 0.05; $t_{2,12} = -0.14$, $p = 0.896$); nor were there differences observed in FDAPA between 2010 (0.48 mg g^{-1} ± 0.09) and 2011 (0.34 mg g^{-1} ± 0.03; $t_{2,12} = 1.48$, $p = 0.218$; Table 3).

Discussion

Diet quality for pronghorn decreased significantly during summer drought (i.e. FN and FDAPA decreased 26% and 27%), yet drought had little effect on dietary quality for gemsbok. In addition, diet overlap was substantially higher than previously reported, particularly during the summer drought period. Since the introduction of gemsbok in New Mexico, few studies have evaluated their impact on native pronghorn. Hoenes (2008) reported that pronghorn and gemsbok generally utilized similar habitats, however, Smith et al. (1998) reported little dietary overlap (0.02–0.19) between the two species when using the Petraitis overlap

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Table 2. Diet composition (percent) based on microhistoligical analyses of feces collected from American pronghorn and South African gemsbok during warm–dry seasons (March–June) in 2010 and 2011 on White Sands Missile Range, New Mexico, USA.

	Warm–dry (2010)		Warm–dry (2011)	
	Pronghorn (n = 18 [90])[1]	Gemsbok (n = 4 [21])	Pronghorn (n = 5 [49])	Gemsbok (n = 10 [53])
Grasses				
Aristida spp.	0.5	4.9	1.0	2.8
Bothriochloa barbinodis	0.0	2.2	0.0	1.0
Bouteloua spp.	2.8	24.3	2.0	15.4
Muhlenbergia spp.	0.0	3.1	0.0	0.5
Pleuraphis mutica	0.0	1.3	0.0	2.4
Schizachyrium scoparium	0.0	0.0	0.0	1.8
Setaria leucopila	0.5	0.5	0.5	0.5
Sporobolus spp.	1.0	11.0	1.7	13.8
Unknown grasses	2.4	6.6	3.5	7.2
Total grasses	7.2	53.9	8.7	45.4
Shrubs				
Aloysia wrightii	1.4	0.0	0.0	0.0
Artemisia spp.	2.6	1.0	5.9	1.0
Atriplex canescens	1.8	0.5	1.9	0.5
Cercocarpus spp.	0.0	1.0	0.0	0.5
Dalea spp.	0.0	0.5	0.0	1.0
Ephedra spp.	0.0	0.0	0.5	0.5
Fallugia paradoxa	1.2	2.0	2.9	0.5
Juniperus spp.	0.0	0.0	1.0	0.5
Krascheninnikovia lanata	1.0	9.9	0.5	0.5
Opuntia spp.	3.8	1.7	24.2	5.7
Prosopsis glandulosa	0.5	0.0	0.5	1.0
Quercus turbinella	0.5	1.7	0.5	0.5
Rhus ssp.	1.5	0.0	1.5	0.5
Rumex spp.	0.5	0.0	0.0	0.0
Yucca spp.	11.1	10.0	10.8	22.5
Unknown shrubs	2.2	1.2	0.5	1.3
Total shrubs	28.1	29.5	50.7	36.5
Forbs				
Ambrosia spp.	1.7	1.6	4.0	0.5
Aphanostephus ramosissimus	5.0	–	0.5	0.0
Croton spp.	9.5	1.0	1.0	1.1
Cryptantha angustifolia	0.0	1.7	0.0	0.0
Garrya spp.	3.8	0.0	0.0	0.0
Gutierrezia sarothrae	0.5	0.0	1.1	0.0
Helianthus petiolaris	2.0	0.0	0.5	0.0
Hoffmannseggia glauca	5.5	1.2	10.1	1.2
Lepidium spp.	3.3	2.2	0.5	0.5
Lesquerella spp.	6.2	4.5	0.0	0.0
Machaeranthera spp.	5.2	0.5	1.5	0.0
Marrubium vulgare	4.6	0.0	0.5	0.0
Mentzelia spp.	5.4	0.0	0.5	0.0
Peganum harmala	0.5	0.0	1.6	0.0
Plantago patagonia	3.2	0.0	0.0	0.0
Solanum ssp.	2.2	0.5	9.8	5.3
Sphaeralcea spp.	3.8	1.9	6.8	9.4
Tidestromia lanuginosa	1.3	0.0	0.0	0.0
Tiquilia ssp.	1.0	0.5	0.5	0.0
Unknown forbs	0.0	1.0	1.7	0.1
Total forbs	64.7	16.6	40.6	18.1

[1]Sample size represents the number of composite fecal samples. Composite samples were comprised of fecal pellets collected from multiple individuals within observed during a single observation. Number in brackets represents the number of pellet groups from individual animals sampled for the composite samples.

index. Unlike the results of Smith et al. (1998), we found overlap was 0.44–0.49 between these two ungulates, a level we considered biologically meaningful for pronghorn. Pronghorn are dependent on high quality forage species (Koerth et al. 1984, Smith and Malechek 1974, Yoakum 2004) resulting in populations being particularly sensitive to changes in rainfall (Bright and Hervert 2005, Brown et al. 2002, 2006). Interspecific competition for forage during drought periods, would certainly exacerbate climate-induced impacts to pronghorn populations.

Differences in dietary overlap between pronghorn and gemsbok in our study and those reported by Smith et al. (1998) were likely attributable to rainfall. Precipitation was 33% above average during 1991 when Smith et al. (1998)

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Table 3. Average concentrations of fecal nitrogen (FN%) and fecal 2,6-diaminopimelic acid (FDAPA mg g^{-1}) for American pronghorn (standard error and sample size[1] in parenthesis) and South African gemsbok on White Sands Missile Range, southcentral New Mexico. Fecal indices were analyzed seasonally from 2010 to 2011 during warm–dry (March–June), warm–wet (July–October) and cool–dry (November–February).

	Fecal N		Fecal DAPA	
Season	Pronghorn	Gemsbok	Pronghorn	Gemsbok
Cool–dry 2010	1.36 (0.08, 9)		0.31 (0.03, 9)	
Warm–dry 2010	1.99 (0.15, 18)	1.47 (0.21, 4)	0.44 (0.04, 18)	0.48 (0.09, 4)
Warm–wet 2010	1.55 (0.07, 22)		0.37 (0.03, 22)	
Cool–dry 2011	1.68 (0.76, 11)		0.33 (0.04, 11)	
Warm–dry 2011	1.48 (0.09, 5)	1.50 (0.05, 10)	0.32 (0.02, 5)	0.34 (0.03, 10)

[1]Sample size represents the number of composite fecal samples. Composite samples were comprised of fecal pellets collected from multiple individuals within observed during a single observation. See Table 1 and 2 for number of animals represented in composite samples.

collected their data; whereas, our study occurred during periods with precipitation ranging from 12 to 93% below average (Western Regional Climate Center 2016). Given the wide difference in precipitation between when Smith et al. (1998) reported low dietary overlap and our study, it is unsurprising that dietary overlap would be increased during the dry conditions observed during our study. Dietary overlap and the potential for competition increase for sympatric herbivores during periods of reduced forage availability (Baldi et al. 2004, Odadi et al. 2011). Similarly, Stephenson et al. (1985) reported that following a period of average rainfall, diet similarity between cattle and pronghorn and sheep and pronghorn increased during a drought in northern New Mexico.

Pronghorn diets are typically composed primarily of forbs followed by shrubs, with grasses ususally contributing less to the diet (Mitchell and Smoliak 1971, Yoakum 2004). In arid areas or during dry periods with limited forage production, shrubs or cacti may compose most of the diet (Stephenson et al. 1985, McInnis and Vavra 1987, Hughes 1991, Ngugi et al. 1991, Smith et al. 1998). Diets of gemsbok in Africa are most commonly reported to be composed primarily of grasses (Ambrose and DeNiro 1986, Gagnon and Chew 2000, Cerling et al. 2003, Sponheimer et al. 2003, Codron et al. 2005). Studies of introduced gemsbok in New Mexico have also reported diets predominated by grasses (Dye 1998, Smith et al. 1998), however using isotopic analyses of various body tissues (i.e. hair, muscle, bone collagen), Marquez and Boecklen (2010) reported a substantial forb and shrub component in the diets of introduced gemsbok in New Mexico. Similarly, Lehmann et al. (2013) reported high dietary plasticity of gemsbok diets in Namibia with C3 plants (i.e. forbs and shrubs) increasing in gemsbok diets during drought. Thus, when abundance and nutritional content of grasses declines, gemsbok readily shift diets to include a larger proportion of forbs and shrubs, thus increasing the potential for competition with pronghorn and possibly other native ungulates (e.g. mule deer) when space use overlaps.

Smith et al. (1998), reported pronghorn and gemsbok shared yucca, plains bristlegrass *Setaria leucopila* and dropseed *Sporobolus* spp. whereas we found that pronghorn and gemsbok shared yucca, prickly pear and globemallow. Yucca and prickly pear combined comprised 35% of the pronghorn diet and 28% of the gemsbok diets during the drought of 2011. Further, prickly pear was a component of the pronghorn diet throughout the study appearing in the diet every season. However, given that prickly pear is typically very high in moisture (i.e. $>75\%$) but protein content is often $<4\%$ (Seegmiller et al. 1990, Hughes 1991, Fox 1997), pronghorn and gemsbok are likely increasing consumption of prickly pear in efforts to satisfy water requirements rather than based on nutrient content of this species (Hughes and Smith 1990, Hervert et al. 2005).

The diet of both species shifted across seasons and between climatic periods, generally reflecting selection of forage species that would best meet nutritional demands given the constraints of rainfall-induced changes in forage availability. Throughout areas where pronghorn were observed foraging, above-ground biomass varied throughout the warm–wet, cool–dry, and warm–dry seasons. Overall biomass estimates reported by Avery (2012) were lower (seasonal means = 67.2–95.1 g m^{-2}) than those reported for grassland systems throughout the Chihuahuan desert (51–184 g m^{-2}; Muldavin et al. 2008). Grasses composed the largest portion of edible forage biomass (64%), followed by forbs (17%) and shrubs (19%). Despite their lower availablity, forbs contributed the highest proportion (68%) and the greatest diversity to pronghorn diet which is consistent with other research on pronghorn diet composition (Beale and Smith 1970, Mitchell and Smoliak 1971, Koerth et al. 1984, Stephenson et al. 1985, Hansen et al. 2001, Brown et al. 2008). While grasses represented the greatest percentage of available forage biomass throughout all seasons (Avery 2012), grasses contributed least to pronghorn diets whereas shrubs increased in the diet during an dry seasons (warm–dry 2011; Stephenson et al. 1985, Brown and Shaw 2005, Brown et al. 2008).

Diet quality is an important indicator of the health of wildlife populations that can be monitored through fecal indices (Gates and Hudson 1981, Holechek et al. 1982b, Robinson et al. 2001). During the warm–dry season of 2010, FN and FDAPA values in the pronghorn diet was likely related to the consumption of forbs. McDonald (2005) compared dietary quality of pronghorn throughout similar environments in the southwestern US and reported FN values (0.86–1.60%) similar to those reported in this study (0.31–1.99%). In contrast, McDonald (2005) reported FDAPA values that were substantially higher (0.82–1.80 mg g^{-1}) than ours (0.310.44 mg g^{-1}) which were below values deemed necessary to support reproduction in pronghorn. In contrast to the pronghorn, dietary quality of gemsbok was not impacted by severe drought. As a larger herbivore,

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gemsbok (180–225 kg) can consume lower quality forage than the smaller pronghorn (40–50 kg) which must consume a higher quality diet and are generally more selective of plant species and plant parts (Bell 1971, Jarman 1974, Koerth et al. 1984, Smith and Malechek 1974, Lehmann et al. 2013). Gemsbok have a clear advantage over pronghorn during periods with low precipitation and thus of poor forage production because gemsbok can utilize forage of lower nutritional quality due to their larger body size and dietary placticity (Lehmann et al. 2013) during drought periods.

Given their requirements for high quality forage, pronghorn population trends and juvenile recruitment are much more sensitive to precipitation than gemsbok. Fawn survival is commonly related to short-term declines in precipitation, where as declines in population abundance are more related to extended drought periods (Simpson et al. 2007). Precipitation during late gestation and early post-parturition affects fawn survival (Bright and Hervert 2005, Simpson et al. 2007, McKinney et al. 2008, Bender et al. 2013) and loss of almost an entire fawn cohort is not uncommon during periods of extreme drought (Bright and Hervert 2005). In addition, rainfall during mid-summer can influence survival of adults (Brown et al. 2006, Bender et al. 2013). Thus, the increased diet overlap and potential for competition that we observed should be considered in the context of more frequent droughts predicted for the southwestern US under various climate change models potentially affecting growth trajectories and persistence of southwestern pronghorn populations (Gedir et al. 2015).

Acknowledgements – Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Capture of study animals and logistical support was provided by L. Bender, P. Morrow, C. Rodden and D. Anderson. A. McComb, D. Alsworth, C. Alsworth, B. Bodgier and M. Painter assisted with field work and laboratory analysis. Comments by P. Krausman improved an earlier draft of this manuscript.
Funding – Funding was provided by the U. S. Geological Survey, Cooperative Research Unit Program and the Dept of Defense, White Sands Missile Range - Environmental Stewardship Branch. Additional support was provided by New Mexico State University and the Dept of Fish, Wildlife and Conservation Ecology.
Permits – Animal capture and handling followed acceptable methods and was approved by New Mexico State University Institutional Animals Use and Care Committee (protocol no. 2009-025).

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