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

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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.
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 from 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 ≤ –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 Erineuron 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 Larrea 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 hemionus and collared peccary Peccari 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.
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...
We considered similarity indices to represent the percentage overlap of the pronghorn diet to the percentage overlap of the pronghorn and gemsbok diet, respectively. For the purpose of this study, the similarity index was determined for each plant species in each composite sample (Holechek and Gross 1982). We then averaged the composite samples collected from each sampling 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 Kulczyński’s similarity index (Oosting 1956) with the diet composition data obtained from microhistological analysis:

$$SI = \frac{2 \sum l_{i} C_{i}}{\sum l_{i} (P_{0} + P_{k})} \times 100$$

where $C_{i}$ is the lesser proportion of plant species $i$ in the diets of both herbivores and $P_{0}$ and $P_{k}$ are the proportions of plant species $i$ in the diet of herbivore $j$ and $k$, respectively. We selected Kulczyński’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 bivore diets (Holechek et al. 1982a, Brown et al. 1995, Osborn and Ginnett 2001) and ranges from 0 to 1, with 1 representing complete bivore diets (Holechek et al. 1984). The reliability of FN as an index 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).
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.

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 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).

**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).**

| Grasses          | Cool–dry (n = 9 [26]) | Warm–dry (n = 18 [90]) | Warm–wet (n = 22 [106]) | Warm–dry (n = 5 [49]) |
|------------------|----------------------|------------------------|-------------------------|-----------------------|
| 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                  |
| Prosopis glandulosa| 0.0               | 0.5                    | 2.2                     | 0.5                   |
| Quercus turbellina| 6.1                  | 0.5                    | 0.5                     | 0.5                   |
| Rhus spp.        | 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                   |
| Carrya spp.      | 0.0                  | 3.8                    | 2.0                     | 0.0                   |
| Cutierrea sarothrae| 1.3              | 0.5                    | 1.2                     | 1.1                   |
| Helianthus petiolaris | 1.8                 | 2.0                    | 5.3                     | 0.5                   |
| Holmimannseggia 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 elaeagniolum | 14.2             | 2.2                    | 3.6                     | 9.2                   |
| Tidestromia laruginosa | 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                  |

1Sample 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.

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.

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).
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) conducted their study. 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.

### Table 2. Diet composition (percent) based on microhistological 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             |
| *Fallopia* 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             |
| *Prosopis* glandulosa | 0.5            | 0.0             | 0.5            | 1.0             |
| *Quercus* turbinella | 0.5            | 1.7             | 0.5            | 0.5             |
| *Rhus* spp.     | 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* angustitolia | 0.0            | 1.7             | 0.0            | 0.0             |
| *Caryya* spp.   | 3.8            | 0.0             | 0.0            | 0.0             |
| *Cuscuta* sarothraae | 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             |
| *Macuaena* 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* spp.  | 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* spp. | 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            |

1Sample 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.
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 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).

| Season         | Fecal N | Fecal DAPA |
|----------------|---------|------------|
|                | Pronghorn | Gemsbok     | Pronghorn     | Gemsbok    |
| Cool–dry 2010  | 1.36 (0.08, 9) | 0.31 (0.03, 9) | 1.99 (0.15, 18) | 0.44 (0.04, 18) |
| Warm–dry 2010  | 1.47 (0.21, 4) | 1.50 (0.05, 10) | 0.40 (0.09, 4)  | 0.48 (0.09, 4)  |
| Warm–wet 2010  | 1.55 (0.07, 22) | 0.37 (0.03, 22)  | 1.68 (0.76, 11) | 0.33 (0.04, 11)  |
| Cool–dry 2011  | 1.48 (0.09, 5)  | 0.32 (0.02, 5)   | 0.30 (0.02, 5)   | 0.34 (0.03, 10)  |
| Warm–dry 2011  | 1.50 (0.05, 10) | 0.34 (0.03, 10)  | 1.55 (0.07, 22) | 0.37 (0.03, 22)  |

1Sample 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 usually 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, Mclinis 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 \textit{Setaria leucopila} and dropseed \textit{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 availability, 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, Holeczek 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 (0.310–0.44 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,
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 plasticity (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).

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References

Acevedo, P. et al. 2012. Co-occurrence and potential for competition between wild and domestic herbivores in a South American desert. – J. Arid. Environ. 77: 39–44.

Acevedo, P. et al. 2007. The Iberian ibex is under an expansion trend but displaced to suboptimal habitats by the presence of extensive goat livestock in central Spain. – Biodivers. Conserv. 16: 3361–3376.

Alipayo, D. et al. 1992. Evaluation of microhistological analysis for determining ruminant diet botanical composition. – J. Range Manage. 45: 148–152.

Ambrose S. H. and DeNiro, M. J. 1986. The isotopic ecology of East African mammals. – Oecologia 69: 395–406.

Anderwald, P. et al. 2015. Influence of migratory ungulate management on competitive interactions with resident species in a protected area. – Ecosphere 6(11): 228.

Anderwald, P. et al. 2016. Heterogeneity in primary productivity influences competitive interactions between red deer and alpine chamois. – PLoS ONE 11(1): e0146458.

Avery, M. M. 2012. Seasonal effects of forage quantity, quality and dietary composition of pronghorn (Antilocapra americana) in a semi-arid environment. – MS thesis, New Mexico State Univ., Las Cruces, NM, USA.

Baldi, R. et al. 2004. High potential for competition between guanacos and sheep in Patagonia. – J. Wildlife Manage. 68: 924–938.

Beale, D. M. and Smith, A. D. 1970. Forage use, water consumption, and productivity of pronghorn antelope in western Utah. – J. Wildlife Manage. 34: 570–583.

Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. – In: Watson, A. (ed.), Animal populations in relation to their food resources. Blackwell, pp. 111–124.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. – Sci. Am. 224: 86–93.

Bender, L. C. et al. 2003. Infectious disease survey of gemsbok in New Mexico. – J. Wildl. Dis. 39: 772–778.

Bender, L. C. et al. 2013. Factors influencing survival and productivity of pronghorn in a semiarid grass–woodland in east-central New Mexico. – Human–Wildl. Interactions 7: 313–324.

Bright, J. L. and Hervert, J. J. 2005. Adult and fawn mortality of Sonoran pronghorn. – Wildl. Soc. Bull. 33: 43–50.

Brown, D. E. and Shaw, H. 2005. Pronghorn use of ephedra during a drought in southwest New Mexico. – In: Cain, J. W. and Krausman, P. R. (eds), Managing wildlife in the southwest. Southwest Sect. Wildl. Soc., pp. 63–66.

Brown, D. E. et al. 2002. Winter precipitation and pronghorn fawn survival in the southwest. – Proc. Bienn. Pronghorn Workshop 20: 115–122.

Brown, D. E. et al. 2006. Effects of midsummer drought on mortality of doe pronghorn (Antilocapra americana). – Southwest. Nat. 51: 220–225.

Brown, D. E. et al. 2008. Pronghorn (Antilocapra americana) food habits on a semidesert grassland range in Arizona. – Proc. Pronghorn Workshop 23: 107–118.

Brown, R. D. et al. 1995. Effects of dietary energy and protein restriction on nutritional indices of female white-tailed deer. – J. Wildl. Manage. 59: 595–609.

Buechner, H. K. 1950. Life history, ecology and range use of the pronghorn antelope in Trans-Pecos Texas. – Am. Midl. Nat. 43: 257–354.

Burkett, D.W. et al. 2002. Gemsbok: the management challenge of an exotic ungulate in the American southwest. – Proc. Wildl. Ranching Symp. 5: 161–171.

Cerling E. T. et al. 2003. Diets of east African bovidae based on stable isotope analysis. – J. Mammal. 84: 456–470.

Codron, D. et al. 2005. Animal diet in the Waterberg based on stable isotopic composition of faeces. – S. Afr. J. Wildl. Res. 35: 43–52.

Davitt, B. B. and Nelson, J. R. 1984. Methodology for the determination of DAPA in feces of large ruminants. – In: Nelson, R. W. (ed.), Proc. W. States and Provinces elk workshop, pp. 133–147.

Dawson, T. J. and Ellis, B. A. 1996. Diets of mammalian herbivores in Australian arid, hilly shrublands: seasonal effects on overlap between euros (hill kangaroos), sheep and feral goats and on dietary niche breadths and electivities. – J. Arid. Environ. 34: 491–506.

Denney, J. J. 2000. Influence of social dominance rank on diet quality of pronghorn females. – Behav. Ecol. 12: 177–181.

Dye, J. 1998. Gemsbok and mule deer diets in southern New Mexico. – MS thesis, New Mexico State Univ., Las Cruces, NM, USA.
Fletcher, T. L. 2000. Diets of gemsbok in creosote shrubland and Great Basin conifer woodland in south central New Mexico. – MS thesis, New Mexico State Univ., Las Cruces, NM, USA.

Fox, L. M. 1997. Nutritional content of forage in Sonoran pronghorn habitat, Arizona. – MS thesis, Univ. of Arizona, Tucson, AZ, USA.

Gagnon, M. and Chew, A. E. 2000. Dietary preferences in extant African bovids. – J. Mammal. 81: 490–511.

Gates, C. G. and Hudson, R. J. 1981. Weight dynamics of wapiti in the boreal forest. – Acta Theriol. 26: 407–418.

Gedir, J. V. et al. 2015. Effects of climate change on long-term population growth of pronghorn in an arid environment. – Ecosphere 6: 189.

Hansen, M. C. et al. 2001. New strategies for pronghorn food habit studies. – Proc. Pronghorn Workshop 19: 71–94.

Hervert, J. J. et al. 2005. Home-range and habitat-use patterns of Sonoran pronghorn in Arizona. – Wildl. Soc. Bull. 33: 8–15.

Hoenes, B. 2008. Identification of factors limiting desert mule deer populations in the greater San Andres Mountains of southwestern New Mexico. – Thesis, New Mexico State Univ., Las Cruces, NM, USA.

Holechek, J. L. 1982. Sample preparation techniques for microhistological analysis. – J. Range Manage. 35: 267–268.

Holechek, J. L. and Vavra, M. 1981. The effect of slide and frequency observation numbers on the precision of microhistological analysis. – J. Range Manage. 34: 337–338.

Holechek, J. L. and Gross, B. D. 1982. Evaluation of different calculation procedures for microhistological analysis. – J. Range Manage. 35: 721–723.

Holechek, J. L. and Valdez, R. L. 1985. Magnification and shrub stemmy material influence on fecal analysis accuracy. – J. Range Manage. 38: 350–352.

Holechek, J. L. et al. 1982a. Methods for determining the nutritive quality of range ruminant diets: a review. – J. Anim. Sci. 54: 363–376.

Holechek, J. L. et al. 1982b. Relationships between performance, intake, diet nutritive quality and fecal nutritive quality of cattle on mountain range. – J. Range Manage. 35: 741–744.

Holechek, J. L. et al. 1984. Methods for determining the botanical composition, similarity, and overlap of range herbivore diets. – In: Committee on developing strategies for rangeland management. Strategies for Rangeland Management, Westview Press, pp. 425–472.

Hughes, K. S. 1991. Sonoran pronghorn use of habitat in southwest Arizona. – MS thesis, Univ. of Arizona, Tucson, AZ, USA.

Hughes, K. S. and Smith, N. S. 1990. Sonoran pronghorn use of habitat in southwest Arizona. Final Report 14-16-009-1564 RWO no. 6. – Arizona Cooperative FishWildl. Res. Unit, Tucson, AZ, USA.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. – Behavior 48: 216–267.

Jenkins, K. J. and Wright, R. G. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. – J. Appl. Ecol. 25: 11–24.

Koerth, B. H. et al. 1984. Estimating seasonal diet quality of pronghorn antelope from fecal analysis. – J. Range Manage. 37: 560–564.

Lehmann D. et al. 2013. Dietary plasticity of generalist and specialist ungulates in the Namibian Desert: a stable isotopes approach. – PLoS ONE 8(8): e72190.

Marquez, M. J. and Boecklen, W. J. 2010. Isoptic shift in an introduced population of gemsbok (Oryx gazella). – J. Arid. Environ. 74: 928–932.

Marshall, J. P. et al. 2008a. Evidence for interspecific competition between feral ass Equus asinus and mountain sheep Ovis canadensis in a desert environment. – Wildl. Biol. 14: 228–236.

Marshall, J. P. et al. 2008b. Body condition of mule deer in the Sonoran desert is related to rainfall. – Southwest. Nat. 53: 311–318.

Marshall, J. P. et al. 2009. Intrinsic and extrinsic sources of variation in the dynamics of large herbivore populations. – Can. J. Zool. 87: 103–111.

Metcalfe, C. R. 1960. Anatomy of the monocotyledons. I. Gramineae. – Clarendon Press.

Metcalfe, C. R. and Chalk, L. 1950. Anatomy of the dicotyledons. 2. Volumes. – Clarendon Press.

McInnis, M. L. and Vavra, M. 1987. Dietary relationships among feral horses, cattle and pronghorn in southeastern Oregon. – J. Range Manage. 40: 60–66.

McKinney, T. and Smith, T. W. 2007. Diets of adults and lambs of desert bighorn sheep during years of varying rainfall in central Arizona. – Southwest. Nat. 52: 520–527.

McKinney, T. et al. 2008. Winter precipitation and recruitment of pronghorns in Arizona. – Southwest. Nat. 53: 319–325.

McDonald, D. T. 2005. Factors affecting pronghorn fawn recruitment in central Arizona. – Thesis, Texas Tech Univ., Lubbock, TX, USA.

Mitchell, G. J. and Smoliak, S. 1971. Pronghorn antelope range characteristics and food habits in Alberta. – J. Wildl. Manage. 35: 238–250.

Muldavin, E. H. et al. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. – Oecologia 155: 123–132.

National Drought Mitigation Center 2012. – <http://www.droughtmonitor.unl.edu/archive.html> accessed 5 August 2012.

Ngugi, K. R. et al. 1991. Range animal diet composition in southwestern Wyoming. – J. Range Manage. 45: 542–545.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. – Annu. Rev. Ecol. Syst. 4: 25–51.

Odadi, W. O. et al. 2011. African wild ungulates compete with or facilitate cattle depending on season. – Science 333: 1753–1755.

Oosting, H. J. 1956. The study of plant communities. – W. H. Freeman Co.

Osborn, R. G. and Ginnett, T. F. 2001. Fecal nitrogen and 2,6-diaminopimelic acid as indices to dietary nitrogen in white-tailed deer. – Wildl. Soc. Bull. 29: 1131–1139.

O'Shaughnessy, R. et al. 2014. Comparative diet and habitat selection of puku and lechwe in northern Botswana. – J. Mammal. 95: 933–942.

Putman, R. J. 1996. Competition and resource partitioning in temperate ungulate assemblies. – Chapman and Hall.

Reid, W. H. and Patrick, G. R. 1983. Gemsbok (Oryx gazella) in White Sands National Monument. – Southwest. Nat. 28: 97–99.

Robinson, M. et al. 2001. Relationship between diet quality and fecal nitrogen, fecal diaminopimelic acid and behavior in a captive group of pronghorn. – Proc. Pronghorn Workshop 19: 28–44.

Saiz, R. B. 1975. Ecology and behavior of the gemsbok at White Sands Missile Range, New Mexico. – Thesis, Colorado State Univ., Fort Collins, CO, USA.

Schwartz, C. C. and Ellis, J. E. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. – J. Appl. Ecol. 18: 343–353.

Seegmiller, R. F. et al. 1990. Nutritional composition of desert bighorn sheep forage in the Harquahala Mountains, Arizona. – Desert Plants 10: 87–90.

Simpson, D. C. et al. 2007. Influence of precipitation on pronghorn demography in Texas. – J. Wildl. Manage. 71: 906–910.
Smith, A. D. and Malechek, J. C. 1974. Nutritional quality of summer diets of pronghorn antelopes in Utah. – J. Wildlife Manage. 38: 792–798.
Smith, C. et al. 1998. Diets of native and non-native ungulates in southcentral New Mexico. – Southwest. Nat. 43: 163–169.
Sparks, D. R. and Malechek, J. C. 1968. Estimating percentage dry weight in diets using a microscopic technique. – J. Range Manage. 21: 264–265.
Sponheimer, M. et al. 2003. Diets of southern African bovidae: stable isotope evidence. – J. Mammal. 84: 471–479.
Stephenson, T. E. et al. 1985. Drought effect on pronghorn and other ungulate diets. – J. Wildlife Manage. 49: 146–151.
Verheyden, H. et al. 2011. Fecal nitrogen, an index of diet quality in roe deer Capreolus capreolus – Wildl. Biol. 17: 166–175.
Voeten, M. M. and Prins, H. H. T. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. – Oecologia 120: 287–294.
Western Regional Climate Center 2016. Climate Summary Bosque del Apache, New Mexico. – <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nm1138> accessed 7 February 2016.
Yoakum, J. D. 2004. Foraging ecology, diet studies and nutrient values. – In: O’Gara, B. W. and Yoakum, J. D. (eds), Pronghorn ecology and management. Univ. Press of Colorado, pp. 447–502.