

## Extreme precipitation variability, forage quality and large herbivore diet selection in arid environments

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Nutritional ecology forms the interface between environmental variability and large herbivore behaviour, life history characteristics, and population dynamics. Forage conditions in arid and semi-arid regions are driven by unpredictable spatial and temporal patterns in rainfall. Diet selection by herbivores should be directed towards overcoming the most pressing nutritional limitation (i.e. energy, protein [nitrogen, N], moisture) within the constraints imposed by temporal and spatial variability in forage conditions. We investigated the influence of precipitation-induced shifts in forage nutritional quality and subsequent large herbivore responses across widely varying precipitation conditions in an arid environment. Specifically, we assessed seasonal changes in diet breadth and forage selection of adult female desert bighorn sheep *Ovis canadensis mexicana* in relation to potential nutritional limitations in forage N, moisture and energy content (as proxied by dry matter digestibility, DMD). Succulents were consistently high in moisture but low in N and grasses were low in N and moisture until the wet period. Nitrogen and moisture content of shrubs and forbs varied among seasons and climatic periods, whereas trees had consistently high N and moderate moisture levels. Shrubs, trees and succulents composed most of the seasonal sheep diets but had little variation in DMD. Across all seasons during drought and during summer with average precipitation, forages selected by sheep were higher in N and moisture than that of available forage. Differences in DMD between sheep diets and available forage were minor. Diet breadth was lowest during drought and increased with precipitation, reflecting a reliance on few key forage species during drought. Overall, forage selection was more strongly associated with N and moisture content than energy content. Our study demonstrates that unlike north-temperate ungulates which are generally reported to be energy-limited, N and moisture may be more nutritionally limiting for desert ungulates than digestible energy.

In north-temperate environments, seasonality is driven by temperature change and snow-melt, resulting in predictable temporal and spatial variation in phenology and forage conditions. Annual variation in onset and duration of green-up notwithstanding, the relatively consistent phenological patterns in north-temperate environments allow animals to more reliably cope with variation in forage resources through seasonal changes in forage selection (Owen-Smith 2002), foraging behaviour (Owen-Smith 1994), habitat selection (van Beest et al. 2010, Merkle et al. 2016), and pre-emptive movements including migration to capitalize on changing forage conditions (Albon and Langvatn 1992). In contrast, changes in phenology

and forage conditions in arid and semi-arid regions are influenced by rainfall, which is unpredictable and highly variable in quantity, timing, and spatial distribution (Noy-Meir 1973). In many arid regions, greater aridity of the environment is associated with greater variability in rainfall and forage (e.g. the Sonoran Desert, USA and Mexico; Marshal et al. 2009). Thus, short-term movement responses of arid-land ungulates to forage and rainfall are often unpredictable and opportunistic. Some species become nomadic in response to rainfall, whereas other desert-dwelling ungulates display limited movements due to naturally fragmented habitats, and must therefore cope with wide variation in forage conditions primarily through adjusting movement patterns within their home range, time allocated to foraging, and diet selection (Owen-Smith 2002, Owen-Smith and Cain 2007).

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Ungulates cope with spatial and temporal variability in forage conditions through changes in diet (Owen-Smith 2002), and may expand their diet breadth to compensate for declining forage abundance and quality (Owen-Smith 1994, Stewart et al. 2011). For example, when abundance of preferred forage species declines during drought periods or when herbivore densities are high, animals often expand their diets to include less-favoured species to maintain intake rates. However, contraction in diet breadth has also been reported in response to seasonal decreases in forage abundance due to climatic conditions or increases in competition (Parker et al. 1999, Nicholson et al. 2006), perhaps reflecting dietary shifts to key resources (Illius and O'Connor 1999) during lean periods. Furthermore, increases in diversity of annual plants and new leaf production on perennial species during wet periods provides more dietary choices for ungulates and often leads to increased dietary breadth (Nicholson et al. 2006, Folks et al. 2014).

Ungulates can be nutritionally limited by protein, energy, and minerals, and forage selection patterns should reflect the most pressing nutritional limitation. For example, white-tailed deer *Odocoileus virginianus* and black-tailed deer *O. hemionus columbianus* inhabiting temperate areas select forage with higher energy content at the expense of protein, indicating that their diets are more energy-limited (Berteaux et al. 1998, Parker et al. 1999, Dumont et al. 2005). In contrast, ungulates in subtropics and tropics are more likely protein-limited (Jarman and Sinclair 1979, Owen-Smith 1982, Prins and Beekman 1989). In arid and semi-arid regions, intermittent loss of leaves in drought-deciduous shrubs and trees during dry periods cause declines in available forage protein resulting in often protein-deficient diets for ungulates. Long periods of low-protein diets, coupled with unpredictable production of high protein forages during brief wet periods, should result in increased selection for high protein diets, particularly during dry periods. Furthermore, ungulates in arid environments with limited surface water may select forage in part based on moisture content, independent of energy or protein levels. When forage moisture declines in the most abundant forage species, the reduced intake of preformed water may lead to ungulates selecting plant species that are high in moisture but low in protein and energy, in an effort to maintain favourable water balance (e.g. cacti generally have high water and low protein content; Alderman et al. 1989, Cain et al. 2008).

Existing research on the diet of desert ungulates is usually descriptive and documents seasonal variation in diet composition or forage nutritional quality. Few studies have encompassed a longer time frame (i.e. >2 years) covering periods of extreme precipitation variability typically observed in arid regions. Moreover, forage quality and diet selection were often not assessed simultaneously, and few have assessed the relationships between potentially limiting nutritional constraints (e.g. protein, energy, forage moisture) and forage selection. Therefore, our objectives were to: 1) investigate how precipitation variability influences seasonal forage nutritional quality; 2) assess seasonal changes in diet breadth and forage selection in response to precipitation-induced shifts in forage quality; and 3) examine the relationship between seasonal forage selection and specific nutritional limitations in desert bighorn sheep

*Ovis canadensis mexicana* across widely varying precipitation conditions. We predicted that desert bighorn sheep select forage more for their protein and moisture content, and less for their energy content, and that this selection would be strongest during dry periods. We also predicted that desert bighorn sheep would expand their diet breadth during drought and dry seasons (summer) to compensate for seasonal and drought-induced declines in availability of more favoured forage species.

## Material and methods

### Study species

Desert bighorn sheep inhabit isolated and rugged desert mountain ranges in the desert regions of the southwestern USA and Mexico. Desert bighorn sheep are adapted to steep, rocky terrain with high levels of visibility where they can escape from predators; therefore, unlike other desert ungulates (e.g. desert mule deer, *Odocoileus hemionus eremicus*), desert bighorn sheep cannot simply adjust their distribution to take advantage of distant rain without crossing broad valleys at significant risk of mortality. While there is some gene flow via limited intermountain range movements, most desert bighorn sheep populations are demographically independent and are either completely isolated or exist as part of a metapopulation. While adapted to harsh, desert conditions, the fragmented and isolated distribution of the desert mountain ranges makes desert bighorn sheep particularly susceptible to climate change and drought (Epps et al. 2004). Anthropogenic developments (e.g. roads and boundary fences) have further reduced movements between some populations (Epps et al. 2005). Therefore, desert bighorn sheep are an ideal species for investigating how desert-dwelling ungulates cope with variability in forage resources associated with highly variable precipitation when the potential for long distance movements to better foraging opportunities are limited.

### Study area

The Cabeza Prieta National Wildlife Refuge (CPNWR) encompasses 3480 km<sup>2</sup> in the Sonoran Desert along the international border between the USA and Mexico in southwestern Arizona. Topography consists of a series of rugged mountain ranges separated by wide alluvial valleys; elevations range from 200–900 m. The study sites were the Sierra Pinta and Cabeza Prieta Mountains located in the western half of the CPNWR.

Annual precipitation was bimodal, with peaks during summer and winter; long-term mean annual precipitation in the area (1969–2005, Tacna, AZ, approx. 64 km north of study area) was 101 mm with high interannual variability (CV = 56%). Mean daily low and high temperatures ranged from 22°C to >45°C in the summer and 3°C to 21°C in the winter (Western Regional Climate Center 2005). We defined January–March as winter, April–June as early summer, July–September as late summer, and October–December as autumn based on long-term climate data.

In the valleys, vegetation was characterized by creosote bush *Larrea tridentata*, white bursage *Ambrosia dumosa*, and ocotillo *Fouquieria splendens* with ironwood *Olneya tesota*, and blue palo verde *Parkinsonia florida* common along washes. Vegetation in the mountains was characterized by ironwood, catclaw acacia *Senegalia greggii*, foothill palo verde *Parkinsonia microphyllum*, white bursage, ratany *Krameria* spp., brittlebush *Encelia farinosa*, and Wright's buckwheat *Eriogonum wrightii*. Prevalent grasses and forbs included three-awn *Aristida* spp., grama *Bouteloua* spp., big galleta grass *Pleuraphis rigida*, globemallow *Sphaeralcea* spp., indian wheat *Plantago patagonica*, and lupine *Lupinus* spp. Common cacti included giant saguaro *Cereus giganteus*, barrel cactus *Ferocactus* spp., fishhook cactus *Mammillaria* spp., teddy bear cholla *Cylindropuntia bigelovii*, buckhorn cholla *C. acanthocarpa* and chain fruit cholla *C. fulgida*.

The only known sources of perennial water available for desert bighorn sheep in our study area included three man-made water catchments in the Sierra Pinta and four in the Cabeza Prieta Mountains. Desert bighorn sheep habitat encompassed approximately 150 km<sup>2</sup> and 315 km<sup>2</sup> in the Sierra Pinta and Cabeza Prieta Mountains, respectively, resulting in one perennial water source per 53 km<sup>2</sup> in the Sierra Pinta and one perennial water source per 78 km<sup>2</sup> in the Cabeza Prieta Mountains.

### Precipitation periods

We used the standardized precipitation index to define precipitation periods (SPI; Guttman 1999). The SPI represents the number of standard deviations that observed cumulative precipitation deviates from the long-term climatological average. We defined a drought event as the period when the SPI was consistently negative and reaches  $\leq -1.0$  with the drought event beginning when the SPI fell below 0, and ending when the SPI becomes positive. We similarly defined wet periods as when the SPI was continuously positive and reached a value  $\geq 1.0$  and periods near average when the SPI fluctuated near 0, not becoming consistently positive or negative. We used long-term (1969–2005) precipitation data from the weather station nearest our study area (Western Regional Climate Center 2005) to calculate the three-month SPI for each month from 2002 through 2005 using program SPI SL 6. Sampling periods were classified as drought, average or wet based on the three-month SPI for the month immediately preceding forage sample collection (i.e. SPI was lagged by approximately 2 weeks).

### Forage sample collection

Between 2002 and 2004, we captured 37 adult female desert bighorn sheep with a net gun fired from a helicopter; we maintained 6–10 radio-collared animals in each mountain range from 2002 to 2005 (Cain et al. 2008). All animals were fitted with a GPS-telemetry collar, equipped with VHF and satellite transmitters (900 g; models 440 and 3580, Telonics, Mesa, AZ), programmed to record one location every 13 h; GPS location data was transmitted every three days via the Argos satellite system.

We used GPS positions from peak morning and afternoon foraging periods of sheep to identify areas for assessing

forage availability and collecting forage samples to determine nutritional content. Sampling times were adjusted for seasonal changes in foraging activity associated with shifts in sunrise and sunset times (Cain et al. 2008). We chose the most recent (i.e.  $\leq 2$  days) GPS locations recorded in the appropriate time period for 8–10 randomly selected animals. We sampled 10 forage plots per range per season, all of which were sampled during a 4–5 day period in the middle of each season (i.e. February, May, August, November). We used a modified line-intercept method to estimate percent cover of each plant species in the foraging areas by setting two 60-m perpendicular line transects that intersected in the center with the orientation determined from a randomly selected compass bearing. We measured all vegetation intercepting each line and estimated percent cover for each plant species. A detailed description for sampling is available in Cain et al. (2008).

To determine seasonal forage moisture and nutritional content we collected  $\geq 100$  g of agave *Agave deserti* barrel cactus, big galleta grass, brittlebush, catclaw acacia, desert lavender *Hyptis emoryi*, fishhook cactus, globemallow, ironwood, palo verde, ratany, rough jointfir *Ephedra aspera*, silverbush *Ditaxis lanceolata*, three-awn, Wright's buckwheat, and white bursage. These 16 species constituted 73–98% ( $\bar{x} = 85.4\% \pm 7.9\%$  SD) of the seasonal diets of desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains in 2002–2005 (Cain unpubl.). Forage samples consisted of current annual growth including green leaves when available, and stems  $\leq 4$  mm in diameter. All forage samples were composites of  $\geq 4$  individual plants unless there were  $< 4$  individuals in the plot. We weighed plant samples immediately post collection to determine fresh weight.

Because we expected precipitation infiltration rates to vary with topographic position and potentially influence forage moisture and nutritional content, we classified each plot as either ridgeline, slope, or drainage line. We classified each forage species as grass, forb, succulent, shrub or tree to assess differences in forage moisture and nutritional content related to forage type. Big galleta and three-awn were the only grass species, globemallow and silverbush were classified as forbs, agave, barrel cactus and fishhook cactus as succulents, brittlebush, desert lavender, ratany, rough jointfir, Wright's buckwheat and white bursage as shrubs, and catclaw acacia, ironwood and palo verde as trees.

### Forage nutritional analyses

We dried forage samples at 50°C in a drying oven to a constant weight, determined dry weight, and calculated percent moisture. We ground dried forage samples through a Wiley mill with a 1 mm mesh screen. We determined nitrogen (N) content using a N-analyser. We determined neutral detergent fibre (NDF) and acid detergent fibre (ADF) following the Van Soest method (Van Soest 1994) using a fibre analyser. We analysed acid detergent lignin (ADL) using the Van Soest ADL assay (Van Soest and Robertson 1980) modified for use with the Ankom fiber bags. Detergent fibre values include residual ash.

Because we were unable to conduct laboratory analysis for in vitro dry matter digestibility or energy content, we

used dry matter digestibility (DMD) as a proxy for energy content of forage, as calculated by Mould and Robbins (1982) for white-tailed deer (Eq. 1; i.e. desert bighorn sheep are primarily browsers, and thus, have a diet more similar to deer than to domestic sheep).

$$\text{DMD} = (1.06\text{NDS} - 18.06) + \text{NDF} \left( \frac{161.39 - 36.95 \ln X}{100} \right) \quad (1)$$

Here NDS is neutral detergent solubles (%;  $100 - \text{NDF}$ ), and X is lignin and cutin (ADL). Our use of DMD as a proxy for energy content is supported by other work describing a strong positive correlation between digestibility and energy content of forages (Moir 1961, Robbins et al. 1975). Therefore, we used three metrics of forage nutritional content to assess the influence of rainfall conditions on forage quality and the influence of these nutritional metrics on diet selection across widely varying precipitation periods: N, DMD and moisture.

### Diet diversity, breadth, and forage selection

We collected 10–20 pellet groups per season per mountain range from adult female desert bighorn sheep to estimate percent diet composition of forage species using microhistological analysis. We assessed three slides per pellet group and sampled 20 randomly selected microscope fields on each slide (Holechek et al. 1982). We assumed that potential biases resulting from differential digestibility of various forage species would be minimal or would equally affect our diet composition across seasons and precipitation periods (Alipayo et al. 1992).

We estimated diet breadth using Levins niche breadth index (Levins 1968). To account for individual level variation in diet composition, we calculated diet breadth for each independent pellet group separately then summarized this data by season and precipitation period.

We estimated forage selection in relation to forage availability using Jacobs' modified electivity D index (Jacobs' D; Eq. 2; Jacobs 1974).

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i} \quad (2)$$

Here  $D_i$  is the Jacobs' D index value for forage species  $i$ ,  $r_i$  is the proportion of forage species  $i$  in sheep pellets (i.e. diet), and  $p_i$  is the proportion of forage species  $i$  in the environment (i.e. availability). Jacobs' D values range from  $-1$  to  $1$ , where negative and positive values indicate species avoidance and preference, respectively. Overall 24 plant species were identified in the pellets which represent  $> 80\%$  of sheep diet in the study area (Cain unpubl.). The plant species that were most prevalent in sheep diet and were analysed for nutritional quality were used to calculate diet selection index ( $n = 16$ ). As part of a separate study examining impacts of water removal on desert bighorn sheep (Cain et al. 2008), water catchments in the Sierra Pinta range were kept empty from March 2004 until the end of the study. Since this may influence sheep forage selection, pellet samples from this time period were removed from diet selection analyses. Given the low density ( $0.01 - 0.02$  perennial water sources  $\text{km}^{-2}$ ) of perennial sources of drinking water on the study area, we expected that forage moisture content would continue to exert an influence on forage selection of desert bighorn sheep, regardless of there being some drinking water

available in man-made water catchments in each mountain range (i.e. three in Sierra Pinta and four in Cabeza Prieta).

### Data analysis

We averaged N, moisture, DMD, NDF, ADF and ADL by forage type, season and precipitation period. If N, DMD, or moisture were limiting, we would expect desert bighorn sheep to select diets to compensate for this nutritional limitation assuming there were sufficient forages with suitable nutritional conditions available. Therefore, we would expect higher values for a limiting nutritional metric in forages selected by desert bighorn sheep than in the available forage as a whole. To assess differences in nutritional metrics between diets consumed by desert bighorn sheep and available forage, we calculated weighted means for each nutritional metric for each season and precipitation period (Eq. 3).

$$\bar{x}_w = \frac{\sum (x_{ijk} \times w_{ijk})}{\sum (w_{ijk})} \quad (3)$$

Here  $x$  is N, DMD or moisture,  $w$  is the proportion of the forage type available in the environment or consumed by sheep for forage type  $i$ , season  $j$  and precipitation period  $k$ . We estimated required N concentrations in forage for desert bighorn sheep as: 0.89% for minimum maintenance requirement, 1.2% for minor accretion of lean body (i.e. protein) mass, 1.5% as the lower limit for lactation, and 1.8% for weaned lamb growth (Church and Pond 1982, DeYoung et al. 2000). The minimum requirement of 0.89% should be considered as the minimum level required by desert bighorn sheep to prevent loss of condition, whereas the 1.2% requirement would allow for moderate ( $10 \text{ g day}^{-1}$ ) accretion of lean body mass and is the level below which the ability to successfully raise lambs may be compromised (National Research Council 2007).

We used ANOVA to assess differences in nutritional quality in relation to precipitation period (drought, average, and wet conditions), season (winter, early summer, late summer and autumn), and forage type (succulent, grass, shrub, tree and forb). We conducted separate analyses, each with N, DMD, or moisture as the response variable, precipitation period, season, and forage type as factors, and topographic position (drainage, slope, and ridgeline) as a blocking factor. Because we had an unbalanced design due to missing cells (e.g. no winter seasons were classified as below average precipitation based on SPI) we used type IV sum of squares in all analyses. We logit-transformed all response variables before analyses; however, estimated marginal means and 95% confidence limits were back-transformed for presentation. We used ANOVA to determine differences in diet breadth across seasons and precipitation periods. We used Levins niche breadth (Levins 1968) as the response variable and season and precipitation period were entered as factors.

We assessed the relationships between forage selection (i.e. Jacobs' D) and nutritional content (N, DMD and moisture) and precipitation periods (reference level – wet) using generalised linear models. To account for the potentially conflicting limitations in desert bighorn sheep diets (e.g. protein versus water), we developed an initial set of 18 a priori models (Supplementary material Appendix 1

Table A1). All models included precipitation period as a fixed effect and some models tested the interaction between forage quality metrics and precipitation period. In addition, to assess the potential for a nonlinear relationship between diet selection and moisture content, we included a quadratic term for moisture. We ran Pearson's pairwise correlations between N, DMD, and moisture to assess the potential for multicollinearity; none of the nutritional metrics were correlated (all  $r \leq 0.35$ ; Supplementary material Appendix 1 Fig A1). We evaluated models using Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). When competing models performed poorer than the highest ranking model with the addition of a single predictor variable, we considered the more complex model to contain an uninformative parameter (Arnold 2010), thus we excluded these models. We calculated model-averaged parameter estimates ( $\pm$  SE) and 95% confidence intervals for variables in the highest ranking models using multi-model averaging (Burnham and Anderson 2002) across all a priori models except for those excluded due to uninformative parameters. We used SPSS 17.0 for all statistical analyses.

## Data deposition

Data available from the USGS data repository: <<https://www.sciencebase.gov/catalog/item/58e3ceb7e4b09da67997eeb9>> and <<https://doi.org/10.5066/F7B856CS>>. Data also available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.p4h15>> (Cain et al. 2017).

## Results

Our data spanned a period of exceptional drought (January through October 2002 being the driest period on record for this region at the time of the study), transitioning through

a period with near average precipitation and into an abnormally wet period. Based on SPI, we classified January 2002 through February 2003 and July 2004 through October 2004 as drought; March 2003 through June 2004 and May to September 2005 were classified as average. November 2004 through April 2005 were classified as wet; Fig. 1).

Concentration of N in forage available to desert bighorn sheep differed among precipitation periods ( $F_{2,1103} = 16.63$ ,  $p < 0.001$ ), seasons ( $F_{3,1103} = 6.37$ ,  $p < 0.001$ ), and forage types ( $F_{4,1103} = 74.38$ ,  $p < 0.001$ ). Differences in N content between precipitation periods depended on season (precipitation period  $\times$  season interaction;  $F_{4,1103} = 3.34$ ,  $p = 0.010$ ). Forage N content did not differ between seasons during drought, but was higher during winter and autumn of average and wet periods than during drought (Fig. 2a). Seasonal N levels in forage during all seasons in drought and in summer during average precipitation were between minimum levels to prevent loss of body condition and minimum level for accretion of lean body mass, and only winter and autumn N levels during average and wet precipitation periods met minimum levels for accretion of lean body mass. The highest N levels occurred in winter under wet conditions (25% and 36% higher than in winter during average and drought conditions, respectively; 40–46% higher than in summer during average precipitation; 52–61% higher than other seasons in drought). Autumn N levels were also high in the average and wet precipitation periods; during the wet period, 26–29% higher than in summer under average conditions and 19–42% higher than in all seasons in drought (Fig. 2a).

Differences in N content between precipitation periods also depended on forage type (precipitation period  $\times$  forage type interaction;  $F_{8,1103} = 3.90$ ,  $p < 0.001$ ). Mean N content of succulents and trees did not differ across precipitation periods, that of grasses was similar between periods of drought and average precipitation, and forb and shrub

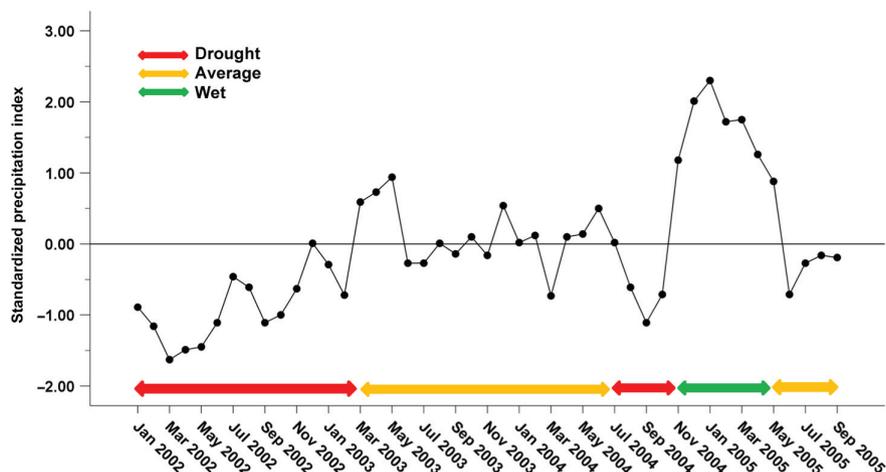


Figure 1. Three-month standardized precipitation index (SPI; i.e. the number of standard deviations that observed cumulative precipitation deviates from the long-term climatological average; see Methods for more details) calculated from long-term (1969–2005) precipitation data from Tacna, Arizona (Western Regional Climate Center 2005) for the period from January 2002 through September 2005. We defined a drought event when the SPI was consistently negative and reaches  $\leq -1.0$  with the drought event beginning when the SPI fell below 0, and ending when the SPI becomes positive. We defined wet periods as when the SPI was continuously positive and reached a value  $\geq 1.0$  and periods near average when the SPI fluctuated near 0, not becoming consistently positive or negative. January 2002 through February 2003 and July 2004 through October 2004 were classified as drought, March 2003 through June 2004 and May to September 2005 were classified as average, and November 2004 through April 2005 were classified as wet.

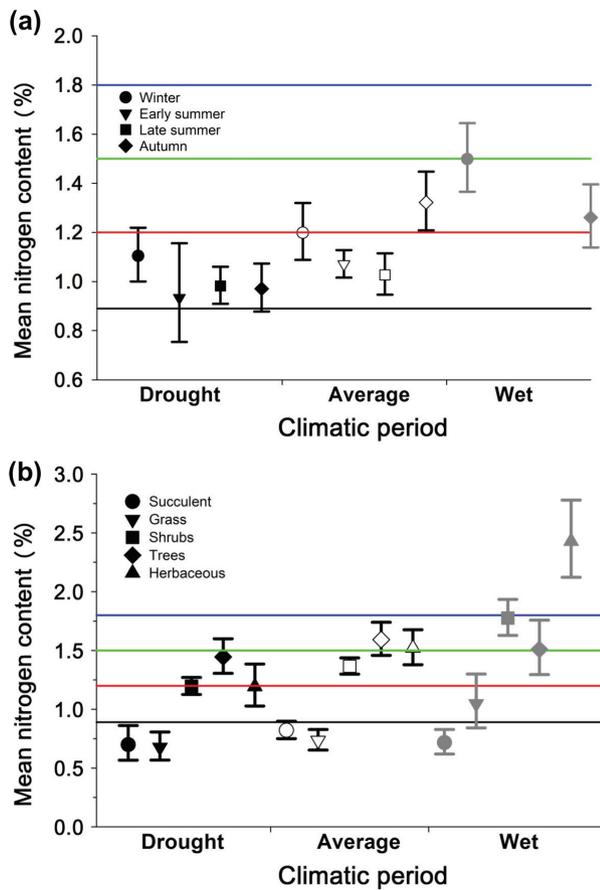


Figure 2. Mean nitrogen content of forage available to adult female desert bighorn sheep in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), by (a) season and (b) forage type in drought (closed black symbols), average (open symbols) and wet (closed grey symbols) conditions. Means and error bars are back-transformed estimated marginal means and 95% confidence intervals. Horizontal reference lines are forage N requirement levels for desert bighorn sheep (DeYoung et al. 2000): 0.89% minimum maintenance (black line), 1.2% accretion of lean body mass (red line), 1.5% lower limit for lactation (green line), and 1.8% minimum for weaned lamb growth (blue line).

N content increased with precipitation (Fig. 2b). Mean N content of succulents was below sheep minimum maintenance levels to prevent loss of condition during all climate periods, and grasses only exceeded this level under wet conditions. Nitrogen content of grasses was 42–55% higher during the wet period than during drought and average precipitation, but was significantly lower than shrubs, trees and forbs across climate periods (Fig. 2b). Nitrogen content of shrubs and forbs were positively correlated with precipitation, increasing from drought to average precipitation (shrubs – 14%; forbs – 35%) and from average to wet conditions (shrubs – 30%; forbs – 60%; Fig. 2). In every precipitation period, N levels in shrubs, forbs and trees were above sheep minimum maintenance requirements, but forbs were the only plant type that met all reproductive requirements of female sheep, and only under wet conditions (Fig. 2b). Mean N content of trees was generally high, meeting sheep lactation requirements during non-drought periods.

Differences in moisture content of forage available to desert bighorn sheep between precipitation periods depended on season (precipitation period  $\times$  season;  $F_{4,1106} = 8.55$ ,  $p < 0.001$ ), forage type (precipitation period  $\times$  forage type;  $F_{8,1106} = 11.50$ ,  $p < 0.001$ ), and season by forage type (precipitation period  $\times$  season  $\times$  forage type;  $F_{28,1106} = 3.54$ ,  $p < 0.001$ ). As expected, succulents had the highest (> 75% and as high as 92%) moisture content of any forage type throughout the study, and showed a slight increasing trend from the drought to the wet period (Supplementary material Appendix 1 Fig. A2). Grasses, forbs and shrubs had low to moderate moisture content, which increased across precipitation periods and during winter and autumn within precipitation periods; lowest moisture content was observed during summer in these forage types. Trees had moderate but consistent moisture content across seasons within precipitation periods and across precipitation periods (Supplementary material Appendix 1 Fig. A2).

Differences in DMD of forage available to desert bighorn sheep between precipitation periods depended on season (precipitation period  $\times$  season;  $F_{4,1108} = 3.34$ ,  $p = 0.010$ ), forage type (precipitation period  $\times$  forage type;  $F_{8,1108} = 5.54$ ,  $p < 0.001$ ), and season by forage type (precipitation period  $\times$  season  $\times$  forage type;  $F_{16,1108} = 2.76$ ,  $p < 0.001$ ). Within forage types, DMD levels were generally consistent across seasons and precipitation periods, although grasses and forbs demonstrated more variability (Supplementary material Appendix 1 Fig. A3). The lowest DMD in each precipitation period (43–62%) occurred in early summer and winter grasses under drought and wet conditions, respectively, and in forbs during average precipitation (Supplementary material Appendix 1 Fig. A3). Alternatively, the highest DMD in each climatic period occurred in succulents (80–81%); early summer in drought, late summer in average precipitation, autumn in wet conditions (Supplementary material Appendix 1 Fig. A3).

Shrubs and trees had the highest availability of all forage types at foraging sites of desert bighorn sheep (Supplementary material Appendix 1 Table A2; Table 1). Correspondingly shrubs and trees composed the bulk of sheep diets across all seasons and climatic periods; however, the proportion of the diet composed of tree species was always substantially higher than availability (winter in non-drought periods excepted), whereas the proportion of shrubs in diets were considerably lower than availability during all seasons (Supplementary material Appendix 1 Table A2; Table 1). Consumption of succulents was highest during drought (17–20%) and the proportion in the diet always exceeded availability (Supplementary material Appendix 1 Table A2; Table 1). With the exception of autumn, forb availability and consumption generally increased with precipitation, particularly during winter (Table 1). With the exception of succulents, N content of forage types that made up the majority of seasonal sheep diets tended to be higher than the mean N averaged across available forages for each season and precipitation period (Table 1). Moisture content of forage types was similarly higher in sheep diets during summer, drought and the average precipitation period. Among forage types that made up the majority of seasonal sheep diets, there was little difference between DMD of diets and the within-season average DMD across forage types, and surprisingly,

Table 1. Mean diet contribution (Diet), forage availability (Avail.), nitrogen (N), moisture (Moist.), and dry matter digestibility (DMD) of adult female desert bighorn sheep forage by forage type, season, and precipitation period in Cabeza Prieta National Wildlife Refuge, Arizona, USA. – = not available; during the study wet conditions did not occur during any summer seasons.

Season <sup>a</sup>	Forage	Drought					Average					Wet				
		Avail. <sup>b</sup>	Diet <sup>c</sup>	N	Moist.	DMD	Avail.	Diet	N	Moist.	DMD	Avail.	Diet	N	Moist.	DMD
ES	forb	0.6	1.1	1.1	42.9	77.9	6.6	8.0	1.4	41.6	56.5	–	–	–	–	–
	grass	1.5	6.1	0.5	16.9	57.1	2.2	1.1	0.7	20.9	59.7	–	–	–	–	–
	shrub	71.8	25.9	1.2	33.6	71.6	63.3	27.1	1.3	42.3	62.2	–	–	–	–	–
	succulent	1.6	19.9	0.8	66.6	71.1	2.7	13.3	0.8	77.4	66.5	–	–	–	–	–
	tree	24.5	44.3	1.6	48.4	67.8	25.2	33.3	1.9	47.8	64.1	–	–	–	–	–
	mean			1.0	41.7	69.1			1.2	46.0	61.8	–	–	–	–	–
LS	forb	1.9	2.9	1.3	28.4	74.0	4.2	7.2	1.7	36.1	44.2	–	–	–	–	–
	grass	2.4	7.9	0.7	14.9	63.3	1.1	4.5	0.6	22.5	74.7	–	–	–	–	–
	shrub	59.9	12.2	1.2	29.9	67.9	71.7	12.2	1.1	37.6	46.6	–	–	–	–	–
	succulent	2.4	20.2	0.7	73.5	74.4	1.6	18.4	0.9	76.1	40.4	–	–	–	–	–
	tree	33.3	41.7	1.6	45.2	71.9	21.2	39.9	1.6	45.8	43.3	–	–	–	–	–
	mean			1.1	38.4	70.3			1.2	43.6	49.8	–	–	–	–	–
A	forb	8.9	6.3	1.2	25.5	64.4	3.0	3.9	1.7	52.4	63.9	4.9	17.1	1.9	61.5	62.2
	grass	1.5	1.6	0.8	12.2	78.5	2.2	1.7	1.0	43.4	60.1	1.2	2.5	1.0	30.5	59.9
	shrub	58.2	27.6	1.4	33.9	68.4	58.6	27.4	1.9	55.1	68.6	58.2	16.9	1.9	60.8	68.1
	succulent	1.5	16.5	0.7	69.8	69.0	1.2	16.3	0.9	81.6	77.3	4.2	9.5	0.7	91.6	75.9
	tree	29.9	40.8	1.5	47.1	72.5	35.0	42.1	1.6	52.9	67.5	31.5	42.1	1.6	52.8	69.1
	mean			1.1	37.7	70.6			1.4	57.1	67.5			1.4	59.4	67.0
W	forb	4.8	4.6	1.4	33.0	65.9	6.9	15.3	1.6	51.7	73.5	22.3	13.9	3.5	70.1	51.3
	grass	1.2	0.8	1.0	14.8	75.3	4.5	2.1	0.8	29.7	76.4	2.4	2.4	1.2	61.6	32.5
	shrub	74.1	27.3	1.3	38.9	57.1	58.3	33.0	1.6	47.1	66.9	53.2	28.8	1.9	63.4	54.4
	succulent	2.9	18.1	0.9	76.7	73.1	2.4	6.5	0.9	75.2	75.8	1.4	11.7	0.8	88.5	41.4
	tree	16.4	43.2	1.5	42.3	62.1	27.9	19.2	1.6	42.5	73.4	20.4	19.1	1.5	42.6	36.7
	mean			1.2	41.1	66.7			1.3	49.2	73.2			1.8	65.2	43.3

<sup>a</sup>Season: ES = early summer, LS = late summer, A = autumn, W = winter.

<sup>b</sup>Avail. = Percent forage availability.

<sup>c</sup>Diet = Percent diet contribution.

some predominant seasonal forage types in sheep diets (i.e. >20%) were actually lower in DMD than the within-season precipitation period average (Table 1).

Across all seasons in drought, the weighted mean N and moisture contents were 12–18% and 14–37%, respectively, higher in sheep diets than in available forage, and a similar pattern was found in summer under average precipitation conditions (Fig. 3). Winter during non-drought periods was the only season when N content was higher in available forage than in sheep diets (Fig. 3). Differences in DMD between sheep diets and available forage were minor (i.e. 0.1–4%) and showed no consistent pattern across seasons or precipitation periods (Fig. 3). Similarly, NDF, ADF and ADL did not show consistent differences between sheep diets and available forage across all seasons and precipitation periods (Supplementary material Appendix 1 Fig. A4, Table A3) and differences were generally <9%.

Each of the three nutritional metrics, N, DMD and moisture, appeared in at least one model in the confidence set of models (i.e. models with  $\sum w_i \geq 0.95$ ) for forage selection by desert bighorn sheep (Table 2). However our top model had 3 and 10 times more support than the next two highest ranking models, respectively. Forage selection by female desert bighorn sheep increased with increasing forage N and moisture content; however, after accounting for the effects of N and moisture, forage selection was negatively associated with DMD (Table 3, Fig. 4). Sheep forage selection had a quadratic relationship with moisture content, and model-averaged parameter estimates indicated that selection was strongest at intermediate levels (Table 3,

Fig. 4c). Models with interactions between precipitation period and nutritional metrics had less support than those including precipitation period as an additive term (Table 2) indicating that the influence of each nutritional metric on sheep forage selection was independent of climate periods (e.g. selection for N did not depend on climate period).

Desert bighorn sheep diet breadth across seasons depended on precipitation (precipitation period  $\times$  season;  $F_{4,340} = 22.04$ ,  $p < 0.001$ ), and was generally lowest during drought and increased with rainfall (Fig. 5). Diet breadth was similar among seasons during drought, whereas under average and wet conditions sheep diet breadth exhibited high variability among seasons, but generally increased across precipitation periods (Fig. 5).

## Discussion

Our hypothesis that desert bighorn sheep are more limited by forage moisture and protein than by energy content was supported by our data; N (i.e. protein) and moisture content were more strongly associated with forage selection than energy content as proxied by DMD. Selection of forage species increased with increasing N content. The relationship between sheep forage selection and moisture content was nonlinear; forage selection increased with increasing moisture when levels were lower during drought and summer, then peaked at intermediate moisture levels, before declining with further increases in forage moisture. This reduced selection at higher moisture levels likely reflected a dietary

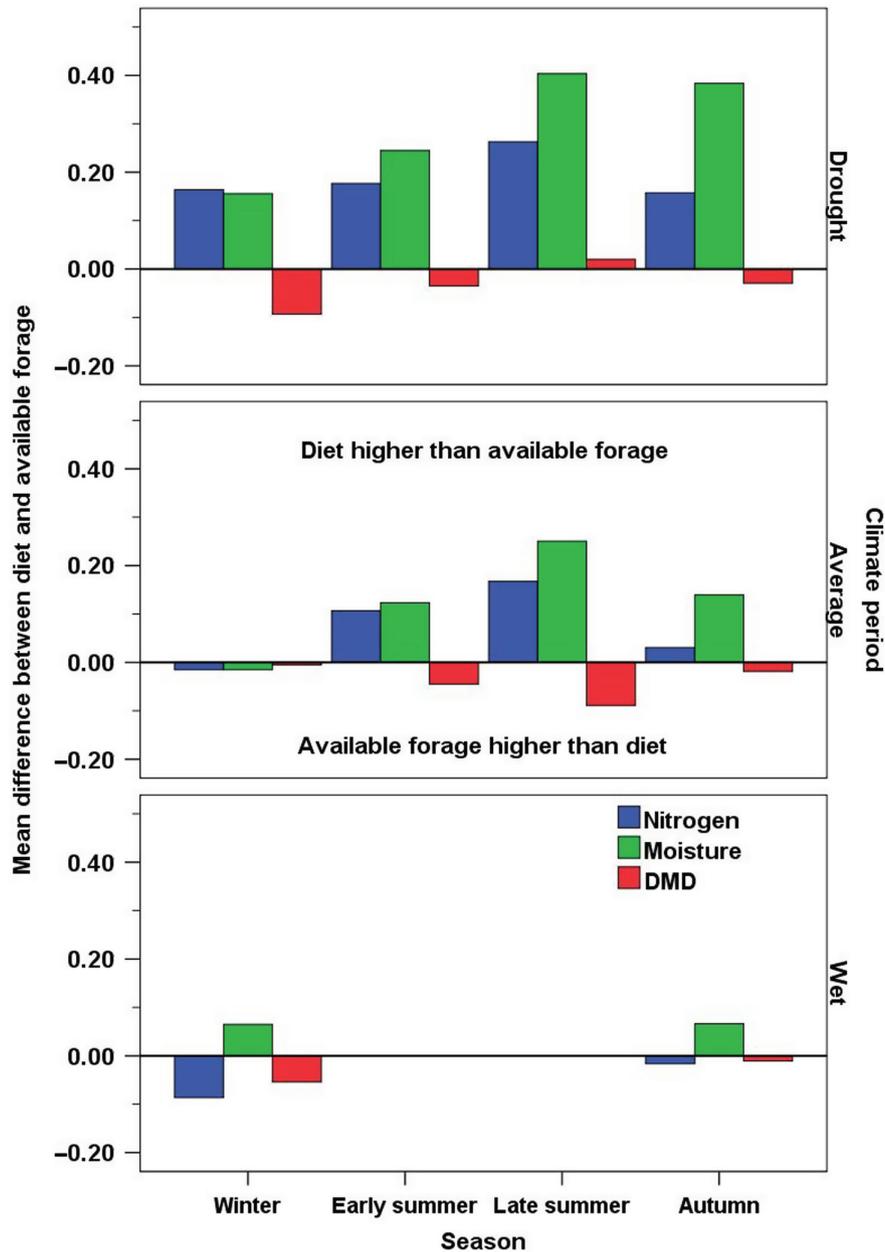


Figure 3. Seasonal differences (weighted means) for nitrogen, moisture and dry matter digestibility (DMD) of adult female desert bighorn sheep diets and available forage in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), during drought, average and wet conditions. Values > 0 indicate nutritional metrics were higher in diet selected by desert bighorn sheep than in available forage; values < 0 indicate that nutritional metrics were higher for available forage than selected diet. There are no bars for early and late summer under wet conditions because during the study wet conditions did not occur during any summer seasons.

Table 2. Highest ranking a priori models with a  $\Delta AIC_c \leq 10$  assessing the relationship between forage selection by adult female desert bighorn sheep (Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005) and nutritional quality and precipitation period. Number of parameters (K), Akaike's information criterion adjusted for small sample size ( $AIC_c$ ),  $\Delta AIC_c$ , and Akaike weights ( $w_i$ ) are given.

Model	K	$AIC_c$	$\Delta AIC_c$	$w_i$
N + DMD + Precipitation	5	426.60	0.00	0.643
N + DMD + Moisture + Precipitation	5	428.70	2.10	0.225
DMD + Precipitation	4	431.32	4.72	0.061
DMD + Moisture + Precipitation	5	433.73	6.73	0.018
Moisture + Moisture <sup>2</sup> + Precipitation	5	434.64	7.13	0.012
N + DMD + Precipitation + N × Precipitation + DMD × Precipitation	9	435.26	8.04	0.008
N + Moisture + Moisture <sup>2</sup> + Precipitation	6	435.55	8.66	0.007

Table 3. Model-averaged coefficient estimates, standard errors (SE), and 95% confidence limits for variables in the top models testing the relationship between forage selection by adult female desert bighorn sheep in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), and forage nutritional content and precipitation period.

Variable	Model-averaged parameter estimate		95% Confidence limits	
	Estimate	SE	Lower CL	Upper CL
N	19.26	7.52	4.51	34.01
DMD	-2.23	0.52	-3.24	-1.23
Moisture	1.91	0.13	0.94	1.45
Moisture <sup>2</sup>	-3.73	0.94	-5.57	-1.89
Precipitation (drought)	-0.03	0.46	-0.94	0.87
Precipitation (average)	0.10	0.43	-0.75	0.95

shift away from succulents when they increased in moisture during the wet period (Cain et al. 2008). Our models indicate that after accounting for the influence of moisture and N, sheep selection for forage decreased with increasing DMD. This unexpected result could relate to the fact that

many of the forage species with the highest N content made up the bulk of the diet and had intermediate to high selection indices but had lower DMD (e.g. trees and shrubs). Similarly, both N content and selection for forbs increased with precipitation from the drought to average period, however, DMD decreased with precipitation likely due to increased fibre content of forbs when conditions were more suitable for forb growth. Alternatively, many species with the higher DMD had lower selection indices, many of which had lower N and moisture. Succulents for example generally had low N and high DMD and when DMD increased (along with moisture) during wet periods, sheep selection of succulents declined. The DMD of grasses and forbs was variable and largely reflected changes in seasonal precipitation patterns, but overall there was little change in DMD across precipitation periods. The DMD of succulents, trees and shrubs were largely unresponsive to either seasonal changes or precipitation periods. The low variability and moderate to high DMD in most forages likely allowed desert bighorn sheep to focus their selection on plants with more variability in other potential nutritional constraints such as N and moisture

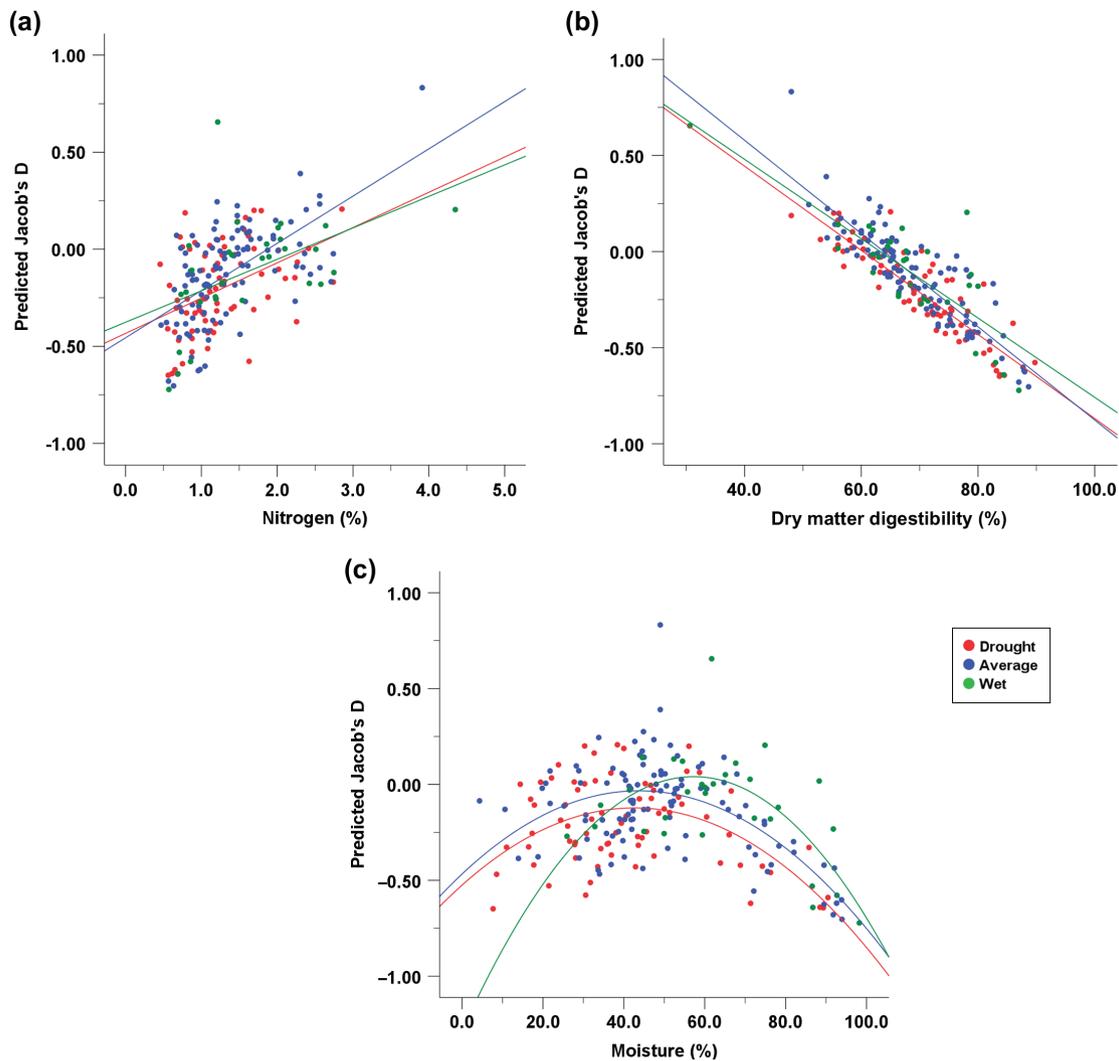


Figure 4. Predicted levels of forage selection (Jacob's D) by female desert bighorn sheep in relation to forage (a) nitrogen, (b) dry matter digestibility and (c) moisture content on the Cabeza Prieta National Wildlife Refuge, Arizona, USA. Predicted values based on highest ranking model.

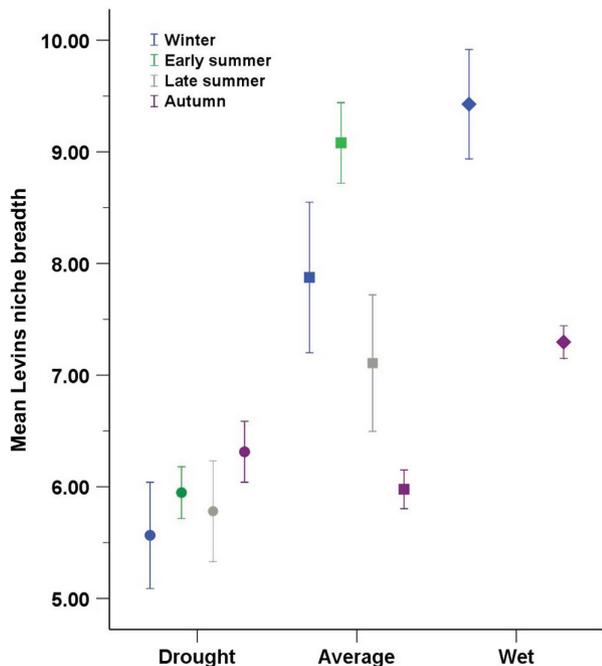


Figure 5. Mean seasonal Levins niche breadth of adult female desert bighorn sheep diets in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), during drought (closed circles symbols), average (open squares) and wet (closed diamond) conditions. Blue symbols are winter (Jan–Mar), green are early summer (Apr–Jun), grey are late summer (Jul–Sep), and purple are autumn (Oct–Dec).

content. Contrary to our prediction, selection for high N content forages did not differ between precipitation periods, but rather desert bighorn sheep displayed consistently high selection for forage species with higher N content.

The moisture and N content of grasses, forbs, and shrubs were most responsive to changes in precipitation conditions, varying among seasons and increasing as climatic conditions ranged from severe drought to above-average precipitation. Trees had consistently high N content (> 1.4%, higher than any of the forage classes, except forbs during wet conditions) and moderate moisture content (40–50%) throughout the study. The DMD of shrubs, succulents, and trees was relatively consistent throughout the study, whereas DMD of forbs and grasses was more variable and reflected seasonal changes in precipitation. As expected, succulents were always high in moisture (> 75%) but very low in nitrogen ( $\leq 0.9\%$ ) and varied little in association with changes in precipitation.

Ungulates typically select diets to obtain the optimal balance of required nutrients given their morphological and physiological digestive restrictions, the nutritional content of available forage, and levels of secondary plant compounds in the forage (Westoby 1974, 1978, Bryant et al. 1992, Van Soest 1994). Ungulates have the ability to distinguish between forages with differing nutrient levels (Hochman and Kotler 2006) and when limited by a particular nutritional constraint (e.g. energy, protein), should select forages to overcome this limitation (McNaughton 1990, Ben-Shahar and Coe 1992, Wang and Provenza 1997). Many species of north-temperate ungulates are reportedly nutritionally limited by energy

content of forage, particularly during winter (Parker et al. 1999, Dumont et al. 2005). Berteaux et al. (1998) experimentally showed that when white-tailed deer were presented with food varying in protein and energy during winter, they selected diets higher in energy and with lower protein, consistent with being energy-limited. Our results are more consistent with findings from ungulates in the tropics and subtropics which tend to have diets more limited by protein than energy (Jarman and Sinclair 1979, Owen-Smith 1982, Prins and Beekman 1989, Spalton 1999). Cattle in semi-arid savannas of Kenya reduced consumption of forbs (with their higher protein content) in favour of graminoids when supplemented with protein, an indication that protein content drives forage selection of unsupplemented cattle (Odadi et al. 2013). It is widely recognized that N and energy content of forages are often correlated (Robbins 1993, Owen-Smith 2002), making it difficult to disentangle the influence of energy and N content on forage selection. However, this was not the case with our study, DMD (our proxy for energy) was moderate to high throughout the study, and levels of DMD were relatively constant for those forage types that made up the bulk of the desert bighorn sheep diets across seasons and climate periods. Nitrogen and moisture content were much more variable, being lowest during periods with little rainfall. In addition, N and moisture content of selected diets was higher than in available forage, whereas there were no consistent differences in DMD or fibre content of selected forages compared to available forage.

The N content of shrubs, trees, and forbs in the desert bighorn sheep diets in our study were above maintenance levels but were not excessively high (especially during drought). With the exception of forbs during the wet period, none of the forage species exceeded the 1.8% N required for weaned lamb growth (Church and Pond 1982). Nitrogen content of succulents remained below minimum maintenance levels throughout the study and that of grasses only exceeded minimum requirements during the wet period. However, plant secondary compounds, particularly tannins can act to reduce the forage N that can be utilised by ungulates (Mould and Robbins 1982). Although little is known about the tannin content of the forage species of desert bighorn sheep in this study, our estimates of forage N likely overestimated the total N biologically-available to sheep. This suggests that utilizable N was probably closer to or below sheep maintenance requirements and that N was nutritionally limiting. Furthermore, desert-adapted ungulates generally have lower metabolic rates than temperate species, which are commonly associated with lower water turnover rates for species inhabiting water-limited environments, as well as decreased total energy requirements (Macfarlane and Howard 1972, Maloiy et al. 1979, Cain et al. 2006). This pattern has also been reported among conspecifics with a wide latitudinal distribution range. White-tailed deer in the southern portion of their range have lower energy requirements than northern conspecifics, which Strickland et al. (2005) attributed to adaptation to a low productivity environment. In addition, desert bighorn sheep may have enhanced digestive capacity compared with other desert ungulates. Kay and Goodall (1976) reported that digestibility was higher and forage retention time longer in domestic sheep compared to red deer; desert bighorn sheep may share

this adaptation. Indeed, Krausman et al. (1988) reported higher digestibility in desert bighorn sheep than in domestic sheep. Therefore, we suggest that in the context of this study, N is more nutritionally limiting to desert bighorn sheep than DMD.

The consistently low N content and extremely high water content of succulents consumed by desert bighorn sheep indicates that their consumption was most likely related to moisture content, particularly during drought and dry seasons. Furthermore, succulent moisture increased with precipitation, and sheep selection for succulents had a quadratic relationship with moisture content. Succulent consumption by sheep increased as precipitation increased from the drought to the average period, then decreased with further increases in moisture during the wet period, coinciding with increases in moisture and nutritional content of other forages. Similar patterns of succulent use have been documented in other species, with increased consumption of high moisture forages during periods with limited surface water availability and low overall forage moisture content (Taylor 1969, Jarman 1973, Williamson 1987, Manser and Brotherton 1995).

Diet selection allows animals to maximize nutrient gains to build body reserves during periods with favourable foraging conditions and to minimize the loss of body reserves during adverse periods. Unlike north-temperate ungulates which experience nutritional bottlenecks during winter, desert ungulates typically face the most critical period of nutritional stress during the summer months, with winter having much more favourable forage conditions. Trees are a critical dietary component, providing relatively consistent sources of N and moisture across seasons and climatic periods, and serve as key buffer resources for desert bighorn sheep, particularly during extreme drought (Illius and O'Connor 1999). Ironwood and palo verde trees were especially important for desert bighorn sheep in our study, comprising 19–43% of their seasonal diets, with dietary contribution being >40% during drought. Palo verde is a drought-deciduous species which drops its leaves during dry periods, but quickly regrows leaves shortly after sufficient rainfall, whereas ironwood retains its leaves for most of the year. Both species have photosynthetically active stems; only the youngest stems of ironwood, but all stems (with exception of the base of the trunk) of palo verde are photosynthetically active year round. The N content of small palo verde branches varies little throughout the year, which is attributable to year-round photosynthetic activity (Barth and Klemmedson 1986). Palo verde and ironwood had relatively constant moisture content across seasons and precipitation periods indicating they are less water-stressed than shrubs (Szarek and Woodhouse 1976). Thus, moderate and consistent N and moisture content illustrate the overall importance of these two forage species, particularly during dry periods when nutritional quality of other forages decline.

Our prediction that desert bighorn sheep diet breadth would expand during drought and summer dry seasons was not supported. Rather, diet breadth was narrowest during drought and expanded with increases in precipitation in all seasons (autumn in average precipitation excepted). Ungulates can either increase diet breadth during periods with reduced forage abundance by including less-favoured forage

species in their diet, or they can contract diet breadth, relying on a few forage species that serve as buffer resources during critical periods, provided there is sufficient biomass of these species (Owen-Smith 1994, Parker et al. 1999, Nicholson et al. 2006, Stewart et al. 2011). In our study, the drought period was extreme (i.e. rainfall was 92% below average), and as such, the extreme aridity likely severely limited the number of forage species available in sheep habitat and rendered other species inedible. Thus, the desert bighorn sheep were presumably forced to rely on a reduced number of forage species to comprise their diet, and this would explain the contracted diet breadth we observed during drought. In desert environments, precipitation prompts rapid and significant increases in forage diversity through new production of annual forbs and leaf growth in drought-deciduous shrubs and trees, and thus, sheep would have a wider variety of forages on offer under average and wet conditions, and their diet breadth would expand accordingly.

High spatial and temporal variability of rainfall in desert systems results in unique constraints for the arid-adapted ungulates that inhabit them. Many ungulates can simply move to areas where rain has provided a higher abundance of forage; however, the fragmented habitat of desert bighorn sheep often does not afford them the opportunity to migrate when forage conditions deteriorate, and they must modify their behaviour to overcome forage nutritional limitations, particularly during periods of extreme drought. Selection of forage species targeting specific qualities, changing diet breadth to minimize diet deficiencies during periods of nutritional and/or water stress, and relying on key forage resources are adaptive strategies that help to minimize negative effects of climatically-induced declines in forage conditions. Because drought conditions are expected to be exacerbated in the future by changing climate and rainfall regimes (Duncan et al. 2012), responses of forage and ungulate diets to those changes provide an indication of the capacity of large ungulates in arid environments to adapt in the long-term. Forage N and moisture content were more strongly associated with desert bighorn sheep forage selection than energy content as proxied by DMD. Forage selection by ungulates should be influenced by attempts to overcome the most limiting nutritional constraint, and our findings indicate that protein and moisture can be more nutritionally limiting for desert ungulates than digestible energy.

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*Permits* – We followed acceptable methods for capture and handling of study animals (Univ. of Arizona Institutional Animal Care and Use Protocols 01-191 and 04-180).

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Supplementary material (available online as Appendix oik-04282 at <[www.oikosjournal.org/appendix/oik-04282](http://www.oikosjournal.org/appendix/oik-04282)>). Appendix 1.