

Drought but not population density influences dietary niche breadth in white-tailed deer in a semiarid environment

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Abstract. A premise in ungulate foraging theory is that animals become less selective and expand the breadth of their dietary niche as the availability of palatable forage declines with increasing herbivore population density or drought. Increased niche variation resulting from intraspecific competition is thought to create less similar diet composition and decreased diet overlap between individuals within a population at higher densities than between individuals within less dense populations. These ideas were largely developed in relatively mesic environments and their applicability to ungulate foraging in semiarid environments is unclear. We tested the idea that white-tailed deer (*Odocoileus virginianus*) contract dietary niche breadth; reduce dietary plant species diversity, richness, and evenness; and become more individualistic in forage choices in response to a fourfold difference in population density (12 deer/km² versus 50 deer/km²) in semiarid shrubland in Texas, USA. We used the bite count method to determine diet composition of tame female white-tailed deer seasonally during summer 2009 to spring 2011. We were able to determine impacts of drought on foraging dynamics a posteriori because sampling during each season fortuitously occurred under both drought and non-drought conditions. Population density did not affect diet richness, diversity, breadth, evenness, overlap, and similarity. Diet richness, diversity, breadth, and evenness tended to be greater in non-drought conditions. For white-tailed deer, the idea that dietary niches expand in response to increasing population density is not robust across environments. In semiarid environments, variation in precipitation has a much stronger influence on dietary niche breadth and intraspecific diet overlap of deer than population density does.

Key words: density dependence; diet breadth; diet evenness; diet selection; diversity; *Odocoileus virginianus*; precipitation; southern Texas, USA.

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INTRODUCTION

A premise in ungulate foraging theory is that

as population density increases, resource competition results in depletion of palatable plant species (Stephens and Krebs 1986, Pianka 1988).

In response to the decline in palatable plants, foragers become less selective and expand the breadth of their dietary niche (Svanbäck and Bolnick 2007). Dietary niche expansion at high ungulate densities is thought to result in greater dietary plant species diversity, species richness, and evenness because as palatable plant species become depleted animals broaden their dietary niche by including less palatable plant species in diets (Augustine and McNaughton 1998, Sargeant 2007). Increased niche variation resulting from intraspecific competition is predicted by foraging theory to cause diet composition to be less similar and diet overlap to decline among individuals within a population at higher densities than among individuals within less dense populations (Svanbäck and Bolnick 2007). These ideas were developed primarily in mesic environments. Their applicability in semiarid environments where environmental stochasticity may drive plant–animal interactions (Ellis and Swift 1988, Briske et al. 2003) is unclear.

Resource depletion may result from environmental variables such as drought. Resource depletion resulting from environmental factors should result in dietary niche expansion in a manner similar to increased deer density (Roughgarden 1972, Owen-Smith 1994, Rödel et al. 2004). Diet diversity, richness, evenness, and niche breadth of herbivores should increase in response to drought because palatable forages become less available and herbivores are forced to consume lower quality plants (Owen-Smith 1994).

Density-dependent dietary niche expansion has been documented in white-tailed deer. For example, a two-fold increase in deer densities in southern Texas resulted in fewer herbaceous dicots in deer diets and increased graminoids (Kie et al. 1980). In southern Quebec, deer from a high density (14 deer/km²) population shifted their diet from forbs to greater prevalence of fruits, grasses, and farm crops compared to deer in a low density (1 deer/km²) population (Daigle et al. 2004).

Dietary shifts of deer in response to resource depletion do not always follow predictions of foraging theory. For example, Nicholson et al. (2006) compared a low-density with a high-density mule deer (*Odocoileus hemionus*) population in southern California, USA, and found that

the low-density population had greater diet breadth. Narrowed dietary niches in mule deer at a high population density possibly resulted because foraging by deer at high population densities reduced forbs, forcing deer to consume browse. White-tailed deer (*Odocoileus virginianus*) likewise prefer forbs and switch to browse when forbs are depleted (Rooney 2009, Fulbright and Ortega-S 2013). Nicholson et al. (2006) suggested that dietary niche broadens when forbs are available to deer. In Tennessee, white-tailed deer became less selective when high-quality forage was abundant and were more selective during autumn and winter when forage was less abundant (Weckerly and Kennedy 1992). Increased selectivity when forage was less abundant suggests that the dietary niche of deer may have contracted, rather than expanding as predicted by foraging theory.

Indices of diversity including the Shannon-Wiener and Simpson's indices are often used as estimates of dietary niche breadth (Sargeant 2007). Diversity indices are based on species richness and evenness and increase in magnitude as the values of these variables increase (Sargeant 2007). Evenness is greatest when proportions of each plant species in the diet are similar; if one plant species composes most of the diet then evenness is low. Estimating richness and evenness, therefore, helps to explain whether the number of plant species consumed or relative amount of each species consumed has greater influence on estimates of niche breadth.

Our objectives were to determine whether a fourfold increase in white-tailed deer population density resulted in (1) differences in niche breadths, plant species diversity, richness, and evenness of white-tailed deer diets and (2) greater relative amounts of browse in white-tailed deer diets. We hypothesized that resource depletion at higher population densities should result in reduced intraspecific diet overlap and less similarity between individual deer at the plant species scale compared to low deer densities. Therefore, we compared mean diet similarity and diet overlap between pairs of individuals within each deer density at the plant species scale. A third objective was to determine if drought results in dietary niche breadth contraction and reduced dietary plant species diversity, richness, and evenness. We developed

the third objective a posteriori because climate conditions during our study were such that sampling during each season fortuitously occurred under both drought and non-drought conditions.

METHODS

Study locations

Our field studies were conducted at two different locations (28.60° N, 100.09° W and 28.28° N, 100.00° W) in Dimmit County near Carrizo Springs, TX within the Texas-Tamaulipan Thornscrub ecoregion (Griffith et al. 2004). Research facilities were established at each location in 2004 as part of a long-term research project. Predominant soils are sandy to clay loams of the Randado-Tonio-Brundage and Tonio-Webb-Uvalde-Zapata soil associations (Natural Resources Conservation Service 1985). Mean annual temperature for the western portion of south Texas from 1900 to 2000 was 21.2°C, with mean annual minimum and maximum temperatures of 14.5°C and 28°C, respectively (Norwine et al. 2007). Mean annual precipitation from 1900 to 2000 in the region was 593 mm. Annual precipitation is highly variable with a coefficient of variation of 35% (Norwine and Bingham 1985).

Vegetation at the study sites is diverse when rainfall is adequate. Prominent shrubs include blackbrush (*Acacia rigidula*), honey mesquite (*Prosopis glandulosa*), granjeño (*Celtis pallida*), whitebrush (*Aloysia gratissima*), guajillo (*Acacia berlandieri*), guayacán (*Guaiacum augustifolium*), and twisted acacia (*Acacia schaffneri*). Forbs include lazy daisy (*Aphanostephus* spp.), low menodora (*Menodora heterophylla*), rain lily (*Cooperia drummondii*), orange zexmenia (*Wedelia hispida*), sida (*Sida* spp.), and field ragweed (*Ambrosia confertiflora*); grasses such as pink pappusgrass (*Pappophorum bicolor*), buffelgrass (*Cenchrus ciliare*), red grama (*Bouteloua trifida*), Hall's panicum (*Panicum hallii*), and curly mesquite (*Hilaria belangeri*); and cacti include prickly pear (*Opuntia* spp.) and tasajillo (*Opuntia leptocaulis*).

At each location in 2004, we constructed 2 81-ha research enclosures surrounded by a 2.5-m tall woven-wire fence to prevent movement of deer among enclosures. Water troughs were centrally

located in each enclosure. Deer density treatments were randomly assigned to enclosures at each location. Target numbers of deer for low and high deer densities in our research enclosures were 10 (12 deer/km²) or 40 (50 deer/km²), respectively, at each of the two locations. All enclosures had a target sex ratio of 1 male to 1.5 females. We based selection of these target densities on the range of white-tailed deer densities documented using mark-resight techniques from helicopters within the western portion of south Texas (DeYoung 1985, DeYoung et al. 1989). Deer were stocked into or removed from enclosures to achieve desired densities at both locations, and all deer handled were marked with uniquely colored and numbered ear tags. Dense vegetation in enclosures restricted visibility of deer; therefore, we estimated deer populations twice each year (October and January) using trail camera surveys (Moore et al. 2013). Each survey was 4–6 weeks long and four cameras were placed in each enclosure. We used mark-resight models in Program MARK to estimate deer populations (White and Burnham 1999). Estimates of population sizes during the study period (summer 2009–spring 2011) were 15 (SE = 1, $n = 4$) deer/km² and 17 (SE = 1) deer/km² in low deer density enclosures during June and January, respectively, and 52 (SE = 5) deer/km² and 51 (SE = 6) deer/km² in high density enclosures during June and January, respectively (N. Cook, unpublished data). Population size was adjusted during March and December each year to maintain target densities. We used aerial gunning to remove deer and aerial captures from a helicopter to add deer (DeYoung 1988). Deer placed in enclosures were free-ranging and were caught using a net-gun fired from a helicopter <15 km from the enclosures.

Bite counts

Tame white-tailed deer forage similarly to wild deer (Spalinger et al. 1997, Davis 2003). We used tame females to estimate deer diets at our study sites using the bite count method (e.g., Parker et al. 1993). Study animals were either captured as fawns in the wild or were taken from their mothers at the Alfred and Margaret Alkek Ungulate Research Facility, Texas A&M University, Kingsville, USA. Fawns were acclimated to human presence and were bottle-fed until

weaned. They were marked with numbered ear tags for identification. When ≥ 1 year of age, females selected for the study were fitted with radio transmitters and released into the enclosures. Each tame female deer resided permanently in the enclosure in which they were released. Deer were used for sampling when they were in an enclosure for ≥ 4 weeks. We attempted to maintain three tame female white-tailed deer in each enclosure for a total of 12 tame deer (3 tame deer \times 2 deer densities \times 2 enclosures). Occasional mortalities caused tame deer numbers to vary from 10 to 12 during each sampling season. Each tame female was visited at least once/week to maintain familiarity with humans and facilitate data collection. We conducted bite counts during each of 4 seasons each year from summer 2009 to spring 2011: winter (January–February), spring (April–May), summer (June–August), and autumn (October–November).

Our goal was to record 2 hr of foraging time per deer during each sampling season for a total of 12 hr of foraging time/density/season/year (3 deer/enclosure \times 2 hr \times 2 enclosures/density). Bite count sessions took place around dawn and dusk because most white-tailed deer foraging is crepuscular (Webb et al. 2010). We attempted to record equal foraging time during morning and evening (e.g., ≈ 1 hr morning time and ≈ 1 hr evening time for each deer). We recorded no more than 45 minutes of foraging data during a single bite count session to ensure that data accurately represented each deer's foraging habits and were not biased towards its choices during that visit.

During sampling, we located study animals using radio telemetry. Once the focal animal began foraging, we used a digital voice recorder to record data. We recorded a start time and only recorded data while the deer was actively foraging. We defined active foraging as any time a deer was biting, chewing, or manipulating vegetation for consumption. If we lost sight of a deer, a stop time was recorded followed by a restart time once the deer was found and renewed foraging activity. Distances from focal animals during data collection ranged from < 1 m to 30 m, but a majority of observations were ≤ 10 m.

We identified plants consumed to species when possible; otherwise, plants were identified

to genus. For each bite, we recorded the part of each plant consumed (e.g., leaves, flowers, stem, or mast) and described the size of each bite using the following criteria:

- Bite 1: Leaves only on a shrub; a small bite on herbaceous plants, mast, or flowers (how small, medium, and large bites of each class were quantified is presented later).
- Bite 2: Leaves and little stem (mostly non-lignified) on a shrub; a moderate-sized bite on herbaceous plants, mast, or flowers.
- Bite 3: Leaves and lignified portions of stem on a shrub (often clipped with molars); a large bite on herbaceous plants, mast, or flowers.

Bite sizes varied for each species and plant part in each season. We recorded flower bites only if the tame female specifically ate flowers. If the deer incidentally ate a flower along with a large bite of a shrub or forb leaves, we recorded this as a shrub or forb bite. Once a foraging session ended, we recorded the stop time and ended the recording. We uploaded voice recordings to a computer. We then totaled bites by size and species.

Forage collection and analysis

During each sampling period, we collected representative bites of each bite size category for each forage item that comprised $> 0.1\%$ of the total bites recorded for an enclosure. We determined the average mass per bite for each bite size category for each species by drying the representative bites at 40°C (or by lyophilization in the case of cacti and some mast) to a constant mass, measuring the dry mass, then dividing by the total number of representative bites collected.

We assigned plant species and parts consumed into nine forage classes (forbs, shrubs, grasses, half-shrubs, cacti/succulents, mast, fungi, flowers, and litter [dead leaves of shrubs]). We determined relative percent composition of each species and forage class in the diet on a dry matter basis during each sampling period by multiplying the bite weight and bite total for each forage item for each deer. For those forage items that comprised $\leq 0.1\%$ of a female's diet, we assigned an average bite weight from the corresponding forage class of that item.

Drought assessment

We used the Palmer Z Index (National Oceanic and Atmospheric Administration 2012a) to assess drought conditions during bite count sampling periods. Because of potential climate-related lag effects and sampling periods typically lasting 1 month, we used the 2-month average Palmer Z Index value for each sampling period (summer = June/July, autumn = October/November, winter = December/January, and spring = March/April). We defined drought on our study sites as any period with a Palmer Z Index value <0 and non-drought as any period with a value ≥ 0 .

Data and statistical analyses

Mean forage class percent composition, diet diversity, and diet breadth/deer.—Differences between treatments in mean percent composition of each forage class in the diet/deer/enclosure were compared using ANOVA. To explore how deer density may influence diet diversity, we first determined dietary plant species richness for each deer in each sampling period by tallying all plant and fungi species each deer consumed (≥ 1 bite taken). If a female deer took bites from more than one forage class from a single plant species in a season (e.g., bites taken of both prickly pear mast and pads), we counted that species only once. We calculated the Shannon-Wiener measure of diet diversity (Whittaker 1972) at the species and forage class scales for each deer in each season as follows:

$$H' = -\sum_{i=1}^n p_i \log p_i$$

where n is dietary plant species or forage class richness and p_i is the proportion of the i th species or forage class used by each individual. The greater H' , the more diverse the diet. We also calculated Simpson's index of diversity (Whittaker 1972) at the forage class and species scales for each deer in each season as follows:

$$C = \sum_{i=1}^n p_i^2$$

where n is dietary plant species or forage class richness and p_i is the proportion of the i th species or forage class used by each individual. We subtracted each Simpson index value from 1

(Whittaker 1972) so that the greater the value, the more diverse the diet. Proportions used in the calculations of all diet indices were relative amounts of each species on a dry matter basis in the diet of each deer. We used the number of species eaten/deer/enclosure and the Shannon-Wiener and Simpson values calculated for each deer/enclosure as dependent variables in statistical analyses.

To test for differences in diet equitability, we also calculated diet breadth (Pianka 1973) at the species and forage class scales for each deer in each season using the equation:

$$B = 1 / \sum_{i=1}^n p_i^2.$$

This equation is simply the inverse of Simpson's index with values ranging from 1 (diet concentrated on one species) to the total number of species consumed by a deer (even distribution of forage species in the diet). We determined diet evenness (e.g., Wegge et al. 2006) at both the forage class and species scales using:

$$J' = \frac{H'}{\ln n}$$

where H' is the Shannon-Wiener diversity index value and n is the number of species or forage classes used by each individual. The evenness measure provides a standardized scale of the Shannon-Wiener index with values ranging from 0 (diet concentrated on one species) to 1 (even distribution of forage species in the diet). We used the breadth and evenness values/deer/enclosure as dependent variables in statistical analyses.

Diet similarity and overlap among pairs of individuals.—To test whether or not density influenced how similar individuals foraged with respect to one another, we determined diet similarity among deer within enclosures in each season at the species scale using Sorensen's similarity index (Koleff et al. 2003) for presence/absence data. We calculated similarity between all possible pairs of deer within an enclosure as follows:

$$S_S = \frac{2a}{2a + b + c}$$

where a is the number of species common to both deer, b is the number of species unique to deer 1,

and c is the number of species unique to deer 2. We also calculated the Bray-Curtis index (Bray and Curtis 1957) between all pairs of deer within an enclosure, which incorporates the proportion of each species in the diet of an individual deer. The Bray-Curtis index is calculated as:

$$S_{BC} = 100 \left(1 - \frac{\sum_i^n |p_{ij} - p_{ik}|}{\sum_i^n p_{ij} + \sum_i^n p_{ik}} \right)$$

where p_{ij} and p_{ik} are the proportions of the i th species in the diets of the j th and k th deer, respectively. Sorensen and Bray-Curtis index values were calculated using the “resemblance” procedure in PRIMER v6 (Clarke and Gorley 2006), and were expressed as percent similarity. We calculated diet overlap among all pairs of deer within an enclosure at both the forage class and species scales following Pianka (1973):

$$O_{ij} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of the i th species or forage class in the diets of the j th and k th deer, respectively. Pianka’s overlap equation was calculated using package “pgirmess” (Giraudoux 2011) in R version 2.13.0 (R Development Core Team 2008). Values for Pianka’s overlap equation range from 0 (no overlap) to 1 (complete overlap), but we expressed these as percent overlap. Because these diet similarity and overlap indices only make pair-wise comparisons, a single similarity and overlap value was determined for each enclosure by averaging the values calculated between all possible pairs within an enclosure in each sampling period. This value was used as the dependent variable in statistical analyses.

Statistical model

Distributional properties of ecological diversity indices should be considered when parametric statistical techniques are used to compare treatments with respect to these indices. For example, species richness is a discrete random variable that represents a count datum, and as such it may be questioned whether richness follows a normal distribution. Bowman et al. (1971) studied distributional properties of Shannon’s index and a modification of Simpson’s index. He found that Shannon’s index may be more nearly normally

distributed when probabilities of species’ occurrence in a sample follow MacArthur’s “broken stick” model or are equally probable than the modification of Simpson’s index.

Permutation-based analysis of variance provides an alternative approach for analyzing variables whose distributional properties may not satisfy normal-based theory. In this approach, the “usual” F statistic is computed from the data. Data are then “randomly permuted” among the experimental units, and an F statistic is calculated for each “reshuffled” data set. The significance of the initial F statistic is evaluated by comparing it to the generated population of F statistics from the permutation data sets rather than the tabular F statistic that relies on parametric assumptions.

We used permutation-based analyses (using 10,000 permutations) with the software PERMANOVA+ (Clarke and Gorley 2006) and normal-based analyses (PROC MIXED; SAS Institute, Cary, North Carolina, USA; Littell et al. 2006) for the diversity indices. In general, both techniques led to very similar conclusions, particularly if the permutation analyses used Monte Carlo tests, suggesting that the diversity indices approximately followed a normal distribution; therefore, we chose to use normal distribution-based statistical techniques to analyze diversity index data.

The study design was a randomized complete block with repeated measures across seasons (4) for 2 years, resulting in eight sampling periods. Blocking by location, we used a repeated measures analysis of variance (ANOVA) with Satterthwaite’s degrees of freedom in SAS 9.2 (Littell et al. 2006) to test for differences in deer diet selection. We included location and location \times treatment as random effects. Independent variables in the model were treatment (density) and the eight sampling periods.

For tests of diet diversity (richness, Shannon, Simpson), equitability (breadth, evenness), and forage class utilization (percent composition), we used deer as the subject in the model. We also modeled 6 covariance structures (first order autoregressive, Toeplitz, univariate autoregressive-moving average, variance components, heterogeneous autoregressive, and compound symmetry) in two steps. First, we modeled the covariance structures for the error term that tested the effects of period and period \times density

Table 1. Two-month average Palmer Z Index values (Texas, Climate Division 9; National Oceanic and Atmospheric Administration 2012a) and drought conditions for bite count sampling seasons from summer 2009 to spring 2011 in Dimmit County, Texas.

Sampling season	Begin-end date	Months selected for Palmer	Palmer Z value	Condition
Summer 2009	6 Jul–5 Aug	Jun/Jul	–2.69	Drought
Autumn 2009	19 Oct–22 Nov	Oct/Nov	0.88	Non-drought
Winter 2010	9 Jan–5 Feb	Dec/Jan	2.29	Non-drought
Spring 2010	15 Apr–7 May	Mar/Apr	3.50	Non-drought
Summer 2010	21 Jun–25 Jul	Jun/Jul	4.48	Non-drought
Autumn 2010	11 Oct–14 Nov	Oct/Nov	–1.41	Drought
Winter 2011	7 Jan–24 Jan	Dec/Jan	–0.12	Drought
Spring 2011	20 Apr–3 May	Mar/Apr	–2.58	Drought

and selected the model with the lowest AIC_C value. We then modeled the same six covariance structures for the error associated with deer-deer variation (while keeping the covariance structure selected in step 1 set for the error term testing period and period \times density), and again selected the model with the lowest AIC_C value to use as the final model. When 2 AIC_C values were similar (<2 units apart), we selected the model with the covariance structure that estimated the fewest parameters.

For tests of diet similarity (Sorensen, Bray-Curtis) and overlap within enclosures, we used enclosure as the subject because we determined an average similarity and overlap value among all possible pairs within an enclosure. We modeled the same six covariance structures for the error term that tested the effects of period and period \times density alone because there was no longer an error term associated with deer-deer variation. We chose the model with the lowest AIC_C value following the criteria described above.

We used contrast statements to test for the effects of season, drought (which was defined as a combination of year and season, based on Palmer Z Index results), and their interaction, and interactions of season \times density, drought \times density, and drought \times season \times density. Significant interactions were followed by tests of simple main effects and simple effects (Kirk 1995). Given the spatial scale of our experiment, it was impractical to install more than two true replications (study locations). Under these conditions, we were concerned about failing to detect real effects in our data, and so we increased our nominal alpha level to 0.10 for all statistical tests. Standard errors are presented

with means unless otherwise stated.

RESULTS

During the two years of our study, we observed 2 animals/enclosure during 41% of our sampling time and 3 animals/enclosure 59% of the time. Combined, we observed 241,166 bites taken from 137 plant species during 165 hr of recorded foraging time. We also recorded bites removed from a lichen, an ephemeral fungus of twisted acacia stems (“rust”), an unidentified mushroom, and 5 unidentified forb species.

Drought patterns

Our study began at the end of a severe drought in summer 2009, followed by four consecutive wet periods through summer 2010; drought began again in autumn 2010 and continued through the end of our study (Table 1). The period January–July 2010 was the second wettest 7-month period in history for the region; the period October 2010–April 2011 was the second driest 7-month period (National Oceanic and Atmospheric Administration 2012b).

Diet diversity, breadth, and evenness

White-tailed deer density did not significantly ($P > 0.17$) affect measures of diet richness (number of species eaten/deer), diversity, breadth, or evenness; and there were no interactions between density and drought or density and season. The effect of drought on diet richness and values of the Shannon-Wiener, Simpson, evenness, and breadth indices varied ($P < 0.07$) by season (Tables 2 and 3). Averaged across deer densities, diet richness was 34–75% greater in non-drought conditions than in drought condi-

Table 2. Seasonal least square means (\pm SE) of index values for plant species (richness/deer, Shannon, Simpson, Evenness, Breadth, Sorenson) or forage classes (diet overlap among individuals) in white-tailed deer diets averaged across density treatments in drought and non-drought conditions in summer and autumn from 2009 to 2010, in Dimmit County Texas. Significant differences between drought and non-drought means ($P < 0.10$) for each index are denoted with an asterisk (*).

Index	Summer		Autumn	
	Drought	Non-drought	Drought	Non-drought
Richness/deer	18 \pm 4	28 \pm 4*	19 \pm 4	23 \pm 4
Shannon	1.34 \pm 0.20	1.65 \pm 0.19	1.49 \pm 0.20	1.60 \pm 0.20
Simpson	0.61 \pm 0.05	0.63 \pm 0.06	0.65 \pm 0.06	0.68 \pm 0.06
Evenness	0.45 \pm 0.04	0.50 \pm 0.05	0.52 \pm 0.04	0.51 \pm 0.04
Breadth	2.88 \pm 0.56	3.78 \pm 0.83	3.19 \pm 0.63	3.78 \pm 0.62
Sorensen (%)	68 \pm 4	60 \pm 4	63 \pm 4	62 \pm 4
Bray-Curtis (%)	64 \pm 8	43 \pm 8	60 \pm 8	58 \pm 8
Overlap (%)	98 \pm 4	79 \pm 4*	85 \pm 4	95 \pm 4

tions during summer, winter, and spring but was similar during autumn. Diversity, breadth, and evenness tended to be greater in all non-drought periods but only differed significantly during spring. We found no significant ($P > 0.10$) main effects or interactions of density, drought, or season for diet diversity, breadth, or evenness at the forage class scale.

Diet similarity and overlap among individuals

Mean diet overlap and similarity among individuals within enclosures did not vary significantly ($P > 0.18$; no interactions between density and drought or season) between density treatments. For diet similarity, drought and season interacted ($F_{3,16} = 2.48$, $P = 0.098$) based on presence/absence data as measured by the Sorensen similarity index, but mean similarity did not differ significantly between drought and

non-drought in any season (Tables 2 and 3). Sorensen similarity among individuals tended to be greater in drought conditions during summer and autumn and greater in non-drought conditions during spring and winter. We did not detect any significant ($P > 0.15$) effects of density, drought, or season based on the Bray-Curtis similarity index or diet overlap at the species scale, although Bray-Curtis similarity tended to be greater in drought conditions during all seasons. At the forage class scale, the effect of drought on diet overlap among individuals within enclosures varied ($F_{3,5.08} = 9.81$, $P = 0.015$) with season with overlap among individuals being significantly lower in non-drought conditions during summer.

Diet composition at the forage class scale

Averaged across seasons, treatments, and

Table 3. Seasonal least square means (\pm SE) of index values for plant species (richness/deer, Shannon, Simpson, Evenness, Breadth, Sorenson) or forage classes (diet overlap among individuals) in white-tailed deer diets averaged across density treatments in drought and non-drought conditions in winter and spring from 2010–2011, in Dimmit County Texas. Significant differences between drought and non-drought means ($P < 0.10$) for each index are denoted with an asterisk (*).

Index	Winter		Spring	
	Drought	Non-drought	Drought	Non-drought
Richness/deer	17 \pm 4	26 \pm 4*	10 \pm 4	42 \pm 4*
Shannon	1.67 \pm 0.19	2.01 \pm 0.20	1.18 \pm 0.20	2.63 \pm 0.19*
Simpson	0.72 \pm 0.05	0.78 \pm 0.05	0.54 \pm 0.08	0.89 \pm 0.04*
Evenness	0.60 \pm 0.02	0.62 \pm 0.03	0.51 \pm 0.07	0.70 \pm 0.01*
Breadth	4.10 \pm 0.75	5.32 \pm 0.86	2.66 \pm 0.61	9.57 \pm 0.90*
Sorensen (%)	70 \pm 4	74 \pm 4	62 \pm 4	67 \pm 4
Bray-Curtis (%)	59 \pm 8	52 \pm 8	49 \pm 8	45 \pm 8
Overlap (%)	60 \pm 16	92 \pm 4	94 \pm 4	79 \pm 12

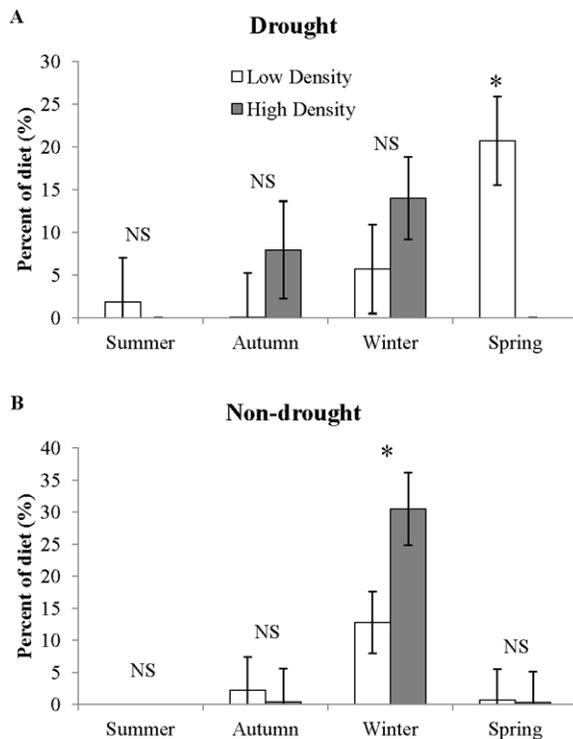


Fig. 1. Seasonal least square means for proportion of cacti/succulents (% of diet \pm SE) in white-tailed deer diets in high and low density treatments under drought (A) and non-drought (B) conditions from summer 2009 to spring 2011, in Dimmit County, TX. Where no bar is present, cacti/succulents were not consumed. Pairs of means accompanied by an asterisk are significantly different ($P < 0.10$).

moisture conditions, shrubs comprised a majority of diets (43%), followed by forbs (23%), mast (22%), cacti/succulents (6%), flowers (4%), half-shrubs (1%), grasses (1%), litter (<1%), and fungi (<1%).

Cacti/succulents.—Drought and season interacted ($F_{7,65.1} = 65.1$, $P = 0.019$) with treatment for percent composition of cacti/succulents, so we examined the nature of the interaction using contrast statements. During drought, deer in low density enclosures consumed more cacti than deer in high density enclosures during spring (Fig. 1A). Cacti consumption was similar between density treatments in all other seasons. During non-drought, cacti consumption was 138% greater in the high density treatment during winter and was similar in all other

seasons (Fig. 1B).

Flowers.—Consumption of flowers was not statistically different ($F_{1-7,14.3} = 0.16-0.28$, $P > 0.606$) between density treatments (Fig. 2). Averaged across treatments and moisture conditions, flower consumption was greatest ($F_{3,14.3} = 2.68$, $P = 0.086$) in spring and <1% in all other seasons (Table 4).

Forbs.—Forb composition of deer diets was similar between density treatments ($F_{1-7,6.38-6.97} = 0.33-3.14$, $P > 0.121$; Fig. 2). We detected an interaction ($F_{3,6.88} = 3.13$, $P = 0.098$) between drought and season for forb consumption. Averaged across treatments, the percentage of forbs in deer diets was greater in non-drought conditions during summer, winter, and spring, but was similar during autumn (Table 5).

Fungi and litter.—Density had no effect on the percentage of fungi ($F_{1-7,1.02-16.1} = 0.04-2.24$, $P > 0.123$) and litter ($F_{1-7,2-22.3} = 0.87-1.12$, $P > 0.302$) in deer diets (Fig. 2).

Grasses.—Averaged across all seasons and drought/non-drought, grass composed <2% of deer diets. Percentage of grass in deer diets was greater in high-density enclosures ($1.3 \pm 0.4\%$) than low density ($0.3 \pm 0.3\%$; $F_{1,2} = 4.33$, $P = 0.059$). The effect of drought on grass consumption varied by season ($F_{3,17.2} = 3.34$, $P = 0.044$). Averaged across density treatments, the proportion of grass in deer diets was 2.2 percentage points greater under non-drought conditions during summer, and similar between drought categories in all other seasons (Table 5).

Half-shrubs.—Deer density had no effect ($F_{1-7,1.98-13.5} = 0.43-2.04$, $P > 0.176$) on the proportion of half-shrubs in deer diets (Fig. 2). We detected a drought \times season interaction ($F_{3,13.5} = 4.12$, $P = 0.028$) for half-shrub consumption. The percentage of half-shrubs in deer diets was about 4.2 percentage points greater under drought conditions during winter, and was similar between drought and non-drought in all other seasons (Table 5).

Mast.—Mast consumption did not vary ($F_{1-7,15} = 0.00-0.22$, $P > 0.651$) between density treatments (Fig. 2). Mast in diets did vary ($F_{3,15} = 7.59$, $P = 0.003$) among seasons when averaged across treatment and drought and non-drought. Mast consumption was greatest during summer and the least during winter (Table 4).

Shrubs.—Percentage of shrubs in diets was

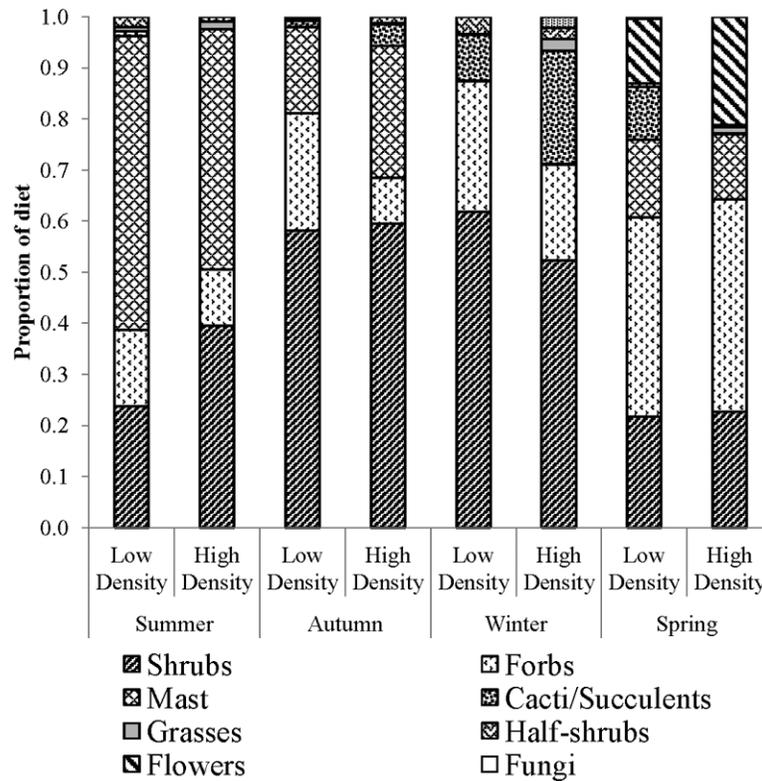


Fig. 2. Seasonal least square means for percent composition of 9 forage classes consumed by white-tailed deer averaged across drought and non-drought from summer 2009 to spring 2011, in Dimmit County, TX.

similar ($F_{1-7,15.4} = 0.09-0.57$, $P > 0.629$) between deer densities (Fig. 2). When averaged across seasons and density treatments, the proportion of shrubs in deer diets was 65% greater ($F_{1,15.4} = 7.54$, $P = 0.015$) under drought conditions than non-drought conditions ($53 \pm 22\%$ vs. $32 \pm 22\%$, respectively). Consumption of shrubs varied

($F_{3,15.4} = 5.65$, $P = 0.008$) seasonally when averaged across treatment and drought/non-drought. The proportion of shrubs in deer diets was greatest during winter and autumn (Table 4).

DISCUSSION

Greater numbers of competitors did not result in dietary niche expansion by female white-tailed deer as predicted by foraging theory. In contrast to predictions based on foraging theory, differences in food resources between deer densities were too subtle for differences in dietary niche breadth to occur, despite low and high densities in the enclosures having been maintained for >5 years before the study began. The prediction that dietary niche breadth expands with increased animal density is based on the theory that selective foraging reduces resource availability, forcing deer to forage on a wider variety of plants (Svanbäck and Bolnik 2007). Predictions of

Table 4. Least square means (\pm SE) for percent composition of forage classes in white-tailed deer diets averaged across density treatments and moisture conditions from summer 2009-spring 2011, in Dimmit County, TX. Seasonal means within forage classes with the same letter are not statistically different ($P > 0.10$).

Forage class	Season			
	Summer	Autumn	Winter	Spring
Flowers	0 \pm 0 ^a	<1 \pm 6 ^a	0 \pm 0 ^a	17 \pm 6 ^b
Mast	51 \pm 14 ^a	21 \pm 14 ^b	<1 \pm 14 ^c	14 \pm 14 ^{bc}
Shrubs	31 \pm 23 ^a	57 \pm 23 ^b	58 \pm 23 ^b	23 \pm 23 ^a

Table 5. Least square means (\pm SE) for percent composition of forage classes in white-tailed deer diets averaged across density treatments from summer 2009–spring 2011, in Dimmit County, TX. Effect of drought varied among seasons for all forage classes presented. Significant tests of drought within season ($P < 0.10$) are denoted with an asterisk (*).

Forage class	Summer		Autumn		Winter		Spring	
	Drought	Non-drought	Drought	Non-drought	Drought	Non-drought	Drought	Non-drought
Forbs	0 \pm 0	28 \pm 8*	6 \pm 8	25 \pm 8	4 \pm 8	41 \pm 8*	10 \pm 8	74 \pm 8*
Grasses	<1 \pm 0	2 \pm 1*	<1 \pm <1	<1 \pm <1	<1 \pm <1	2 \pm 2	1 \pm 1	1 \pm <1
Half-shrubs	2 \pm 1	1 \pm 1	1 \pm 1	1 \pm 1	5 \pm 1	1 \pm 1*	0 \pm 1	1 \pm 1

traditional theory may be less applicable to herbivore impacts on vegetation in arid and semiarid environments (Augustine and McNaughton 1998). Several investigators have suggested that grazing animals and vegetation are more weakly coupled in environments such as southern Texas where precipitation is highly variable than in more stable, mesic environments (Ellis and Swift 1988, Illius and O'Connor 1999, Gordon and Prins 2008).

Environmental stochasticity was likely a major reason for the lack of differences in resource availability between deer density treatments. In the following discussion, we first present evidence supporting our conclusion that differences in resource availability between density treatments were minimal. Second, we posit how variation in precipitation along with temporally heterogeneous phenology of vegetation and foraging strategies of white-tailed deer may result in a lack of differences in dietary niche breadth despite a four-fold difference in deer density. Our results may help to clarify some of the ways in which highly variable patterns of precipitation and timing of plant growth may drive plant-herbivore interactions.

The similarity in forage class composition of deer diets between densities is evidence for the lack of a reduction in food availability between deer densities. We observed subtle differences, such as a slight, but statistically insignificant, increase in grass consumption and increased use of succulents during winter at high densities. However, we did not observe a shift from forbs to other forage classes such as occurred in response to increasing white-tailed deer density in studies by Kie et al. (1980) and Daigle et al. (2004).

Data collected in companion studies conducted at the same time in our enclosures on diet quality,

forb and browse standing crop, and plant species richness between density treatments also supports the contention that increasing deer density did not result in resource depletion. Diet quality should decline with increasing density because higher quality plants should become less available (Nicholson et al. 2006). However, diet quality was similar between densities in studies with tame deer conducted concurrently with the research reported herein (Gann 2012). These results suggest that there was little difference in availability of high quality plants between densities. Lack of differences in resource availability between treatments is also supported by vegetation data collected in companion studies in our enclosures. Forb standing crop, forb species richness, percent canopy cover of forbs and browse palatable to deer, and browse standing crop were also similar between densities during 2004–2012; however, these vegetation parameters varied substantially among years (Crider 2012, Priesmeyer 2013).

Resource availability and dietary niche breadth were similar between deer density treatments in part because switching from periods of high precipitation to drought apparently overrode herbivore impacts on plants; i.e., lack of precipitation reduced plant biomass more than deer did. Forage was abundant during periods of high precipitation and was not depleted at high densities. Consequently, deer diet composition was similar between density treatments; June–July 2010 is an example of such a period (Table 1; Crider 2012). Periods of moisture availability were relatively short-lived; e.g., by October 2010 drought prevailed. During severe drought, such as June–July 2009, dietary niche expansion was restricted because forbs were absent from deer diets and drought-deciduous shrubs defoliated. Browse standing crop was 3.5 times greater

during the wet period in summer 2010 than in summer 2009, averaged across deer densities (Crider 2012).

Seasonal variation in abundance of forbs and mast also increases the complexity of herbivore–plant interactions, and partly explains lack of dietary niche expansion in response to increased deer density. Asynchronous phenology of vegetation in semiarid environments may limit foraging selectivity of ungulates (Augustine and McNaughton 1998, Searle et al. 2010). Production of alternative food resources at different times of the year may reduce the likelihood that an individual food resource will be depleted. Mast was produced primarily during summer and composed up to 80% of deer diets in summer during our study regardless of deer density (Timmons et al. 2010). *Prosopis glandulosa* pods and *Opuntia lindheimeri* fruits were important components of the mast consumed (Timmons et al. 2010). Mast production of these species is not reduced by drought (Lee and Felker 1992, Bowers 1997). Evidently, *Prosopis glandulosa* may increase pod production during drought (Lee and Felker 1992). Presence of mast as an alternative food resource alleviated foraging pressure on woody plants during summer and browsing was most pronounced during autumn and winter. Reduced foraging pressure perhaps provided time for compensatory growth of woody plants when moisture was available (Teaschner and Fulbright 2007). Forbs comprised a large portion of deer diets during moist springs, which may have further reduced browsing pressure on shrubs. About 44% of the forb species eaten by deer in our study area are annuals that are most productive during late winter and spring. In addition, many of the perennial forbs in our study area function like annuals (Schaal and Leverich 1982). The ephemeral nature of annual forbs allow them to avoid foraging pressure during most of the rest of the year, thereby attenuating effects of high deer densities.

A final reason that dietary niche breadth was similar between densities is that white-tailed deer are highly plastic foragers. White-tailed deer consume a variety of different plant species, and part of the feeding strategy of ruminants such as white-tailed deer is to mix diets to optimize nutritional content and avoid malaise

caused by ingestion of plants high in secondary compounds (Provenza et al. 2003). Niche breadth may remain similar between densities because deer employ this foraging strategy regardless of density. In years of higher precipitation when more plant species were available, white-tailed deer expanded their dietary niche to take advantage of the more diverse plant community. The more diverse plant community resulting from greater rainfall enabled deer to mix a greater variety of plant species to optimize diet quality than was possible during drought.

Drought would be expected to result in increased dietary niche width (Owen-Smith 1994), the opposite of our findings. Dietary niches were contracted during drought compared to non-drought in our study simply because fewer plant species were available; only species in the community that are drought-resistant or drought-tolerant are present for consumption. Environmental stochasticity can also drive plant-animal interactions in mesic environments; for example, depletion of forage by deer browsing may limit food choices during severe winters and cause diet expansion (Brown and Doucet 1991). Lack of diet expansion in our study occurred because lack of precipitation limited food choices rather than forage depletion by deer browsing.

Plant species richness of diets and dietary plant diversity were greater during non-drought periods in part because species richness of vegetation in our enclosures was up to threefold greater during greater during periods of non-drought than during drought (Priesmeyer 2013). Additionally, dietary plant species richness was greater during non-drought periods because plant species tended to be more evenly represented in deer diets during non-drought periods when forage was abundant.

Our results demonstrate that, for white-tailed deer, the expectation of dietary niche expansion in response to increasing population density is not robust across environments. Expression of density-dependent effects may be lacking in stochastic environments where environmental fluctuations have a greater impact on vegetation dynamics, and hence resource availability, than do herbivores (Ellis and Swift 1988). Much of the research on white-tailed foraging ecology and plant-animal interactions has been conducted in

regions with humid and subhumid climates (Russell et al. 2001, Rooney and Waller 2003) where density-dependent effects are more pronounced (Briske et al. 2003). Weak density-dependent effects resulting from environmental stochasticity have broad implications for our understanding of interactions between white-tailed deer and vegetation across the geographic range of the species.

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