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Linking White-Tailed Deer Density, Nutrition, and Vegetation in a Stochastic Environment

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ABSTRACT Density-dependent behavior underpins white-tailed deer (*Odocoileus virginianus*) theory and management application in North America, but strength or frequency of the phenomenon has varied across the geographic range of the species. The modifying effect of stochastic environments and poor-quality habitats on density-dependent behavior has been recognized for ungulate populations around the world, including white-tailed deer populations in South Texas, USA. Despite the importance of understanding mechanisms influencing density dependence, researchers have concentrated on demographic and morphological implications of deer density. Researchers have not focused on linking vegetation dynamics, nutrition, and deer dynamics. We conducted a series of designed experiments during 2004–2012 to determine how strongly white-tailed deer density, vegetation composition, and deer nutrition (natural and supplemented) are linked in a semi-arid environment where the coefficient of variation of annual precipitation exceeds 30%. We replicated our study on 2 sites with thornshrub vegetation in Dimmit County, Texas. During late 2003, we constructed 6 81-ha enclosures surrounded by 2.4-m-tall woven wire fence on each study site. The experimental design included 2 nutrition treatments and 3 deer densities in a factorial array, with study sites as blocks. Abundance targets for low, medium, and high deer densities in enclosures were 10 deer (equivalent to 13 deer/km^2), 25 deer (31 deer/km^2), and 40 deer (50 deer/km^2), respectively. Each study site had 2 enclosures with each deer density. We provided deer in 1 enclosure at each density with a high-quality pelleted supplement *ad libitum*, which we termed enhanced nutrition; deer in the other enclosure at each density had access to natural nutrition from the vegetation. We conducted camera surveys of deer in each enclosure twice per year and added or removed deer as needed to approximate the target densities. We maintained >50% of deer ear-tagged for individual recognition. We maintained adult sex ratios of 1:1–1:1.5 (males:females) and a mix of young and older deer in enclosures. We used reconstruction, validated by comparison to known number of adult males, to make annual estimates of density for each enclosure in analysis of treatment effects. We explored the effect of deer density on diet composition, diet quality, and intake rate of tractable female deer released into low- and high-density enclosures with natural nutrition on both study sites (4 total enclosures) between June 2009 and May 2011, 5 years after we established density treatments in enclosures. We used the bite count technique and followed 2–3 tractable deer/enclosure during foraging bouts across 4 seasons. Proportion of shrubs, forbs, mast, cacti, and subshrubs in deer diets did not differ ($P > 0.57$) between deer density treatments. Percent grass in deer diets was higher ($P = 0.05$) at high deer density but composed only $1.3 \pm 0.3\%$ (SE) of the diet. Digestible protein and metabolizable energy of diets were similar ($P > 0.45$) between deer density treatments. Likewise, bite rate, bite size, and dry matter intake did not vary ($P > 0.45$) with deer density. Unlike deer density, drought had dramatic ($P \leq 0.10$) effects on foraging of tractable deer. During drought conditions, the proportion of shrubs and flowers increased in deer diets, whereas forbs declined. Digestible protein was 31%, 53%, and 54% greater ($P = 0.06$) during non-drought than drought during autumn, winter, and spring, respectively. We studied the effects of enhanced nutrition on the composition and quality of tractable female deer diets between April 2007 and February 2009, 3 years after we established density treatments in enclosures. We also estimated the proportion of supplemental feed in deer diets. We used the 2 low-density enclosures on each study site, 1 with enhanced nutrition and 1 with natural nutrition (4 total enclosures). We again used the bite count technique and 2–3 tractable deer living in each enclosure. We estimated proportion of pelleted feed in diets of tractable deer and non-tractable deer using ratios of stable isotopes of carbon. Averaged across seasons and nutrition treatments, shrubs composed a majority of the vegetation portion of deer diets (44%), followed by mast (26%) and forbs (15%). Enhanced nutrition influenced the proportion of mast, cacti, and flowers in the diet, but the nature and magnitude of the effect varied by season and year. The

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trend was for deer in natural-nutrition enclosures to eat more mast. We did not detect a statistical difference ($P = 0.15$) in the proportion of shrubs in diets between natural and enhanced nutrition, but deer with enhanced nutrition consumed 7–24% more shrubs in 5 of 8 seasons. Deer in enhanced-nutrition enclosures had greater ($P = 0.03$) digestible protein in their overall diet than deer in natural-nutrition enclosures. The effect of enhanced nutrition on metabolizable energy in overall diets varied by season and was greater ($P < 0.04$) for enhanced-nutrition deer during summer and autumn 2007 and winter 2008. In the enhanced-nutrition treatment, supplemental feed averaged 47–80% of the diet of tractable deer. Of non-tractable deer in all density treatments with enhanced nutrition, 97% ($n = 128$ deer) ate supplemental feed. For non-tractable deer averaged across density treatments, study sites, and years, percent supplemental feed in deer diets exceeded 70% for all sex and age groups. We determined if increasing deer density and enhanced nutrition resulted in a decline in preferred forbs and shrubs and an increase in plants less preferred by deer. We sampled all 12 enclosures via 20, 50-m permanent transects in each enclosure. Percent canopy cover of preferred forbs was similar ($P = 0.13$) among deer densities averaged across nutrition treatments and sampling years (low density: = 8%, SE range 6–10; medium density: 5%, 4–6; high density: 4%, 3–5; SE ranges are presented because SEs associated with backtransformed means are asymetrical). Averaged across deer densities, preferred forb canopy cover was similar between nutrition treatments in 2004; but by 2012 averaged 20 ± 17–23% in enhanced-nutrition enclosures compared to 10 ± 8–13% in natural-nutrition enclosures ($P = 0.107$). Percent canopy cover of other forbs, preferred shrubs, other shrubs, and grasses, as well as Shannon's index, evenness, and species richness were similar ($P > 0.10$) among deer densities, averaged across nutrition treatments and sampling years. We analyzed fawn:adult female ratios, growth rates of fawns and yearlings, and survival from 6 to 14 months of age and for adults >14 months of age. We assessed adult body mass and population growth rates (lambda apparent, λ_{APP}) to determine density and nutrition effects on deer populations in the research enclosures during 2004–2012. Fawn:adult female ratios declined ($P = 0.04$) from low-medium density to high density in natural-nutrition enclosures but were not affected ($P = 0.48$) by density in enhanced nutrition enclosures although, compared to natural nutrition, enhanced nutrition increased fawn:adult female ratios by 0.15 ± 0.12 fawns:adult female at low-medium density and 0.44 ± 0.17 fawns:adult female at high density. Growth rate of fawns was not affected by deer density under natural or enhanced nutrition ($P > 0.17$) but increased 0.03 ± 0.01 kg/day in enhanced-nutrition enclosures compared to natural nutrition ($P < 0.01$). Growth rate of yearlings was unaffected ($P > 0.71$) by deer density, but growth rate increased for males in some years at some density levels in enhanced-nutrition enclosures. Adult body mass declined in response to increasing deer density in natural-nutrition enclosures for both adult males ($P < 0.01$) and females ($P = 0.10$). Enhanced nutrition increased male body mass, but female mass did not increase compared to natural nutrition. Survival of adult males was unaffected by deer density in natural- ($P = 0.59$) or enhanced- ($P = 0.94$) nutrition enclosures. Survival of adult females was greatest in medium-density enclosures with natural nutrition but similar at low and high density ($P = 0.04$). Enhanced nutrition increased survival of females ($P < 0.01$) and marginally for males ($P = 0.11$). Survival of fawns 6–14 months old was unaffected ($P > 0.35$) by density in either natural- or enhanced-nutrition treatments but was greater ($P = 0.04$) under enhanced nutrition. Population growth rate declined ($P = 0.06$) with increasing density in natural-nutrition enclosures but not ($P = 0.55$) in enhanced nutrition. Enhanced nutrition increased λ_{APP} by 0.32. Under natural nutrition, we found only minor effects of deer density treatments on deer diet composition, nutritional intake, and plant communities. However, we found density-dependent effects on fawn:adult female ratios, adult body mass, and population growth rate. In a follow-up study, deer home ranges in our research enclosures declined with increasing deer density. We hypothesized that habitat quality varied among home ranges and contributed to density-dependent responses. Variable precipitation had a greater influence on deer diets, vegetation composition, and population parameters than did deer density. Also, resistance to herbivory and low forage quality of the thornshrub vegetation of our study sites likely constrained density-dependent behavior by deer. We posit that it is unlikely that, at our high-density (50 deer/km^2) and perhaps even medium-density (31 deer/km^2) levels, negative density dependence would occur without several wet years in close association. In the past century, this phenomenon has only happened once (1970s). Thus, density dependence would likely be difficult to detect in most years under natural nutrition in this region. Foraging by deer with enhanced nutrition did not result in a reduction in preferred plants in the vegetation community and had a protective effect on preferred forbs because ≤53% of deer diets consisted of vegetation. However, enhanced nutrition improved fitness of individual deer and deer populations, clearly demonstrating that nutrition is limiting for deer populations under natural conditions in western South Texas.

KEY WORDS density dependence, forbs, nutrition, *Odocoileus virginianus*, selective foraging, shrubs, South Texas, stochasticity, supplemental feeding, vegetation dynamics.

Relier la Densité de Cerf de Virginie, la Nutrition et la Végétation dans un Environnement Stochastique

RÉSUMÉ Les comportements dépendants de la densité du cerf de Virginie (*Odocoileus virginianus*) orientent la compréhension et la gestion de ce dernier en Amérique du Nord, bien que l'intensité ou la fréquence de ce phénomène varie en fonction de la répartition géographique de l'espèce. L'effet modificateur des environnements stochastiques et des habitats de faible qualité sur les comportements qui dépendent de la densité est reconnu chez les populations d'ongulés à travers le monde, notamment chez les populations du cerf de Virginie dans le sud du Texas, États-Unis. Malgré l'importance de comprendre les mécanismes influençant la densité-dépendance, les chercheurs se sont davantage concentrés sur l'impact de la densité de cerfs sur la démographie et la morphologie de ceux-ci, au lieu d'établir des liens entre la dynamique de la végétation, l'alimentation et la dynamique des populations de cerfs. Nous avons mis en place une série de dispositifs expérimentaux durant la période 2004–2012 afin de déterminer la force des liens entre la densité de cerfs de Virginie, la composition de la végétation et l'alimentation (naturelle et dans des conditions d'approvisionnement). L'étude a eu lieu dans un environnement semi-aride dans lequel le coefficient de variation des précipitations annuelles excède 30%. Nous avons reproduit notre étude dans deux sites d'étude dont le couvert végétal est composé d'arbustes épineux, dans le comté de Dimmit, Texas. À la fin de l'année 2003, nous avons construit 6 enclos de 81 ha entourés d'une clôture barbelée de 2,4 m de hauteur dans chaque site d'étude. Le dispositif expérimental comprenait 2 traitements d'alimentation et 3 densités de cerfs dans un plan factoriel, avec les sites d'étude en blocs. L'abondance de cerfs ciblée pour représenter les faible, moyenne et forte densités a été établi à 10 cerfs (équivalent à 13 cerfs/km^2), 25 cerfs (31 cerfs/km^2) et 40 cerfs (50 cerfs/km^2), respectivement. Chaque site d'étude comprenait 2 enclos contenant chacun les 3 densités de cerfs. Dans l'un des deux enclos et pour chaque densité, les cerfs étaient nourris *ad libitum* d'une moulée de haute qualité, condition ci-après nommée alimentation enrichie. Dans le deuxième enclos et pour chaque densité, les cerfs s'alimentaient de la végétation naturellement présente dans le milieu. Nous avons effectué le suivi des cerfs dans chacun des enclos 2 fois par année, à l'aide de caméras. Nous avons ajouté ou retiré des cerfs pour conserver chaque densité de cerfs et >50% des cerfs étaient marqués à l'oreille pour la reconnaissance individuelle. Nous avons maintenu un sex-ratio adulte de 1:1–1:1.5 (mâles:femelles) dans les enclos, ainsi qu'un mélange de cerfs plus jeunes et plus âgés. Nous avons utilisé la reconstitution, validée en comparant le nombre connu de mâles adultes, pour estimer la densité annuelle de cerfs pour chaque enclos dans l'analyse des effets du traitement. Nous avons étudié les effets de la densité de cerfs sur la composition du régime alimentaire, la qualité du régime alimentaire et le taux d'ingestion des cerfs femelles domestiquées, relâchées dans des enclos à faible et forte densité. Elles avaient une alimentation naturelle dans les deux sites d'étude (4 enclos au total) entre juin 2009 et mai 2011, et ce 5 ans après que nous ayons établi les traitements de densité dans les enclos. Nous avons utilisé la technique du décompte de bouchées et avons suivi 2–3 cerfs domestiqués/enclos durant les périodes d'alimentation, pendant 4 saisons. La proportion d'arbustes, d'herbacées, de faînes, de cactus et de petits arbustes dans le régime alimentaire des cerfs n'était pas différente ($P > 0.57$) entre les traitements de densité de cerfs. Le pourcentage de graminées dans le régime alimentaire des cerfs était plus élevé ($P = 0.05$) dans le traitement à forte densité de cerfs, mais ne composait que 1.3 ± 0.3(ES) % du régime alimentaire. Les protéines digestibles et l'énergie métabolisable des régimes alimentaires étaient similaires ($P > 0.45$) entre les traitements de densité de cerfs. Également, le taux de bouchées, la taille des bouchées et l'ingestion de matière sèche ne variaient pas ($P > 0.45$) entre les traitements de densité de cerfs. Comparativement à la densité de cerfs, la sécheresse a eu des effets dramatiques ($P \leq 0.10$) sur l'alimentation des cerfs domestiqués. Dans des conditions de sécheresse, la proportion d'arbustes et de fleurs augmentait dans le régime alimentaire des cerfs alors que la proportion d'herbacées diminuait. Les protéines digestibles étaient 31%, 53%, et 54% supérieures ($P = 0.06$) durant la période sans sécheresse, comparativement à la période de sécheresse à l'automne, à l'hiver et au printemps, respectivement. Nous avons étudié les effets d'une alimentation enrichie sur la composition et la qualité du régime alimentaire de cerfs femelles domestiquées entre avril 2007 et février 2009, 3 ans après l'établissement des traitements de densité dans les enclos. Nous avons également estimé la proportion de suppléments dans les régimes alimentaires des cerfs. Nous avons utilisé 2 enclos à faible densité pour chaque site d'étude, dont un avec une alimentation enrichie et un avec une alimentation naturelle (4 enclos au total). Nous avons utilisé la technique du décompte de bouchées sur 2–3 cerfs domestiqués pour chaque enclos. Nous avons estimé la proportion de moulée dans les régimes alimentaires des cerfs domestiques et non-domestiques en utilisant des ratios d'isotopes stables du carbone. Les arbustes composaient la majorité de la portion végétation des régimes alimentaires des cerfs (44%), suivi des faînes (26%) et des herbacées (15%), corrigés pour les saisons et les traitements d'alimentation. L'alimentation enrichie influençait la proportion de faînes, de cactus et de fleurs dans le régime alimentaire, mais le sens et l'ampleur de l'effet variait selon la saison et l'année. La tendance pour les cerfs dans les enclos en condition d'alimentation naturelle était de consommer davantage de faînes. Nous n'avons pas détecté de différence

significative ($P = 0.15$) dans la proportion d'arbustes entre les traitements d'alimentation naturelle et d'alimentation enrichie, mais les cerfs avec une alimentation enrichie consommaient 7–24% plus d'arbustes pour 5 saisons sur 8 (interaction saison-année). Les cerfs avec une alimentation enrichie avaient une plus grande ($P = 0.03$) quantité de protéines digestibles dans leur régime alimentaire global que les cerfs dans les enclos en condition d'alimentation naturelle. L'effet de l'alimentation enrichie sur la quantité d'énergie métabolisable pour tous les régimes alimentaires variait selon la saison et était plus élevé ($P < 0.04$) pour les cerfs avec alimentation enrichie pendant l'été et l'automne 2007 et l'hiver 2008. Dans le traitement d'alimentation enrichie, les suppléments alimentaires représentaient en moyenne 47–80% des régimes alimentaires des cerfs domestiqués. De tous les cerfs non-domestiqués de chaque traitement de densité avec l'alimentation enrichie, 97% ($n = 128$ cerfs) ont consommé des suppléments alimentaires durant l'automne. Pour les cerfs non-domestiqués, le pourcentage de suppléments alimentaires dans les régimes alimentaires dépassait 70% pour tous les sexes et les groupes d'âge, corrigés pour les traitements de densités, les sites d'études et les années. Nous avons déterminé si l'augmentation de la densité de cerfs et l'alimentation enrichie entraînaient un déclin des herbacées et arbustes préférés et une augmentation des plantes moins prisées par le cerf. Nous avons échantillonné les 12 enclos via 20 transects permanents de 50 m à l'intérieur de chacun des enclos. Le pourcentage de couvert des herbacées préférées était similaire ($P = 0.13$) entre les densités de cerfs, corrigés pour les traitements d'alimentation et les dates d'échantillonnage (basse densité: $\bar{x} = 8\%$, étendue de ES 6–10, densité moyenne: 5%, 4–6, et densité élevée: 4%, 3–5; les étendues des ES sont présentées parce que les ES associées aux moyennes transformées sur l'échelle originale sont asymétriques). Corrigé pour toutes les densités de cerfs, le couvert d'herbacées préférées était similaire entre les traitements d'alimentation en 2004, mais en 2012, il était en moyenne de 20% (ES 17–23) dans les enclos d'alimentation enrichie, comparativement à 10% (ES 8–13) dans les enclos d'alimentation naturelle ($P = 0.107$). Le pourcentage de couvert des autres herbacées, des arbustes préférés, des autres arbustes et des graminées, tout comme l'indice de Shannon, l'indice de diversité et la richesse spécifique étaient similaires ($P > 0.10$) entre les densités de cerfs, corrigées pour les traitements d'alimentation et les années d'échantillonnage. Nous avons analysé les ratios faon:femelle adulte, les taux de croissance des faons et des juvéniles, la survie de 6 à 14 mois, la survie des adultes >14 mois, la masse corporelle des adultes et les taux de croissance de la population (lambda apparent, λ_{APP}) pour déterminer les effets de la densité et de l'alimentation sur les populations de cerfs dans les enclos expérimentaux entre 2004 et 2012. Les ratios faon:femelle adulte ont décliné ($P = 0.04$) entre les densités faibles-moyennes et la forte densité dans les enclos d'alimentation naturelle, mais n'étaient pas affectés ($P = 0.48$) par la densité dans les enclos d'alimentation enrichie. L'enrichissement de l'alimentation a entraîné une augmentation des ratios faon:femelle adulte de $0.15 \pm$ ES 0.12 faon:femelle adulte à faible et moyenne densité à 0.44 ± 0.17 faon:femelle à forte densité. Le taux de croissance des faons n'était pas affecté par la densité de cerfs dans les conditions d'alimentation naturelle ou enrichie ($P > 0.17$), mais a augmenté de 0.03 ± 0.01 kg/jour dans les enclos d'alimentation enrichie, comparativement aux enclos d'alimentation naturelle ($P < 0.01$). Le taux de croissance des juvéniles n'était pas affecté ($P > 0.71$) par la densité de cerfs, mais le taux de croissance a augmenté pour les mâles dans les enclos d'alimentation enrichie. La masse corporelle des adultes a décliné en réponse à l'augmentation de la densité de cerfs dans les enclos d'alimentation naturelle pour les mâles ($P < 0.01$) et les femelles ($P = 0.10$). L'enrichissement de l'alimentation a entraîné l'augmentation de la masse corporelle des mâles, bien que la masse corporelle des femelles n'ait pas augmentée, comparativement aux conditions d'alimentation naturelle. La survie des mâles adultes n'était pas affectée par la densité de cerfs dans les enclos d'alimentation naturelle ($P = 0.59$) ou enrichie ($P = 0.94$). La survie des femelles adultes était supérieure dans les enclos à densité moyenne avec une alimentation naturelle ($P = 0.04$), mais similaire à faible et forte densité. L'enrichissement de l'alimentation a entraîné l'augmentation de la survie des femelles ($P < 0.01$) et, de manière marginale, celle des mâles ($P = 0.11$). La survie des faons de 6 à 14 mois n'était pas affectée ($P > 0.35$) par la densité dans les traitements d'alimentation naturelle ou enrichie, mais elle était supérieure ($P = 0.04$) dans le traitement d'alimentation enrichie. Le taux de croissance de la population a diminué ($P = 0.06$) avec l'augmentation de la densité dans les enclos d'alimentation naturelle, mais pas ($P = 0.55$) dans les enclos d'alimentation enrichie. L'enrichissement de l'alimentation a entraîné une augmentation de 0.32 du λ_{APP}. Dans les conditions d'alimentation naturelle, nous avons seulement trouvé des effets mineurs des traitements de densité de cerfs sur la composition du régime alimentaire des cerfs, l'apport nutritionnel et les communautés végétales. Cependant, nous avons trouvé des effets densité-dépendants dans les ratios faon:femelle adulte, la masse corporelle des adultes et le taux de croissance de la population. Dans une étude subséquente, les domaines vitaux des cerfs présents dans nos enclos de recherche diminuaient avec la densité de cerfs et nous supposons que la qualité de l'habitat variait au sein des domaines vitaux et contribuait aux réponses dépendantes de la densité. La variable précipitation a eu une plus grande influence sur le régime alimentaire des cerfs, la composition de la végétation et les paramètres populationnels que n'en a eu la densité de cerfs. Aussi, la résistance à l'herbivorie et à la basse qualité de la végétation arbustive épineuse de nos sites d'études a probablement contraint le comportement densité-dépendant des cerfs. Nous supposons qu'il est peu probable que la forte densité de cerfs (50/km^2), de même que la densité moyenne de cerfs

(31 cerfs/km^2), pour lesquelles nous avons détecté de la densité-dépendance négative, puissent survenir sans la succession de plusieurs années pluvieuses. Au cours du siècle dernier, ce phénomène n'est arrivé qu'une seule fois (années 1970). Par conséquent, la densité-dépendance serait probablement difficile à détecter pour la majorité des années, dans des conditions d'alimentation naturelle, dans cette région. Le broutement par les cerfs avec une alimentation enrichie n'a pas engendré une diminution des plantes préférées dans la communauté végétale et a eu un effet protecteur sur les herbacées préférées parce que ≤53% du régime alimentaire des cerfs était composé de végétaux. Cependant, l'alimentation enrichie a amélioré la valeur adaptative individuelle et populationnelle des cerfs, démontrant clairement que l'alimentation est limitante pour les populations de cerfs dans des conditions d'alimentation naturelle dans le sud-ouest du Texas.

Relación entre la Densidad de Venado Cola Blanca, la Nutrición y la Vegetación en Ambientes Variables

RESUMEN El comportamiento del venado cola blanca (*Odocoileus virginianus*) dependiente de la densidad apoya la aplicación de la teoría y manejo en Norte América, sin embargo, la potencia o la frecuencia de este fenómeno varía a través de la distribución geográfica de la especie. El efecto de los ambientes variables y la calidad pobre del hábitat sobre el comportamiento dependiente de la densidad en las poblaciones de ungulados ha sido reconocido alrededor del mundo incluyendo las poblaciones de venado cola blanca en el Sur de Texas en Estados Unidos. A pesar de la importancia de entender los mecanismos que influencian la dependencia de la densidad, los investigadores se han concentrado en la demografía y las implicaciones morfológicas de la densidad de venados. La investigación no se ha enfocado a establecer enlaces entre la dinámica de la vegetación, nutrición, y la dinámica de los venados. El objetivo de estos estudios conducidos de 2004 a 2012 fue determinar la intensidad de la relación entre la densidad de venados y la composición de la vegetación, y la nutrición de los venados (con y sin suplementación) en ambientes semiáridos con un coeficiente de variación en la precipitación anual de más de 30%. El estudio se estableció en dos sitios en la zona de matorral espinoso en Dimmit County, Texas, en Estados Unidos. Durante 2003 se construyeron 6 potreros de 81 ha con malla para venados de 2.4 m de altura en cada sitio (repetición). El diseño experimental incluyó 2 tratamientos de nutrición y 3 densidades de venados en un arreglo factorial considerando sitios como bloques. La abundancia aproximada para las densidades baja, media, y alta en los potreros fueron 10 venados (equivalente a 13 venados/km^2), 25 venados (31 venado/km^2), y 40 venados (50 venados/km^2), respectivamente. En cada sitio se tuvieron 2 potreros para cada densidad, y la suplementación de alimento peletizado de alta calidad se ofreció *ad libitum* en uno de los potreros de cada densidad con el propósito de mejorar nutrición; mientras que en el otro potrero en cada densidad los venados solamente tuvieron acceso a la nutrición natural que provee la vegetación. En cada potrero se realizaron censos con cámaras fotográficas para estimar la densidad de venados y se removieron o agregaron venados de acuerdo a la densidad aproximada correspondiente a cada tratamiento. Para la identificación individual de los venados se mantuvo más del 50% de la población con aretes numerados. Adicionalmente, se mantuvo una relación de sexos de animales adultos de 1:1–1:1.5 (machos:hembras) y una mezcla de animales jóvenes y adultos en cada potrero. Las estimaciones anuales de densidad por tratamiento (potrero) para el análisis de los efectos de tratamiento se realizaron mediante la reconstrucción validada por la comparación con el número conocido de venados machos adultos. En este estudio se evaluaron los efectos de la densidad de venados sobre la composición de la dieta y la velocidad de consumo en venadas mansas (criadas artificialmente para incrementar mansedumbre) que se liberaron en los tratamientos de baja y alta densidad sin suplementación en los dos sitios de estudio (cuatro potreros en total) por un período de 5 años entre junio de 2009 y mayo de 2011. Los muestreos se realizaron utilizando la técnica de conteo de mordidas con 2–3 venadas mansas durante periodos cortos de forrajeo en las 4 estaciones del año. La proporción de arbustos, hierbas, frutos, cactáceas, y arbustos de porte bajo en las dietas de los venados fue similar ($P > 0.57$) entre los tratamientos de densidad de venados. El porcentaje de zacates en las dietas de los venados fue más alto ($P = 0.05$) en el tratamiento de densidad alta de venados, sin embargo, solamente constituyó el 1.3 ± 0.3% (SE) de la dieta. La proteína digestible y la energía metabolizable fueron similares ($P > 0.31$) entre los tratamientos de densidad. Similarmente, no existió diferencia ($P > 0.45$) entre las densidades de venados en la velocidad de consumo (número de mordidas), tamaño de la mordida, y consumo de materia seca. A diferencia de la densidad de venados la sequía tuvo un efecto dramático ($P \leq 0.10$) en el forrajeo de las venadas. Bajo condiciones de sequía, la proporción de arbustos y flores se incrementó en las dietas de los venados mientras que el porcentaje de hierbas declinó. La proteína digestible fue 31%, 53%, y 54% más alta ($P = 0.06$) durante el otoño, invierno, y primavera, respectivamente, cuando no hubo sequía en comparación con los valores durante la sequía. En el caso de los tratamientos de suplementación se analizaron las mismas variables respuesta descritas

anteriormente entre abril de 2007 y febrero de 2009, por un período de 3 años una vez establecidas las densidades de venados en los tratamientos. Adicionalmente se estimó la proporción de suplemento en las dietas de los venados. Se evaluaron los dos tratamientos de densidad baja de venados con y sin suplementación en los dos sitios de estudio (4 potreros en total). Nuevamente, se utilizó la técnica de conteo de mordidas con las venadas mansas de cada uno de los tratamientos. La proporción de suplemento peletizado en la dieta de las venadas mansas y el resto de los venados se estimó utilizando la relación de isotopos estables de carbono. En promedio de estaciones y tratamientos de nutrición los arbustos constituyeron la mayor parte de las dietas de los venados (44%), posteriormente los frutos (26%), y las hierbas con (15%). El mejoramiento de la nutrición mediante la suplementación afectó la proporción de frutos, cactáceas, y flores en la dieta, sin embargo, el efecto y su magnitud variaron con la época del año. En el tratamiento sin suplementación los venados tendieron a consumir más frutos. No se detectó diferencia ($P = 0.15$) en la proporción de arbustos las dietas de los venados con y sin suplementación, sin embargo, los venados con suplementación consumieron de 7–24% más arbustos en 5 de los 8 estaciones del año analizadas. La proteína digestible en la dieta fue más alta ($P = 0.03$) en los venados con suplementación comparado con los sin suplementación. El efecto de la suplementación sobre la energía metabolizarle en las dietas varió por estación y fue más alta ($P < 0.04$) para los venados con suplementación durante el verano y otoño de 2007 y el invierno de 2008. En el tratamiento con suplementación, el suplemento promedió 47–80% de la dieta de las venadas mansas. En el resto de los venados en todos los tratamientos de densidad con suplementación, 97% ($n = 128$ venados) consumieron suplemento durante el otoño, en estos venados el consumo de suplemento en promedio de tratamientos de densidad, sitios de estudio, y años fue de más de 70% independientemente del sexo y grupos por edad. En este estudio también se determinó el efecto de la suplementación sobre la reducción de hierbas y arbustos preferidos por los venados y un incremento en las plantas menos preferidas. Se colectó información de 20 transectos permanentes de 50 m de longitud en cada uno de los 12 potreros del estudio. El porcentaje de cobertura aérea de las hierbas preferidas fue similar ($P = 0.13$) entre los tratamientos de densidad de venados en promedio de los tratamientos de suplementación y años de muestreo (densidad baja; $x = 8\%$, SE rango 6–10, densidad media; 5%, 4–6, densidad alta; 4%, 3–5; los rangos de SE se presentan debido los SE's asociados con los datos transformados convertidos a promedios reales son asimétricos). La cobertura aérea de hierbas en promedio de las densidades de venado, fue similar entre los tratamientos con y sin suplementación en 2004, sin embargo para 2012 el promedio fue de 20 ± 17–23% en los tratamientos con suplementación comparado con 10 ± 8–13% para los tratamientos sin suplementación ($P = 0.107$). La cobertura aérea de otras hierbas, arbustos preferidos, otros arbustos y zacates además del Shannon's index, uniformidad, y riqueza de especies fueron similares ($P > 0.10$) entre las densidades de venado en promedio de los tratamientos de suplementación y años de muestreo. Otras variables respuesta evaluadas de 2004 a 2012 incluyeron la relación cervato:venada adulta, el índice de crecimiento en cervatos y venados de un año de edad, la sobrevivencia de los venados entre 6–14 meses y en adultos de más de 14 meses de edad. Adicionalmente de 2004 a 2012 se evaluaron la masa corporal de adultos y el índice de crecimiento de la población (lambda aparente, λ_{APP}) para determinar los efectos de la densidad de venados y la suplementación. La relación cervato venada adulta declinó ($P = 0.04$) conforme la densidad de venados se incrementó de baja-media a alta en los tratamientos sin suplementación, sin embargo, no se detectó ($P = 0.48$) un efecto entre densidades en los tratamientos con suplementación, sin embargo, comparado con los tratamientos sin suplementación, los tratamientos con suplementación la relación cervato:venada adulta se incrementó 0.15 ± 0.12 cervatos:venada adultaen los tratamientos de densidad baja-media de venados y 0.44 ± 0.17 cervatos:venada adulta en la densidad alta. En los tratamientos sin suplementación la densidad no afectó ($P > 0.17$) el índice de crecimiento de los cervatos, sin embargo, en los tratamientos con suplementación el índice de crecimiento incremento 0.03 ± 0.01 kg/dia ($P < 0.01$), comparado con los tratamientos sin suplementación. La densidad de venados no afectó ($P > 0.71$ el índice de crecimiento de los venados de un año de edad, sin embargo, el índice de crecimiento para venados machos se incrementó en algunos años en los tratamientos con suplementación. El peso de los venados adultos machos ($P < 0.01$) y hembras ($P = 0.10$) en los tratamientos sin suplementación declinó conforme la densidad de venados incrementó. La suplementación incremento el peso corporal de los venados machos, sin embargo, el peso de las hembras fue similar en los tratamientos con y sin suplementación. La densidad de venados no afectó la sobrevivencia de venados adultos en los tratamientos con ($P = 0.59$) y sin ($P = 0.94$) suplementación. La sobrevivencia más alta ($P = 0.04$) de venadas se obtuvo en los tratamientos de densidad media sin suplementación y fue similar a los tratamientos de densidades baja y alta. La suplementación incremento la sobrevivencia de las venadas ($P < 0.01$) y marginalmente la de los venados machos ($P < 0.01$). La densidad de venados no afectó ($P > 0.35$) la sobrevivencia de cervatos de 6–14 meses de edad en los tratamientos con y sin suplementación, sin embargo, la sobrevivencia fue más alta ($P = 0.04$) en los tratamientos con suplementación. El índice de crecimiento de la población declinó ($P = 0.06$) con el incremento en la densidad de venados en los tratamientos sin suplementación pero no tuvo efecto ($P = 0.55$) en los tratamientos con suplementación. La

suplementación resultó en un incremento del 0.32 en λ_{APP} por 0.32. Las densidades de venados en los tratamientos sin suplementación tuvieron solamente un efecto mínimo en la composición de la dieta de los venados, consumo de nutrimentos y las comunidades vegetales. Sin embargo, se encontraron efectos dependientes de la densidad en la relación cervato:venadas adultas, peso corporal de los venados adultos, y el índice de crecimiento de la población. En un estudio posterior, los ámbitos hogareños de los venados en los potreros experimentales declinaron conforme la densidad incrementó y se considera la hipótesis de que la calidad del hábitat varió entre los ámbitos hogareños y contribuyó a las respuestas dependientes de la densidad. La precipitación variable tuvo la mayor influencia en las dietas de los venados, la composición de la vegetación, y los parámetros de la población comparado con las densidades de población de los venados. Adicionalmente, la resistencia al forrajeo y la baja calidad del forraje de la vegetación de matorrales espinosos en el estudio posiblemente inhibieron el comportamiento dependiente de la densidad de los venados. La información de este estudio postula que es improbable que los niveles de alta densidad de venados (50 deer/km^2) y aun los de densidad media (31 deer/km^2), los efectos negativos de la dependencia de la densidad asociada pudieran ocurrir sin el efecto asociado de varios años húmedos. En el siglo pasado, este fenómeno solamente ha ocurrido en una ocasión (1970′s). Por lo tanto, la dependencia de la densidad posiblemente sería muy difícil de detectar en la mayoría de los años bajo las condiciones naturales de nutrición de la región. El forrajeo de los venados bajo condiciones de suplementación no resultó en una reducción de las plantas preferidas por el venado en la comunidad vegetal y la suplementación tuvo un efecto protector de las plantas herbáceas preferidas debido a que la vegetación constituyó menos del ≤53% de las dietas de los venados. Sin embargo, la suplementación mejoró la condición individual de los venados y de las poblaciones, claramente demostrando que la nutrición es un factor limitante para las poblaciones de venados bajo condiciones naturales de nutrición en el oeste del Sur de Texas.

Contents

BACKGROUND

Density-dependent behavior by ungulate populations has been widely documented (Caughley 1977, Fowler 1981*a*, Skogland 1985, McCullough 1999, Bonenfant et al. 2009, Bowyer et al. 2014). Density dependence can take many forms but basically involves constrained productivity and/or increased mortality as population density increases. In addition to a fundamental role in ungulate population ecology, density dependence is foundational in ungulate harvest theory, some of which originated from Ricker-type models in fishery science (Ricker 1958, McCullough 1979). These models posit a carrying capacity, that when approached by a harvested population, results in the harvest being partly or completely compensatory with natural mortality (Caughley 1985).

Embedded in density-dependence theory is the idea that herbivores and vegetation are strongly linked (Ellis and Swift 1988, Briske et al. 2003, Derry and Boone 2010). Herbivores and vegetation interact with one another over time and space, with palatable vegetation declining as herbivore populations increase (Noy-Meir 1975, Caughley 1976, Choquenot 1991, McCullough 1999). Density-dependent behavior, consequently, is attributed most frequently to intraspecific competition for food (Bonenfant et al. 2009, DeYoung 2011). Sometimes intrasexual (female-female) competition is inferred (McCullough 1979, Clutton-Brock et al. 1982, Portier et al. 1998). More commonly, total density or abundance (males + females) is correlated with density-dependent behavior of some vital rate (Mysterud et al. 2002, Bonenfant et al. 2009).

Parallel to the development of models of density dependence and harvesting by animal ecologists, rangeland and plant ecologists developed theory explaining effects of herbivory on vegetation dynamics. Parallels between density-dependence theory in ungulates and plant succession included the idea that as herbivore density increases, plant community composition shifts as palatable plants decline in response to selective foraging and are replaced by unpalatable species and plants more tolerant to herbivory (Stoddart et al. 1975). This theory of plant response to herbivory mirrors theories of density dependence in ungulates in that plant communities subjected to intense herbivory ultimately become dominated by unpalatable plants or heavily defended plants, which in turn provide less and lower-quality forage for herbivores. Increased herbivore densities thereby are assumed to have similar consequences with both hypotheses—a reduction in quantity and quality of forage. A somewhat different idea was that herbivores could maintain vegetation in a relatively stable condition compositionally different from the true climax, referred to as a zootic climax (Daubenmire 1952). The zootic climax was regarded as a deteriorated state by range ecologists (Dyksterhuis 1983). Thus, ungulate density dependence, ungulate harvesting, and dynamics of plant communities producing ungulate food are based on intertwined theories. Presence of an equilibrium phase or phases is a commonality in theories of Daubenmire (1952), Stoddart et al. (1975), Caughley (1976), and McCullough (1999).

Ecosystem equilibrium is at best a temporary phenomenon in stochastic environments. In fact, usefulness of the carrying-capacity concept for large mammals in variable environments has been questioned (McLeod 1997). Applied ecologists have debated density dependence in domestic ungulates in non-equilibrium or disequilibrium environments (Illius and O'Conner 1999, Sullivan and Rohde, 2002, Briske et al. 2003, Vetter 2005, Derry and Boone 2010, Silcock and Fensham 2013). Ungulates and vegetation are 2 dynamic systems (McCullough 1999), and the argument has been about whether there is tight coupling between ungulate-plant systems (equilibrium) or de-coupling (disequilibrium) because frequent droughts in variable systems prevent populations from increasing to a level where density dependence becomes apparent (Derry and Boone 2010). Equilibrium versus disequilibrium plant-ungulate systems can be viewed as a continuum of responses among environments that vary from stable to extremely variable (Briske et al. 2003).

Typically, density dependence is expressed by increased age of puberty of females and reduced survival of young, fetal rate, pregnancy rate, and (rarely) adult survival (Gaillard et al. 2000, Bonenfant et al. 2009, Monteith et al. 2014). Environmental variation, usually precipitation flux but sometimes cold, snowy winters, interacts with density-dependent tendencies to affect ungulate population sizes (Bowyer et al. 2014). Some researchers argue that density dependence is expressed throughout the spectrum of a population's size, from low density to carrying capacity (McCullough 1979, Bowyer et al. 2014). Others posit that density dependence becomes apparent only after a population grows near carrying capacity (McCullough 1999).

Density-dependent influences can be expressed through many aspects of ungulate biology and ecology including demography, diet composition, diet quality, and body growth and condition (Leberg and Smith 1993, Keyser et al. 2005).

White-tailed deer (*Odocoileus virginianus*) are ungulates with a wide distribution in the Americas (Heffelfinger 2011). In boreal and temperate forested regions, they can be abundant, and exhibit strong density dependence (McCullough 1979). In locations with poor soils or high environmental stochasticity, overt density-dependent behavior can be rare (DeYoung 2011). However, there are different types of stochastic environments and Pierce et al. (2012) and Monteith et al. (2014) reported density-dependent behavior in migratory mule deer (*O. hemionus*) populations occupying environments with variable winter precipitation.

Density-dependent behavior in white-tailed deer has been proposed to be a function of the distribution of food quality and quantity as well as deer numbers (DeYoung 2011). Cook et al. (2016) made a similar proposal for density dependence in elk (*Cervus elaphus*). Understanding the dynamics of plant communities that provide the food supply is clearly important to understanding the population dynamics of large herbivores (Bonenfant et al. 2009), including white-tailed deer. However, few researchers have undertaken studies that included detailed data collection on both plant community and deer dynamics across levels of deer density in a designed experiment.

Providing high-quality food to deer may obfuscate density-dependent responses because of increased fecundity and ungulate densities that typically result (Bishop et al. 2009, Milner et al. 2014). Availability of high-quality feed also may result in changes in foraging behavior and diet composition (Timmons et al. 2010), thereby potentially altering the manner at which increasing densities of ungulates influence vegetation composition and dynamics. White-tailed deer foraged more selectively when provided with supplemental feed (Murden and Risenhoover 1993), suggesting the potential for affecting vegetation dynamics differently than deer that are not provided feed.

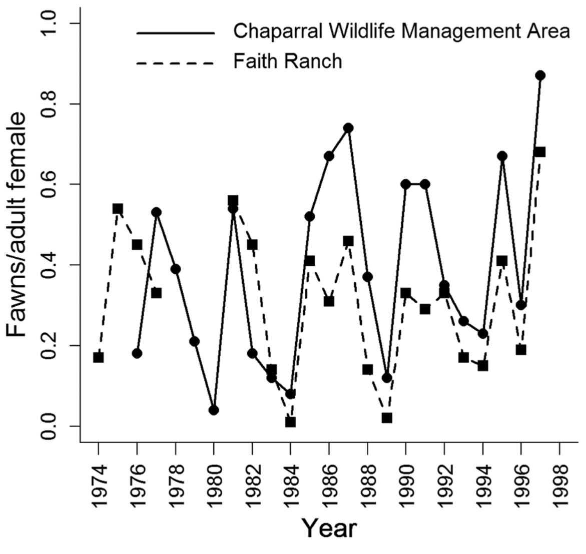

Figure 1. White-tailed deer fawn survival estimated during autumn surveys by helicopter on 2 South Texas, USA, study areas, showing effects of environmental stochasticity, 1974–1998. Data from DeYoung et al. (2008).

DeYoung et al. (2008) questioned the utility of simple density-dependent models to describe dynamics of white-tailed deer in South Texas, USA, a semi-arid region with a stochastic environment (Fig. 1). They analyzed time series of long-term deer counts across the region and concluded there was a declining gradient of the likelihood of density dependence from east to west. We conducted a series of designed experiments, replicated on 2 large ranches, examining the relationship between plant communities and deer density in the western part of South Texas where density-dependent behavior was expected to be infrequent. We also included a nutrition treatment to assess the interacting effect of nutrition on that relationship.

ENVIRONMENT

Our study sites were on the Comanche and Faith ranches in Dimmit County, Texas (Fig. 2) in the Tamaulipan biotic province (Blair 1950). The ranches were used for cattle grazing in the late nineteenth century and most of the twentieth century. Comanche Ranch (until 2000 known as Farias Ranch) was also grazed by sheep (Lehmann 1969), but it is unclear if this was the case with Faith Ranch. Cattle were removed from Comanche Ranch in 2000 and from Faith Ranch in 2003. Both ranches supported essentially unmanaged and lightly hunted (<0.1 deer/km^2/year) white-tailed deer populations for decades, if not centuries. Comanche Ranch was hunted through a commercial lease system until 2000, but anecdotal reports showed <1 adult male/km^2/year was harvested. Deer hunting on Faith Ranch was historically incidental. Records of helicopter survey of deer on Faith Ranch date back to the 1970s and showed elevated population levels at that time (DeYoung et al. 2008). Rainfall records showed that the 1970s were the wettest period during 1900–1983 in South Texas (Norwine and Bingham 1986).

White-tailed deer were commonly encountered by early Spanish explorers in southern Texas along with pronghorn (*Antilocapra americana*), and at times, bison (*Bison bison*; Inglis 1964, Fulbright 2001). Large and medium-sized predators included wolf (*Canis lupus* or *C. rufus*), jaguar (*Panthera onca*), mountain lion (*Puma concolor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and black bear (*Ursus americanus*).

Based on early historical records, the region was cooler and wetter than today from 1500 until about 1850. This difference was due to effects of the Little Ice Age climatic phenomenon (Naftz et al. 1996). Annual rainfall in recent decades has varied from about 65 cm in the eastern portion of the region to 55 cm in the western portion with a coefficient of variation of about 35% (Norwine and Bingham 1986). Rainfall is significantly influenced by El Nino-Southern Oscillation (ENSO) cycles, with wetter El Nino phases every 3–5 years (McCreary and Anderson 1984). This cycling has led to South Texas being described as a pulsed environment (DeYoung 2011).

Western South Texas and north-central Mexico have a climatic classification similar to north-central and southern Africa, central India, east-central South America, and northern and eastern Australia (Peel et al. 2007). Early European explorers described a landscape of grasslands

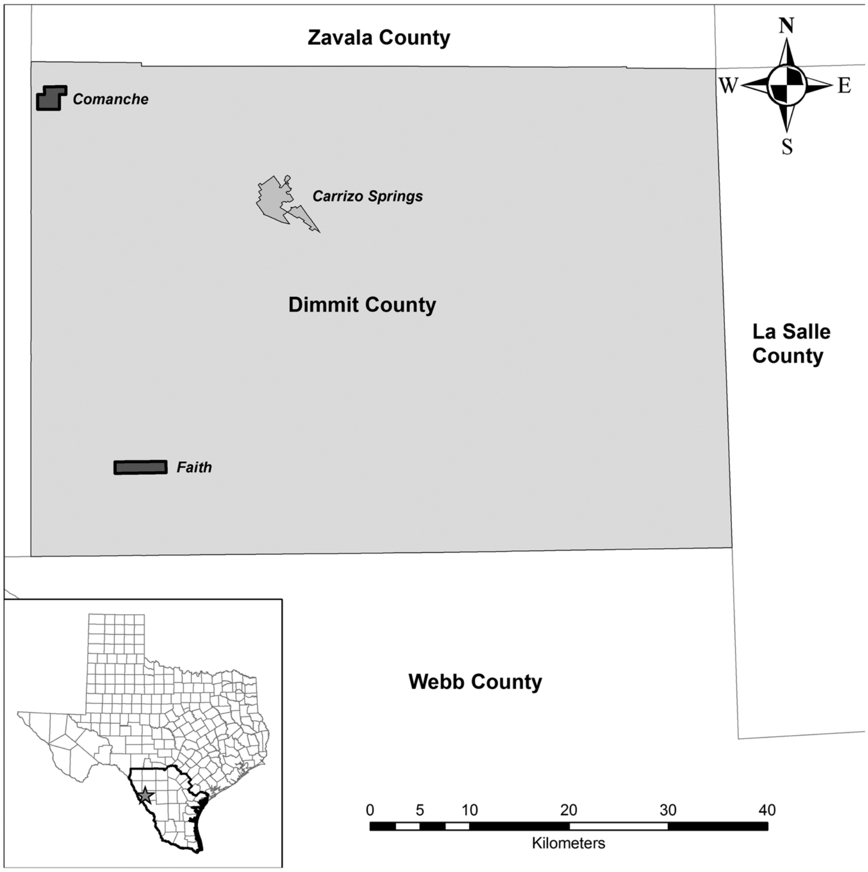

Figure 2. Location of Comanche and Faith Ranch study areas, South Texas, USA.

interspersed with thornshrub, especially along drainages. Over the past 400 years, shrubs have increased significantly in density and distribution (Archer 1989). Shrub increase has been attributed to climate change, lack of fire, and anthropogenic practices such as brush control and livestock grazing (Archer et al. 1988). Although famous for cattle ranching, millions of domestic sheep were grazed in the region in the late 1800s (Lehmann 1969).

Vegetation of southern Texas is diverse, with >100 plant species yearly in deer diets (Folks et al. 2014). Herbaceous dicotyledons include many cool-season forbs preferred by deer. Many forbs are annual and occur only in years when moisture is sufficient for seed germination. Others are perennial but act like annuals in dry periods. Perennial forbs may have little or no above-ground tissue during droughts and exist as stem and root belowground until rainfall and temperature are sufficient for growth. Many species of cacti occur in the region with fruits of prickly pear (*Opuntia engelmanni*) particularly important in the diet of deer (Arnold and Drawe 1979).

Approximately 190 species of trees, shrubs, subshrubs, and cacti occur in southern Texas, many only in the Rio Grande Valley of the extreme south (Everitt and Drawe 1993). Many shrubs in western South Texas are drought-deciduous and exhibit defenses to grazing, including thorns, chemical defenses, and responses such as compensatory growth and branching (Teaschner and Fulbright 2007, DeYoung 2011). At least some species in this suite of woody plants evolved under a rich group of grazers and browsers far more disruptive to plant communities than white-tailed deer. Although the evolutionary histories of many shrubs are obscure, large grazers present in the region in the late Pleistocene included large ground sloths (*Paramylodon harlani* and *Megalonyx jeffersonii*), flat-headed peccary (*Platygonus compressus*), camelids, 3 species of *Equis*, and 3 species of Proboscideans (Baskin and Thomas 2007).

Many, maybe most, areas of South Texas received some type of mechanical or chemical treatment to reduce thornshrub canopy and enhance grass production for cattle in the 1960s and 1970s (Helms 1981). Some or all of Comanche Ranch may have received a mechanical chaining treatment (Scifres et al. 1976) in the 1970s. Chaining involves dragging a large anchor chain between 2 large tractors to break off and sometimes uproot woody stems. The Faith Ranch has been owned by the same family since the 1930s and has never been subjected to brush management.

Greater than 95% of the South Texas region is private land, and non-agency managers commonly provide pelleted feed to improve deer productivity that is otherwise constrained by the stochastic environment. Rainfall variability, lack of irrigation water, and poor quality of soils limits farming of food plots for deer as is common in the southeastern United States. Providing enhanced nutrition to free-ranging white-tailed deer has been a common practice in South Texas since the 1970s (Zaiglin and DeYoung 1989, McBryde 1995, Bartoskewitz et al. 2003, Timmons et al. 2010, Priesmeyer et al. 2012). Murden and Risenhoover (1993) suggested that habitat enhancement for deer could lead to overuse of preferred forage plants and Cooper et al. (2006) documented increased browsing pressure near feed sites. However, despite concern over negative effects of feeding of deer on plant communities (Brown and Cooper 2006), long-term and comprehensive research on the subject is lacking.

Results of research on the effects of supplemental feeding on the diets of ungulates other than deer contradict the idea posited by Murden and Risenhoover (1993) that herbivores provided supplemental feed will consume the most palatable and nutritious plants, leading to their overuse. Iberian red deer (*C. elaphus*) in Spain, for example, consumed forages that contained nutrients lacking in their supplemental feed rather than consuming the most preferred and nutritious plants (Miranda et al. 2015). Plant species composition of the diets of derby eland (*Taurotragus derbianus derbianus*) and western giant eland (*Tragelaphus derbianus derbianus*) in Senegal were unchanged by supplemental feeding (Hejcmanová et al. 2010, 2013). Supplementally fed cattle in Africa

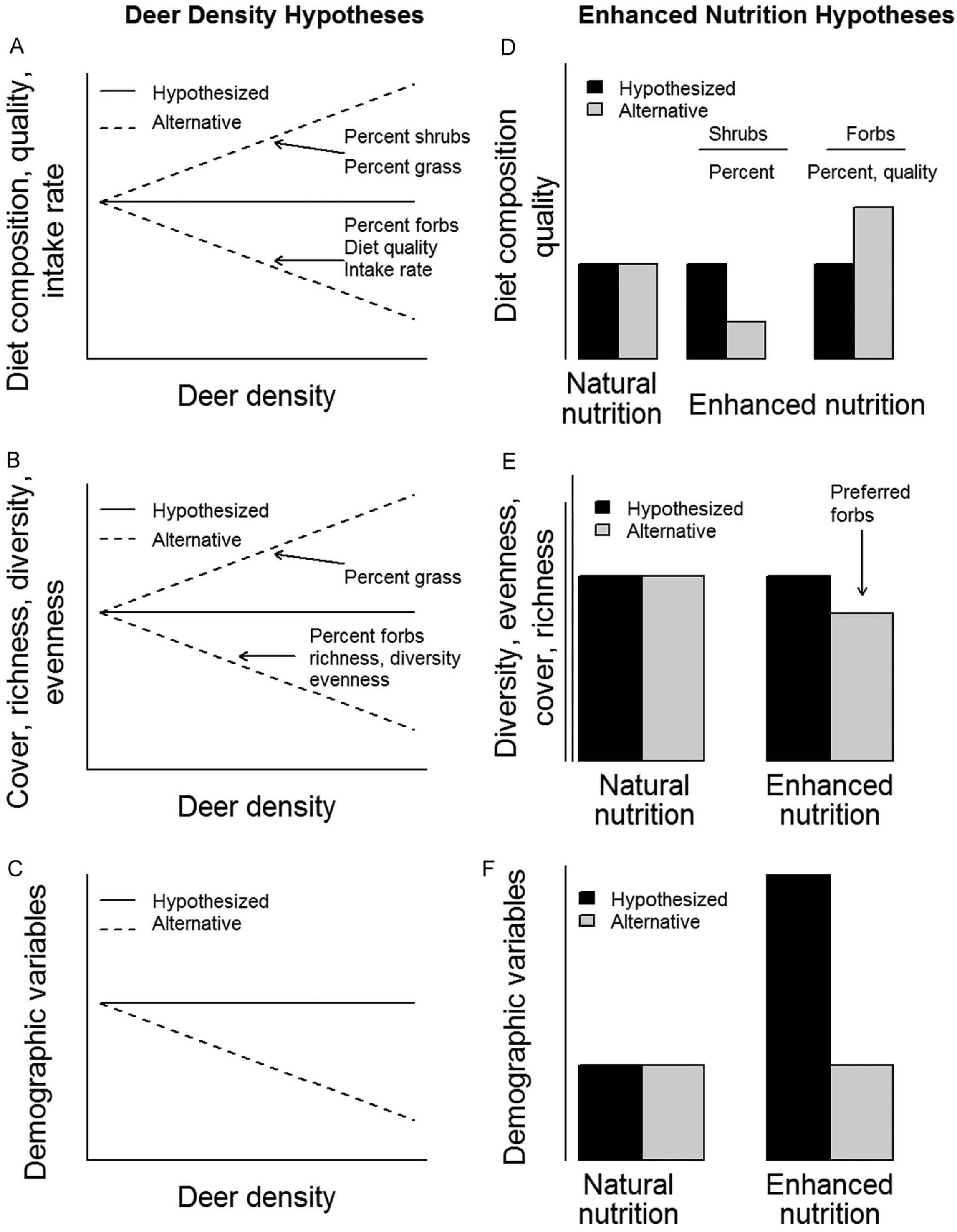

Figure 3. Hypotheses of effects of white-tailed deer density (A-C) and enhanced nutrition (D-F) on diet composition and quality, vegetation parameters, and deer demographics, South Texas, USA.

consumed more low-protein grasses and fewer protein-rich forbs (Odadi et al. 2013).

OBJECTIVES

Our primary motivation for conducting this study was to develop guidance for wildlife managers in South Texas who are interested in producing the maximum number of large-antlered deer without incurring vegetation retrogression from high densities. In addition to these practical objectives, we recognized the rare opportunity to conduct a controlled experiment in ungulate population ecology.

Density dependence is predicated to a considerable extent on existence of a strong linkage between deer and vegetation. In particular, density dependence requires a linkage between deer fitness and food quality and quantity. In the ecological literature, however, the strength of this linkage for ungulates in stochastic environments has been questioned (Mackie et al. 1990, Owen-Smith 1990, Bonenfant et al. 2009); therefore, the ubiquity of density dependence in ungulates also has been questioned. We hypothesized that under natural nutrition the linkages between deer and vegetation are not detectable (Fig. 3A–C); therefore, density dependence is weak in a stochastic environment like South Texas. In addition, because deer populations are frequently constrained by nutrition in stochastic environments, supplemental feeding (hereafter referred to as enhanced nutrition) should increase metrics of deer productivity and population growth rates (Fig. 3F). We hypothesized that enhanced nutrition will not result in increased foraging pressure on palatable plants or a decline in abundance of palatable plants (Fig. 3D,E) but will increase deer productivity and population growth rate regardless of deer density (Fig. 3F).

We tested the following predictions based on these hypotheses: 1) foraging behavior and deer diets under natural nutrition should be similar among different deer densities (Gann et al. 2019*a*), 2) enhanced nutrition will not cause deer to selectively forage on the most palatable plants (Darr et al. 2019), 3) increasing deer density and providing enhanced nutrition will have little effect on vegetation dynamics (Gann et al. 2019*b*), 4) population demographics will be similar among deer densities under natural and enhanced nutrition (Cook et al. 2019), and 5) enhanced nutrition will result in an increase in deer demographic and morphological parameters in comparison to natural nutrition. Finally, we discuss and summarize results of all facets of the overall study (DeYoung et al. 2019*b*). We considered evidence of an effect of increasing deer density on foraging behavior and deer diets, vegetation dynamics, morphometrics, and demographic parameters to support the alternative hypotheses that deer exhibit density-dependent responses and that deer and vegetation are closely linked.

Study Areas, Experimental Design, and General Methods for Studying Vegetation and White-Tailed Deer Dynamics in Tamaulipan Thornshrub

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INTRODUCTION

Collecting data on deer populations over a range of deer densities under both natural and enhanced nutrition was necessary to meet our goals. We present a general description of research enclosures on the replicate study sites and how we collected population data. We detail how we selected a range of deer densities for the enclosures and established and maintained deer populations in research enclosures through 9 years of the study. We also describe how and why we removed coyotes, feral hogs (*Sus scrofa*), and collared peccary (*Pecari tajacu*) from the research enclosures. Finally, we evaluate our success in achieving design goals for deer density, sex ratio, and age structure. Detailed descriptions of how plant communities, deer diets, and deer population productivity were affected by the various experimental treatments are in Gann et al. (2019*a*,*b*); Cook et al. (2019); Darr et al. (2019); and DeYoung et al. (2019*b*). All research activities were approved by the Texas A&M University–Kingsville Institutional Animal Care and Use Committee (numbers 2004-2-9, 2009-11-5A, and 2012-11-28A).

STUDY AREAS

Study areas were on the Comanche (28.60°N–100.09°W) and Faith (28.28°N–100.00°W) ranches, located in Dimmit County, Texas, near the town of Carrizo Springs (Fig. 2). In late 2003, we constructed 6 enclosures of 81 ha each on both ranches (Fig. 4). The size of enclosures was a compromise between being large enough for realism but small enough to 1) inventory and manage deer population sizes, and 2) minimize spatial variation in abiotic and biotic factors such as soils and plant species composition among experimental units. The sites of enclosure complexes were designated by the respective ranches and were in areas of native thornshrub vegetation (Crider et al. 2015) that were as uniform as possible. We randomly assigned treatments within enclosure complexes. Clay-loam to sandy-loam soils of Maverick–Dilly–Randado and Copita–Pryor–Dant soil associations predominated (Stevens and Arriaga 1985). Elevation within enclosures was flat to slightly rolling with occasional shallow drainages in some enclosures.

Precipitation was variable with an annual average of 51.3 cm (1971–2000), with about 69% of this rainfall typically occurring in May and September (National Climatic Data Center 2001). We monitored precipitation monthly during the present study (2004–2012) on each of the 2 study sites using a combination of electronic and standard rain gauges (Gann et al. 2019*b*). Between 1981 and 2010, monthly average high temperatures ranged from 37°C during August to 19°C in December (U.S. Climate Data 2018).

Scientific names of plants follow those in the Plants Database (U.S. Department of Agriculture Natural Resources Conservation Service 2017). Vegetation of the study areas was Tamaulipan thornscrub (Blair 1950) and common shrub species included honey mesquite (*Prosopis glandulosa*), spiny hackberry (*Celtis ehrenbergiana*), blackbrush acacia (*Vachellia rigidula*), Texas lignum-vitae (*Guaiacum angustifolium*), whitebrush (*Aloysia gratissima*), brasil (*Condalia hookeri*), guajillo (*Senegalia berlandieri*), purple sage (*Leucophyllum frutescens*), Texas kidneywood (*Eysenhardtia texana*), and twisted acacia (*Vachellia bravoensis*). Forbs included lazy daisy (*Aphanostephus* spp.), low menodora (*Menodora heterophylla*), rain lilly (*Cooperia drummondii*), hairy wedelia (*Wedelia hispida*), sida (*Sida* spp.), and field ragweed (*Ambrosia confertiflora*). Common cacti included prickly pear (*Opuntia engelmanni*) and tasajillo (*Cylindropuntia leptocaulis*), and grasses belonged to the *Aristida*, *Bouteloua*, *Chloris*, *Eragrostis*, *Pappaphorum*, *Pennisetum*, and *Tridens* genera (Timmons et al. 2010).

The enclosures were surrounded by net wire material 2.4 m tall. The fencing had smaller mesh at the bottom, grading to 15.2-cm × 15.2-cm mesh approximately 0.75 m above ground. Before the experiment began, we decided to remove coyotes, the main predator of deer in South Texas (Cook et al. 1971, Beasom 1974, Guthery and Beasom 1977). We wanted the research to focus on dynamics of vegetation and deer without significant predation so that density-dependent responses based on food limitation would be clear. To exclude coyotes, all exterior fences of the enclosure complexes (Fig. 4) had 1.2 m of net wire material buried on the outside stretching horizontally from the bottom of the fences to deter coyotes from digging under. After we observed coyotes passing through the 15.2-cm × 15.2-cm mesh of the upright portion of fences, we covered the existing wire mesh on exterior fences of the complexes with 10.2-cm × 10.2-cm mesh wire to a height of 1.5 m on the existing exterior fences in 2007. We poured concrete under all exterior gates to also exclude coyotes from digging under. Throughout the study, we removed coyotes within the enclosures with leg hold traps, snares, shooting from ground and helicopter, and use of M-44 cyanide devices. These efforts kept coyote

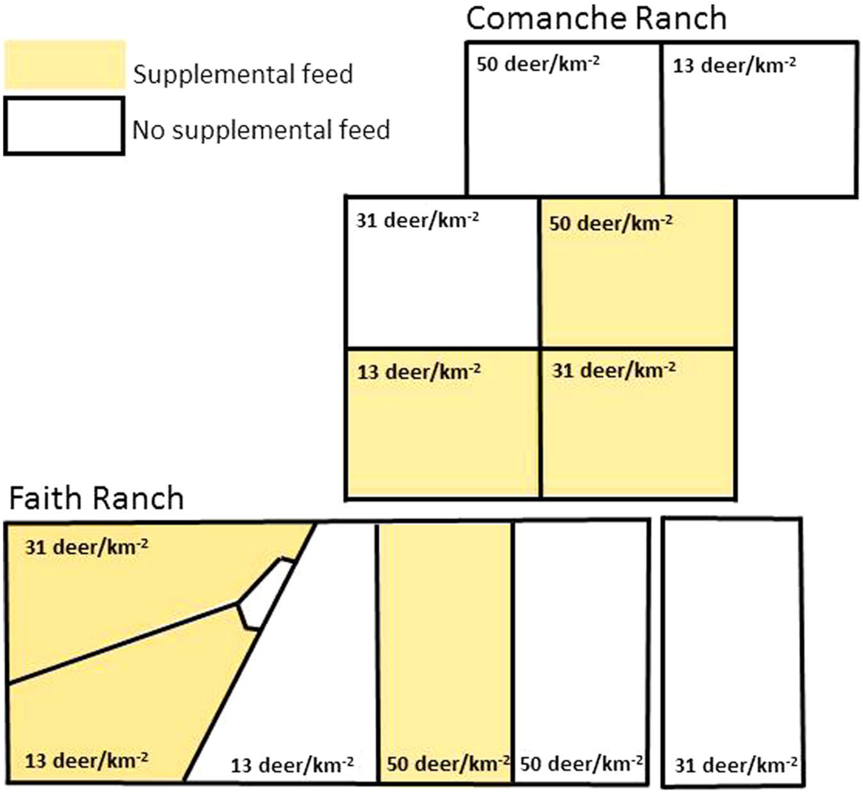

Figure 4. Layout of 81-ha enclosures with nutrition and white-tailed deer density treatments, Comanche and Faith ranches, South Texas, USA.

numbers low or non-existent for periods, but coyotes continued to occasionally enter enclosures through temporary holes under fences created by running water after heavy rains. During 2006–2012, 2-week camera surveys of the 12 enclosures with 1 camera/20 ha revealed photos of coyotes in an average of 1.9 enclosures/survey ($n = 11$, SE = 0.5).

Feral swine and collared peccaries consume and sometimes uproot vegetation. We removed feral pigs from the enclosures within the first year of the study by trapping and shooting. We removed collared peccary by trapping and transplanting. Bobcats (*Lynx rufus*) were present in the enclosures, but we made no effort to remove them because they could climb fences and are not generally a serious predator of white-tailed deer (Fulbright 2011). Mountain lions (*Puma concolor*) are known but rare on both ranches and we never found conclusive evidence of a lion in any enclosure during the 9 years of study.

METHODS

The overall design of our experiment was a randomized complete block with study areas as blocks. We randomly assigned a factorial combination of deer density and nutrition enhancement treatments to 81-ha enclosures within each block. Our goal was to design an experiment with a sufficient range of deer densities to reveal effects on enclosure deer populations and the vegetation they fed upon (Bowyer et al. 2014). The only published density estimates of deer in western South Texas thornshrub were mark-resight estimates based on sightings from a helicopter. DeYoung (1985) estimated 15.8 deer/km^2 (mean of 6 flights) on the Zachry Blanco Ranch (100 km southeast of Faith Ranch) and 19.3 deer/km^2 (8 flights) on the Chaparral Wildlife Management Area (80 km east of Faith Ranch). DeYoung et al. (1989) estimated 35.9 (5 flights) and 40.1 (4 flights) deer/km^2 on the Camaron Ranch (125 km east of Faith Ranch) and 11.2 (4 flights) and 18.1 (5 flights) deer/km^2 on the Faith Ranch. DeYoung (2011) provided 2 estimates of nutrition-based carrying capacity from Strickland (1998) of 45 deer/km^2 (10 trials, 11 Oct 1994–25 Nov 1995) and 41 deer/km^2 (11 trials, 12 Mar 1996–30 May 1997) made on our Faith Ranch study area using the tame deer technique. This technique consists of placing tractable deer in small enclosures for about 30 days and allowing them to feed on the natural vegetation. Change in deer mass while in the enclosures is used to calculate carrying capacity using equations that predict digestible energy intake based on mass change. McCall et al. (1997) validated the tame deer technique by comparing it to estimates using traditional forage-based methods of estimating carrying capacity. Based on these published density ranges and estimates of carrying capacity, treatments were assigned at random to enclosures with a goal of 13 deer/km^2 (equivalent to 10 deer), 31 deer/km^2 (25 deer), or 50 deer/km^2 (40 deer; Fig. 4). Both ranches had 2 enclosures with each density goal: 1 provided with enhanced nutrition in the form of a pelleted feed via 2 centrally located feeders and the other providing only natural nutrition from the vegetation. All enclosures had a centrally located water trough. The pelleted feed was 22% crude protein with 3.0 kcal/g digestible energy and was available *ad libitum* year around.

Some deer were present in all enclosures after fences were erected in late 2003. We were initially reluctant to use a helicopter over enclosures for inventory and capture because deer were not used to boundary fences. We feared that deer would hit fences running from the helicopter and be injured. We could not directly count deer because of the dense thornshrub, but we gained an approximate count initially by baiting roads and open lanes with shelled corn (*Zea mays*) and counting deer that appeared. Subsequently, in early 2004, we captured deer outside the enclosures by helicopter and net gun (DeYoung 1988) and translocated them into enclosures to bring each up to the randomly assigned density goal. Population reconstruction later allowed us to estimate how close each enclosure was to the density goal early in the experiment. We aged captured deer by tooth replacement and wear (DeYoung 1989), weighed them, and tagged them in both ears with numbered and colored cattle ear tags (Allflex USA, Inc., Dallas, TX, USA) for individual recognition.

We classified deer as known age in the 0–1 and 1–2-year age classes based on tooth replacement (Severinghaus 1949). We assigned ages of older deer by tooth wear (Severinghaus 1949, DeYoung 1989). We extracted an incisor from dead deer >2 years old and submitted incisors to Matson's Laboratory (Manhattan, MT, USA; DeYoung 1989) for age estimation using cementum annuli. We used age determined with cementum annuli throughout the study when available.

Beginning in 2005, we surveyed enclosures yearly using trail cameras for 2 consecutive 14-day periods during September–October (autumn) and again in December–January (winter; Moore et al. 2014). We used the photo data and a composite of population estimators to judge if each enclosure was at, above, or below density goal of 10, 25, or 40 deer. We carried out adjustments to maintain density goals after the surveys in early December based on the autumn estimates and again in late March or early April based on the winter estimates.

We used 4 cameras in each enclosure for each survey. In natural-nutrition enclosures, we placed 1 camera over the water source and the remaining cameras were along deer trails. We sometimes used bait piles of shelled corn to increase the number of photos in natural-nutrition enclosures. For enhanced-nutrition enclosures, 1 camera was over the water source, 1 at feeders, and 2 along deer trails. To avoid errors in reading the number and color of ear tags, we placed a steel post painted bright yellow 10 m from each camera in all enclosures and tallied only deer between the camera and the post. Bait (shelled corn) or feed (enhanced nutrition) resulted in adult deer photos biased toward males (Moore et al. 2014).

We used a composite of mark-resight (Lancia et al. 2005) and camera (Jacobson et al. 1997) estimators to determine if enclosure deer populations differed from our goal of 10, 25, or 40 deer after the autumn and winter surveys. These population estimates were for temporary use to make each biannual density adjustment and were not used for later population analyses, which were based on reconstruction. We estimated number of adult males by individual ear tags or antler characteristics for untagged deer (Jacobson et al. 1997). We estimated number of adult females by mark-resight using the ratio of individually tagged to unmarked deer (Lancia et al. 2005). There were no marked fawns in autumn surveys and our experience showed fawns were underrepresented in photos in autumn (McCoy et al. 2011). We made a preliminary estimate of fawns in autumn using the ratio of adult female photos to fawn photos (Jacobson et al. 1997). At the yearly December population adjustment, we captured, tagged, and released several fawns in each enclosure. In the subsequent winter survey, we estimated fawns by mark-resight (Lancia et al. 2005). We summed adult male, adult female, and fawn estimates to obtain a total population estimate.

In enclosures that we estimated to be below density goal, we stocked additional deer captured outside the enclosures. In enclosures that we estimated to be above goal, we shot surplus animals from the ground (early years) or a helicopter (later years). Also, in most years, we captured and tagged additional deer inside enclosures to maintain a high percentage of marked animals. In maintaining densities in enclosures through stocking or removal, we maintained adult sex ratios (male:female) of 1:1–1:1.5, and age structures with declining proportions from young to older animals.

We developed and evaluated a unique population reconstruction estimator to obtain a retrospective monthly estimate of number of deer in each enclosure. Our reconstructions used age-at-harvest data and picked-up skulls, as have previous studies (McCullough 1979, Fryxell et al. 1988), but we relied mainly on date of translocation into enclosures, frequent capture and tagging of unmarked deer, and biannual camera surveys of tagged deer to document survival. Subsequently, we used reconstruction estimates in all analyses for evaluation of deer density and nutrition treatments. Reconstruction provided several advantages in our studies. All deer in low-density treatments and fawns in all treatments could not be estimated with mark-resight procedures in Program MARK (White and Burnham 1999) because of low sample size (Donohue 2010, Cook 2014). Also, reconstruction was more flexible in providing a year-around monthly estimate. Certain parameters were more realistically estimated in months other than those where a point estimate was available from MARK. Finally, we did not begin camera surveys until 2005, so only reconstruction provided population estimates for 2004.

Our reconstruction estimator was an accounting procedure whereby we developed a spreadsheet for each enclosure with each individual deer in a column by month for as long as it lived. Deer entered the reconstruction in several ways. Deer captured on the ranches and translocated into enclosures entered the reconstruction in the month of their translocation. Untagged deer captured in enclosures and subsequently tagged and released entered in the month of capture. We extended their histories back to either the beginning of the study in March 2004 or to July of their known or estimated birth year. We applied the same procedure to unmarked deer harvested in enclosures to reduce density to treatment goal. We also picked up untagged dead deer in enclosures during annual intensive and comprehensive vegetation sampling described in Crider et al. (2015) and Gann et al. (2016, 2019*b*). Untagged dead deer entered the reconstruction in an estimated month of death and extended back in the reconstruction based on known or estimated age.

We removed deer from the reconstruction in the month of harvest during density reductions. We removed tagged deer from reconstruction when they did not appear in trail camera photos for 2 consecutive sets of 2-week surveys. In this case, we removed deer from reconstruction in the month half way between the middle of the second camera survey where they did not appear and the last survey where they were photographed. We removed tagged deer from reconstruction that we picked up dead in the month half way between when we found them and the month of the last camera survey that we photographed them. Exceptions to the halfway rule for picked up-deer were occasional situations where the deer had obviously died recently. In these cases, we removed deer from reconstruction in the estimated month of death.

We validated reconstruction estimates by comparing adult male reconstruction estimates with a tally of total number of marked and unmarked males that we identified by ear tags and unique antler characteristics during camera surveys. We termed the tally known number of males because Moore et al. (2014) reported that only 2.8% of marked deer in our enclosures were not identified during an autumn or winter camera survey. Although we had no evaluation of number of untagged males missed in camera surveys, we assumed it was similar to marked males and thus low. For each of the 12 enclosures, we determined known number of males for 2-week camera surveys in autumn and winter beginning with autumn 2007 through winter 2013 ($n = 144$). We fit a simple linear mixed regression model with reconstruction as the independent variable and known males as the dependent variable. The model accounted for possible lack of independence, and we forced the intercept through 0 and tested for slope = 1.

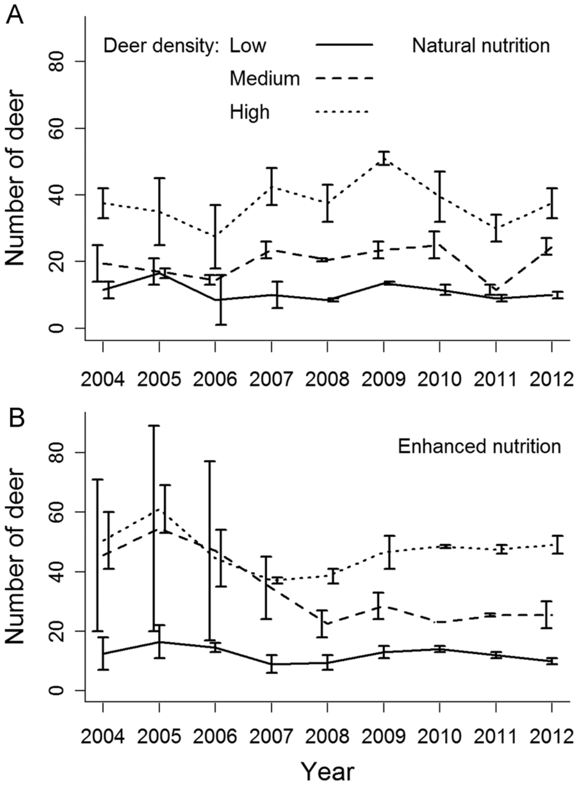

Figure 6. May mean (±SE) number of white-tailed deer in 2 replicate 81-ha enclosures with natural nutrition (A) and enhanced nutrition (B) and low, medium, and high white-tailed deer density treatments, South Texas, USA, 2004–2012. Some error bars are slightly off-set for clarity.

RESULTS

Our regression validation (Fig. 5) showed reconstruction provided reliable estimates of the number of males in enclosures. There was a 1:1 relationship ($P = 0.20$; Fig. 5) between known males and reconstruction males. Thus, we used reconstruction population estimates in subsequent analyses because they provided reliable information. They also provided estimates in all months, during early parts of the study when we had no camera data, and when sample sizes were too small to analyze with Program MARK.

It was a challenge to maintain target densities of wild deer in dense thornshrub vegetation through 9 years of study in 81-ha

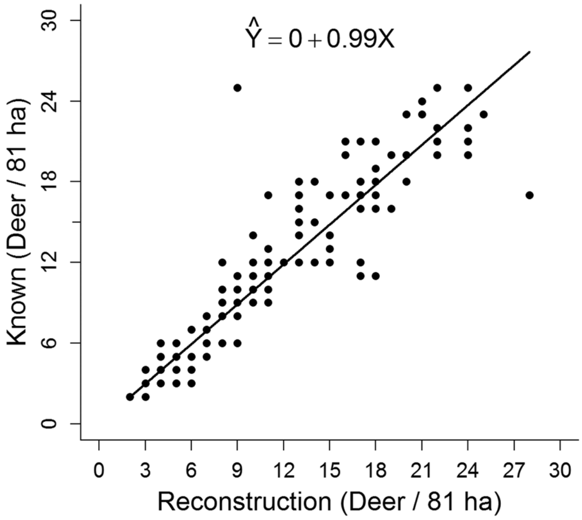

Figure 5. Regression of number of white-tailed deer males estimated by reconstruction and known number of males identified by tags or unique antlers in autumn and winter camera surveys in 81-ha enclosures, South Texas, USA, 2007–2012. Some dots in figure represent more than 1 data point ($n = 144$ total).

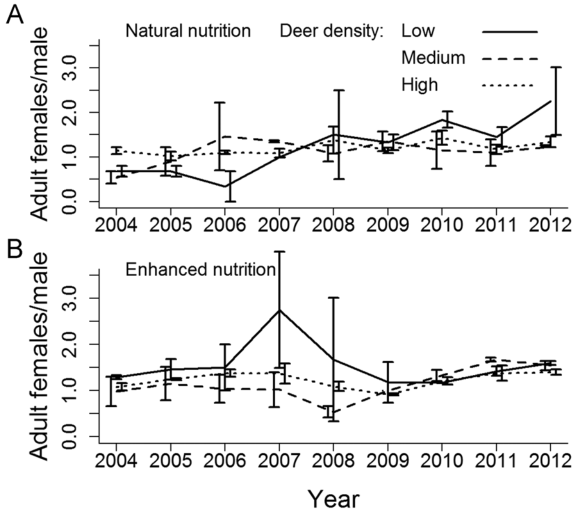

Figure 7. May means (±SE) of 2 replicates for adult white-tailed deer sex ratios (females/male) in 81-ha enclosures with natural nutrition (A) and enhanced nutrition (B) and low, medium, and high deer density treatments, South Texas, USA, 2004–2012. Some error bars are slightly off-set for clarity.

enclosures. We maintained the natural-nutrition enclosures close to goal (Fig. 6A). Low-density deer numbers in natural-nutrition enclosures averaged 11.0 ± 1.7 (SE) deer (equivalent 13.6 deer/km^2) versus the goal of 10, medium-density averaged 19.5 ± 0.7 deer (24.0 deer/km^2) versus the goal of 25, and high-density enclosures averaged 37.6 ± 3.67 deer (46.4 deer/km^2) versus the goal of 40. Deer in enhanced-nutrition enclosures were very productive (Cook et al. 2019) and high populations in the medium-density enclosure on the Faith Ranch resulted in numbers over goal for medium density (enhanced) for the first years of the study (Fig. 6B). Over the 9 years, enhanced low-density enclosures averaged 12.3 ± 2.6 deer (15.2 deer/km^2) versus our goal of 10, medium-density enclosures averaged 34.1 ± 11.7 deer (42.1 deer/km^2) versus our goal of 25, and high-density enclosures averaged 47.0 ± 2.0 deer (58.0 deer/km^2) compared to our goal of 40 deer (Fig. 6B). For the last 5 years of the study, the medium-density enhanced-nutrition treatment averaged 25.0 ± 1.0 deer.

Sex ratios of natural-nutrition enclosures averaged 1.23 ± 0.2 females/male for low-density enclosures, 1.08 ± 0.01 for medium density, and 1.2 ± 0.01 for high density (Fig. 7A). Corresponding sex ratios in enhanced-nutrition enclosures averaged 1.56 ± 0.3, 1.14 ± 0.1, and 1.2 ± 0.03 females/male, respectively (Fig. 7B).

For natural-nutrition enclosures, adult female ages averaged 4.6 ± 0.10 years in low-density enclosures, 5.2 ± 0.6 years in medium density, and 5.2 ± 0.4 years in high density (Fig. 8A). In enhanced-nutrition enclosures, adult female ages averaged 4.3 ± 0.10 years at low density, 5.1 ± 0.6 years for medium density, and 5.9 ± 0.3 years in the high-density treatments (Fig. 8B). For males in natural-nutrition enclosures, adults averaged 4.7 ± 0.3 years at low density, 5.1 ± 0.6 years for medium density, and 5.2 ± 0.3 years at high density (Fig. 9A). Males in enhanced-nutrition enclosures averaged 4.4 ± 0.6 years at low density, 4.9 ± 0.9 years at medium density, and 5.8 ± 0.1 years at high density (Fig. 9B).

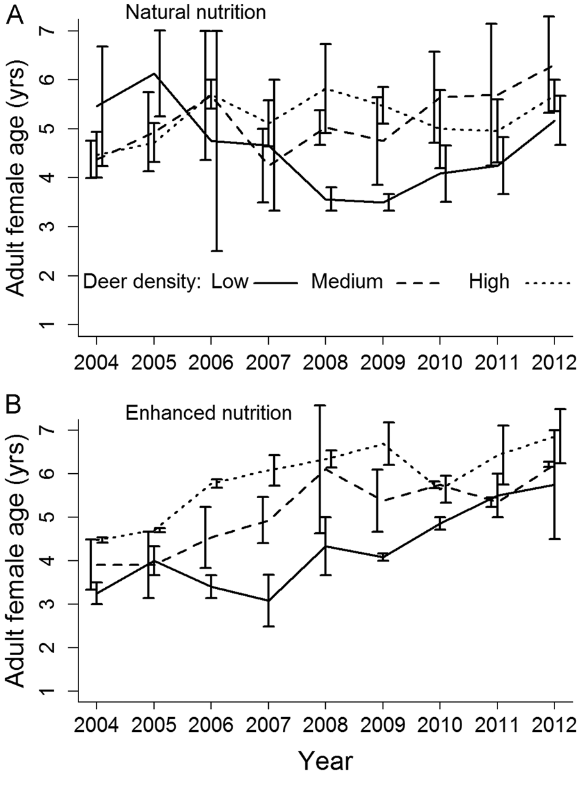

Figure 8. July means (±SE) of 2 replicates for adult white-tailed deer female ages in 81-ha enclosures with natural nutrition (A) and enhanced nutrition (B) and low, medium, and high deer density treatments, South Texas, USA, 2004–2012. Some error bars are slightly off-set for clarity.

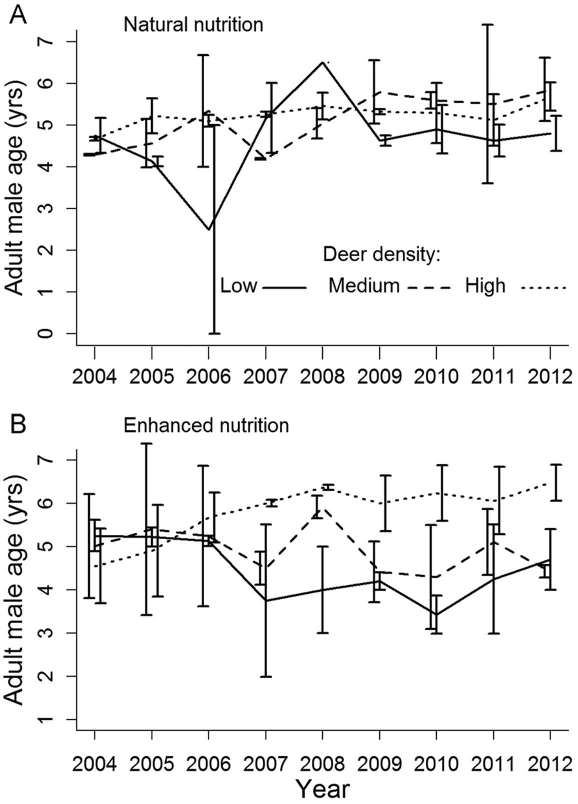

Figure 9. July means (±SE) of 2 replicates for adult male white-tailed deer ages in 81-ha enclosures with natural nutrition (A) and enhanced nutrition (B) and low, medium, and high deer density treatments, South Texas, USA, 2004–2012. Some error bars are slightly off-set for clarity.

DISCUSSION

We removed potential herbivore competitors of deer from our enclosures because we wanted our experiments to focus on intraspecific competition for food. Before our experiments began in 2004, both ranches removed cattle, and we removed feral hogs and collared peccary. Cattle diets tend to be dominated by grasses (Bryant et al. 1979) and deer diets are dominated by browse and forbs (Darr et al. 2019). However, competition for food between deer and cattle can occur at critical times (Bryant et al. 1979). Feral hogs in South Texas are mainly grazers and may have the highest diet overlap with deer in spring when forbs are most available (Taylor and Hellgren 1997). In eastern South Texas, collared peccary diets were dominated by forbs and grasses, followed by *Opuntia* cactus (Ilse and Hellgren 1995). Thus, all 3 of the potential herbivore competitors that were absent on our study sites have some documented diet overlap with white-tailed deer. The collective degree of competition among sympatric deer, cattle, feral hogs, and collared peccary is unknown.

We also significantly suppressed coyotes in research enclosures to focus on intraspecific competition among deer. Coyotes can be significant predators of neonatal fawns in South Texas (Beasom 1974) and depredate some adult deer (Heffelfinger et al. 1990). However, in western South Texas, coyote predation was not a significant factor in deer dynamics in some years (Guthery and Beasom 1977). Ballard et al. (2001) reviewed deer-predator relationships in North America and concluded that predator impacts on deer density dependence were complex and may be related to level of deer populations relative to carrying capacity.

Our goal was to design an experiment that assessed the effect of a range of deer densities on vegetation and deer dynamics. We set our high-density treatment goal at 50 deer/km^2, slightly above the carrying-capacity estimates (McCall et al. 1997, Strickland 1998) and highest population estimate (DeYoung 1985, DeYoung et al. 1989). The lowest published density for South Texas thornshrub was 11.2 deer/km^2 (average of 4 flights) from our Faith Ranch study area (DeYoung et al. 1989). We set our low-density goal at the slightly higher density of 13 deer/km^2 to have enough deer to estimate most population processes (10 deer/81-ha enclosure). We achieved the goal of maintaining a low, medium, and high density of deer with the natural-nutrition enclosures over the 9 years of study. Although some enhanced-nutrition enclosures exceeded goal early in the study, we attained the desired range of densities for the last 5 years.

We used an accounting process to reconstruct enclosure populations monthly, 2004–2012. Previous researchers using reconstruction have relied on age-at-harvest data (Fryxell et al. 1988, Gove et al. 2002, Skalski et al. 2007) or age-at-harvest plus picked-up skulls (McCullough 1979). Statistical models are commonly used to reconstruct populations from age-at-harvest data (Skalski et al. 2005). Our approach was different and had several advantages. We had age-at-harvest data from semi-annual population adjustments in the enclosures. We also had picked-up skulls collected during intensive vegetation sampling (Gann et al. 2019*b*) and other fieldwork in the 81-ha enclosures. However, the best data for the reconstructions were from capture, tagging, and aging of deer and semi-annual camera surveys in which approximately 98% of marked deer were identified (Moore et al. 2014). A high proportion of enclosure populations were tagged for individual identification. We aged and tagged deer initially stocked into enclosures and captured, aged, and tagged additional untagged deer. Disappearance of individually tagged deer from 2 consecutive camera surveys provided strong evidence the animal was dead because it was very rare that any deer was sighted alive after going missing for 2 surveys (Moore et al. 2014). We did not have to wait until all animals died to reconstruct populations because we had an inventory of tagged animals. Finally, we had the ability to validate our reconstruction estimates by comparing them against known numbers of males from tagged individuals and unique antler configuration of untagged individuals in camera surveys.

Experimental designs for studying population dynamics of ungulates must consider several elements (McCullough 1990, Bonenfant et al. 2009, Bowyer et al. 2014). Scale and habitat heterogeneity can influence detection of density dependence. McCullough (1990) argued that smaller study areas might exhibit density dependence across the spectrum of low to high density, whereas a larger study area might see what he termed a ramp. The ramp would result from no density dependence until the population approached ecological carrying capacity. We selected 81 ha as the size of each of our experimental units as a compromise between being large enough for most natural population processes to occur yet small enough to intensively sample the plant and deer populations over 9 years.

The more diverse the habitat, the more likely ungulates can use rich patches during critical periods and off-set effects of intraspecific competition (Searle et al. 2010). On a ranch adjacent to our Faith Ranch study area, Hood and Inglis (1974) estimated home ranges of 167 ha and 252 ha for free-ranging females and males, respectively. Thus, presumably deer in our 81-ha enclosures would have access to less habitat heterogeneity, thereby making expression of density dependence by enclosure deer populations more likely.

DeYoung et al. (2008) reported sex ratios of deer determined from helicopter survey averaged 1.58 ± 0.09 during 1981–1997 for the Faith Ranch when hunter harvest was non-existent or incidental. Leon et al. (1987) reported no bias by sex in adult deer sightings from helicopter surveys in South Texas thornshrub. Sex ratios over our 9-year study varied from 1.08 to 1.56 among treatments. Experimental sex ratios close to natural are presumably important for enclosure deer populations to express natural social behavior (DeYoung and Miller 2011), which affects population dynamics. Obviously, breeding-age females are needed for population productivity (DeYoung 2011).

For males in age-structured populations, researchers have recently (DeYoung et al. 2009) shown that males 3.5 years old and older sire about 70% of fawns. Ages of adult males in our enclosures averaged 4.4–5.8 years across treatments, which should have ensured breeding success similar to natural free-ranging populations. Ages of adult females averaged 4.3–5.9 years across the various treatments during the study. Older white-tailed deer females are more productive than young females (DeYoung 2011) so our enclosure ages ensured ample population productivity.

MANAGEMENT IMPLICATIONS

Designed experiments for understanding ungulate population dynamics are valuable in developing management applications (Caughley 1985). Our experiment, which spanned 9 years and included 3 density levels and 2 nutrition treatments, will aid managers only if treatment levels mirrored unexploited, free-ranging deer populations in semi-arid, stochastic environments. With the possible exception of the medium-density, enhanced-nutrition level for the first 4 years, we maintained density treatments close to goal during the 9 years. We maintained sex ratios and age structures of enclosure populations reasonably parallel with published data on white-tailed deer living in thornshrub habitat. We simplified the enclosure ecosystems by removing collared peccary, feral hogs, and coyotes. With this caveat, managers can be confident that results of our experiments will provide reliable information for managing white-tailed deer in habitats and environments similar to our study areas.

Deer Density Effects on White-Tailed Deer Diets and Foraging Behavior Under Natural Nutrition

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INTRODUCTION

Understanding ecological processes determining the number of animals that live in an area is fundamental to ecology and wildlife management (Sibley et al. 2003, Guthery and Shaw 2013). Density-dependent relationships have been proposed as a primary factor influencing white-tailed deer population processes and thereby population size (Bowyer et al. 2014). These density-dependent relationships are often assumed to act through declines in forage quantity and quality as deer density increases (McCullough 1979, DeYoung 2011). A relationship between forage quality and deer density is intuitive because deer are selective foragers, preferentially eating some forages and avoiding others (Augustine and McNaughton 1998). If selective foraging is sufficiently intense, vegetation communities change and diet quality declines, causing a reduction in productivity of deer and a decline in population growth rate (Daigle et al. 2004, Tremblay et al. 2005, Simard et al. 2010, White 2012, Lashley et al. 2015). Despite the importance of understanding mechanisms influencing density dependence, most research on density dependence in white-tailed deer has concentrated on demographic and morphological implications of deer density (McCullough 1979; Keyser et al. 2005; Simard et al. 2010, 2014; DeYoung 2011), whereas research on the consequences of deer density on foraging dynamics and diet quality is less common (Kie et al. 1980, Stewart et al. 2011).

Our objectives were to use our natural-nutrition enclosures to 1) determine the effect of deer density on diet composition, diet quality, and intake rate of white-tailed deer in rangelands of southwestern Texas; and 2) assess the effect of environmental stochasticity, as measured by variation in a drought index, on white-tailed deer diet composition, diet quality, and intake rate. To address our first objective, we hypothesized that because density dependence may be difficult to detect in stochastic environments (DeYoung et al. 2008), differences in diet composition of white-tailed deer at different densities will not be evident (Fig. 3A). We predicted that diet composition would not shift toward shrubs and grass, forages that were less preferred and more resistant to deer browsing, and away from forbs in enclosures with higher deer density as would be expected if deer populations were density dependent. We also predicted that diet quality and intake rates of dry matter (DM), digestible protein (DP), and metabolizable energy (ME) would be similar at high deer density compared to low deer density.

For our second objective, we hypothesized that drought would cause a shift in diet composition toward drought-resistant forages and that diet quality and intake rate would decline during drought compared to periods of average or above-average precipitation. We predicted that during drought, shrubs would be a larger proportion of deer diets and forbs would be a lower proportion compared to non-drought periods. We also predicted that intake of DP and ME would decline during drought but that DM intake rate would not change during drought because abundant shrubs would enable deer to maintain intake rate despite the decline in herbaceous forage.

METHODS

We conducted our study between June 2009 and May 2011 in 81-ha research enclosures that were not provided with enhanced nutrition (DeYoung et al. 2019*a*). We used the low and high deer density enclosures on each of the 2 study sites. Target deer densities of 13 deer/km^2 and 50 deer/km^2, respectively, had been maintained in these enclosures since spring 2004 (DeYoung et al. 2019*a*), 5 years before our study began.

Diet Composition

Folks et al. (2014) provided a description of our study deer and sampling procedures. We summarize these methods below. We quantified composition and quality of deer diets using the bite count method (Meyer et al. 1984, Parker et al. 1999). We collected foraging data from 10 to 12 adult, female white-tailed deer each season. All deer were hand-reared in captivity and acclimated to humans at the Alfred and Margaret Alkek Ungulate Research Facility, Texas A&M University–Kingsville, Kingsville, Texas. We fitted deer with very high frequency radio-collars and released them into their respective enclosures ≥4 weeks before any data collection; they remained in the research enclosures permanently. We allocated deer between

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high- and low-density enclosures across both study sites, so that ≥2 deer were present in each enclosure during each season.

We obtained bite count data during summer (Jun–Jul), autumn (Oct–Nov), winter (Jan–Feb), and spring (Apr–May) from summer 2009 to spring 2011 for a total of 8 sampling periods. During each sampling period, we randomly selected a study site on which to begin observations and alternated observations between deer in the low- and high-density enclosures. We located the deer chosen for observation during a given morning or evening foraging period by homing on the deer's radio-transmitter. Once located, we followed the focal deer and started a digital voice recorder when the deer began actively foraging (biting, chewing, and manipulating forage). We paused the recording ≤5 seconds after the deer stopped foraging and resumed recording when the deer continued foraging. Distances from focal animals during data collection ranged from <1–30 m, but most observations were ≤10 m. We collected about 2 hours of constant foraging data from each deer during each season with <45 minutes of data during any 1 foraging session. We attempted to record equal foraging time during morning and evening foraging bouts. For each bite taken, we recorded the plant species, plant part (leaf, stem, flower, or mast), and bite size (1, 2, or 3). Bite size categories varied by species and season. Generally, for browse, bite 1 included leaves only; bite 2 included leaves and some stem, mostly non-lignified and removed with the incisors; bite 3 included leaves and stem removed with the molars. For subshrubs, forbs, flowers, mast, fungi, and grass, we recorded bites as 1, 2, or 3 based on species-specific amounts of material removed from the plant. After bite counts, we transcribed the voice recordings and totaled bites by species, plant part, and bite size for each deer. We then assigned all plant parts to 1 of 10 forage classes: forbs, browse, subshrubs, grasses, cacti-succulents, mast, grasses, fungi, flowers, and litter (dead leaves of shrubs).

Intake Rate and Forage Quality

When bite counts concluded at each site each season, we picked ≥5 representative bites of each bite size category for each plant and plant part that composed >0.1% of total bites in each enclosure each season and dried the samples at 40°C to a constant mass. We used the dry mass of each representative bite to determine average bite mass for each bite size. We also collected 60 g (wet mass) of each plant and plant part totaling >0.1% of total bites per enclosure per season to use for nutritional analyses. We dried all plant samples at 40°C to a constant mass. Plant samples that were exceedingly moist, like cacti, or that had a high sugar content, like Texas persimmon (*Diospyros texana*) and mesquite mast, were stored in a freezer at −20°C until dried via cryodessication (Labconco FreeZone 18, Kansas City, MO, USA). For shrub species, we assumed bite 1 and bite 2 tissues were nutritionally similar because bite 2 tissues only contained a small portion of non-lignified stem. We performed nutritional analysis on bite 1 tissues and assigned these values to bite 2 tissues. We collected and analyzed bite 3 tissues separately if they made up >0.1% of the total bites in each enclosure. For all other forage classes, we collected and analyzed the tissue of bite sizes 1, 2, and 3 in the same sample because we assumed all bites had the same nutritional quality. For all forage items constituting <0.1% of diets, we assigned the average bite mass and nutritional values for the corresponding forage class. We then used the dry mass of each bite size, the number of bites taken, and the nutritional quality of each bite to determine the quality of each deer's diet.

To determine the nutritional content of forages consumed by deer, we ground all samples in a Wiley mill to pass through a 1.0-mm screen. We then conducted nutritional analyses including detergent fiber, tannin, gross energy, and crude protein at the Lehmann Forage Laboratory, Texas A&M University–Kingsville, Kingsville, Texas. We used sequential detergent analysis (Goering and Van Soest 1970) to determine neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) using an ANKOM Technology Fiber Analysis System (Macdeon, NY, USA). We used sodium sulfite for all samples in this analysis to prevent the overestimation of ADF, NDF, and ADL in tannin-containing forages (Hanley et al. 1992).

We estimated the protein-binding potential of tannins in forage samples using the radial diffusion technique (Hagerman 1987, 2002*a*). We purified pentagalloyl glucose from tannic acid and used it as a standard for the radial diffusion analysis (Hagerman 2002*b*). Ensuing calculations required tannin quantified using precipitation of labeled bovine serum albumin (BSA; Asquith and Butler 1985). Because we did not use this precipitation technique, we converted radial diffusion results to match labeled protein precipitation values using the equation $y = 4.56x$, where y is the BSA precipitation (mg BSA/100 mg plant tissue) and x the radial diffusion precipitation (mg tannin/100 mg plant tissue; Hagerman 1987). We measured percent nitrogen in the forage samples using a Vario Macro CN Elemental Analyzer (Elementar Americas, Inc., Mt. Laurel, NJ, USA), then multiplied percent nitrogen by 6.25 to estimate percent crude protein (Robbins 1993). We measured gross energy (kcal/g DM) content of the samples using a Parr 6300 Bomb Calorimeter (Parr Instrument Co., Moline, IL, USA). We determined gross energy for the top 5 shrub, subshrub, forb, grass, fungi, litter, and cacti species, based on the number of bites taken during a season. We then applied the average for each forage class to the remaining species in that forage class. We analyzed all flower and mast samples for gross energy.

We assessed diet quality using DP and ME. We calculated DP from the equation $\mathrm{DP} = -3.87 + 0.9283x - 11.82y$, where DP is the digestible protein (g/100 g DM plant tissue), x the percent crude protein, and y the BSA precipitation (mg BSA/mg forage DM; Robbins et al. 1987*a*, Hanley et al. 1992). We calculated ME by first estimating the digestible dry matter content with the equation

$$\begin{aligned}\mathrm{DDM} = {} & [(0.9231e^{-0.0451A} - 0.03B)(\mathrm{NDF})] \\ & + [(-16.03 + 1.02\mathrm{NDS}) - 2.8P]\end{aligned}$$

where DDM is the digestible dry matter (g/100 g forage DM), A the lignin and cutin content as a percentage of NDF [((ADL − ash)/NDF) × 100], B the percent biogenic silica content of monocots, NDS = (100 − percent NDF), and P the reduction of protein digestion by tannins ($11.82y$ from the above DP equation; Robbins et al. 1987*b*, Hanley et al. 1992). We assumed $B = 0$ because deer did not eat much grass.

Next, we determined the diet's digestible energy coefficient (DEC) using the equation $DEC = (-0.49 + (0.99 \times DDM))$. We used this value to calculate digestible energy (DE) with the equation $DE = [(DEC/100)\ (\text{gross energy})]$. Finally, we calculated ME (kcal/g DM) as $ME = DE \times MEC$, where MEC is the metabolizable energy coefficient. We considered $MEC = 0.81$ for woody plant stems and cacti and 0.82 for woody plant leaves, forbs, mast, flowers, fungi, and grass (Robbins 1993).

Some forb samples collected during winter 2010, especially those forbs in the rosette stage, had extremely high ash values due to sand that adhered to the plant sample. We divided DP and ME by 1-decimal percent of ash to account for the high ash content. Bite weights for these species did not include sand.

We summed total foraging time, number of bites, DM, DP, and ME intake across bite count trials for each deer within a season. We then used these totals to calculate bite rate (bites/min), DM intake rate (g DM/min), ME intake rate (kcal/min), DP intake rate (g DP/min), and average bite size (g/bite).

Statistical Analysis

We used repeated-measures analysis of variance (ANOVA) in SAS 9.2 (PROC MIXED; SAS Institute Incorporated, Cary, NC, USA) to compare the following dependent variables: dietary DP and ME, DP and ME intake, and the proportion of each forage class in deer diets, with each deer serving as an experimental unit. We combined fungi, flower, and litter forage categories into a forage class called other for this analysis. We designated seasonal sampling periods as periods 1–8. Independent variables included in the models were seasonal sampling period (4 seasons × 2 years = 8 sampling periods), treatment (low and high deer density), and their interaction. We included study site and interactions between study site and treatment and between study site and year nested within treatment as random variables. Because of rainfall variability during this study, we used contrast statements to complete *post hoc* tests on the effect of season and drought conditions on diet quality.

We determined drought using the Palmer *Z* Index because of its ability to assess short-term drought conditions on a monthly scale (National Climatic Data Center 2001). We averaged drought index values for the 2-month time span encompassing each sampling period. We considered sampling periods with Palmer *Z* Index values <0 to be drought and periods with values >0 to be non-drought (Table 1). Rainfall variability during this study fortuitously resulted in each sampling season (summer, autumn, winter, and spring) having 1 drought and 1 non-drought period, allowing for the inclusion of season and drought as independent variables in the analysis. We assessed 6 possible variance–covariance structures for each repeated-measures ANOVA: variance components, Toeplitz, heterogeneous autoregressive, first-order autoregressive, compound symmetry, and univariate autoregressive moving average. We selected variance–covariance structures in 2 steps. First, we modeled the variance–covariance structure associated with the error term for period and the period × treatment interaction and selected the structure with the smallest Akaike's Information Criterion corrected for sample size (AIC_c). We then modeled the variance–covariance structure associated with the error term for deer-to-deer variation and selected the structure with the smallest $AICc$, while keeping the variance–covariance structure selected in the first step. We set the significance level for statistical tests at $P = 0.10$ to reduce the probability of a Type II error. We used least square means with standard errors for all statistical analyses.

RESULTS

During the 2 years of the study, we collected data from an average of 2.6 deer/enclosure during each of 8 periods, resulting in 241,166 bites being observed during 165 hours of active foraging time. Deer consumed 137 vascular plant species, 1 species of lichen, and 2 species of fungi. The fungi consisted of 1 mushroom species and an ephemeral rust (*Ravenelia subtortuosae*) growing on the stems of twisted acacia.

Deer Density

Diets of deer in low-density enclosures contained a higher percent of cactus during spring (11 ± 4% [SE] vs. 0%) and a lower percent of cactus during winter (9 ± 4% vs. 22 ± 4%) than did diets of deer in high-density enclosures (Fig. 10B). Percent grass in deer diets was greater in high-density (1.3 ± 0.4%) than low-density (0.3 ± 0.3%) enclosures (Fig. 10B). Composition of deer diets did not differ between deer density treatments for any other forage category (Fig. 10; Table 2).

Metabolizable energy content of deer diets did not vary significantly ($P = 0.45$) between low (2.25 ± 0.05 kcal/g) and high (2.20 ± 0.05 kcal/g) deer density treatments (Fig. 11A). Digestible protein in deer diets was similar ($P = 0.54$) between deer density treatments and averaged 9.9 ± 1.3% for the low-density treatment and 9.3 ± 1.3% for the high-density treatment (Fig. 11B).

Table 1. Two-month average Palmer *Z* Index values (Texas, Climate Division 9; National Climatic Data Center 2011) and drought conditions for seasonal bite count sampling of white-tailed deer from summer 2009–spring 2011 on the Comanche and Faith ranches in Dimmit County, Texas, USA.

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

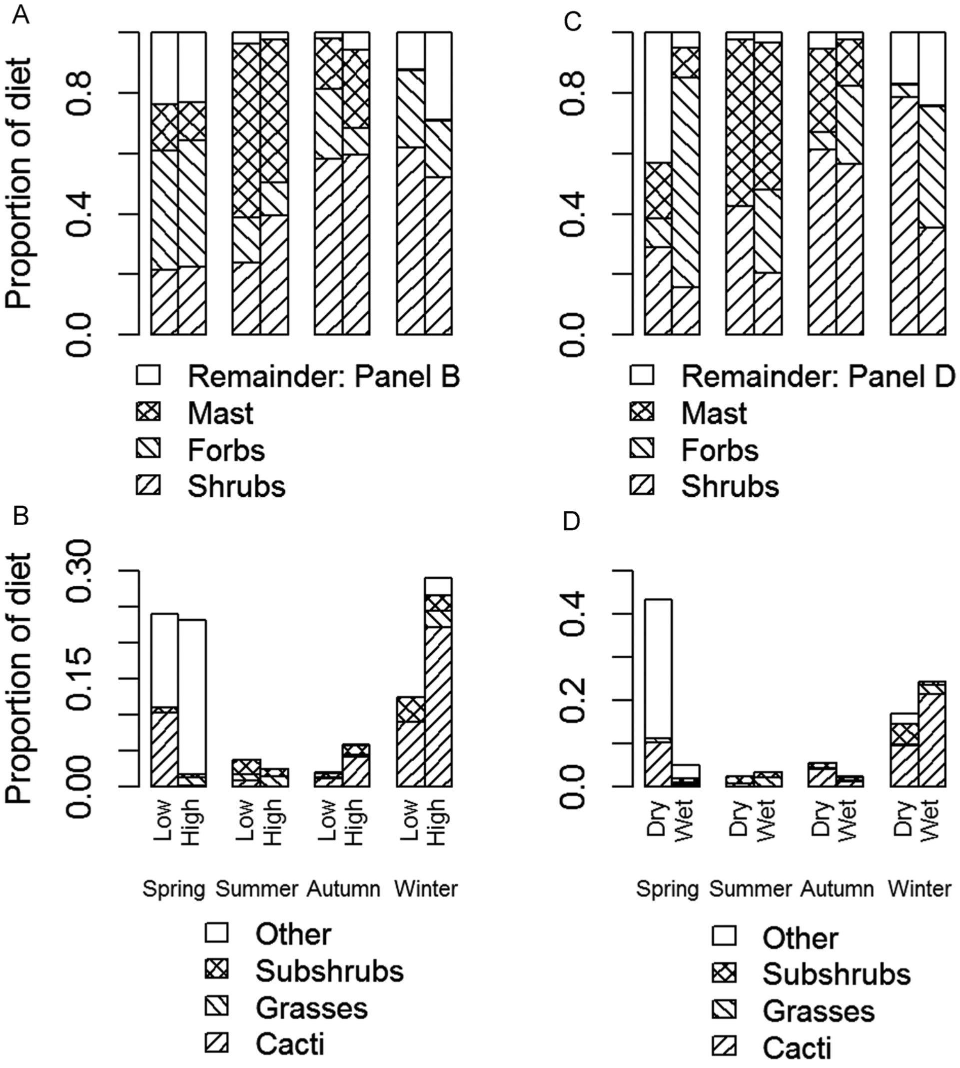

Figure 10. Seasonal least square means for proportion of major (A) and minor (B) forage classes in white-tailed deer diets in high and low deer density treatments averaged across drought conditions, and of major (C) and minor (D) forage classes in deer diets during dry and wet climatic conditions averaged across deer density treatments from summer 2009–spring 2011, in Dimmit County, Texas, USA. The forage class other is composed of flowers (dominant during spring), litter, and fungi.

Bite rate, bite size, and DM intake rate did not vary with deer density (Table 3). Averaged across seasons and drought conditions, bite rate was 25 ± 2 and 24 ± 2 bites/minute for deer in the low- and high-density treatments, respectively. Bite size averaged 0.13 ± 0.02 g/bite in low-density and 0.14 ± 0.02 g/bite in high-density enclosures. Dry matter intake rate averaged 2.85 ± 0.44 and 3.05 ± 0.44 g/minute for deer in low- and high-density enclosures, respectively. Neither DP (low density = 0.25 ± 0.02 g/min; high density = 0.24 ± 0.02 g/min) nor ME intake rate (low density = 6.3 ± 0.91 kcal/min; high density = 6.6 ± 0.91 kcal/min) varied with deer density (Table 3).

Drought

Precipitation conditions had a larger impact on deer diets than did deer density (Fig. 10C,D). Mast and other were the only forage classes that did not change significantly with drought (Table 2). However, the proportion of flowers, the main component of the other forage class, in deer diets during spring changed from 3 ± 8% during non-drought to 32 ± 8% during drought (Fig. 10D). During drought conditions, the proportion of shrubs increased in deer diets, whereas forbs decreased to 0–10% of the diet, depending on the season. The effect of drought on cactus consumption varied with season. Cactus consumption was greater during drought in the spring and during wet conditions in winter. Subshrubs were a larger proportion of winter diets during drought than non-drought and grass consumption during summer and winter decreased during drought.

Percent DP was 31%, 53%, and 54% greater during non-drought than drought during autumn, winter, and spring, respectively ($P = 0.06$). During summer, DP was 19% greater during drought than non-drought. Metabolizable energy did not vary between drought and non-drought ($P = 0.75$).

Average bite rate decreased in drought conditions during spring, whereas bite size increased during autumn and spring relative to non-drought (Fig. 12A,B; Table 3). Changes in bite size influenced DM intake rate, which was greater in drought conditions than non-drought during autumn and spring (Fig. 12C). Our analysis suggested an interaction between season and

Table 2. Analysis of variance mixed models evaluating the effect of deer density, period (8 seasonal periods across 2 years), and density by period interaction on the percent of white-tailed deer diets composed of 7 forage classes during summer 2009–spring 2011, in Dimmit County, Texas, USA. We used contrast statements to derive *P*-values for tests of drought category (dry or wet), season, and deer density.

Forage category	Source of variation	df	*F*	*P*	Forage category	Source of variation	df	*F*	*P*
Shrub	Density	1, 15.4	0.09	0.773	Forb	Density	1, 2.01	0.45	0.569
	Period	7, 15.4	4.11	0.010		Period	7, 14.1	3.09	0.034
	Period × density	7, 15.4	0.41	0.883		Period × density	7, 14.1	0.23	0.972
	Drought	1, 15.4	7.54	0.015		Drought	1, 14.1	14.93	0.002
	Season	3, 15.4	5.65	0.008		Season	3, 14.1	1.33	0.305
	Drought × density	1, 15.4	0.24	0.629		Drought × density	1, 14.1	0.80	0.386
	Season × density	3, 15.4	0.57	0.645		Season × density	1, 14.1	0.19	0.900
	Drought × season	3, 15.4	1.80	0.189		Drought × season	3, 14.1	9.66	0.590
Mast	Density	1, 15	<0.01	0.945	Cacti	Density	1, 2.02	0.08	0.802
	Period	7, 15	3.38	0.023		Period	7, 65.1	5.18	<0.001
	Period × density	7, 15	0.15	0.991		Period × density	7, 65.1	2.62	0.019
	Drought	1, 15	0.63	0.439		Drought	1, 65.2	0.03	0.874
	Season	3, 15	7.59	0.003		Season	3, 65.2	8.60	<0.001
	Drought × density	1, 15	0.21	0.651		Drought × density	1, 65.2	1.42	0.238
	Season × density	3, 15	0.22	0.884		Season × density	3, 65.2	4.40	0.007
	Drought × season	3, 15	0.68	0.576		Drought × season	3, 65.1	5.72	0.002
Grass	Density	1, 14.9	4.59	0.049	Subshrub	Density	1, 1.98	0.43	0.580
	Period	7, 11.8	1.62	0.221		Period	7, 13.4	3.27	0.030
	Period × density	7, 11.7	0.88	0.547		Period × density	7, 13.4	0.83	0.582
	Drought	1, 15.5	4.53	0.050		Drought	1, 13.5	2.73	0.121
	Season	3, 17	2.41	0.103		Season	3, 13.5	2.82	0.077
	Drought × density	1, 15.5	2.14	0.164		Drought × density	1, 13.5	2.04	0.176
	Season × density	3, 17	1.02	0.408		Season × density	3, 13.5	0.54	0.665
	Drought × season	3, 17.5	2.99	0.059		Drought × season	3, 13.5	4.12	0.028
Other	Density	1, 14.2	0.28	0.606					
	Period	7, 14.2	2.26	0.091					
	Period × density	7, 14.2	0.23	0.972					
	Drought	1, 14.2	2.27	0.153					
	Season	3, 14.2	2.76	0.081					
	Drought × density	1, 14.2	0.43	0.525					
	Season × density	3, 14.2	0.14	0.935					
	Drought × season	3, 14.2	2.04	0.154					

Table 3. *P*-values for analysis of variance mixed models evaluating the effect of deer density, period (8 seasonal periods across 2 years), and density by period interaction on measures of foraging behavior of tractable white-tailed deer during summer 2009–spring 2011, in Dimmit County, Texas, USA. We used contrast statements to derive *P*-values for tests of drought category (dry or wet), season, and deer density.

Variable	Source of variation	df	*F*	*P*	Variable	Source of variation	df	*F*	*P*
Bite rate	Period	7, 14.6	6.97	<0.001	Bite size	Period	7, 7.63	3.87	0.042
	Period × density	7, 14.5	0.34	0.921		Period × density	7, 7.31	1.44	0.317
	Density	1, 17	0.60	0.448		Density	1, 5.41	0.47	0.520
	Season	3, 14.3	14.10	<0.001		Season	3, 16.9	6.34	0.004
	Drought	1, 16.2	4.20	0.057		Drought	1, 30.9	5.65	0.024
	Season × density	3, 14.3	0.46	0.713		Season × density	3, 16.9	2.11	0.137
	Drought × density	1, 16.2	0.07	0.796		Drought × density	1, 30.9	0.22	0.643
	Drought × season	3, 14.7	12.58	<0.001		Drought × season	3, 17.6	2.87	0.066
Dry matter intake rate	Period	7, 6.12	9.53	0.007	Digestible protein intake rate	Period	7, 6.22	3.59	0.067
	Period × density	7, 5.89	1.67	0.277		Period × density	7, 5.8	0.55	0.773
	Density	1, 3.69	0.37	0.580		Density	1, 1.25	0.20	0.722
	Season	3, 10.5	17.66	<0.001		Season	3, 6.5	8.31	0.012
	Drought	1, 25.4	3.75	0.064		Drought	1, 9.69	0.02	0.904
	Season × density	3, 10.5	2.23	0.144		Season × density	3, 6.5	0.70	0.584
	Drought × density	1, 25.4	0.20	0.656		Drought × density	1, 9.69	0.15	0.703
	Drought × season	3, 11.2	15.09	<0.001		Drought × season	3, 6.82	7.58	0.014
Metabolizable energy intake rate	Period	7, 4.06	7.34	0.035					
	Period × density	7, 4.03	1.07	0.502					
	Density	1, 2.55	0.19	0.698					
	Season	3, 6.46	13.27	0.004					
	Drought	1, 13.7	3.62	0.078					
	Season × density	3, 6.46	1.40	0.327					
	Drought × density	1, 13.7	0.42	0.530					
	Drought × season	3, 6.54	10.01	0.008					

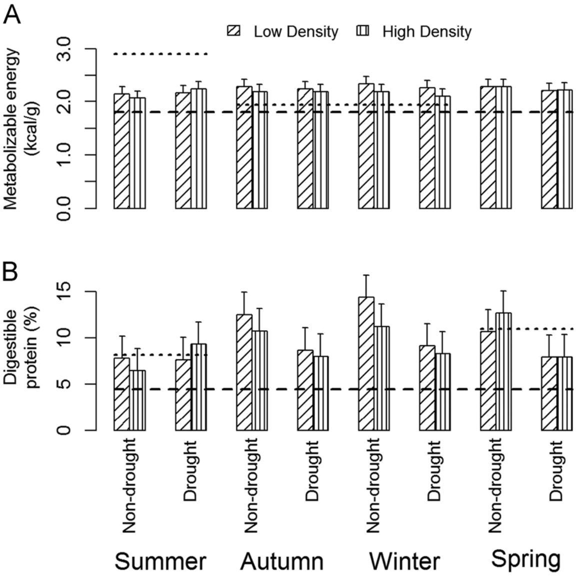

Figure 11. Least square means (+SE) for metabolizable energy (A; kcal/g dry matter) and digestible protein (B; g/100 g dry matter) in seasonal diets of tame female white-tailed deer in 81-ha enclosures with low and high deer densities from July 2009 to May 2011 on the Comanche and Faith ranches in Dimmit County, Texas, USA. Long-dashed lines are maintenance requirements and short-dashed lines are gestation (winter and spring) or lactation (summer) requirements.

drought for both DP and ME intake but none of the drought status comparisons within season were significant ($P > 0.16$).

DISCUSSION

The effect of white-tailed deer density on diet composition is rarely quantified (Kie et al. 1980); however, many researchers have reported changes in vegetation communities from deer foraging sufficient to change composition of deer diets (Rooney and Waller 2003, Cornett et al. 2010, White 2012, Simard et al. 2014). In contrast, we found few differences attributed to deer density in deer diet composition and no differences in diet quality or foraging parameters even though enclosures in our study were maintained with a 3.4-fold difference in deer density for 5 years. This design allowed for possible accumulated impacts on the vegetation of different deer densities as well as current-year impacts. The effects of deer density on cactus consumption depended on season and drought conditions and were not consistent with respect to deer density. Percent grass in the diet was greater in high-density than low-density enclosures, consistent with predictions of cumulative impacts from deer foraging (Kie et al. 1980, Rooney and Waller 2003), but grass was a minor component of the diet (≤2.3%) and differences were not sufficient to affect diet quality. Thus, our hypothesis that differences in diet composition of white-tailed deer at different densities will not be evident in a stochastic environment was supported (Fig. 3A). Furthermore, Folks et al. (2014) used diet composition data from our study to test the hypothesis that intraspecific competition would cause deer in enclosures with a high deer density to broaden their diet and for diets to become less similar among deer in an enclosure. They found no effect of deer density on diet richness, diversity, breadth, evenness, overlap, or similarity.

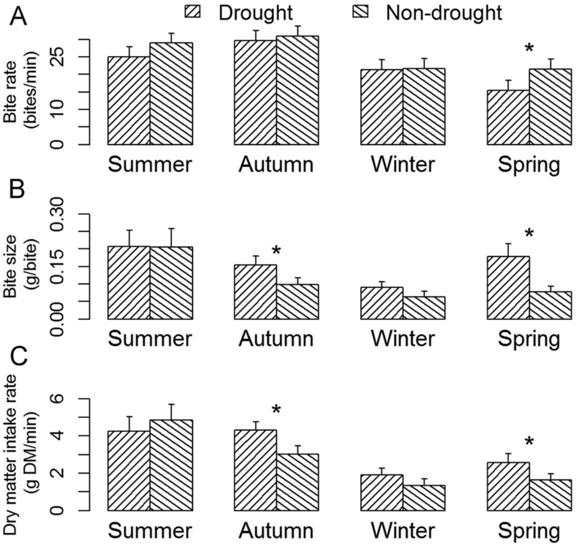

Figure 12. Seasonal bite rate (A; least square means + SE), bite size (B), and dry matter intake rate (C) of tractable female white-tailed deer in 81-ha enclosures during periods of drought and non-drought (averaged across 2 deer densities) from July 2009 to May 2011 on the Comanche and Faith ranches in Dimmit County, Texas, USA. Pairs of bars with an asterisk above are different ($P < 0.1$).

We provide 3 reasons why deer in our study may not have altered their diet in response to our density treatments. First, deer density may not have been maintained long enough for browsing to affect vegetation sufficiently to alter foraging patterns. However, in the George Reserve of Michigan, the white-tailed deer population increased from 6 deer in 1927 to 160 deer in 1933 (1.3 deer/km^2 to 34.5 deer/km^2) and the "deer population in the mid-1930s began to have a dramatic and highly visible impact upon the vegetation of the reserve" (McCullough 1979:8). The deer density that altered vegetation in the George Reserve was 30% below the deer density maintained for 5 years in our high-density enclosures. A 5-fold difference in elk density was sufficient to cause detectable dietary changes after 1 year (Stewart et al. 2011). Horsley et al. (2003) investigated white-tailed deer impacts on vegetation in a northern hardwood forest using a replicated, manipulative study with 4 deer densities ranging from 4 deer/km^2 to 25 deer/km^2, an upper deer density half that in our high-density enclosures. Five years after treatment by clear-cutting, herbaceous species preferred by deer declined with increasing deer density, whereas cover of unpalatable ferns increased. Deer density also reduced the height growth and density of trees 5 years after clear cut. Although not as dramatic as in clear-cut forests, deer density reduced *Rubus* ground cover, density of American beech (*Fagus grandifolia*), and species richness of woody plants in thinned forests 5 years after thinning. Thus, cervids can affect vegetation in a 5-year period in some ecosystems.

A second reason why deer in our study did not alter their diet in response to high deer density may be that the vegetation community did not change significantly as a result of varying deer density. In contrast to other systems in which deer can have a large influence on vegetation, 50 deer/km^2 had little detectable impact on the shrub-dominated vegetation on our study sites (Gann et al.

2019*b*). Most studies documenting changes in vegetation communities because of white-tailed deer browsing are in temperate forests (Russell et al. 2001). In contrast to temperate regions, vegetation in our study area appears recalcitrant to deer browsing (Crider et al. 2015; Gann et al. 2016, 2019*b*).

A third reason why we did not detect a change in deer diets in response to variation in deer density may be that changes in deer diet composition and especially in diet quality are not necessarily expected, even in areas where differences in deer density alter the vegetation community. White-tailed deer are flexible in their foraging behavior and can adapt to large changes in vegetation caused by past deer foraging. Intake rate of browsing herbivores is more sensitive to bite size than to biomass (Spalinger and Hobbs 1992). Thus, depending on the distribution of bites available from different forage classes, changes in the relative biomass of forage classes may not result in changes in deer intake rate or diet composition. Furthermore, white-tailed deer are selective browsers and can alter feeding strategies to maintain nutrient intake in response to forage depletion by past browsing (Kohlmann and Risenhoover 1994). Browsing may even result in higher-quality diets as a result of browse regrowth (du Toit et al. 1990) and deer may choose heavily browsed over moderately browsed patches because nutrient intake is higher (Kohlmann and Risenhoover 1994). Finally, deer are remarkably adept at using novel food items as preferred forages become scarce, and thereby can maintain adequate dietary intake (Miyaki and Kaji 2004, Tremblay et al. 2005, Le Saout et al. 2014). For example, in our study during drought when forb biomass was low, diets of deer during spring contained 32% flowers, primarily of blackbrush acacia and prickly pear. During non-drought, flowers were <5% of deer diets.

Our inability to detect meaningful changes in diet composition with 3.4-fold changes in deer density was consistent with Gann et al. (2019*b*), who found only subtle changes in vegetation communities in the same enclosures after 9 years of deer density treatments. Similarly, fawn and yearling growth rates, adult survival, and survival of fawns from 6 to 14 months old did not change with deer density in natural-nutrition enclosures, although fawn:adult female ratios, adult male and female body mass, and population growth rates declined with increasing deer density in the same research enclosures (Cook et al. 2019). Our nutrition and foraging data are limited to adult females and it is possible that nutritional impacts of increasing deer density are different on adult males and fawns (Kie and Bowyer 1999). Furthermore, the dramatic morphological and demographic response of deer in our study area to enhanced nutrition (Cook et al. 2019) shows clearly that deer consuming natural forage are nutritionally limited, even at low deer density. In such situations, deer may be especially sensitive to small changes in nutritional conditions and our tractable-deer technique may not have been sufficiently sensitive to detect changes in forage that affect fawns <6 months old and adult males.

The environmental stochasticity in our study areas resulting from variation in precipitation had a larger influence on deer diet composition and quality than did deer density. In accordance with changes in vegetation as a result of drought status (Gann et al. 2019*b*), deer diets contained a higher proportion of herbaceous forages when conditions were wet and a higher proportion of shrubs during dry conditions (Fig. 10). The proportion of mast in the diet did not change with moisture conditions because 2 primary mast-producing species, mesquite and prickly pear, are drought adapted and continue to produce mast despite drought. In fact, mesquite pods are produced at a higher rate during drought (Lee and Felker 1992), providing a valuable forage resource during summer, a particularly challenging season for deer during drought (Meyer et al. 1984).

White-tailed deer consume forbs, when available, because forbs are generally higher in DE and DP than shrubs (Hewitt 2011, Fulbright and Ortega-Santos 2013). Stochastic precipitation resulted in variable forb availability and when forb biomass was low, deer shifted their diets to other forages such as flowers, shrubs, and succulents. This dietary shift reduced DP in deer diets in autumn, winter, and spring during drought, compared to the same seasons during non-drought. The same effect was not evident during summer, when DP in deer diets did not increase during the non-drought summer. Mast, primarily from prickly pear, made up a large portion of deer diets during both drought and non-drought summers (53% and 48%, respectively) and was 52–90% during summer in an earlier study at our study sites (Timmons et al. 2010). Mast is low in DP (range in DP of prickly pear mast = 0.5–3.1%) but appears to be an important food item for deer because it can be abundant, highly visible, and provides large bites, thus facilitating high DM intake rates (Spalinger and Hobbs 1992) and therefore high ME intake.

Digestible protein in deer diets appeared sufficient to meet maintenance requirements for adults (4.5%, calculated from crude protein in National Research Council 2007) during all seasons, regardless of rainfall conditions. However, DP in diets fell below levels necessary for late gestation (11%) during the dry spring and for lactation with a single fawn (8.2%) during both summers (calculated from crude protein in National Research Council 2007). Meyer et al. (1984) reported crude protein levels of deer diets never falling below maintenance levels along the Coastal Bend of South Texas, but they found potential crude protein deficiencies for lactation by females during summer when forage availability and quality is reduced. Digestible protein was deficient for pregnant females in late gestation during drought in our study because of the increased consumption of forages low in DP and high in ME, such as flowers (particularly prickly pear flowers), succulents, and mast. High prickly pear mast consumption during summer caused DP in diets to be below optimum levels for gestation and lactation, a finding also noted by Timmons et al. (2010) who hypothesized that deer may consume large amounts of mast to meet ME requirements at the expense of reduced DP in diets.

In addition to reducing dietary DP below levels necessary for production in adult females, drought conditions may decrease DP in diets to levels insufficient for optimal growth of young deer. Fawns require 13–16% crude protein for optimum growth (French et al. 1956), which is 8.2–11.0% DP (assuming no reduction in protein digestion from tannins). During drought in autumn, winter, and spring, DP in deer diets was reduced to levels that bordered inadequacy, ranging from 8.1% to 8.4% DP.

Drought had no effect on the quality of ME in deer diets. This finding conflicts with results from Meyer et al. (1984), who found reduced dietary DE during hot, dry summers along the Coastal Bend of South Texas. Assuming a deer mass of 50 kg, dry mater intake of 28 g/kg$^{0.75}$/day (Parker et al. 1999), and an MEC of 81.8% (Robbins 1993), deer could maintain ME in diets >1.80 kcal/g, which is necessary for maintenance (Robbins 1993), throughout our study. Below this level of ME, deer are unable to consume adequate amounts of forage necessary to meet energy requirements because of limited gastrointestinal capacity and passage rates (Amman et al. 1973, Spalinger 1980, Robbins 1993). Metabolizable energy in diets was also sufficient for pre-breeding and mean gestation during autumn and winter (ME = 1.94 kcal/g; Pekins et al. 1998, our calculation). Diets selected by deer in our study during autumn and winter provided excess energy, which allowed deer to restore body condition and accumulate body reserves to be used during periods of insufficient energy intake (Parker et al. 1999).

Metabolizable energy in deer diets did not meet nutritional requirements for peak gestation and lactation during spring and summer (2.9 kcal/g ME; National Research Council 2007). However, the high energy requirements necessary for peak gestation and lactation often result in negative energy balance, requiring tissue catabolism to meet energy requirements (Parker et al. 1999). Surplus energy available to our study animals during autumn would enable deer to replace tissue catabolized during peak gestation and lactation.

Deer in our study may have been able to maintain ME at stable levels despite the stochastic environment by consuming forages high in ME and low in DP. During the dry spring, cacti, flowers (primarily prickly pear flowers), and mast were about 60% of deer diets, whereas mast made up 48% to 53% of diets during each summer. Throughout these periods, which also coincided with elevated ME requirements for females, deer appeared to maximize ME intake at the expense of DP.

We may have underestimated the decline in diet quality during drought. Shrub species, particularly guajillo and blackbrush acacia, composed large portions of deer diets during the dry autumn and winter. These species are high in plant secondary metabolites (PSMs; Clement et al. 1997, 1998) that result in high gross energy estimates (about 5 kcal/g gross energy for guajillo). These energy-rich plant chemicals may reduce DDM and, if absorbed, are excreted through the urine, resulting in decreased energy available to the animal. We did not test for PSMs other than tannins in forage samples, but we did use an MEC of 81.8% to compensate for urinary energy losses associated with PSMs (Robbins 1993). However, our calculations resulted in ME values for these browse species during drought being as high as forbs during non-drought (e.g., 2.5 kcal/g ME for guajillo). However, in vivo estimates of ME in guajillo foliage during summer are <1.6 kcal/g (calculated from Barnes et al. 1991 using 1.6–1.9 kcal/g DE and MEC of 0.8; Campbell and Hewitt 2005), suggesting an overestimate of ME available to the animal during periods of high browse consumption. Similarly, DP may have been overestimated because blackbrush acacia and guajillo contain non-protein nitrogen (Clement et al. 1997, 1998). Guajillo also contains large amounts of non-digestible fiber-bound nitrogen (Campbell and Hewitt 2005). These sources of nitrogen raise the crude protein values of these forages but do not contribute to the amount of nitrogen available to the animal. Thus, DP also may be overestimated for these forages (Campbell and Hewitt 2005).

Female deer in our study areas appeared to maintain suitable nutrient intake across a range of deer densities. This apparently unusual finding is likely a result of the unique vegetation community in which browse is a continuously available forage that does not decline with changes in deer density up to 46 deer/km^2 (Gann et al. 2019*b*). This browse resource is moderate in nutritional quality and sufficient to meet maintenance requirements of adult deer but not reproductive requirements of late gestation or lactation. Conversely, forbs can meet nutrient requirements for reproduction but are sporadic and only available during wet periods (Gann et al. 2019*b*). As a result, nutrition and therefore demographics of deer populations in this stochastic region are influenced more by precipitation patterns than by deer density.

Results of our study should not be extrapolated to longer time periods, greater deer densities, or ecosystems beyond those evaluated by our research. Effects of deer foraging on vegetation communities could accrue over a longer period than we studied, thereby changing deer diet composition. Furthermore, high herbivore densities influence composition of vegetation communities worldwide. Although the semi-arid rangelands of western South Texas appear recalcitrant to deer foraging, there is no reason to doubt a threshold deer density capable of changing vegetation communities in our study area. Finally, our findings of only minor changes in deer diets with increased deer density are likely a product of the unique vegetation community and environmental conditions in western South Texas. Deer alter vegetation communities in a wide variety of North American ecosystems (Russell et al. 2001, Tremblay et al. 2005, White 2012) and as a result, it is likely that changes in deer density have different effects in portions of the species' range outside western South Texas.

MANAGEMENT IMPLICATIONS

Wildlife managers in the western part of South Texas have greater latitude in managing deer densities without influencing deer diet composition or quality than do managers in other portions of the species' range. Such management flexibility is founded on a base of diverse vegetation. Therefore, maintaining and promoting diverse vegetation communities should be a management goal. Until more is known about their effects, land management actions that reduce diversity of vegetation communities, such as root-plowing (Ruthven et al. 1993, Ruthven and Hellgren 1995) or promoting invasive grasses, should be avoided or applied judiciously.

Effects of Enhanced Nutrition on White-Tailed Deer Foraging Behavior

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INTRODUCTION

Foraging by large herbivores can alter vegetation communities, affect ecological processes such as nutrient cycling, soil erosion, and fire behavior, and therefore have ecosystem-wide impacts (Hobbs 1996, Augustine and McNaughton 1998, Danell et al. 2006). The direction and degree of many of these impacts are determined by the herbivores' patterns of forage selection and the amount of forage eaten. Forage selection is a complex behavior that integrates chemical constituents and spatial distribution of forage, herbivore anatomy and nutritional requirements, energy and time investment in harvesting and processing forage, social interactions, and constraints from predation risk and environmental conditions (Hanley 1982, Stephens and Krebs 1987). Predicting how changes in available food will affect forage selection is important because of the pervasive consequences of forage selection on ecosystem composition and function. However, the complex and integrative nature of foraging behavior has made such predictions difficult.

Provisioning livestock and wildlife with supplemental food is a common management practice that changes a large herbivore's forage choices and therefore may alter forage selection patterns (Putman and Staines 2004, Priesmeyer et al. 2012, Milner et al. 2014). Proposed or documented effects of such nutrition enhancement on forage selection include promoting intake of poor-quality forage (Dziba et al. 2007, Miranda et al. 2015), reducing intake of poor-quality forage (Schmitz 1990, Murden and Risenhoover 1993), and reducing consumption of high-quality forages or crops (Smith 2001, Putman and Staines 2004, Timmons et al. 2010, Milner et al. 2014). Furthermore, nutrition enhancement may occur for anthropogenic or natural reasons other than the provision of supplement, and predicting the effect on herbivore forage-selection patterns can help managers plan for possible impacts. For example, many agricultural crops are a vast source of high-quality food. Disturbance that sets back succession can result in a flush of high-quality forage, as can natural phenomena such as synchronized mast crops (e.g., acorns [*Quercus* spp.]).

Optimal foraging and energy and nutrient maximization models predict that providing a high-quality, easily accessible supplement should cause the herbivore to reduce consumption of poor-quality forages (Schmitz 1990, Murden and Risenhoover 1993). If herbivores reduce consumption of poor-quality forage while continuing to consume the highest-quality forages, poor-quality forages may obtain a competitive advantage and become more dominant. Alternatively, models of forage selection based on postingestive feedback predict that herbivores will select a diet consistent with their nutritional requirements, anatomy, physiology, and impacts of plant secondary metabolites (PSMs; Provenza 1995, Miranda et al. 2015). Under the postingestive feedback model, the effects of nutritional enrichment will be situationally dependent. The effect of supplementation on forage selection will depend on the other forages available, the nutrient and PSM content of forages and the supplement, and the requirements of the herbivore. Measuring changes in forage selection resulting from enhanced nutrition, such as provision of a supplement, may offer insight into the forage selection process.

Our study's primary objective was to determine botanical composition and quality of white-tailed deer diets in the presence of a high-quality nutritional supplement compared to natural nutrition in semi-arid rangelands of southern Texas. This objective was necessary to our broader study investigating density-dependent relationships of white-tailed deer in southwestern Texas because the enhanced-nutrition treatment helped us understand the extent to which nutrition is limiting in this environment. However, understanding resulting changes in deer foraging behavior was necessary to interpret effects of enhanced nutrition on vegetation. A second objective was to estimate the proportion of deer that consume supplement and the proportion of their diet composed of supplement.

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For our first objective, we tested the hypothesis that enhancing nutrition would not result in increased foraging pressure on palatable plants (Fig. 3D). This hypothesis was based on predictions of the postingestive feedback hypothesis that deer would not increase forb consumption if offered a high-quality supplement because forbs are generally high quality and therefore represent a competing diet item. Under this hypothesis we also expected deer would continue eating shrubs because the fiber and PSMs that tend to be higher in shrubs than other forage categories may be important for proper digestive-tract function when deer eat a high-quality supplement (Provenza 1995, Timmons et al. 2010). We predicted that the botanical composition of the vegetation portion of deer diets (i.e., not including the supplemental feed as a diet component) in enclosures with enhanced nutrition would be similar to botanical composition of deer diets under natural nutrition. Our alternative hypothesis was that enhancing deer nutrition with a high-quality supplement would enable deer to concentrate their foraging on the highest-quality forages and reduce consumption of low-quality forage as predicted by the optimal foraging hypothesis. Under our alternative hypothesis, we predicted forbs would increase and shrubs would decrease in the vegetation portion of the diet. Our second objective was descriptive and we did not pose hypotheses or predictions.

METHODS

Our study was conducted in 81-ha research enclosures on the Comanche and Faith ranches in South Texas. Enclosure complexes on each ranch contained 6 enclosures with 3 deer densities (low, medium, and high) and half were provided a pelleted supplement, whereas deer in the remaining enclosures were exposed to natural nutrition. Research design and details of enclosure construction and maintenance are described by DeYoung et al. (2019*a*).

To maximize forage choices available to research animals and to standardize deer density, we used the 2 low-density enclosures on each study site: 1 enhanced-nutrition enclosure that was provided with pelleted supplement and 1 natural-nutrition enclosure (DeYoung et al. 2019*a*). We maintained target deer numbers of 10 deer in these enclosures beginning in spring 2004 (DeYoung et al. 2019*a*), 3 years before our study began. To document vegetation similarity among research enclosures, we estimated canopy cover using line-intercept techniques for shrubs and cacti and 25-cm × 50-cm plots for herbaceous plants during summer 2007 and 2008 (Gann et al. 2019*b*). Forage categories had similar availability in natural and enhanced-nutrition enclosures ($P > 0.27$), although enhanced-nutrition enclosures had about 10% greater canopy cover of shrubs and subshrubs (Table 4).

Table 4. Backtransformed least squares means for percent woody and herbaceous canopy cover during summer 2007–2008 in 4 81-ha enclosures (2 enclosures with no supplemental feed [natural nutrition] and 2 with pelleted supplement [enhanced nutrition]) with low white-tailed deer density on the Comanche and Faith ranches, Carrizo Springs, Dimmit County, Texas, USA. Standard errors were asymmetric because of backtransformation.

	Natural		Enhanced		Test of nutrition effect	
Forage class	$\bar{x}$	**±SE**	$\bar{x}$	**±SE**	***F***	***P***
Shrubs	65.0	53.7, 75.5	75.6	65.1, 84.8	$F_{1,1} = 4.49$	0.281
Forbs	22.7	16.1, 30.0	25.7	18.8, 33.3	$F_{1,1} = 0.26$	0.700
Grasses	45.0	41.0, 49.0	39.1	35.1, 43.0	$F_{1,3} = 1.78$	0.274
Cacti	3.0	1.5, 5.0	5.2	3.2, 7.7	$F_{1,1} = 1.08$	0.489

Bite Counts

We used tractable deer and the bite count technique as described by Gann et al. (2019*a*) to quantify deer diet composition and quality between April 2007 and February 2009. We calculated a foraging efficiency index as the amount of time each deer foraged divided by the total time active during observations (Berger 1978). We performed bite counts quarterly with spring sampling conducted in March–April, summer in July–August, autumn in October–November, and winter in December–February. On the Comanche Ranch, we placed 3 females into the enhanced-nutrition enclosure and 2 into the natural-nutrition enclosure. On the Faith Ranch, we placed 2 females into the enhanced-nutrition enclosure, and 3 into the natural-nutrition enclosure. These tractable deer lived in the enclosures and were counted against the target 10 deer/enclosure. We replaced deer lost to mortality or that could not be approached for observation, and replacements resided in the enclosures for ≥4 weeks before data collection began. We sampled foraging bouts of tractable deer as described by Gann et al. (2019*a*). We hand-picked simulated bites of forage plants and analyzed them for nutritive content as per Gann et al. (2019*a*)

We ranked vegetation species composing ≥0.1% of all bites within a given season and site by digestible protein (DP) and metabolizable energy (ME) content and divided plants into 3 categories separately for DP and ME representing low, medium, and high nutritional quality. Categories contained equal numbers of plants because there were no natural breaks in the distribution of forage nutritional quality; however, when the total number of forages was not a multiple of 3, we divided similar numbers of plants into the low and high categories and placed the remainder in the medium-quality category. For each deer, we divided the dry matter (DM) of forages consumed in each forage-quality category by the total DM of all vegetation consumed to obtain the percent DM consumed from each diet-quality category for every deer.

Statistical Analysis

We used repeated-measures analysis of variance (ANOVA) for mixed models in SAS 9.3 (PROC MIXED; SAS Institute Incorporated, Cary, NC, USA) for all analyses to determine if enhanced nutrition influenced the proportion of high-quality and low-quality vegetation in deer diets. Our dependent variables were the proportion of each forage class (shrubs, subshrubs, forbs, cacti, mast, grasses, dead leaves, flowers, and fungi) in deer diets, forage-based dietary ME and DP, DM intake, ME intake, DP intake, and foraging efficiency index. We analyzed the proportion of the vegetation portion of the diet composed of low- and high-quality forages, using DP and ME separately as measures of quality. We also tested for differences in overall diet quality (forage and supplement).

Our independent fixed variables were season (spring, summer, autumn, winter), year (2007, 2008), treatment (natural vs. enhanced nutrition), and all possible interactions. We included study site and interactions between study site and treatment and between study site and year nested within treatment as random variables. We used contrast statements to assess treatment effects when treatment interacted with season or year. We assessed 6 possible variance–covariance structures for each repeated-measures ANOVA: variance components, Toeplitz, heterogeneous autoregressive, first-order autoregressive, compound symmetry, and univariate autoregressive moving average. We chose the structure with the lowest Akaike's Information Criterion corrected for finite population size (AIC_c; Littell et al. 2006). We set the significance level for statistical tests at $P = 0.10$ to reduce the probability of a Type II error. We used descriptive statistics to summarize estimates of the percent of supplemental feed in diets of tractable and non-tractable deer. We present least square means with standard error in text and figures.

Pelleted Supplement in Diets

We used ratios of stable isotopes of carbon to estimate the proportion of pelleted supplement in deer diets. In addition to formulating our pelleted supplement to have high concentrations of DP and ME (DeYoung et al. 2019*a*), we designed the supplement to differ in ratios of carbon stable isotopes from the natural vegetation. Pre-sampling from deer in enclosures without supplement indicated that the average isotope ratio of vegetation consumed by deer was $\delta^{13}C = -22.8 \pm 0.3‰$ across both study sites. Because variation in isotope ratios among food sources is necessary for dietary reconstruction (Fry 2006), we formulated our supplemental feed (Lindner Mills, Comfort, TX, USA) to contain 65% of feed ingredients from C_4 plants including corn, sorghum, and sugar cane. Ingredients of C_3 legumes, such as alfalfa, were added to maintain nutritional balance. The supplemental feed had a mean $\delta^{13}C = -17.5 \pm 0.4‰$ during the 2 years of our study.

We estimated the proportion of supplement in the diet and the proportion of individuals eating supplement for 2 groups of deer. First, we used tractable deer in the bite count portion of the present study seasonally during spring 2007–summer 2008. Second, we sampled non-tractable deer captured or harvested during annual population adjustments in December and April 2006–2010 (DeYoung et al. 2019*a*).

We used stable isotope ratios in deer tissues to determine percentages of supplement and natural vegetation in diets of tractable deer in low-density enclosures. Our tissue collection regimen was structured around tissue turnover rate, which determined the period during which stable isotopes in the tissue were influenced by diet. Turnover periods for tissues of interest in other species include the entire growth period for hair (i.e., months), 1 week for serum, and 2–3 months for red blood cells (Tieszen et al. 1983, Hilderbrand et al. 1996, Cerling et al. 2006). We assumed that these turnover periods are similar in white-tailed deer. We collected hair and blood samples from each tractable deer after spring and summer bite counts following sedation with xylazine hydrochloride and Telazol (Fort Dodge Animal Health, Overland Park, KS, USA).

We estimated the carbon isotope ratio of vegetation consumed by supplemented tractable deer using tissues collected from deer from natural-nutrition enclosures, accounting for trophic shifts (McCutchan et al. 2003, Darr and Hewitt 2008). We estimated the mean $\delta^{13}C$ of vegetation eaten by deer within each season by averaging these corrected values from natural-nutrition deer with respect to tissue type, turnover rate, and season. To increase the sample size of deer on which we based estimates of stable isotope ratios resulting from consumption of vegetation, we collected hair and blood from non-tractable deer in natural-nutrition enclosures during spring by capturing them using a net fired from a helicopter (DeYoung 1988). Hair collected during spring, which occurred before onset of summer pelage growth, corresponded to diet during autumn bite counts. Red blood cells collected during spring represented winter diet, and serum reflected the diet during the season it was collected. We used antlers collected from enclosures with natural nutrition during spring to represent diet during the previous summer. We assumed the majority of isotope incorporation in antler occurs during the final month of development (Brown 1983). We considered shed antler color, fading, and damage to ensure that antlers were shed during the same year as collected.

We collected blood in vacuum-filled tubes with no anticoagulant and centrifuged the samples to separate serum and red blood cells, which we then lyophilized (Felicetti et al. 2003). We cleaned hair samples with soap and water, dried them at 40°C, soaked them in acetone for 8 hours, and reduced samples to <3 mm with scissors (Hilderbrand et al. 1996, Roth and Hobson 2000). Although the isotope values of hair can vary along an individual shaft with diet change (Darimont and Reimchen 2002, Cerling et al. 2006), we included the entire shaft to obtain an average diet across the entire hair growth period. We sectioned antler samples using a miniature miter saw then ground samples in a Wiley mill over a 1.0-mm screen. We did not extract collagen from antler samples because of negligible differences in whole antler and antler collagen isotope values (Darr and Hewitt 2008). The Analytical Chemistry Laboratory at the University of Georgia, USA, analyzed stable isotope samples using a Carlo Erba NA1500 CHN Combustion Analyzer (Carlo Erba Corporation, Milan, Italy) with a Thermo-Finnigan Conflo III Interface coupled to a Thermo-Finnigan Delta Plus isotope ratio mass spectrometer (Thermo-Finnigan Corporation, Bremen, Germany). Technicians calibrated $\delta^{13}C$ values using poplar (*Populus* spp.; $\delta^{13}C = -27.0 \pm 0.1‰$) and BSA standards ($\delta^{13}C = -21.2 \pm 0.03‰$), then standardized values with international standards. Precision was ±0.15‰ using replicates of standard material after every tenth sample.

We used the Stable Isotope Sourcing Using Sampling (SISUS) multiple-source mixing model (E. B. Erhardt, University of New Mexico, Albuquerque, NM, USA; http://statacumen.com/sisus/; Erhardt 2007) to estimate the proportion of each deer's diet that was composed of supplemental feed. Source isotope ratios were those of supplemental feed and of natural vegetation eaten by deer as backcalculated from tissues of deer in natural-nutrition enclosures (see above); we derived mixture isotope ratios from deer tissues collected in enhanced-nutrition enclosures. We included source discrimination, concentration, and assimilation efficiency values to increase accuracy of the results. Source discrimination came from Darr and Hewitt (2008). Source concentration corrects for the percentage of carbon within each source that can contribute to the $\delta^{13}C$ of the mixture (Felicetti et al. 2003, Fry

Table 5. Source concentration and assimilation efficiency values for carbon, shown as percentages, used in the Stable Isotope Sourcing Using Sampling (SISUS) multiple-source mixing model to estimate supplemental feed consumption by female white-tailed deer on the Faith and Comanche ranches, Dimmit County, Texas, USA.

Study area	Source concentration		Assimilation efficiency	
Season	Vegetation	Feed	Vegetation	Feed
Faith Ranch				
Spring 2007	37.1	40.9	61.6	79.2
Summer 2007	39.0	40.1	47.9	79.7
Autumn 2007	40.5	38.1	52.0	75.8
Winter 2008	41.8	38.8	58.6	78.5
Spring 2008	41.8	38.3	61.8	79.0
Summer 2008	41.7	38.7	35.2	80.2
Comanche Ranch				
Spring 2007	39.5	40.9	60.3	79.2
Summer 2007	39.0	40.1	55.8	79.7
Autumn 2007	42.3	38.1	52.4	75.8
Winter 2008	41.7	38.8	58.6	78.5
Spring 2008	41.7	38.3	63.5	79.0
Summer 2008	42.3	38.7	65.2	80.2

2006). We derived average source concentration values from all vegetation consumed and supplemental feed on a seasonal basis (Table 5). Source assimilation efficiency is the proportion of a consumed element that is absorbed by the animal. The assimilation efficiency is generally unknown for most forages and must be estimated (Martinez del Rio and Wolf 2005). We estimated relative carbon assimilation efficiency using the average DDM of diets consumed during bite counts and of supplemental feed on a seasonal basis (Table 5). Digestible dry matter was calculated as described in Gann et al. (2019*a*).

We estimated the proportion of deer diets composed of supplemental feed for non-tractable deer using hair collected from captured or harvested deer during December and April population adjustments, 2006–2010 (DeYoung et al. 2019*a*). Hair collected from all enhanced-nutrition enclosures on both study areas (DeYoung et al. 2019*a*) was composed of the deer's winter coat, and therefore was assumed grown during the preceding autumn (Sep–Oct). We also collected hair from animals in natural-nutrition enclosures to determine the stable isotope ratio of vegetation consumed on our study areas as described above. We processed and analyzed hair and estimated diet composition using the techniques described for tractable deer. Stable isotope ratios in 25 hair samples exceeded the mixing space on the supplemental feed boundary. For those deer only, we recalculated a diet with the 2 sources being supplemental feed and C_4 grasses and crassulacean acid metabolism (CAM) plants. We used average $\delta^{13}C$ and % carbon from plants collected near the study sites and the average DDM of C_4 and CAM plants collected in the enclosures during the respective season and year.

RESULTS

To test the effect of enhanced nutrition on deer foraging behavior, the supplement must be higher quality than the vegetation consumed by deer in the absence of supplement. Our supplement was higher in DP in all 6 periods in which we compared the quality of supplement and vegetation and had higher ME in 4 of 6 periods (Fig. 13). Deer selected a diet with ME similar to that of the supplement during spring and summer 2008.

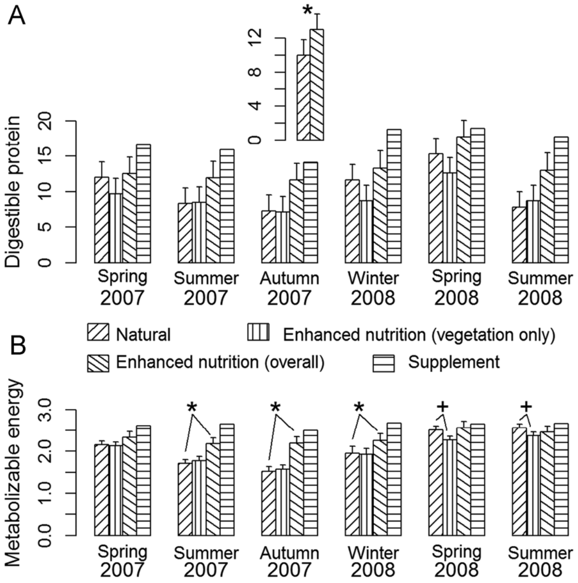

Figure 13. Seasonal digestible protein (A; g/100 g dry matter + SE) and metabolizable energy (B; kcal/g dry matter + SE) in diets of tractable white-tailed deer in 81-ha enclosures with natural nutrition, pelleted feed (vegetation portion only), pelleted feed (overall diet, vegetation plus supplement), and the supplement alone, April 2007–August 2008, in Dimmit County, Texas, USA.

We recorded foraging data from 10 deer during 5 of the 8 periods. We observed 5 enhanced nutrition and 4 natural-nutrition deer during autumn 2007, 5 natural- and 4 enhanced-nutrition deer during autumn 2008, and 5 enhanced-nutrition and 3 natural-nutrition deer during winter 2008. We recorded 213,245 bites, with an average of 26,656 ± 2,064 bites/period and 2,806 ± 97 bites/deer each season ($n = 76$).

Diet Composition

Tractable deer consumed 170 vascular plant species and 3 species of fungi. Averaged across seasons and treatments, shrubs composed a majority of the vegetation portion of deer diets (44%), followed by mast (26%), forbs (15%), flowers (4%), cacti (4%), grasses (2%), dead leaves (2%), subshrubs (2%), and fungi (1%). Enhanced nutrition did not influence the proportion of forbs or fungi in deer diets (Table 6; Fig. 14) as predicted by our hypothesis that enhanced nutrition would not result in greater foraging pressure on palatable plants. The effect of the enhanced-nutrition treatment on the proportion of shrubs in deer diets varied with season and year (Table 6), but none of the treatment effects within a season and year were significant ($P > 0.15$). However, there was no evidence that deer with enhanced nutrition consistently reduced the proportion of shrubs in their diet, which would be expected if foraging pressure on palatable plants (forbs) increased as predicted by the optimal foraging hypothesis. The proportion of shrubs in deer diets was 7–24% greater for enhanced nutrition deer in 5 of 8 season × year combinations, whereas the proportion of shrubs differed by <2% in 2 periods. Only during spring 2007 were shrubs 8% greater in deer diets in natural-nutrition deer compared to enhanced-nutrition deer. The effect of the nutrition treatment on the proportion of deer diets composed of subshrubs varied with season (Table 6) although subshrubs were <5% of the diet in all

Table 6. Analysis of variance mixed models evaluating the effect of supplemental feed, season, and year on the percent of white-tailed deer diets composed of 9 forage classes during spring 2007–winter 2009, in Dimmit County, Texas, USA.

Forage category	Source of variation	df	*F*	*P*	Forage category	Source of variation	df	*F*	*P*
Shrub	Nutrition (N)	1, 4.01	0.94	0.387	Forb	Nutrition (N)	1, 20	0.05	0.817
	Year (Y)	1, 4.01	0.20	0.675		Year (Y)	1, 20	16.95	<0.001
	N × Y	1, 4.01	0.41	0.555		N × Y	1, 20	0.01	0.941
	Season (S)	3, 19.7	63.73	<0.001		Season (S)	3, 17.3	17.43	<0.001
	S × N	3, 19.7	0.37	0.772		S × N	3, 17.3	0.13	0.938
	Y × S	3, 19.7	6.84	0.002		Y × S	3, 17.3	10.03	<0.001
	Y × S × N	3, 19.7	6.8	0.002		Y × S × N	3, 17.3	0.41	0.750
Mast	Nutrition (N)	1, 23.9	4.19	0.052	Cacti	Nutrition (N)	1, 1.98	0.02	0.909
	Year (Y)	1, 23.9	13.35	0.001		Year (Y)	1, 1.88	0.08	0.802
	N × Y	1, 23.9	0.04	0.839		N × Y	1, 1.88	3.24	0.222
	Season (S)	3, 16.1	94.27	<0.001		Season (S)	3, 56.5	2.92	0.042
	S × N	3, 16.1	4.52	0.018		S × N	3, 56.5	0.26	0.853
	Y × S	3, 16.1	13.68	0.001		Y × S	3, 56.5	0.49	0.690
	Y × S × N	3, 16.1	2.59	0.089		Y × S × N	3, 56.5	3.17	0.031
Grass	Nutrition (N)	1, 15.9	0.89	0.360	Subshrub	Nutrition (N)	1, 1.37	1.82	0.357
	Year (Y)	1, 15.9	9.47	0.007		Year (Y)	1, 28.9	5.11	0.032
	N × Y	1, 15.9	0.58	0.459		N × Y	1, 28.9	0.73	0.400
	Season (S)	3, 19.2	7.02	0.002		Season (S)	3, 25.2	9.25	<0.001
	S × N	3, 19.2	6.60	0.003		S × N	3, 25.2	3.08	0.046
	Y × S	3, 19.2	2.39	0.100		Y × S	3, 25.2	1.37	0.276
	Y × S × N	3, 19.2	2.73	0.072		Y × S × N	3, 25.2	0.11	0.954
Flowers	Nutrition (N)	1, 2.9	5.64	0.101	Dead leaves	Nutrition (N)	1, 60	3.63	0.062
	Year (Y)	1, 2.8	11.31	0.048		Year (Y)	1, 60	2.76	0.102
	N × Y	1, 2.79	6.55	0.090		N × Y	1, 60	1.41	0.240
	Season (S)	3, 56.2	23.55	<0.001		Season (S)	3, 60	5.37	0.002
	S × N	3, 56.2	8.55	<0.001		S × N	3, 60	3.43	0.022
	Y × S	3, 56.2	34.22	<0.001		Y × S	3, 60	2.61	0.059
	Y × S × N	3, 56.2	8.53	<0.001		Y × S × N	3, 60	1.33	0.273
Fungi	Nutrition (N)	1, 3	0.73	0.457					
	Year (Y)	1, 3	5.16	0.108					
	N × Y	1, 3	0.73	0.456					
	Season (S)	3, 48.5	11.21	<0.001					
	S × N	3, 48.5	1.27	0.294					
	Y × S	3, 48.5	11.12	<0.001					
	Y × S × N	3, 48.5	1.25	0.303					

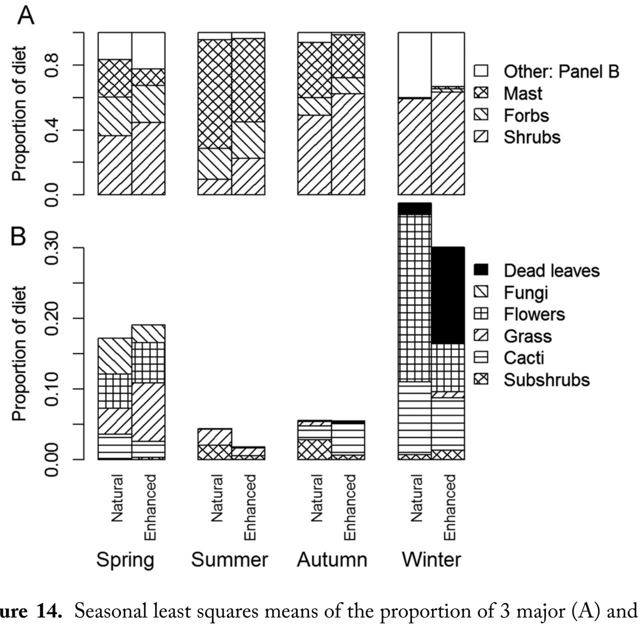

Figure 14. Seasonal least squares means of the proportion of 3 major (A) and 6 minor (B) forage classes in the diets of tractable female white-tailed deer in natural nutrition or enhanced nutrition treatments during April 2007–February 2009 on the Comanche and Faith ranches, Dimmit County, Texas, USA

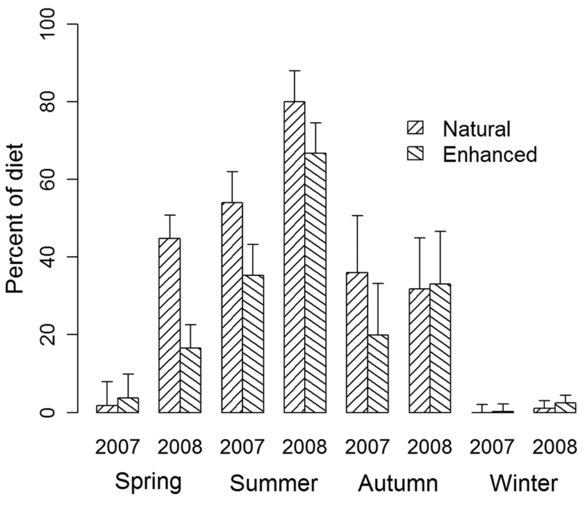

Figure 15. Percent (least square means + SE) of seasonal diet containing mast for natural-nutrition and enhanced-nutrition tractable female white-tailed deer on the Comanche and Faith ranches, Dimmit County, Texas, USA.

Table 7. Analysis of variance for digestible protein and metabolizable energy in overall diets of tractable white-tailed deer and in the vegetation portion of their diets based on independent variables nutrition treatment and seasonal period from spring 2007 through summer 2008 in Dimmit County, Texas, USA.

		Overall diet			Vegetation portion of diet		
Nutrients	**Source of variation**	**df**	***F***	***P***	**df**	***F***	***P***
Digestible protein	Nutrition (N)	1, 6.83	7.91	0.03	1, 10.3	1.06	0.33
	Season (S)	5, 3.99	4.29	0.09	5, 10.3	3.10	0.06
	N × S	5, 3.99	0.45	0.80	5, 10.3	0.35	0.87
Metabolizable energy	Nutrition (N)	1, 14.9	27.97	<0.01	1, 1.69	1.24	0.40
	Season (S)	5, 9.29	25.30	<0.01	5, 2.42	233.6	0.002
	N × S	5, 9.29	6.29	<0.01	5, 2.42	9.92	0.07

seasons and none of the seasonal comparisons between treatments were significant ($P > 0.12$).

Enhanced nutrition influenced the proportion of mast, cacti, flowers, and grass in the vegetation portion of deer diets, but the effect varied with season and year (Table 6). The trend was for diets of deer in natural-nutrition enclosures to contain a higher proportion of mast (Fig. 15) especially during spring 2008. The only significant seasonal differences in percent cacti in deer diets was during winter, but the effect of enhanced nutrition was not consistent across years. Cacti consumption was greater in enhanced-nutrition deer in 2007 (15 ± 5% vs. 1 ± 6%) and in natural-nutrition deer in 2008 (20 ± 5% vs. <1 ± 5%). Flowers were a greater proportion of diets of natural-nutrition deer only during winter 2007 compared to enhanced-nutrition deer (48 ± 4% vs. 14 ± 3%). Flowers were 9–10% of deer diets in both treatments during spring 2008 and were <2% of deer diets in all other seasons. Dead leaves were only eaten during winter and were 14 ± 2% of the diet of enhanced-nutrition deer but only 2 ± 3% of the diet of natural-nutrition deer (Fig. 14). Percent grass in the vegetation portion of deer diets increased during winter 2008 with enhanced nutrition ($P < 0.01$; natural nutrition = 0.1 ± 0.23 and enhanced nutrition = 1.5 ± 0.23), but grass was a minor part of the diet. Grass was a larger percent of deer diets during spring 2008 when there was an indication ($P = 0.14$; natural nutrition = 7.1 ± 3.7 and enhanced nutrition = 15.1 ± 3.7) of increased grass in diets with enhanced nutrition.

Diet Quality

Enhanced-nutrition deer had greater ($P = 0.03$) DP concentration in their overall diet (13 ± 1.8 g/100 g DM) than natural-nutrition deer (10 ± 1.8 g/100 g DM; Table 7; Fig. 13A). The effect of enhanced nutrition on overall diet ME varied (treatment × season interaction; $P = 0.01$) by season (Fig. 13B). Overall diet ME was 0.37 ± 0.16 kcal/g to 0.68 ± 0.11 kcal/g greater ($P < 0.03$) in enhanced- than natural-nutrition deer during summer and autumn 2007 and winter 2008. Overall diet ME did not differ ($P \geq 0.21$) by nutrition treatment in the other 3 seasons.

Deer with access to enhanced nutrition had a similar ($P = 0.33$; Table 7) concentration of DP in the vegetation portion of their diet as natural-nutrition deer (10 ± 1.3 g/100 g DM vs. 9 ± 1.2 g/100 g DM). Metabolizable energy in the vegetation portion of deer diets was influenced by enhanced nutrition, but the effect varied ($P = 0.07$) by season. During spring and summer 2008, ME of the vegetation portion of the diet was 0.24 ± 0.06 kcal/g and 0.19 ± 0.07 kcal/g lower ($P \leq 0.06$) for enhanced- than for natural-nutrition deer, respectively.

The proportion of deer diets composed of low-quality forage did not differ between nutrition treatments when measured using DP ($P = 0.88$; natural nutrition = 34 ± 7% and enhanced nutrition = 35 ± 7%) or ME ($P = 0.29$; natural nutrition = 33 ± 6%, enhanced nutrition = 41 ± 6%). The proportion of deer diets composed of high-quality forages, when measured using DP, was greater ($P = 0.01$) for deer in the natural-nutrition (41 ± 4%) than the enhanced-nutrition (24 ± 4%) treatments. The proportion of high-quality forage in the diet as defined by ME did not differ ($P = 0.51$) between nutrition treatments (natural nutrition = 40 ± 11%, enhanced nutrition = 29 ± 11%).

Foraging Behavior

Bite rate was 12% higher ($P = 0.05$; Fig. 16, inset) for deer in natural-nutrition enclosures than for deer in enhanced-nutrition enclosures, and this effect was independent of year ($P = 0.42$), season ($P = 0.10$), and the year-by-season combination ($P = 0.11$; Table 8; Fig. 16). Bite size was similar ($P = 0.54$) between treatments (natural nutrition = 0.15 ± 0.02 g/bite and enhanced nutrition = 0.14 ± 0.02 g/bite). Dry matter ($P = 0.28$), DP ($P = 0.31$), and ME ($P = 0.52$) intake rates did not vary between natural- and enhanced-nutrition deer (Fig. 17). During observation, enhanced-nutrition deer foraged 39 ± 2.7% of the time, whereas natural-nutrition deer foraged 50 ± 2.8% of the time ($P = 0.01$).

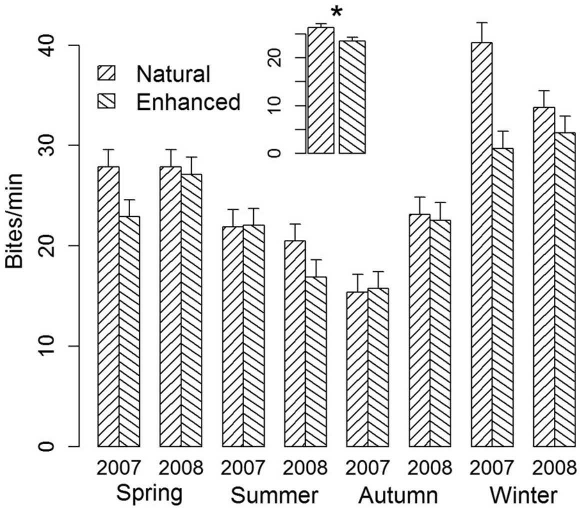

Figure 16. Seasonal and study-wide (inset) bite rate (+SE) of tractable white-tailed deer in 81-ha enclosures with natural or enhanced nutrition from spring 2007 through winter 2008 in Dimmit County, Texas, USA. Pairs of bars with an asterisk above are different ($P < 0.10$)

Table 8. Analysis of variance for bite rate, bite size, dry matter intake, digestible protein intake, metabolizable energy, and percent time foraging of tractable white-tailed deer based on independent variables nutrition treatment, season, and year during spring 2007–winter 2009, in Dimmit County, Texas, USA.

Variables	Source of variation	df	*F*	*P*	Variable	Source of variation	df	*F*	*P*
Bite rate	Nutrition (N)	1, 3.88	7.42	0.05	Bite size	Nutrition (N)	1, 3.91	0.46	0.54
	Year (Y)	1, 3.88	0.77	0.43		Year (Y)	1, 3.91	0.18	0.69
	N × Y	1, 3.88	0.82	0.42		N × Y	1, 3.91	0.53	0.51
	Season (S)	3, 9.98	66.94	<0.01		Season (S)	3, 9.09	11.73	<0.01
	S × N	3, 9.98	2.75	0.10		S × N	3, 9.09	0.10	0.96
	S × Y	3, 9.98	9.06	<0.01		S × Y	3, 9.09	0.59	0.64
	S × Y × N	3, 9.98	2.64	0.11		S × Y × N	3, 9.09	0.92	0.47
Dry matter intake rate	Nutrition (N)	1, 14.8	1.24	0.28	Digestible protein intake rate	Nutrition (N)	1, 20.4	1.09	0.31
	Year (Y)	1, 14.8	0.02	0.88		Year (Y)	1, 20.4	0.15	0.70
	N × Y	1, 14.8	0.14	0.71		N × Y	1, 20.4	0.05	0.83
	Season (S)	3, 13.9	4.86	0.02		Season (S)	3, 15.8	3.37	0.05
	S × N	3, 13.9	0.13	0.94		S × N	3, 15.8	0.05	0.98
	S × Y	3, 13.9	2.24	0.13		S × Y	3, 15.8	0.98	0.43
	S × Y × N	3, 13.9	0.47	0.71		S × Y × N	3, 15.8	0.42	0.74
Metabolizable energy intake rate	Nutrition (N)	1, 16.1	0.43	0.52	Percent of time foraging	Nutrition (N)	1, 14.2	9.11	<0.01
	Year (Y)	1, 16.1	1.81	0.20		Year (Y)	1, 14.2	0.45	0.52
	N × Y	1, 16.1	0.01	0.97		N × Y	1, 14.2	0.05	0.82
	Season (S)	3, 13.8	4.55	0.02		Season (S)	3, 10.5	14.26	<0.01
	S × N	3, 13.8	0.18	0.91		S × N	3, 10.5	1.22	0.35
	S × Y	3, 13.8	1.83	0.19		S × Y	3, 10.5	0.50	0.69
	S × Y × N	3, 13.8	0.51	0.68		S × Y × N	3, 10.5	0.35	0.79

Consumption of Supplemental Feed

Supplemental feed averaged 47–80% of the diet of tractable deer, depending on the season (Fig. 18). Deer on the Faith Ranch had a lower percent supplement in their diet (39 ± 5%), averaged across seasons, than deer on the Comanche Ranch (72 ± 4%).

Ninety-seven percent (*n* = 128) of non-tractable deer in enhanced-nutrition enclosures consumed supplemental feed during early autumn. Of the 4 animals without evidence of supplemental feed consumption, 2 were males and 2 were females. Averaged across density treatments, study sites, and years, percent supplemental feed in deer diets was 70 ± 4% for yearling females, 75 ± 7% for yearling males, 70 ± 3% for adult females, and 81 ± 3% for adult males.

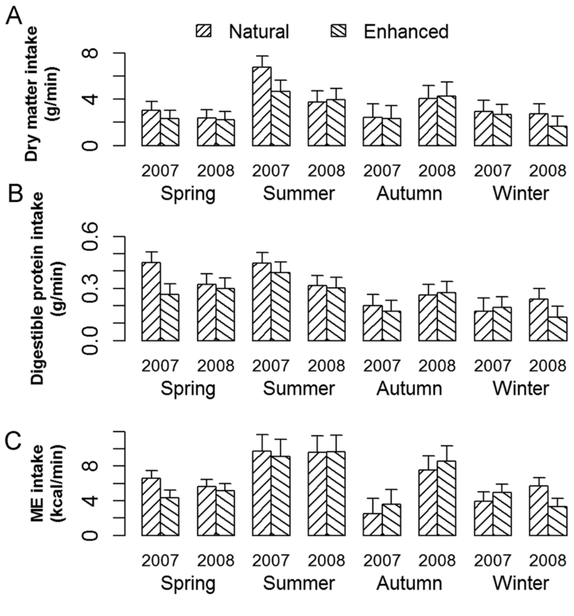

Figure 17. Seasonal dry matter (A), digestible protein (B), and metabolizable energy (ME) intake (C; +SE) of tractable white-tailed deer in 81-ha enclosures with natural or enhanced nutrition in Dimmit County, Texas, USA.

DISCUSSION

As we hypothesized, deer provided a high-quality supplement did not increase the proportion of their diets composed of high-quality, preferred forage classes, specifically forbs and mast. Instead, nutritionally enhanced deer increased consumption of dead leaves, did not reduce consumption of shrubs, and reduced intake of mast. Enhanced nutrition also influenced the quality of the diet selected, as measured by DP and ME. In all instances in which a change in diet quality was noted, deer with enhanced nutrition chose vegetation lower in DP or ME or chose a diet composed of a lower proportion of high-quality forage, although the overall diet of enhanced-nutrition deer was still of higher

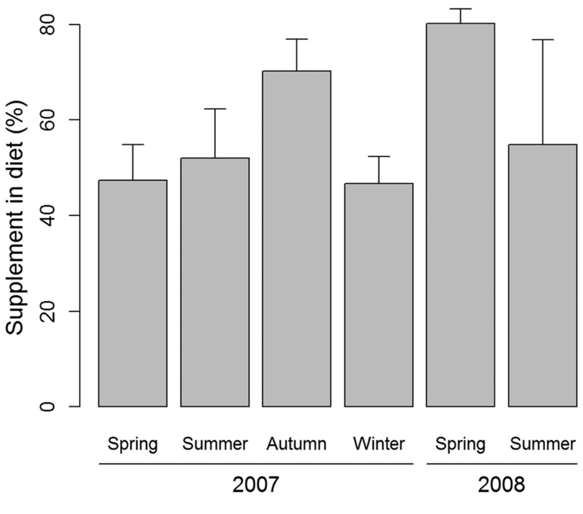

Figure 18. Percent (+SE) pelleted supplement in diets of tractable female white-tailed deer seasonally from spring 2007 through summer 2008 determined using stable isotope ratios of carbon on the Comanche and Faith ranches in Dimmit County, Texas, USA

quality. Thus, patterns of forage selection are influenced by the quantity and quality of foods available as predicted by post-ingestive feedback models of forage selection, a finding supported by studies of red deer and cattle (Odadi et al. 2013, Miranda et al. 2015). Supplemented cattle in Kenya reduced consumption of forbs by 76% and increased consumption of protein-poor grasses (Odadi et al. 2013). Timmons et al. (2010) reported a similar effect of enhanced nutrition, which caused white-tailed deer to select diets with lower proportions of mast and higher proportions of browse during spring and autumn. However, they also reported that deer in enhanced-nutrition enclosures increased consumption of forbs during autumn, a finding consistent with nutrition enhancement causing an increase in selective foraging. Our findings that deer do not necessarily reduce the proportion of lower-quality forages in their diet are consistent with reports that deer with access to supplemental feed continue to browse on shrubs or tree bark (Cooper et al. 2006, van Beest et al. 2010, Garrido et al. 2014, Mathisen et al. 2014, Månsson et al. 2015). Conversely, supplemental food has been used to protect economically valuable timber from damage by foraging from large herbivores. Supplementation caused European bison (*Bison bonasus*) to reduce intake of woody plants (Kowalczyk et al. 2011) and captive red deer to reduce consumption of tree bark (Rajský et al. 2008).

Several reasons may explain why deer with access to a high-quality pelleted feed would consume browse and dead leaves, which are poorer quality than the supplement and other available forages. First, the supplemental feed was a pellet with 75% grain products and >20% crude protein. This diet would be expected to ferment rapidly in the rumen, potentially resulting in acidosis or high concentrations of ammonia. Sheep challenged with acidosis from a diet high in grain learn to consume foods that alleviate the acidosis (Villalba et al. 2006). Deer may have attempted to reduce the negative effects of acidosis and excess ammonia by consuming forages high in fiber, thereby diluting the rapidly fermenting grains. The browse species consumed also have PSMs (e.g., blackbrush acacia and guajillo [*Senegalia berlandieri*]; Clement et al. 1997, 1998; Cash and Fulbright 2005) that may have reduced metabolism of rumen microbes and thereby the rate of DM and protein degradation in the rumen, thus reducing the rate of volatile fatty acid and ammonia production.

A second reason deer may have continued to consume browse is that the DP and ME in the supplemental feed may have enabled deer to continue to eat the abundant but heavily defended browse species. Increased dietary protein or energy can increase the amount of forages defended with PSMs that a herbivore can consume (Villalba et al. 2002*a*,*b*; Villalba and Provenza 2005). Supplemental macronutrients increase the herbivore's ability to detoxify and excrete PSMs by providing energy and substrates for increased enzyme synthesis, conjugates for phase II detoxification, and proteins for binding tannin (Provenza et al. 2003, McLean and Duncan 2006). A third reason deer may continue to eat shrubs is that PSMs in shrubs may have positive health effects, such as reducing the severity of endoparasite infections (Lisonbee et al. 2009, Villalba et al. 2013) or improving immune function (Provenza and Villalba 2010).

We implemented the enhanced-nutrition treatment to determine if nutrition was limiting, and thereby help us understand the context of our tests of density dependence in deer populations in this region. If nutrition was not limiting, then the traditional model of density dependence operating through deer impacts on vegetation, and thereby deer nutrition, would not be expected. To the contrary, our enhanced-nutrition treatment improved diet quality, as measured by DP and ME, of white-tailed deer in our study areas during most seasons. Only during spring and summer of 2008 did deer in the natural-nutrition enclosures eat a diet equivalent in ME as the overall diet (pelleted supplement and vegetation) of deer in the enhanced-nutrition enclosures. The difference in diet quality between our natural- and enhanced-nutrition treatments enabled us to identify nutrition as a limiting factor for deer in this region and to demonstrate that the morphological and demographic improvement of deer in the enhanced-nutrition enclosures (Cook et al. 2019) were due to improved nutrient status.

Our estimates of diet composition from analysis of stable isotope ratios in deer tissue suggest that deer diets were 47–80% supplemental feed. Our estimates of supplement in diets of non-tractable deer were based on hair grown in September and October and thus represent diet composition during autumn only. Nutrient requirements may be high during autumn because female deer are recovering from nutrient deficits incurred during reproduction and male deer are accumulating fat reserves to use during breeding (Hewitt 2011). Thus, deer may be using supplement more during autumn than other seasons and these results may not apply throughout the year.

To the extent that daily DM intake of deer remained constant across nutrition treatments, deer in enhanced-nutrition enclosures may have reduced consumption of vegetation by ≥50%. An increase in daily DM intake could occur because pelleted feed has a faster passage rate than vegetation (Robbins 1993), allowing higher intake if rumen-fill limited intake of vegetation. Conversely, the higher ME content of the supplemental feed may have caused a decline in DM intake because deer could meet energy requirements with a lower daily intake. Additional evidence that deer reduced intake of preferred forbs comes from measurements of cover of preferred forbs, which were greater in enhanced-nutrition enclosures than natural-nutrition enclosures (Gann et al. 2019*b*). Although deer browsing increases near feed sites (Cooper et al. 2006), supplemental feed may reduce the impact of deer on vegetation at larger scales in our study environment at similar deer densities and supplement presentation.

MANAGEMENT IMPLICATIONS

Managers who wish to enhance the nutrition of white-tailed deer in the western part of South Texas may use supplemental feed without the risk of changes in vegetation communities at deer densities ≤12 deer/km^2. Most deer will eat supplement and grazing pressure on vegetation may decline. Our results apply to *ad libitum* availability of supplement and 1 feeder site per 81 ha. Although we did not measure the effects of enhanced nutrition on deer foraging at higher deer densities, vegetation measurements show that enhanced nutrition will not cause declines in forage species that deer prefer up to 50 deer/km^2 over a 9-year time frame (Gann et al. 2019*b*). These results should not be extrapolated to different vegetation communities because of the possibility of differences in deer response to the supplement and vegetation response to deer browsing.

Vegetation Response to White-Tailed Deer Density and Enhanced Nutrition

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INTRODUCTION

Traditional theory regarding plant community responses to increasing white-tailed deer density is based on the assumption that deer selectively forage on the most palatable and nutritious plants in the community (Augustine and McNaughton 1998, Manier and Hobbs 2006). Foraging pressure on preferred plants should intensify with increasing deer density, resulting in a decline of these palatable and nutritious plants over time (Rooney and Waller 2003). This decline in high-quality forage results in a decline in deer natality and survival as populations near carrying capacity (Ballard et al. 2001). Plants that are not preferred by deer or are tolerant of herbivory may competitively displace preferred plants, bringing about changes in vegetation composition in favor of plants that are less preferred or are more resistant to herbivory (Côté 2011). Overall plant cover and plant species richness may decline as plants that are resistant to deer foraging become dominant (Côté et al. 2004). These predictions can be related to traditional range management theory that has roots in Clementsian ecology (e.g., Clements 1920, Weaver and Clements 1938, Dyksterhuis 1949, Westoby 1979): with increasing herbivory, grazing and browsing animals will seek out preferred plants that will decline in abundance in the plant community (hence the label decreaser) with a concomitant increase in less preferred species. Animal population ecology and equilibrium concepts of vegetation succession thus share some commonality in conceptual basis.

Most research on the effects of white-tailed deer on vegetation has been conducted in forested environments with relatively mesic climates (Russell et al. 2001, Côté et al. 2004, Côté 2011). Vegetation dynamics and herbivores tend to be closely linked in mesic environments (Ellis and Swift 1988, Derry and Boone 2010), such as the eastern deciduous forests of the United States where annual precipitation is evenly distributed temporally and exceeds 76 cm/year (Odum 1971). High deer densities in forested ecosystems of the United States typically result in a decline in the abundance of broad-leaved herbaceous plants (forbs) and an increase in grasses (Horsley et al. 2003, Rooney and Waller 2003, Rooney 2009). Forbs decline because they compose a large portion of deer diets when they are available and are generally preferred by deer over grasses which usually compose <20% of deer diets (Fulbright and Ortega-Santos 2013). Understory shrub cover often also declines in abundance in response to high deer densities (Russell et al. 2001, Frerker et al. 2014). In contrast to the effects of high deer densities, moderate levels of deer browsing promoted herbaceous species richness and abundance in West Virginia, USA (Royo et al. 2010).

The linkage between animal population dynamics and vegetation ecology may not follow traditional models in environments where non-equilibrium vegetation dynamics are likely. Responses of vegetation to different densities of white-tailed deer may be dissimilar between mesic climates and highly variable semi-arid environments where the linkage between herbivores and vegetation dynamics tends to be weaker (Ellis and Swift 1988, Derry and Boone 2010). Various authors have challenged the idea that directional succession occurs in environments where the inter-annual coefficient of variation in precipitation exceeds 33% (Derry and Boone 2010). Vegetation in these systems may not change toward an equilibrium state, rather the vegetation exists in a non-equilibrium state where environmental factors drive fluctuations in vegetation composition and abundance. In these systems, consequently, reduction of disturbance from deer foraging may not result in change toward the vegetation composition that originally existed (i.e., the climax community).

Besides density effects, a prediction of foraging theory is that deer become more highly selective when resources are abundant (Weckerly and Kennedy 1992). It follows that if nutritious food resources are artificially provided, deer may forage more selectively on the most nutritious and palatable plants in the

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vegetation (Murden and Risenhoover 1993). Access to high-quality food resources may allow deer to meet their nutritional needs so that they can spend more time foraging on the most palatable and nutritious foods in their environment and reduce consumption of poor-quality forages (Murden and Risenhoover 1993, Baraza et al. 2010). Increased deer densities may exacerbate the reduction of preferred plants if deer forage more selectively with enhanced nutrition, and allow poor-quality plants to increase (Priesmeyer et al. 2012). Potential changes in diet composition resulting from availability of high-quality food resources have caused concern among biologists that supplemental feeding will lead to loss of preferred plants, particularly if enhanced nutrition results in population growth (Butler et al. 2005, Brown and Cooper 2006, Inslerman et al. 2006, Milner et al. 2014).

Alternatively, presence of high-quality food resources may result in dietary changes that do not cause a reduction in higher quality plants and may favor them. Models of forage selection based on postingestive feedback predict that selection depends on the forages available, the nutrient and PSM content of these forages and of the supplement, and nutritional requirements of the herbivore (Provenza 1995, Miranda et al. 2015). Cattle in a semi-arid savanna ecosystem in Africa, for example, that were provided with high-protein feeds consumed less forbs and more low-protein grasses than cattle not provided supplemental feed (Odadi et al. 2013). Cattle possibly consumed low-protein grasses to increase the dry matter content of their diet, which was lacking in the high protein feed. Derby eland and western giant eland in Senegal consumed less natural vegetation, but species composition of native vegetation in their diet did not change when they were supplementally fed (Hejcmanová et al. 2010, 2013). Although potential effects of enhanced nutrition on white-tailed deer diets have been discussed in the literature, documentation that supplemental feeding causes degradation of the vegetation or has a protective effect on vegetation is lacking (Priesmeyer et al. 2012).

Our objective was to determine vegetation response to 3 white-tailed deer densities that were low, moderate, and high relative to regional population densities (DeYoung et al. 2019*a*). We hypothesized that white-tailed deer density and vegetation dynamics would be weakly linked in the stochastic environment of our South Texas study areas (Fig. 3B). We also hypothesized that presence of high-quality food would not influence vegetation dynamics regardless of deer population density (Fig. 3E). We tested these predictions: 1) canopy cover of preferred forbs and shrubs, relative standing crop of forbs, density of selected half shrubs, and plant species richness, diversity, and evenness will not decline with increasing white-tailed deer population density; 2) canopy cover of forbs and shrubs that are not preferred and grasses will not increase with increasing deer population density; and 3) these vegetation characteristics will not change when high-quality food is provided regardless of deer density.

METHODS

Study areas were on the Comanche (28.61°N, 100.09°W) and Faith (28°N, 100°W) ranches in Dimmit County, Texas (DeYoung et al. 2019*a*). Vegetation was Tamaulipan thornscrub (Timmons et al. 2010). Soils on both study sites included gravely loams, clayey loams, and fine sandy loams of the Tonio–Uvalde–Zapata–Webb–Duval–Randado–Chacon soil associations (DeYoung et al. 2019*a*). We monitored precipitation monthly during the study (2004–2012) on each study site using a combination of electronic and standard rain gauges.

We constructed 6 81-ha enclosures surrounded by 2.4-m-tall woven wire on each ranch (DeYoung et al. 2019*a*). The experimental design included ranches as blocks and a 2 nutrition-level (enhanced vs. natural) × 3 deer-density-level factorial array of treatments. Targets for low, medium, and high deer densities were 13 deer/km^2 (10 deer), 31 deer/km^2 (25 deer), and 50 deer/km^2 (40 deer), respectively. We randomly assigned deer density and nutrition treatments (DeYoung et al. 2019*a*) to the 6 enclosures on each of the 2 ranches in February 2004.

Vegetation Sampling

We annually estimated percent canopy cover of herbaceous and woody vegetation to address our objectives of determining the effects of increasing white-tailed deer density and enhanced nutrition on forb and shrub canopy cover and herbaceous plant species richness, diversity, and evenness. Forbs included herbaceous plants and woody-based plants with non-woody stems (subshrubs). To facilitate vegetation sampling, we placed 20, 50-m permanent transects within each of the 12, 81-ha enclosures across both ranches using restricted randomization. We determined locations of these transects using Arc GIS 9.1 software to construct 20 identical, 4-ha polygons in each enclosure (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We assigned a random coordinate inside each polygon to serve as the starting transect position and allocated a random cardinal direction to determine directional orientation of the transect. We recreated directions if transects fell within 50 m of an enclosure perimeter fence.

We estimated percent cover of forbs in 3, 25-cm × 50-cm sampling frames placed 20-m apart along each of the transects within each of the 6 enclosures on each ranch annually during June 2004–2012 (2 frames/transect in 2004). We used the line-intercept method to estimate percent canopy cover of shrubs within the central 30 m of each of the 20 transects annually during June 2004–2012 (Canfield 1941). We estimated percent canopy cover of herbaceous and woody vegetation during June because the first bimodal rainfall peak in the study area typically occurs in May (Norwine and John 2007) and we wanted to collect data during a period of active plant growth.

We ranked forbs and shrubs as preferred or other plants (not preferred) based on data collected at our study sites on the botanical composition of deer diets (Gann et al. 2019*a*). To separate forbs and shrubs into preferred or other classes, we calculated a relative preference index (RPI) that was based on estimates of botanical composition of deer diets and estimates of forb and shrub canopy cover (Krueger 1972):

$$\text{RPI} = \frac{\text{\% deer diet composition}}{\text{\% vegetation composition}}$$

where RPI is the relative preference index, % deer diet composition is the relative percentage of plant species i in the diet, and % vegetation composition is the relative percentage of plant

Table 9. Forb and woody plant species considered to be preferred by white-tailed deer. Relative preference index values are based on composition of plants in deer diets and relative percent canopy cover averaged across high- and low-density enclosures with natural nutrition on the Comanche and Faith ranches in Dimmit County, Texas, USA, April–May 2010. Forb and subshrub species encountered in white-tailed deer diets but not in vegetation sampling were also considered to be preferred by white-tailed deer. Common and scientific names follow the United States Department of Agriculture Natural Resources Conservation Service (2017).

Species
Preferred forbs and subshrubs
Lindheimer's globeberry (*Ibervillea lindheimeri*)
Awnless bushsunflower (*Simsia calva*)
Common yellow oxalis (*Oxalis stricta*)
West Indian shrubverbena (*Lantana urticoides*)
Texas bindweed (*Convolvulus equitans*)
Whitemouth dayflower (*Commelina erecta*)
Scaleflower dodder (*Cuscuta squamata*)
Euphorbia (*Euphorbia* spp.)
American wild carrot (*Daucus pusillus*)
Pitseed goosefoot (*Chenopodium berlandieri*)
Pennsylvania pellitory (*Parietaria pensylvanica*)
Gray's feverfew (*Parthenium confertum*)
Bundleflower (*Desmanthus* spp.)
Redseed plantain (*Plantago rhodosperma*)
Hoary blackfoot daisy (*Melampodium cinereum*)
Dozedaisy (*Aphanostephus* spp.)
Sida (*Sida* spp.)
Bearded prairie clover (*Dalea pogonathera*)
Bushland subverbena (*Lantana achyranthifolia*)
Berlandier's trumpets (*Acleisanthes obtusa*)
Indian blanket (*Gaillardia pulchella*)
Guara (*Guara* spp.)
Hairy wedelia (*Wedelia texana*)
Threelobe false mallow (*Malvastrum coromandelianum*)
Smartweed leaf flower (*Phyllanthus polygonoides*)
Prairie broomweed (*Amphiachyris dracunculoides*)
Angel's trumpets (*Acleisanthes longiflora*)[a]
Elmendorf onion (*Allium elmendorfii*)[a]
Purple poppymallow (*Callirhoe involucrata*)[a]
Stiffstem flax (*Linum rigidum*)[a]
Crowpoison (*Nothoscordum bivalve*)[a]
Showy evening primrose (*Oenothera grandis*)[a]
Hooker's plantain (*Plantago hookeriana*)[a]
Texas vervain (*Verbena halei*)[a]
Desert tobacco (*Nicotiana obtusifolia*)[a]
Smallflower groundcherry (*Physalis cinerascens*)[a]
Huisache daisy (*Amblyolepis setigera*)[a]
Lambsquarters (*Chenopodium album*)[a]
Devil's bouquet (*Nyctaginia capitata*)[a]
Roughpod bladderpod (*Lesquerella lasiocarpa*)[a]
Stragler daisy (*Calyptocarpus vialis*)[a]
False nightshade (*Chamaecrista coronopus*)[a]
Golden tickseed (*Coreopsis tinctoria*)[a]
Texas stork's bill (*Erodium texanum*)[a]
Snapdragon vine (*Maurandella antirrhiniflora*)[a]
Spear globe mallow (*Sphaeralcea hastulata*)[a]
Squarebud daisy (*Tetragonotheca texana*)[a]
Rue of the mountains (*Thamnosma texana*)[a]
Hartweg's sundrops (*Calylophus hartwegii*)[a]
Smallflowered milkvetch (*Astragalus nuttallianus*)[a]
Chinese lantern (*Quincula lobata*)[a]
Pink ladies (*Oenothera speciosa*)[a]
Stemless evening primrose (*Oenothera triloba*)[a]
Louisiana vetch (*Vicia ludoviciana*)[a]
Bedstraw (*Galium* spp.)[a]
Small Venus' looking-glass (*Triodanis biflora*)[a]
Preferred woody plant species
Texas kidneywood (*Eysenhardtia texana*)
Brasil (*Condalia hookeri*)
Spiny hackberry (*Celtis ehrenbergiana*)
Lotebush (*Ziziphus obtusifolia*)
Berlandier's wolfberry (*Lycium berlandieri*)
Texas swampprivet (*Forestiera angustifolia*)
Bravo acacia (*Vachellia bravoensis*)
Clapweed (*Ephedra antisyphilitica*)
Texas lignum-vitae (*Guaiacum angustifolium*)

(*Continued*)

Table 9 (Continued)

[a] Encountered in white-tailed deer diets but not during vegetation sampling.

species *i* in the vegetation (Krueger 1972). We calculated these relative preference indices separately for forbs and shrubs. We obtained estimates of botanical composition of deer diets from bite counts conducted in companion research using tame adult females during April–May, 2010 in high- and low-density enclosures without nutrition enhancement on each ranch (Gann et al. 2019*a*). We determined the relative amount of each species of forb and shrub in deer diets on a dry matter basis for each tame female ($n = 6$; Folks 2012). We included forb or shrub species with a RPI ≥ 1 and forb or shrub species encountered in deer diets but not in vegetation sampling in the preferred class; we classified all other species as other forbs or other shrubs (Table 9).

We annually estimated density of awnless bushsunflower (*Simsia calva*) and hairy wedelia (*Wedelia acapulcensis* var. *hispida*) because they were present on both ranches, are commonly eaten by white-tailed deer (Folks 2012, Gann 2012), and are less ephemeral than many herbaceous dicots in the region because they are woody-based perennials. We estimated density of hairy wedelia and bushsunflower within 3-m × 50-m belts along each of the 20 transects within each of the 6 enclosures on each ranch annually during June 2004–2012. We recorded hairy wedelia and bushsunflower as <0.5 m tall to include seedlings and younger plants because deer herbivory may prevent recruitment (Russell et al. 2001), and >0.5 m tall to include mature plants.

We estimated standing crop of grasses and forbs during spring (Mar 2005–2012) and summer (Aug 2004–2012) to determine effects of white-tailed deer density and enhanced nutrition on standing crop of forbs relative to grasses. We placed a 0.25-m^2 sampling frame at a random distance between 2 m and 10 m in a random direction from the beginning of each transect within each enclosure where no other vegetation sampling was conducted. We estimated standing crop of forbs (including subshrubs) and grasses in 20 plots in each of the 6 enclosures on each ranch (Wilm et al. 1944). We clipped forbs and grasses to ground level excluding dead material (all above-ground herbaceous material was clipped on subshrubs). We dried samples at 40°C until we obtained a constant mass and weighed samples. We calculated standing crop of forbs relative to total herbaceous vegetation (hereafter; relative standing crop of forbs) using standing crop data separately for spring (Mar and Apr) and summer (Aug).

Statistical Analysis

We analyzed data using repeated-measures analysis of variance for a factorial arrangement of deer density and nutrition enhancement treatments blocked by ranch (SAS 9.3, PROC MIXED; SAS Institute Inc., Cary, NC, USA). Enclosures were the experimental unit in statistical analyses. White-tailed deer density and enhanced nutrition treatments were main effects with year as the repeated measure. We designated ranch and the interaction of ranch with nutrition treatment and deer density as random effects, whereas year, deer density, and nutrition treatment were fixed effects. Dependent variables included percent canopy cover of forbs; percent canopy cover of shrubs; relative standing crop of forbs; species richness, diversity, and evenness of forbs; and density of bushsunflower and hairy wedelia.

Species richness was the number of different forb species encountered/enclosure on each sampling date (species/7.5 m^2, summed across 60 25-cm × 50-cm frames/enclosure). We calculated the Shannon–Wiener measure of diversity (Whittaker 1972) using percent canopy cover of forb species as follows:

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

where n is plant species richness and p_i is the proportion of the ith species. The greater H', the more diverse the vegetation. We determined forb species evenness (Wegge et al. 2006) using:

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

where H' is the Shannon–Wiener diversity index value and n is the number of species. The evenness measure provides a standardized scale of the Shannon–Wiener index with values ranging from 0 (all individuals present of the same species) to 1 (even distribution of species in the vegetation).

We tested normality of residuals using Shapiro–Wilks *W*-statistic (Shapiro and Wilk 1965) and transformed data when needed to stabilize variation (Zar 2010). We report backtransformed means and standard errors in the results following Bland and Altman (1996). We report standard error ranges for backtransformed standard errors because backtransformed standard errors are asymmetrical on either side of the mean (Bland and Altman 1996). We also used a mixed model to compare covariance structures (first-order autoregressive, first-order autoregressive moving average, compound symmetry, unstructured, Toeplitz, and variance components) and selected the covariance structure that provided the best fit using Akaike's Information Criterion (Burnham and Anderson 2010). We used a protected least significant difference test to compare means (Carmer and Swanson 1971). We considered means to be significantly different when $P \leq 0.10$.

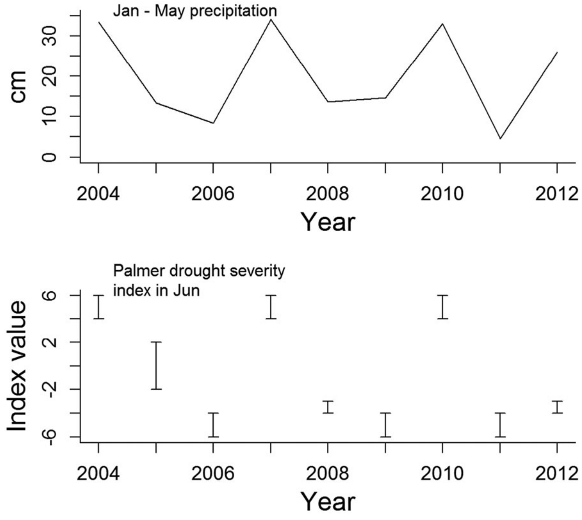

Figure 19. Annual January to May (before Jun vegetation sampling) precipitation averaged across study sites (top) and values for the Palmer Drought Severity Index in June (bottom), 2004–2012, Dimmitt County, Texas, USA. Palmer drought severity indices are extreme drought (<–4), severe drought (–3.99 to –3), moderate drought (–2.99 to –2), midrange (–1.99 to 1.99), moderately moist (3 to 3.99), and extremely moist (>4; National Oceanic and Atmospheric Administration 2016).

RESULTS

The inter-annual coefficient of variation in precipitation during our study was 37% ($n = 9$ years) on the Comanche Ranch and

Table 10. Analysis of variance for the dependent variables canopy cover (%) of preferred forbs, other forbs, preferred shrubs, other shrubs, and grasses and independent variables white-tailed deer density, nutrition treatment, and year, Dimmitt County, Texas, USA, 2007–2012.

Source of variation	df[a]	*F*	*P*
Preferred forbs			
Year (Y)	8, 48	31.6	<0.001
Density (D)	2, 5	3.1	0.133
D × Y	16, 48	0.8	0.675
Nutrition (N)	1, 5	3.9	0.107
N × Y	8, 48	1.4	0.220
N × D	2, 5	0.2	0.825
D × N × Y	16, 48	0.3	0.996
Other forbs			
Year (Y)	8, 48	63.2	<0.001
Density (D)	2, 5	0.8	0.489
D × Y	16, 48	2.4	0.009
Nutrition (N)	1, 5	<0.1	0.882
N × Y	8, 48	2.2	0.044
N × D	2, 5	0.0	0.997
D × N × Y	16, 48	0.5	0.946
Preferred shrubs			
Year (Y)	8, 48	15.8	<0.001
Density (D)	2, 5	2.2	0.203
D × Y	16, 48	1.2	0.307
Nutrition (N)	1, 5	2.0	0.219
N × Y	8, 48	0.6	0.778
N × D	2, 5	1.6	0.292
D × N × Y	16, 48	0.7	0.790
Other shrubs			
Year (Y)	8, 36	20.1	<0.001
Density (D)	2, 5	1.9	0.241
D × Y	16, 35	0.4	0.969
Nutrition (N)	1, 5	0.1	0.727
N × Y	8, 36	1.5	0.185
N × D	2, 5	2.3	0.194
D × N × Y	16, 35	1.3	0.277
Grasses			
Year (Y)	8, 48	25.1	<0.001
Density (D)	2, 5	1.3	0.360
D × Y	16, 48	0.6	0.881
Nutrition (N)	1, 5	0.4	0.575
N × Y	8, 48	0.4	0.937
N × D	2, 5	1.1	0.402
D × N × Y	16, 48	0.2	1.000

[a] We computed degrees of freedom using a Kenward–Rogers approximation (Kowalchuk et al. 2004).

41% on the Faith Ranch. Precipitation in January–May, the 5 months before vegetation sampling in June, varied from 4.5 cm during 2011 to 34.0 cm in 2007 (Fig. 19). The Palmer Drought Severity Index (National Climatic Data Center 2001), a measure of dryness using precipitation and temperature data, indicated that during the study, 3 Junes were extremely moist (2004, 2007, and 2010), 1 was average (2005), and 5 were severe to extreme drought (2006, 2008–2009, and 2011–2012; Fig. 19). The drought of 2011 was the most intense in recorded Texas history (Nielsen-Gammon 2012). The Palmer Drought Severity index reached the lowest value ever recorded in Texas in September 2011.

Canopy Cover, Diversity, and Standing Crop

Percent canopy cover of preferred forbs was similar ($P = 0.13$) among deer densities averaged across sampling years and nutrition treatments (low density: $\bar{x} = 8\%$, SE range = 6–10; medium density: 5%, SE = 4–6; high-density: 4%, SE = 3–5; Table 10). Canopy cover of preferred forbs was greater (7%, SE = 6–8) in enclosures with enhanced nutrition than in enclosures with natural nutrition (4%, SE = 3–5), although the nutrition treatment main effect was only marginally significant ($P = 0.11$). Canopy cover of preferred forbs was greater at the end of the study than at the beginning averaged across deer densities and nutrition treatments (Fig. 20). This difference was driven largely by an increase in preferred forbs in enclosures with enhanced nutrition. Preferred forb canopy cover was similar between enhanced- and natural-nutrition enclosures at the beginning of the study (6%, SE = 5–8 and 6%, SE = 4–8, respectively), but averaged twice as high in enhanced-nutrition enclosures at the end of the study in 2012 (20%, SE = 17–23 and 10%, SE = 8–13, respectively). However, no interactions were statistically significant.

Deer density and nutrition treatment independently interacted with sampling year for percent canopy cover of other forbs (Table 10; Fig. 21). Canopy cover of other forbs was greater in enclosures with low deer densities than in other enclosures in 2004 averaged across nutrition treatments; however, during the last 6 years of the study, canopy cover of other forbs was similar among deer densities (Fig. 21A). Within each sampling year, canopy cover of other forbs was similar in enhanced- and natural-nutrition enclosures, averaged across deer densities (Fig. 21B), except in 2004 when forb cover was greater in natural-nutrition enclosures. Percent canopy cover of preferred shrubs and percent canopy cover of other shrubs were similar among deer densities and between nutrition treatments (Table 10). There were no interactions for percent canopy cover of preferred or other shrubs. Percent canopy cover varied among sampling years for preferred and other shrubs, with a general increasing trend over time for other shrubs (Table 10; Fig. 22).

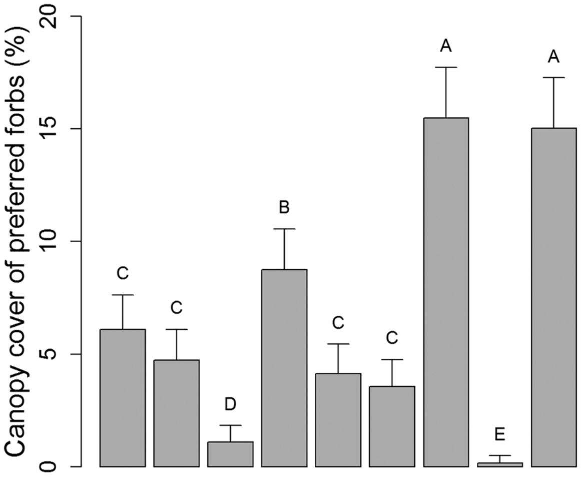

Figure 20. Backtransformed least square means (+SE, $n = 12$) of preferred forb canopy cover averaged across 3 white-tailed deer population densities and 2 nutrition treatments during 2004–2012, Dimmitt County, Texas, USA. Means associated with the same letter are not significantly different ($P > 0.10$).

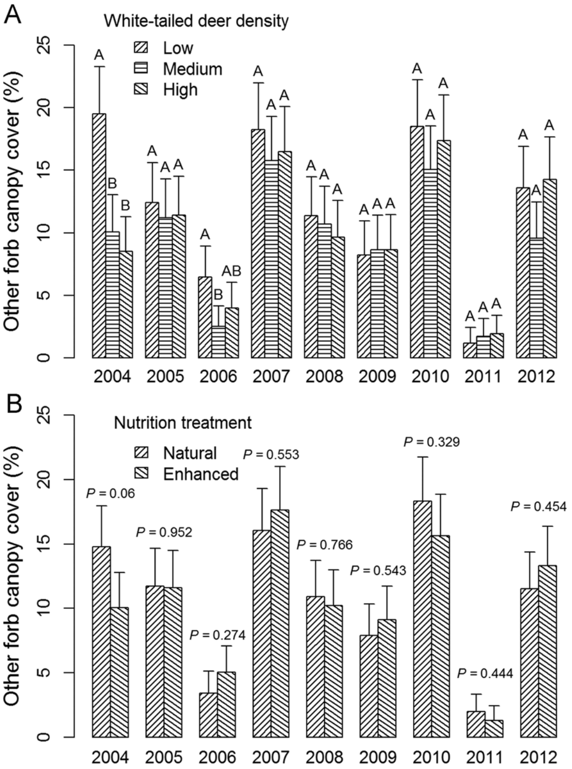

Figure 21. Backtransformed least square means (+SE) of other forb canopy cover in response to 3 white-tailed deer density treatments (A) and 2 nutrition treatments (B), June 2004–2012, Dimmitt County, Texas, USA. Means within a graph and within a cluster of columns associated with the same letter are not significantly different ($P > 0.10$).

Percent canopy cover of grasses was similar among deer densities and nutrition treatments (Table 10). There were no interactions for grass canopy cover. As with forbs, grass canopy cover varied dramatically among sampling years, ranging from 58% (SE ± 3, $n = 12$) in 2004 to 21% (SE ± 3) in both 2006 and 2012, averaged across deer density and nutrition treatments (Fig. 23).

Forb species richness, Shannon's index, and evenness were similar among deer densities (Table 11). Forb species richness was 24% greater in enclosures with enhanced nutrition than in enclosures with natural nutrition (31 ± 4 species/7.5 m^2 vs. 25 ± 4 species/7.5 m^2, respectively), although the difference was not statistically significant ($P = 0.13$). Shannon's index was 2.43 ± 0.1 and 2.15 ± 0.1 in the enhanced- versus

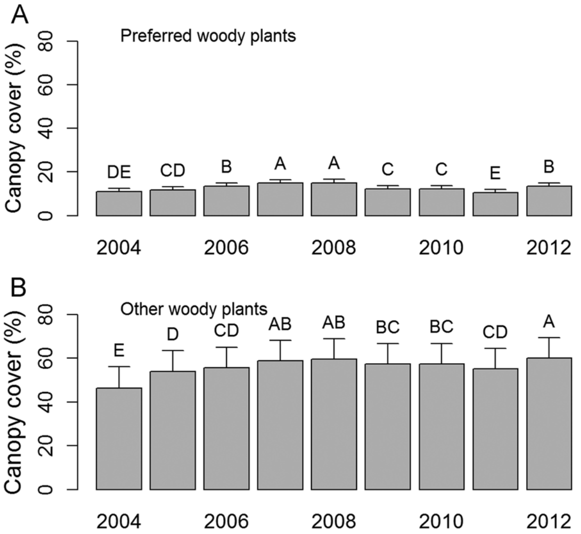

Figure 22. Backtransformed least square means (+SE, $n = 12$) of preferred (A) and other (B) woody plant canopy cover among sampling years averaged across nutrition treatments and 3 white-tailed deer population densities, June 2004–2012, Dimmitt County, Texas, USA. Means associated with the same letter are not significantly different ($P > 0.10$).

natural-nutrition enclosures, respectively. Evenness was 7% greater in enclosures with enhanced nutrition (0.73 ± 0.02) than in enclosures with natural nutrition (0.68 ± 0.02). Forb species diversity, Shannon's index, and evenness varied among sampling years (and there were no interactions for these variables).

Relative standing crop of forbs during spring was similar among white-tailed deer densities and between nutrition treatments during the 9 years of study (Table 12; Fig. 24). In summer, relative standing crop of forbs was similar among deer densities, but there was an interaction of nutrition treatment and sampling year (Table 12). Forbs in enhanced-nutrition enclosures composed more of the herbaceous vegetation in 2012 than in enclosures with natural nutrition, averaged across deer densities. There were no other interactions or main effects during spring or summer except that relative standing crop of forbs varied dramatically among sampling years.

Awnless Bushsunflower and Hairy Wedelia Density

The density of awnless bushsunflower plants >0.5 m tall interacted between sampling year and deer density, and between sampling year with nutrition treatment (Table 13). However, a comparison of bushsunflower density among the 3 deer densities within each sampling year did not reveal any statistically significant ($P > 0.10$) differences (Fig. 25A). Density of bushsunflower plants >0.5 m tall was 4.4 to 6 times greater in enclosures with enhanced nutrition than in enclosures with natural nutrition in 2004, 2007, and 2009–2010, but densities of the plant were similar between treatments in other sampling years (Fig. 25B). As with density of bushsunflower >0.5 m tall, bushsunflower <0.5 m tall varied among sampling years (Table 13). However, there were no other treatment main effects or interactions for density of bushsunflower plants <0.5 m.

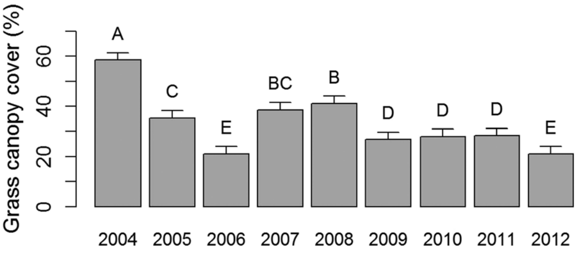

Figure 23. Least squares mean canopy cover (+SE, $n = 12$) of grasses among sampling years averaged across nutrition treatments and 3 white-tailed deer population densities, June 2004–2012, Dimmitt County, Texas, USA. Means associated with the same letter are not significantly different ($P > 0.10$).

Table 11. Analysis of variance for the dependent variables Shannon's diversity index, evenness, and forb species richness (plants/7.5 m^2) and independent variables white-tailed deer density, nutrition treatment, and year, Dimmitt County, Texas, USA, 2004–2012.

Source of variation	df[a]	*F*	*P*
Shannon's Index			
Year (Y)	6, 17	76.9	<0.001
Density (D)	2, 5.6	0.6	0.579
D × Y	12, 18	0.4	0.980
Nutrition (N)	1, 5.6	3.9	0.099
N × Y	7, 33	0.7	0.676
N × D	2, 5.6	0.0	0.972
D × N × Y	14, 32.3	0.3	0.983
Evenness			
Year (Y)	6, 17	18.3	<0.001
Density (D)	2, 6	1.0	0.436
D × Y	12, 18	1.6	0.173
Nutrition (N)	1, 6	1.0	0.094
N × Y	6, 17	0.9	0.504
N × D	2, 6	0.2	0.850
D × N × Y	12, 18	0.3	0.981
Species richness			
Year (Y)	7, 31.5	96.2	<0.001
Density (D)	2, 5.0	0.4	0.712
D × Y	14, 31	0.3	0.995
Nutrition (N)	1, 5.0	3.2	0.133
N × Y	7, 31.5	1.3	0.282
N × D	2, 5.0	0.1	0.894
D × N × Y	14, 31.0	0.9	0.616

[a] We computed degrees of freedom using a Kenward–Rogers approximation (Kowalchuk et al. 2004).

For density of hairy wedelia plants >0.5 m tall, there was a 3-way interaction among sampling year, deer density, and nutrition treatment (Table 13). We examined this interaction by first comparing means for hairy wedelia density among deer densities

Table 12. Analysis of variance for the dependent variable standing crop of forbs relative to grasses (%) in spring and summer and independent variables white-tailed deer density, nutrition treatment, and year, Dimmitt County, Texas, USA, 2004–2012.

	Spring			Summer		
Source of variation	df[a]	*F*	*P*	df	*F*	*P*
Year (Y)	7, 13.9	49.6	<0.001	8, 48	8.1	<0.001
Density (D)	2, 5.3	0.0	0.972	2, 5	0.7	0.542
D × Y	14, 15.1	0.4	0.955	16, 48	0.9	0.610
Nutrition (N)	1, 5.3	0.0	0.950	1, 5	0.8	0.421
N × Y	7, 13.9	0.7	0.654	8, 48	2.1	0.051
N × D	2, 5.3	1.4	0.327	2, 5	2.2	0.205
D × N × Y	14, 15.1	0.8	0.652	16, 48	1.0	0.442

[a] We computed degrees of freedom using a Kenward–Rogers approximation (Kowalchuk et al. 2004).

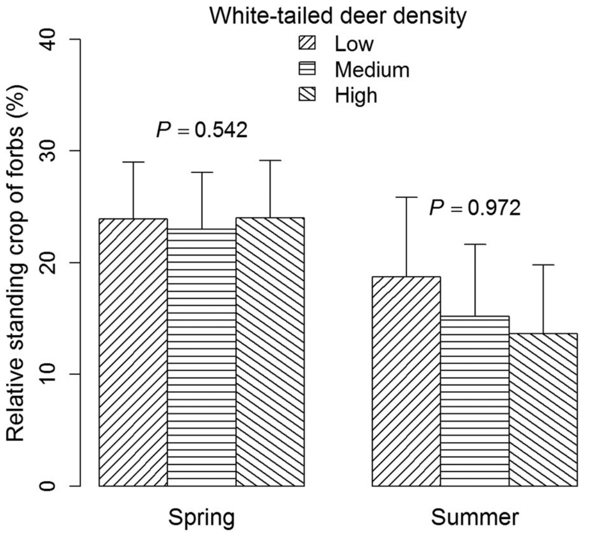

Figure 24. Least squares mean relative standing crop (+SE, $n = 36$) of forbs during spring and summer (backtransformed values) at 3 white-tailed deer population densities averaged across nutrition treatments and sampling years, June 2004–2012, Dimmitt County, Texas, USA.

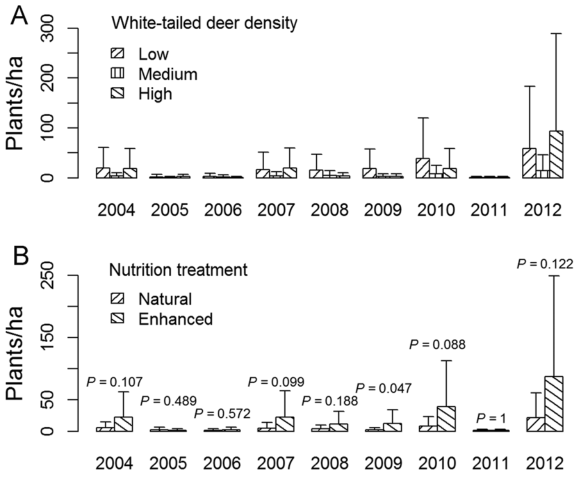

Figure 25. Backtransformed least squares mean density (+SE, $n = 4$) of awnless bushsunflower plants >0.5 m tall at 3 white-tailed deer population densities averaged across nutrition treatments (A) and in enclosures with enhanced nutrition and natural nutrition averaged across 3 white-tailed deer population densities (B), June 2004–2012, Dimmitt County, Texas, USA.

within each sampling date, and then by comparing hairy wedelia means between nutrition treatments within each sampling date. Hairy wedelia >0.5 m tall was denser in enclosures with low deer densities and enhanced nutrition than in enclosures with high deer densities throughout the study except during severe drought. Similarly, hairy wedelia was denser ($P < 0.082$) in low- than medium deer density treatments when averaged across nutrition treatments, although hairy wedelia density was similar ($P > 0.33$) in the low- and medium deer density treatments during the first 2 sampling years (2004 and 2005) and during the droughts of 2006 and 2011.

Hairy wedelia plants >0.5 m tall were denser ($P \leq 0.097$) in enclosures with enhanced nutrition than in those with natural nutrition except during severe drought in 2011 (Fig. 26). In enclosures with enhanced nutrition, density of hairy wedelia increased during 2004 to 2012 in low, medium, and high deer density enclosures (protected least significant difference test, $P < 0.01$, $P = 0.01$, and $P = 0.03$, respectively). Under natural nutrition, hairy wedelia density did not change significantly when comparing 2004 to 2012 in low and high deer density enclosures (protected least significant difference test, $P = 0.28$ and 0.82, respectively) but almost doubled ($P = 0.09$) in medium-density enclosures in 2012 compared to 2004.

There were interactions of sampling year with deer density and deer density with nutrition treatment for density of hairy wedelia plants <0.5 m tall (Table 13; Fig. 27A). Averaged across sampling years, hairy wedelia plants <0.5 m tall tended to be denser in enclosures with enhanced nutrition than in enclosures with natural nutrition only at low deer densities (Fig. 27A).

Table 13. Analysis of variance for the dependent variable density (plants/ha) of awnless bushsunflower and hairy wedelia plants either >0.5 m tall or ≤0.5 m tall during June and independent variables white-tailed deer density, nutrition treatment, and year, Dimmit County, Texas, USA, 2004–2012.

	>0.5 m tall			≤0.5 m tall		
Source of variation	**df**[a]	***F***	***P***	**df**	***F***	***P***
Awnless bushsunflower						
Year (Y)	8, 14	14.1	<0.001	8, 37	9.9	<0.001
Density (D)	2, 5	1.2	0.366	2, 5	1.7	0.277
D × Y	16, 15.3	3.1	0.017	16, 36.1	0.6	0.880
Nutrition (N)	1, 5	2.6	0.168	1, 5.0	0.0	0.934
N × Y	8, 14	3.5	0.020	8, 37	0.5	0.877
N × D	2, 5	0.1	0.904	2, 5.0	0.1	0.934
D × N × Y	16, 15.3	0.6	0.834	16, 36.1	0.4	0.981
Hairy wedelia						
Year (Y)	8, 53	21.0	<0.001	8, 37.7	37.2	<0.001
Density (D)	2, 53	50.4	<0.001	2, 5.0	13.6	0.009
D × Y	16, 53	2.7	0.003	16, 36.6	2.5	0.013
Nutrition (N)	1, 53	76.0	<0.001	1, 5.0	7.1	0.045
N × Y	8, 53	4.7	<0.001	8, 37.7	1.4	0.216
N × D	2, 53	38.4	<0.001	2, 5.0	5.9	0.048
D × N × Y	16, 53	2.1	0.022	16, 36.6	1.6	0.121

[a] We computed degrees of freedom using a Kenward–Rogers approximation (Kowalchuk et al. 2004).

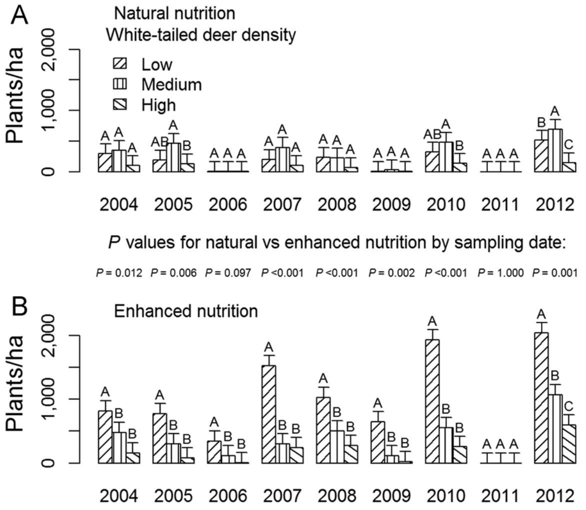

Figure 26. Mean density (+SE, $n = 2$) of hairy wedelia plants >0.5 m tall in enclosures with natural nutrition (A) and enhanced nutrition (B) at 3 white-tailed deer population densities, June 2004–2012, Dimmitt County, Texas, USA. Means within a cluster of columns associated with the same letter are not significantly different ($P > 0.10$).

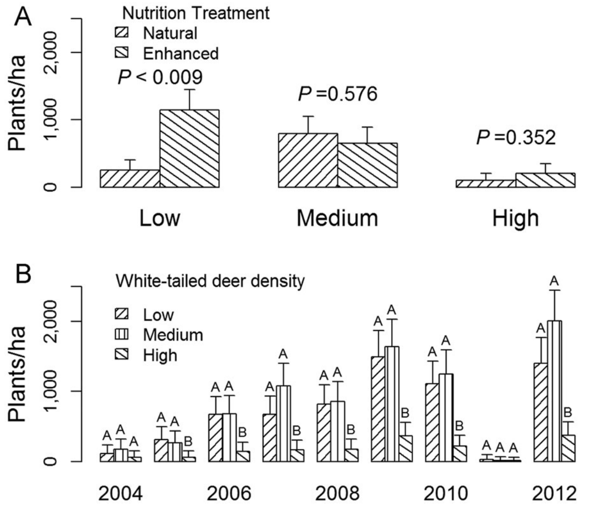

Figure 27. Backtransformed least square mean density (+SE, $n = 18$) of hairy wedelia plants <0.5 m tall in 81-ha enclosures with enhanced nutrition and natural nutrition averaged across sampling years (A) and at 3 white-tailed deer population densities averaged across nutrition treatments (B), June 2004–2012, Dimmitt County, Texas, USA. In the bottom of the figure, means within a cluster of columns associated with the same letter are not significantly different ($P > 0.10$).

Averaged across nutrition treatments, hairy wedelia plants <0.5 m tall were denser in enclosures with low and medium deer densities than in enclosures with high deer densities on 7 of the 9 sampling years (Fig. 27B).

DISCUSSION

Preferred forbs and preferred shrubs did not decrease in response to a 3.4-fold increase in deer density and enhanced nutrition over the 9 years of our study. Forb standing crop was also not reduced by increasing deer density and enhanced nutrition in our study area (Crider et al. 2015). The increase in preferred forb cover, bushsunflower, and hairy wedelia over the course of the study in enclosures with enhanced nutrition and lack of decline with natural nutrition provided further evidence that deer had little effect on preferred forbs within the range of deer densities in our study. Lower density of hairy wedelia plants <0.5 m tall in the high deer density treatment probably resulted from greater foraging pressure; however, results supported the idea that preferred plants would not decline with increasing deer density (Fig. 3B) because density of smaller hairy wedelia plants was greater at the end of the study than during the first 2 years of the study. High deer densities apparently constrained the increase in hairy wedelia relative to other deer densities rather than causing it to decline over time as would be the expected result of heavy use by deer in mesic environments. Our results contrast sharply with the more dramatic decline in preferred plants resulting from selective foraging and increased dominance of unpalatable plants in response to high population densities of white-tailed deer reported in forested environments (Rooney and Waller 2003, Côté et al. 2004, Russell et al. 2005, Shelton et al. 2014). Our results were similar to those of Wester and Wright (1987) in a desert shrub plant community where reduced browsing pressure by mule deer was not reflected in changes in individual species abundance.

We suggest that our results differ from those of the numerous studies in forested environments likely because precipitation was a more influential driver of vegetation change than deer in our study area (Crider et al. 2015). Variable precipitation, however, is not the sole explanation for the differences between our study and those in forested environments. In addition to variable precipitation, characteristics of the vegetation in our region including its ephemeral nature, asynchrony in phenology of different forage classes, plant attributes that directly or indirectly help defend against herbivory, and possibly vegetation change in response to long-term herbivory interacted in a manner that constrained the effects of selective foraging by white-tailed deer on vegetation dynamics. In the subsequent discussion, we explain how these constraints on selective foraging weaken the link between herbivores and vegetation in stochastic, semi-arid environments.

The ephemeral availability of herbaceous vegetation in arid environments may weaken the linkage between vegetation dynamics and herbivores (Silcock and Fensham 2013). Canopy cover and standing crop of vegetation in our study varied dramatically from year to year because of the highly stochastic nature of the semi-arid environment. About 44% of the forb species eaten by deer in our study area were cool-season annuals and many of the perennial forbs function like annuals (Schaal and Leverich 1982, Crider et al. 2015). This life-cycle strategy helps arid-land plants to avoid periods of the year when moisture and temperature are unfavorable for growth (Mulroy and Rundel 1977). Although acting as an adaptation to a variable and arid environment, this strategy also may be important in constraining the effects of selective foraging on annual forbs and perennial forbs that respond to environmental variation in a manner similar to annuals. Growth of forbs when moisture and temperature are favorable results in synchronized pulses of production. These pulses of production may have a swamping effect such that forage is so abundant that the ability of selective foraging by herbivores to have a measurable effect on palatable forbs during the temporary period of time they are available is limited. Cool-season forbs senesce by early summer because of warming temperatures and limited moisture, terminating the pulse of growth. This senescence limits effects of selective foraging because environmental conditions, rather than deer foraging, cause the plants to decline. The ephemeral availability of these forbs also reduces the effects of selective foraging on them by allowing them to avoid herbivory during most of the year (Briske 1996, Silcock and Fensham 2013). We posit that similarity in canopy cover of preferred forbs between the beginning and end of our study at high densities occurred in part because these plants were absent during much of the year and were lacking during severe droughts, such as occurred in 2006 and 2011.

Temporal asynchrony in phenology of vegetation may limit foraging selectivity by deer (Augustine and McNaughton 1998; Fig. 28). Deer may switch to different plant species as they become available, thereby reducing foraging pressure on the plants they were previously consuming. This reduction in foraging pressure when deer switch to other forages may allow plants to avoid excessive herbivory. White-tailed deer in our study area are primarily browsers during autumn and early winter (Timmons et al. 2010, Folks et al. 2014). Forbs in the

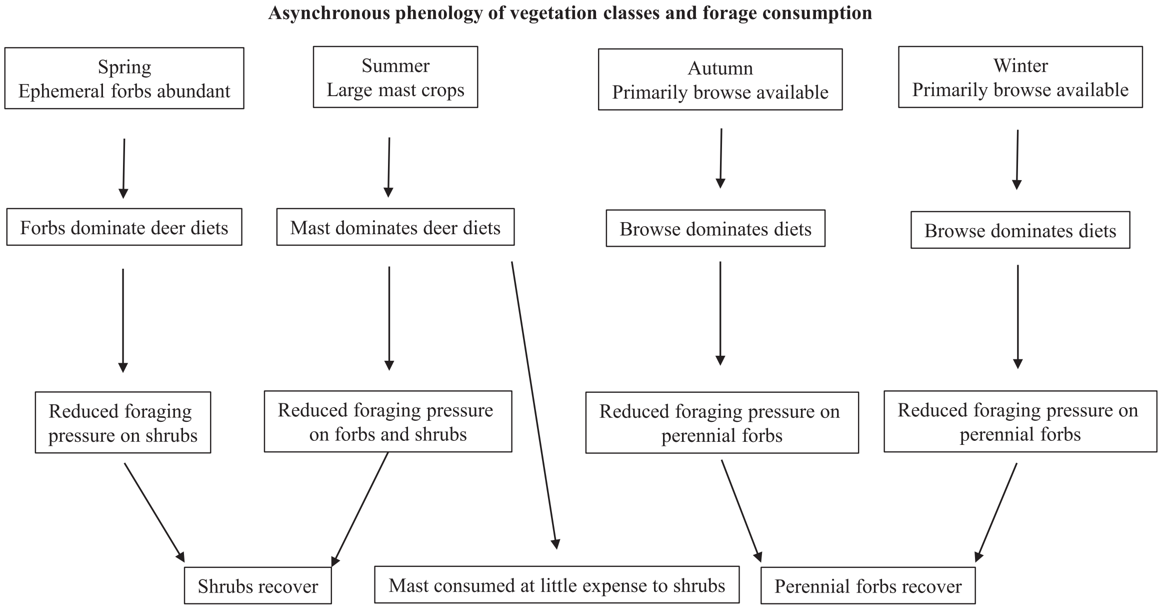

Figure 28. Changes in availability of different forage classes may act to allow recovery of shrubs and perennial forbs from the effects of browsing by white-tailed deer, thereby reducing the potential for overuse of preferred plants.

region are primarily cool-season plants and peak in growth during spring. In years with sufficient precipitation, deer diets are dominated by forbs during spring. During drought, forbs are less abundant in spring and many perennial shrub species including desert yaupon (*Schaefferia cuneifolia*), lotebush (*Ziziphus obtusifolia*), spiny hackberry, and whitebrush (*Aloysia gratissima*) are drought deciduous (Archer 1990, Liu et al. 2013, Felger et al. 2015). During dry winters and springs when forbs are lacking and drought deciduous shrubs have lost their leaves, deer switch foraging activity to evergreen shrubs, particularly Texas lignum-vitae (*Guaiacum angustifolium*), that receive little use during wet years (Folks 2012). In addition, deer consume prickly pear pads during dry winters and springs (Folks 2012). Mesquite and prickly pear mast are produced during summer, and mast composed 53% and 48% of deer diets during drought and non-drought summers, respectively, in natural-nutrition enclosures (Gann et al. 2019*a*). Mast is available from these species even during drought and mesquite mast production may increase in response to drought (Lee and Felker 1992). Foliage of mesquite is unpalatable to deer; therefore, high deer densities are unlikely to cause a reduction in photosynthetic tissue that would, in turn, reduce carbon allocation to mast production. The reduction in use of browse by deer during spring and summer allows shrubs time to recover from browsing that took place during the previous autumn and winter. When drought-deciduous shrubs lose their leaves during summer, consumption of mast by deer allows evergreen shrubs to recover from the effects of browsing. In addition, the high level of mast consumption during summer allows preferred perennial forbs such as hairy wedelia to recover from foraging during spring.

Foraging by high densities of deer may have had little effect on preferred shrubs in part because plant species in our study area possess a variety of characteristics that may limit effects of selective foraging. Local shrubs possess anti-herbivore adaptations such as compensatory growth, structural characteristics that protect leaves within the canopy from browsing, thorns, and secondary compounds (Cooper et al. 2003, Cash and Fulbright 2005, Gann et al. 2016). These traits in part explain why shrub canopy cover was less influenced by deer density and enhanced nutrition than forbs. Many of the dominant shrubs in the region that are important in deer diets, such as spiny hackberry and blackbrush acacia, produce compensatory growth in response to defoliation (Teaschner and Fulbright 2007, Fulbright et al. 2011, Gann et al. 2016). Compensatory growth during late spring and summer following browsing during autumn and early winter may enhance recovery of shrubs by making more photosynthetic tissue available when browsing is less intense.

Characteristics that help shrubs to maintain substantial leaf tissue even when browsed by deer may aid in compensatory growth following defoliation. For example, canopy architecture of many of the shrub species in the study areas prevents leaves and twigs in the inner part of the canopy from being eaten (Cooper et al. 2003). Shrubs such as spiny hackberry, blackbrush acacia, and guajillo are often sufficiently tall that much of the canopy is above the reach of white-tailed deer. Leaves remaining on the plants following browsing may support compensatory growth of browsed portions of shrubs through photosynthesis.

A final reason why selective foraging on preferred shrubs did not result in a shift in shrub composition to less preferred shrubs is that these shrub species do not vary greatly in tolerance to herbivory, in part as a consequence of development of these communities under intensive herbivory. Much of the landscape in pre-Columbian times in southern Texas was prairie or savanna (Fulbright 2001, Van Auken 2009). In pre-Columbian times, shrub communities were primarily confined to active and ephemeral drainages (Box 1967). Woody vegetation has increased dramatically in the past 200–300 years, forming continuous woodland throughout much of the landscape (Archer et al. 1988, Archer 1989). White-tailed deer spatial distribution expanded from drainages into upland landscapes as woodland developed in former grassland. This replacement of grassland and savannas with woody vegetation occurred concomitantly with the introduction of large numbers of domestic herbivores. For example, in 1882 there were an estimated 2.4 million sheep and goats in South Texas (Lehmann 1969). Dimmit County, where our study areas were located, supported 12 times as many sheep and goats as cattle in 1882. The estimated number of animal units (defined as 1 adult cow) was a 1 animal unit/6 ha, the equivalent of a sheep or goat/1.3 ha. Most of the shrub species that came to dominate the South Texas thornscrub landscape are highly defended against herbivory, possessing secondary chemicals, thorns, or both (Cash and Fulbright 2005).

Research on livestock grazing has shown that variation in rainfall may influence short-term changes in vegetation more than livestock grazing, but grazing intensity determines long-term vegetation trends (Fuhlendorf et al. 2001). Environmental stochasticity affected vegetation more than high deer densities during the time scale of our study; but it is unknown whether these densities may affect vegetation more strongly in the longer term in a manner similar to grazers in other rangeland environments.

Our data supported the hypothesis that providing enhanced nutrition will not cause preferred plants to decline in abundance in a stochastic, semi-arid environment. Providing enhanced nutrition acted to protect preferred forbs from the effects of deer foraging, regardless of white-tailed deer density. The increase in preferred forb canopy cover and hairy wedelia density over time when enhanced nutrition was provided may have occurred because the combination of enhanced nutrition and lower herbivore densities allowed preferred forbs to recover from foraging pressures exerted by ungulates existing before the enclosures were constructed. Large herbivores present before construction of enclosures, in addition to white-tailed deer, included domestic cattle, feral pigs, and collared peccaries. Cattle prefer grasses but may consume 3 times the amount of forbs/day than 1 deer does (Fulbright and Ortega-Santos 2013). Forbs may compose up to 81% of the diet of feral pigs, depending on season, and >50% of the diet of collared peccaries in South Texas (Everitt and Alaniz 1980, Everitt et al. 1981, Corn and Warren 1985, Ilse and Hellgren 1995). Consequently, considerable foraging pressure by ungulates other than deer may have been eliminated by construction of the enclosures, resulting in less intensive herbivory than existed before construction.

Another possible explanation for the increased cover of preferred forbs is reduced competition with perennial grasses during the last 4 years of the study. The drought episodes beginning in 2009 reduced grass canopy cover compared to the first 5 years of the study. High mortality of perennial grasses resulting from drought and high temperatures has been previously reported in southern Texas (Rogers et al. 2004). Many of the preferred forbs are annuals. Annuals germinate and grow rapidly following precipitation events (Mulroy and Rundel 1977) and occupy space previously occupied by perennial grasses.

Providing enhanced nutrition in our study resulted in a reduction in native vegetation consumed by white-tailed deer. Averaged across deer densities, white-tailed deer diets in enclosures with enhanced nutrition were <50% natural vegetation, and may have contained more browse compared to deer in enclosures with natural vegetation (Darr et al. 2019). This reduction in consumption of native plants reduced foraging pressure on forbs, which explains in part why preferred forb cover, species diversity, and evenness increased in enclosures with enhanced nutrition. Continued consumption of shrubs by deer in enclosures with enhanced nutrition may be a response to high rates of rumen fermentation because grain-based supplements may lower rumen pH, causing ruminants to consume forages with higher fiber (Wobeser and Runge 1975, Woolf and Kradel 1977).

Increased diversity of forbs in enclosures with enhanced nutrition may have benefited deer nutritionally. Part of the foraging strategy of ruminants is to consume a variety of species, which enables them to mix diets and optimize diet quality (Provenza et al. 2003). In addition, foraging on a variety of species helps ruminants to avoid malaise caused by ingestion of plants high in secondary compounds.

Response of preferred forbs was more constrained with natural nutrition than with enhanced nutrition. The lack of change in percent canopy cover of preferred forbs over time in enclosures with natural nutrition probably occurred because foraging pressure by deer was greater than occurred with enhanced nutrition. This result could be interpreted as indirect evidence of density-dependent responses of vegetation to deer foraging. Reasoning for this interpretation is that foraging pressure on forbs was much less in enclosures with enhanced nutrition then in enclosures with natural nutrition because <50% of diets were composed of vegetation (Darr et al. 2019). In other words, the greater canopy cover of preferred forbs in enclosures with enhanced nutrition compared to enclosures with natural nutrition resulted in part because fewer forbs were eaten in the enclosures with enhanced nutrition. By reducing the amount of vegetation that deer ate, providing enhanced nutrition may have reduced foraging effects on vegetation in a manner similar to reducing deer densities. Although selective foraging may have constrained preferred forbs in natural-nutrition enclosures, the effect was subtle as there was no difference in overall forb standing crop between enhanced and natural-nutrition enclosures (Crider et al. 2015).

MANAGEMENT IMPLICATIONS

Understanding potential differences in vegetation responses to foraging by white-tailed deer between moist and semi-arid climates will help wildlife managers refine management approaches and make them more applicable to the semi-arid portion of the geographic range of white-tailed deer. Management paradigms for white-tailed deer are often based on the assumption that deer populations are density-dependent. In stochastic, semi-arid systems, traditional management approaches based on the assumption of strong density dependence may be inappropriate. White-tailed deer densities in these systems may be limited by low recruitment and seldom reach population densities high enough to cause degradation of the vegetation. Management actions such as reducing deer densities are unlikely to result in dramatic vegetation changes in these environments with natural nutrition. Providing enhanced nutrition may result in an increase in preferred herbaceous plants.

White-Tailed Deer Population Dynamics at Different Densities in Tamaulipan Thornshrub as Influenced by Nutrition

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INTRODUCTION

Density-dependent behavior by ungulate populations has been widely documented (Caughley 1977, McCullough 1999, Gaillard et al. 2000, Bonenfant et al. 2009, Bowyer et al. 2014). Density dependence can take many forms but basically involves constrained productivity and/or increased mortality as population density increases. Ungulates are found in most major ecosystems of the world (Gaillard et al. 2000), and factors influencing density-dependent behavior reflect the diversity of species and ecosystems (Bonenfant et al. 2009). Influences of predators, disease, and human factors vary with ungulate population density in some situations (Gaillard et al. 2000). Time lags in expression of density dependence, population age structure, and sex ratio can also be factors (Festa-Bianchet et al. 2003, Bonenfant et al. 2009). DeYoung (2011) suggested that the profile of available food quality can dictate whether density responses are possible in some environments (also see Cook et al. 2016). Finally, there is great variability in the effects of temperature and precipitation on density-dependent behavior (Gaillard et al. 2000, DeYoung et al. 2008, DeYoung 2011, Monteith et al. 2014, Cook et al. 2016).

Typically, density dependence is expressed by increased age at breeding for females and reduced survival of young, fetal rate, pregnancy rate, and (rarely) adult survival (Fowler 1981*b*, Gaillard et al. 2000, Bonenfant et al. 2009, Monteith et al. 2014). Phenotypic parameters such as growth rate and body mass are also commonly reduced as density increases (Bonenfant et al. 2009). Environmental variation, usually precipitation flux but sometimes cold winters (Caughley and Gunn 1993), interacts with density-dependent tendencies to affect ungulate population sizes (Bowyer et al. 2014).

Some researchers argue that density dependence is expressed throughout the spectrum of a population's size, from low density to carrying capacity (McCullough 1979, Bowyer et al. 2014). Others posit that density dependence becomes apparent only after a population grows near carrying capacity (McCullough 1999).

McCullough's (1979) experiment on white-tailed deer dynamics on the George Reserve, Michigan, USA, has influenced subsequent population theory (McCullough 1999, Bowyer et al. 2014). The George Reserve experiment revealed strong density dependence across a range of deer densities in relation to carrying capacity. Although McCullough (1979) remains an important part of the body of knowledge on white-tailed deer population dynamics, density dependence has been elusive to demonstrate in other studies (Mackie et al. 1990, Shea et al. 1992, Shea and Osborne 1995, DeYoung et al. 2008). DeYoung et al. (2008) used 2 analytical approaches to study density dependence from east to west across South Texas. They found relatively strong density dependence in the eastern part of the region but could not detect density dependence in the drier, stochastic environment to the west.

Because deer managers in South Texas perceive that the semiarid, stochastic environment limits deer nutrition, pelleted supplemental feed is commonly provided (Zaiglin and DeYoung 1989, Bartoskewitz et al. 2003). The climate and soils of the region preclude common use of food plots, which are used to supplement deer in the southeastern United States (Edwards et al. 2004). There is limited documentation of the effects on deer populations of enhanced nutrition through feeding pellets to deer.

Designed manipulative experiments are needed to clarify the apparent continuum for strong to weak density-dependent dynamics across white-tailed deer range. Our objective was to conduct a series of experiments in western South Texas, where DeYoung et al. (2008) could not detect density dependence, to assess effects of 3 deer density levels and enhanced nutrition in 81-ha enclosures. We assessed the following metrics: fawn:adult female ratios, growth rates of fawns and yearlings, survival from 6 to 14 months, annual survival for adults >14 months, adult body mass, pregnancy rate in fawns and adult females, and population growth rate. Our hypothesis was that under natural nutrition, enclosure deer populations would not exhibit density dependence as density level increased to 50 deer/km^2 (DeYoung et al. 2019*a*; Fig. 3C). Accordingly, we predicted that all

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variables would show no effect as deer density increased. Additionally, we hypothesized that deer under enhanced nutrition would not exhibit density dependence (Fig. 3C) but would have higher productivity than those under natural nutrition (Fig. 3F). Under this hypothesis, we predicted that fawn:adult female ratios, growth rates of fawns and yearlings, survival from 6–14 months and for adults >14 months, adult body mass, pregnancy rate in fawns and adult females, and population growth rate would exhibit an additive effect, but this effect would not interact with density level.

METHODS

We sampled deer populations in 6 81-ha enclosures on each of 2 study sites in Dimmit County, Texas, during 2004–2012. Each site had 2 enclosures with 1 of 3 deer density levels and 1 enclosure at each density on each site was provided with enhanced nutrition. Details on study areas and overall design of our experiment are described in DeYoung et al. (2019*a*). Specific methods to estimate demographic variables are described here.

Demographics

We used reconstruction (Cook 2014, DeYoung et al. 2019*a*) to estimate the number of adult females available to produce fawns in July, the month when most fawns were born (Wilson 2013), of each study year. We also used reconstruction to estimate the number of fawns that survived to December, which was past the time most would be weaned (DeYoung and Miller 2011). Because of low sample size, we combined data from low- and medium-density enclosures for assessing fawn:adult female ratios, resulting in 2 density levels. We divided the number of fawns by the number of adult females to arrive at a fawn:adult female ratio.

We used vaginally inserted transmitters in adult females to catch newborn fawns in our enclosures (Wilson 2013). Average birth date for fawns was 18 July (±1.26 SE, $n = 43$) and there was no difference ($t = -0.98$, $P = 0.17$) between average birth dates in natural ($n = 22$) and enhanced ($n = 21$) enclosures (A. S. Wilson, Caesar Kleberg Wildlife Research Institute, Texas A&M University–Kingsville, unpublished data). Additionally, Wilson (2013) found mean birth mass of 2.53 ± 0.43 kg for fawns in natural-nutrition enclosures and 2.98 ± 0.01 kg for enhanced-nutrition enclosures ($t = 1.88$, $P = 0.03$). We calculated growth rate of fawns and yearlings captured or harvested in December and March–April population adjustments (DeYoung et al. 2019*a*) by subtracting average birth mass from capture or harvest mass and dividing by days since 18 July of each deer's birth year. Because of sample size limitations, data for low and medium-density enclosures were combined for both fawn and yearling analysis, resulting in 2 density levels (low-medium and high). For yearlings, it made biological sense that growth rate would differ by sex. However, the global model would not run because of insufficient data; therefore, we analyzed male and female yearlings separately. For females, we obtained data for 2005–2007 and 2009–2012. For males, we obtained data for 2005–2006 and 2009–2010. We weighed deer >14 months old that we captured or harvested in enclosures in December and March–April to obtain whole body mass (DeYoung et al. 2019*a*). We analyzed adult body mass for males 4–10 years old and females 2–10 years old.

We estimated survival using a multistate model in Program MARK (White et al. 2006) with 2 groups (males and females) and 3 states. State 1 was tagged deer >14 months old that had lived in an enclosure ≥9 months, which provided an annual estimate of adult survival of deer that had been in enclosures long enough to adjust to treatment conditions. State 2 was deer >14 months old that were added to an enclosure from outside range (≤8 km) and remained in the enclosure <9 months. State 3 was fawns captured and tagged in December or March–April and were 6–14 months old, which provided an estimate of annual survival of older fawns. We obtained individual deer capture history annually from camera surveys in September–October or December–January (DeYoung et al. 2019*a*). We included dead recoveries in models and censored harvested deer.

We counted fetuses in fawns and older females harvested in density reductions during March–April annually (DeYoung et al. 2019*a*). However, sample sizes were too small in some treatments to analyze statistically so we present descriptive statistics.

We analyzed population growth rate by annually calculating lambda apparent (λ_{APP}) for each enclosure after accounting for removals or additions as follows:

$$\lambda_{\mathrm{APP}} = \frac{N_{t+1} - A_t}{N_t - C_t}$$

where N is the population estimate in June from reconstruction, A the number of deer added, and C the number of deer removed, after Skalski et al. (2005). The variance of λ_{APP} is 0. Parameters A and C are known so variance = 0. Also, VN_1 and VN_2 are 0 because the reconstruction estimates have no variance. Finally, the covariance between N_1 and N_2 is 0 because the estimates are independent.

Statistical Analysis

For each response variable (fawn:adult female ratio, fawn and yearling growth rate, adult body mass, adult male and female survival, survival of fawns 6–14 months, and population growth rate), we analyzed data with a linear mixed model for a randomized block design (PROC MIXED, SAS 9.3; SAS Institute, Cary, NC, USA), with ranch (Comanche and Faith; DeYoung et al. 2019*a*) as a block effect and a factorial arrangement of deer density and nutrition treatment (natural or enhanced) as fixed factors of interest. Random effects included ranch and the interaction between ranch, nutrition treatment, and deer density. We tested the effect of sex and its interactions with deer density and nutrition treatment with the interaction between sex and ranch nested within nutrition treatment and deer density included as an additional random effect (Milliken and Johnson 2009). We analyzed sampling date (Dec or Mar–Apr) or year as repeated-measures factors with the interaction between sampling date (or year) and ranch nested within ranch, with deer density and nutrition treatment included as a random effect. For adult male and adult female survival analysis, we used 1/standard error^2 as weights for the dependent variable in the mixed model, and obtained standard error of the survival estimate from

Table 14. Analysis of variance (ANOVA) for white-tailed deer fawn:adult female ratio based on independent variables deer density, nutrition treatment, and year. Also, 1-tailed *t* tests for deer density effect by nutrition treatment, Dimmit County, Texas, USA, 2004–2012.

Source of variation	df	*F*	*t*	*P*
ANOVA				
Density (D)	1, 8.65	2.13		0.18
Nutrition (N)	1, 8.65	7.97		0.02
D × N	1, 8.65	1.89		0.20
Year (Y)	8, 16	3.72		0.01
Y × D	8, 16	1.05		0.44
Y × N	8, 16	1.04		0.45
Y × D × N	8, 16	0.79		0.62
1-tailed *t* tests				
Density effect, natural nutrition	8.65		−2.00	0.04
Density effect, enhanced nutrition	8.65		−0.06	0.48

Program MARK. For fawn survival, 33% of survival estimates had a standard error of 0, so we did not use weights for this variable. Other response variables could not be weighted like survival for adult males and adult females. Fawn and yearling growth rate and adult mass were based on actual measurements, not estimates. Fawn:adult female ratio and population growth rate were based on reconstruction, which has no variance. We used information-theory criteria to select an appropriate variance–covariance structure for the repeated-measures effects from among the following candidates: unstructured, variance components, Huynh–Feldt, compound symmetry, first-order autoregressive, and Toeplitz (with heterogeneous variance variants of the latter 2 structures). We analyzed an *a priori* hypothesis of negative deer density effects by fitting linear and quadratic components of a regression model using estimated mean deer densities from DeYoung et al. (2019*a*) and testing with a 1-sided *t* test.

RESULTS

Fawn:adult female ratios declined 0.29 ± 0.15 (SE) fawns:adult female from low-medium to high deer density in the natural-nutrition enclosures but were not affected by deer density in enhanced-nutrition enclosures (Table 14; Fig. 29). Enhanced

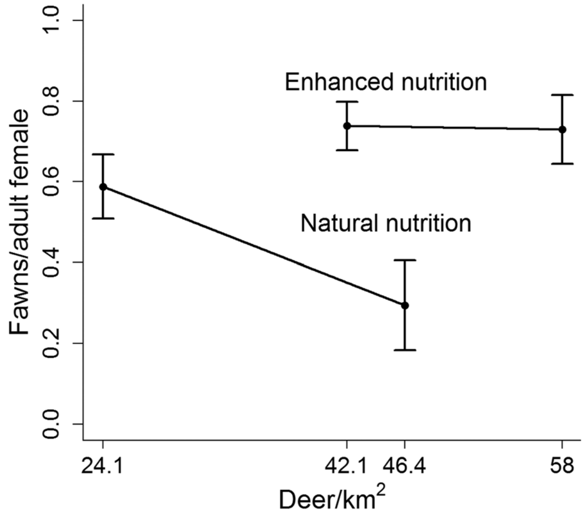

Figure 29. Mean (±SE) fawn:adult female ratios for white-tailed deer in 81-ha enclosures under natural and enhanced nutrition at 2 density levels, South Texas, USA, 2004–2012.

Table 15. Analysis of variance (ANOVA) for white-tailed deer fawn growth rate based on independent variables deer density, nutrition treatment, and year. Also, 1-tailed *t* tests for deer density effect by year, Dimmit County, Texas, USA, 2004–2012.

Source of variation	df	*F*	*t*	*P*
ANOVA				
Density (D)	1, 101	1.04		0.31
Nutrition (N)	1, 101	19.91		<0.01
D × N	1, 101	0.02		0.88
Year (Y)	8, 267	1.87		0.07
Y × D	8, 267	1.39		0.20
Y × N	8, 267	0.60		0.78
Y × D × N	8, 267	0.88		0.53
1-tailed *t* tests				
Density effect, linear, in 2004	194		0.47	0.68
Density effect, linear, in 2005	257		1.49	0.93
Density effect, linear, in 2006	391		−0.96	0.17
Density effect, linear, in 2007	136		0.35	0.64
Density effect, linear, in 2008	201		2.57	0.99
Density effect, linear, in 2009	175		0.34	0.63
Density effect, linear, in 2010	188		−0.23	0.41
Density effect, linear, in 2011	502		0.35	0.64
Density effect, linear, in 2012	102		−0.67	0.25

Table 16. Analysis of variance (ANOVA) for yearling growth rate of female (2005–2007, 2009–2012) and male (2005, 2006, 2009, 2010) white-tailed deer based on independent variables deer density, nutrition treatment, sex, and year. Also, 1-tailed *t* tests for deer density effect by year, Dimmit County, Texas, USA.

Sex	Source of variation	df	*F*	*t*	*P*
Females	ANOVA				
	Density (D)	1, 2.84	0.01		0.94
	Nutrition (N)	1, 2.83	3.37		0.17
	D × N	1, 2.83	0.24		0.66
	Year (Y)	6, 7.60	2.98		0.08
	Y × D	6, 7.60	1.39		0.33
	Y × N	6, 7.61	0.97		0.50
	Y × N × D	6, 7.62	1.36		0.34
	1-tailed *t* tests				
	Density, linear	2.84		−0.08	0.47
	Density, linear, enhanced nutrition, 2005	na		na[a]	na
	Density, linear, enhanced nutrition, 2006	na		na	na
	Density, linear, enhanced nutrition, 2009	na		na	na
	Density, linear, enhanced nutrition, 2010	na		na	na
Males	ANOVA				
	Density (D)	1, 17.6	0.14		0.71
	Nutrition (N)	1, 17.6	13.92		<0.01
	D × N	1, 17.6	0.01		0.92
	Year (Y)	3, 55	4.19		0.01
	Y × D	3, 55	1.18		0.33
	Y × N	3, 55	0.80		0.50
	Y × N × D	3, 55	2.68		0.06
	1-tailed *t* tests				
	Density, linear	na		na[b]	na
	Density, linear, enhanced nutrition, 2005	17.3		0.32	0.63
	Density, linear, enhanced nutrition, 2006	63.1		−2.91	<0.01
	Density, linear, enhanced nutrition, 2009	23.2		0.64	0.74
	Density, linear, enhanced nutrition, 2010	31		1.80	0.96

[a] Tests not performed because of absence of a density × nutrition × year interaction for females; see top portion of table.

[b] Tests not performed because of significant density × nutrition × year interaction for males; see top portion of table.

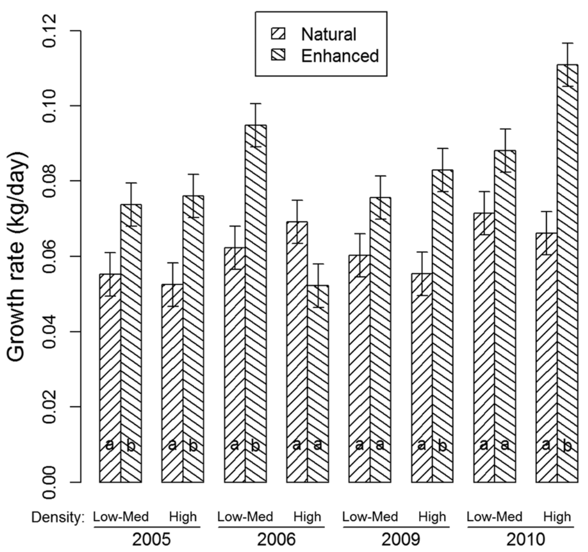

Figure 30. Mean (±SE) growth rate/day for yearling white-tailed deer males in 81-ha enclosures under natural and enhanced nutrition and 2 levels of deer density (low-medium [med] and high), South Texas, USA. Pairs of bars with different letters are different ($P < 0.10$).

nutrition increased fawn:adult female ratios by 0.15 ± 0.12 compared to natural nutrition in low-medium density enclosures and by 0.44 ± 0.17 in high-density enclosures. As would be expected in this stochastic environment, there was a strong effect of year but no interactions were significant (Table 14).

Growth rate of fawns was not influenced by deer density in either the natural-nutrition or enhanced-nutrition enclosures (Table 15). Enhanced nutrition increased fawn growth rates 0.03 ± 0.01 kg/day compared to natural nutrition. For yearlings, neither deer density nor nutrition affected female growth rate (Table 16). For males, year, deer density, and nutrition interacted in their effects on growth rate (Table 16). Deer density had no effect on male growth rate in natural-nutrition enclosures. In enhanced enclosures, however, density effects interacted ($P < 0.01$) with year. We detected a negative density effect ($P < 0.01$) in 2006 (Table 16) when growth rate at low-medium density averaged 0.09 ± 0.01 kg/day but only 0.05 ± 0.01 kg/day at high deer densities. Growth rate was higher with enhanced nutrition in 2005 at both low-medium and high deer densities but only higher at low-medium density in 2006 (Fig. 30). In 2009 and 2010, enhanced nutrition increased growth rate only at high deer densities (Fig. 30).

Body mass of adult deer was marginally affected ($P = 0.11$) by a 3-way interaction involving nutrition, sex, and density (Table 17). Body mass declined linearly 10.55 ± 3.07 kg in response to increasing deer density in natural-nutrition enclosures for males (Table 17; Fig. 31). Females also declined under natural nutrition but in a quadratic relationship, increasing 2.46 ± 2.53 kg from low to medium density then declining 3.73 ± 1.72 kg at high density (Table 17; Fig. 31). In enhanced-nutrition enclosures, male body mass increased in a quadratic relationship with deer density, increasing from low to medium density, then declining slightly at high density (Fig. 31). There was no density effect on female body mass in the enhanced treatment. Sampling date was significant (it would be expected that deer mass would differ between Dec and Mar–Apr in South Texas) and body mass was affected by a 3-way interaction involving deer density, sex, and sampling date (Table 17). For animals captured or collected in the spring, sex and density acted independently ($P = 0.80$) of each other and there were no density effects detected ($P = 0.61$). For animals collected in the winter, however, sex and deer density interacted ($P < 0.01$) in their effects on body mass; body mass of females was not affected ($P = 0.58$) by deer density and body mass of males showed a positive quadratic response to increasing deer density ($P < 0.03$).

Deer sex and density interacted in their effects on annual survival of animals >14 months of age that had lived in enclosures ≥9 months (Table 18). Although survival of males was not affected by deer density, survival of females showed a negative quadratic response to increasing deer density (survival increased from low to medium density then declined to high density; Fig. 32). Survival for both sexes was higher in enhanced enclosures, but the magnitude of the difference was greater for females (female survival: 0.90 ± 0.02 [enhanced] vs. 0.71 ± 0.02 [natural]; Fig. 32).

Table 17. Analysis of variance (ANOVA) for white-tailed deer adult body mass based on independent variables deer density, nutrition treatment, sex, and sampling date (Dec or Mar–Apr). Also, 1-tailed *t* tests for deer density effect by nutrition treatment for each sex, Dimmit County, Texas, USA, 2004–2012.

Source of variation	df	*F*	*t*	*P*
ANOVA				
Density (D)	2, 7.91	2.07		0.19
Nutrition (N)	1, 9.62	39.72		<0.01
D × N	2, 7.84	11.38		<0.01
Sex (S)	1, 9.70	427.97		<0.01
S × D	2, 7.83	4.74		0.04
N × S	1, 9.62	6.20		0.03
N × S × D	2, 7.78	2.94		0.11
Sampling date (SD)	1, 328.00	41.22		<0.01
SD × D	2, 326.00	2.01		0.14
N × SD	1, 327.00	4.77		0.03
N × SD × D	2, 324.00	0.42		0.66
S × SD	1, 326.00	67.59		<0.01
S × SD × D	2, 327.00	2.64		0.07
N × S × SD	1, 321.00	0.18		0.67
N × S × SD × D	2, 326.00	1.12		0.33
1-tailed *t* tests				
Density effect, linear, males, natural nutrition	15.50		−3.79	<0.01
Density effect, quadratic, males, natural nutrition	13.50		−0.45	0.33
Density effect, linear, females, natural nutrition	6.93		−0.88	0.20
Density effect, quadratic, females, natural nutrition	6.76		−1.43	0.10
Density effect, linear, males, enhanced nutrition	29.20		1.91	0.97
Density effect, quadratic, males, enhanced nutrition	12.50		−1.82	0.05
Density effect, linear, females, enhanced nutrition	3.97		2.37	0.96
Density effect, quadratic, females, enhanced nutrition	1.43		2.63	0.92
Density effect, linear, females, winter	24.70		0.96	0.83
Density effect, quadratic, females, winter	17.00		−0.01	0.49
Density effect, linear, males, winter	53.80		−2.33	0.01
Density effect, quadratic, males, winter	56.50		−1.35	0.03

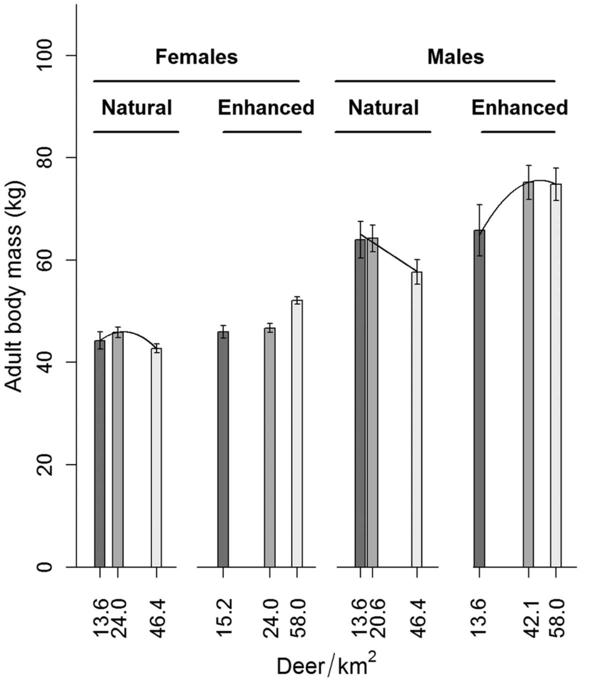

Figure 31. Mean (±SE) adult body mass of white-tailed deer in 81-ha enclosures under natural and enhanced nutrition at different levels of deer density, South Texas, USA, 2004–2012.

Survival of fawns 6–14 months of age was not affected by density in either the natural nutrition or enhanced-nutrition treatments (Table 19). However, survival of fawns 6–14 months of age was greater under enhanced nutrition (0.87 ± 0.09) than natural nutrition (0.62 ± 0.09, Fig. 32).

In natural-nutrition enclosures, only 1 of 13 (8%) fawns was pregnant versus 30 of 89 (34%) pregnant for enhanced-nutrition enclosures. Four of 5 (80%) natural-nutrition yearlings were pregnant compared to 25 of 28 (89%) in enhanced-nutrition enclosures. All females ≥2.75 years old were pregnant in natural- ($n = 18$) and enhanced-nutrition ($n = 44$) treatments.

Population growth rate was higher in enhanced-nutrition enclosures than natural-nutrition enclosures (Table 20; Fig. 33). Although there was no nutrition-density interaction, there was a linear decline in λ from 1.11 ± 0.08 at low-density to 0.93 ± 0.08 in high-density enclosures (Table 20; Fig. 33) for deer with natural nutrition without a similar decline in λ in enhanced-nutrition enclosures ($\lambda_{APP} = 1.32 \pm 0.05$; Table 20; Fig. 33). Enhanced nutrition resulted in an increase in λ_{APP} of 0.32 ± 0.05 relative to natural nutrition.

Table 18. Analysis of variance (ANOVA) for annual survival of white-tailed deer >14 months of age based on independent variables deer density, nutrition treatment, and sex. Also, 1-tailed *t* tests for deer density effect by nutrition treatment for each sex, Dimmit County, Texas, USA, 2004–2012.

Source of variation	df	*F*	*t*	*P*
ANOVA				
Density (D)	2, 6.02	0.63		0.56
Nutrition (N)	1, 6.02	19.47		<0.01
Sex (S)	1, 6.16	0.73		0.42
N × D	2, 6.02	0.49		0.64
S × D	2, 6.17	5.84		0.04
N × S	1, 6.16	22.44		<0.01
N × S × D	2, 6.17	2.23		0.19
1-tailed *t* tests				
Density effect, linear, males	8.79		0.49	0.69
Density effect, quadratic, males	8.79		1.41	0.90
Density effect, linear, females	8.79		1.48	0.91
Density effect, quadratic, females	8.79		−1.66	0.07

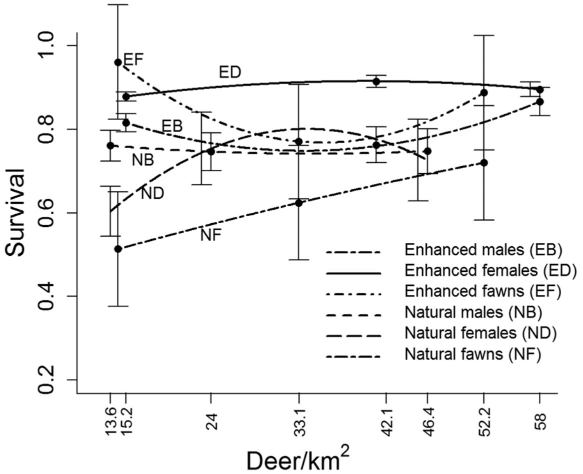

Figure 32. Mean (±SE) annual survival of white-tailed deer in 81-ha enclosures with natural and enhanced nutrition at different deer density levels, South Texas, USA, 2004–2012.

DISCUSSION

Our hypothesis of no density dependence under natural nutrition was not supported as we found declines in fawn:adult female ratios, adult body mass, and population growth rate with increasing density. Density dependence occurs in a predictable pattern in ungulate populations as carrying capacity is approached (Fowler 1981*b*, Bonenfant et al. 2009, Bowyer et al. 2014). The sequence is reduced survival of young, increased age at first reproduction for females, reduced fetal rate, reduced pregnancy rate, and finally, reduced survival of adults. Phenotypic traits such as growth rate and body mass may also be reduced by an increase in density (Bonenfant et al. 2009). We found evidence of reduced survival of young, expressed as fawn:adult female ratio, as density increased in natural-nutrition enclosures. Survival of neonatal young is frequently the most sensitive response to increasing population density

Table 19. Analysis of variance (ANOVA) for survival of white-tailed deer fawns 6–14 months of age based on independent variables deer density, nutrition treatment, and sex. Also, 1-tailed *t* tests for deer density effect by nutrition treatment for each sex, Dimmit County, Texas, USA, 2004–2012.

Source of variation	df	*F*	*t*	*P*
ANOVA				
Density (D)	2, 11	0.34		0.72
Nutrition (N)	1, 11	5.74		0.04
Sex (S)	1, 11	<0.01		0.95
N × D	2, 11	0.84		0.46
D × S	2, 11	1.91		0.19
N × S	1, 11	0.63		0.44
N × D × S	2, 11	1.44		0.28
1-tailed *t* tests				
Density effect, natural nutrition	11		−0.06	0.48
Density effect, enhanced nutrition	11		1.13	0.86

Table 20. Analysis of variance (ANOVA) for population growth rate (λ apparent) of white-tailed deer based on independent variables deer density, nutrition treatment, and year. Also, 1-tailed *t* tests for deer density effect by nutrition treatment, Dimmit County, Texas, USA, 2004–2012.

Source of variation	df	*F*	*t*	*P*
ANOVA				
Density (D)	2, 12.40	0.94		0.42
Nutrition (N)	1, 12.40	36.47		<0.01
D × N	2, 12.40	1.49		0.26
Year (Y)	7, 27.90	3.15		0.01
Y × D	14, 27.90	1.50		0.18
Y × N	7, 27.90	1.92		0.10
Y × D × N	14, 27.90	1.23		0.31
1-tailed *t* tests				
Density effect, linear, natural nutrition	12.40		−1.91	0.04
Density effect, linear, enhanced nutrition	12.40		0.09	0.53

(McCullough 1979). Adult survival is commonly not sensitive to population density (Bowyer et al. 2014) and we found no effect of density on adult males and an inconsistent trend for adult females. Bonenfant et al. (2009) cited studies of roe deer (*Capreolus capreolus*), red deer, mule deer, white-tailed deer, bighorn sheep (*Ovis canadensis*), and caribou (*Rangifer tarandus*) where adult body mass decreased with increasing population density. Likewise, we found a density-dependent reduction in both adult male and adult female body mass under natural nutrition.

Declines in fawn:adult female ratio and adult body mass, and possibly other parameters we did not measure, contributed to the decrease in λ_{APP} below 1.0 in medium and high-density enclosures under natural nutrition. During the 9 years of our study, deer populations >31 deer/km^2 would likely have declined under natural conditions. Gann et al. (2019*b*) described several drought years during our study, which would have contributed to lower deer population productivity, including 2011, the worst drought on record. Stochastic rainfall is characteristic of South Texas and is correlated with fawn survival (Ginnett and Young 2000). The correlation of March–May rainfall with fawns/adult female during 1982–1997 for the Faith Ranch was high ($r = 0.78$, $n = 16$; DeYoung et al. 2008).

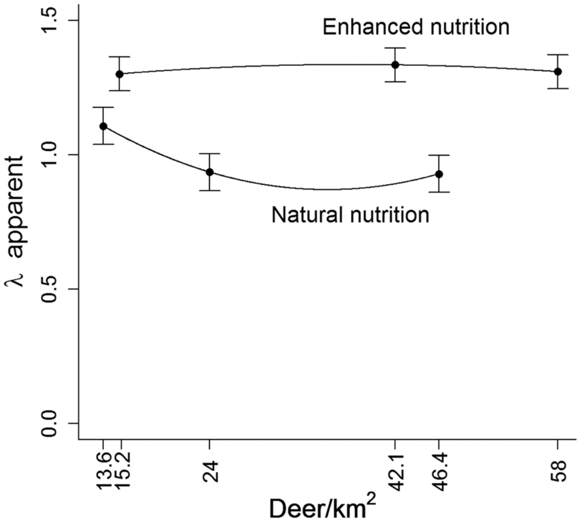

Figure 33. Mean (±SE) apparent population growth (λ) for white-tailed deer in 81-ha enclosures under natural and enhanced nutrition at different density levels, South Texas, USA, 2004–2012.

It is unlikely that a deer population in South Texas thornshrub habitat would have reached our experimental high-density level (i.e., ~50 deer/km^2) without a sequence of average and above-average rainfall years. This state might have happened in the region during the 1970s when there were several wet years (Norwine and Bingham 1986). Adjusting density estimates from Faith Ranch during 1975–1977 from helicopter surveys in DeYoung et al. (2008) by multiplying by 3 to correct for undercount (DeYoung 1985) resulted in a mean of 29.1 ± 1.6 deer/km^2. However, from the same data set in DeYoung et al. (2008), corrected surveys from 1981–1997 averaged 18 ± 1.3 deer/km^2. Additionally, mark-resight estimates of deer from helicopter surveys in South Texas thornshrub averaged 15.8 deer/km^2 and 19.3 deer/km^2 (DeYoung 1985). The only published estimates in South Texas thornshrub that approached our high-density treatment were 35.9 deer/km^2 and 40.1 deer/km^2 from 1986 to 1987, respectively, on the Camaron Ranch (DeYoung et al. 1989). Possibly contributing to these high estimates were intensive experimental coyote control and above-average rainfall, especially in 1987 (Heffelfinger et al. 1990). It is likely that white-tailed deer populations under natural nutrition would only occasionally attain and maintain densities where density-dependent responses would be strong. DeYoung et al. (2008) could not detect density dependence in a time series of helicopter surveys of deer on the Faith Ranch using 2 analytical methods.

Our hypothesis for enhanced-nutrition enclosures was supported as we found no density dependence for most variables but increased productivity in most demography measures. However, Donohue et al. (2013) found that aggressive behavior at feed sites in our enclosures increased with increasing population density. In our study, fawns 6–14 months of age in enhanced-nutrition enclosures had a survival rate of 0.88 ± 0.09, which compares favorably with rates for similar-aged fawns from the upper midwestern region of the United States, which harbors some of the most productive white-tailed deer populations (DeYoung 2011). In Illinois, USA, Nixon et al. (1991) estimated survival of 6–12-month-old fawns at 0.92 for males and 0.95 for females. Researchers in another Illinois study reported that female fawns 6–12 months old had a survival of 0.85 (Etter et al. 2002). We found adult male survival under enhanced nutrition ranged from 0.76 ± 0.04 at medium density to 0.87 ± 0.04 in high-density treatments. Survival of females in enhanced-nutrition enclosures ranged from 0.90 ± 0.04 at high density to 0.92 ± 0.04 in medium-density treatments. These rates compared to the 0.80 survival rate for non-hunted adult females in Nelson and Mech (1986) and the 0.09 non-hunting mortality rate by Fuller (1990), both in Minnesota, USA.

Our enclosure populations occurred with reduced presence of coyotes, considered the main predator of neonatal fawns in South Texas (Cook et al. 1971, Beasom 1974, Guthery and Beasom 1977). Coyotes in South Texas also kill some adult deer (Heffelfinger et al. 1990). Although there were coyotes present in some enclosures during 2004–2012, coyote presence was undoubtedly lower than normal for the region. Bobcats were present throughout the study and undoubtedly took some fawns. Wang et al. (2008) found that large predators in simple, northern ecosystems reduced the strength of density dependence in ungulate populations. It is unclear whether removal of coyotes in our experiment had any effect on density-dependent forces. In southeastern Texas, where annual precipitation averages approximately 65% higher than our study areas, exclusion of coyotes caused deer populations to increase substantially, with strong density-dependent effects (Kie and White 1985).

MANAGEMENT IMPLICATIONS

Deer occupying South Texas thornshrub may show weak or occasional density-dependent responses under natural nutrition. Therefore, compensatory responses to harvest are also likely to be rare and these populations cannot stand much harvest pressure without declining (Foley et al. 2016). Supplemental nutrition supplied plentifully and year-around increases performance of deer populations in this environment and enhanced populations will increase without harvest. Managers should harvest enhanced populations to at or below the level of the high-density treatment in this experiment to maintain healthy deer and their habitat.

Synthesis: Interactions of White-Tailed Deer Populations and Vegetation in South Texas at Different Deer Densities and Nutrition Levels

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INTRODUCTION

Our knowledge of the linkage between vegetation dynamics and ungulate population dynamics in stochastic environments has largely been confined to livestock and rangeland management literature. The results of our study expand our understanding of this linkage to populations of wild ungulates, and our results have implications for ungulate population ecology in other parts of the world with variable environments. Periods where only poor-quality food is available to ungulates do not always result in density-dependent population behavior (Owen-Smith 1990, Cook et al. 2016). On the other hand, there is frequent evidence of density dependence during stress periods for large mammals, including cold climates where winter severity rather than drought may be limiting (Bartmann et al. 1992, Bonenfant et al. 2009). More attention needs to be given to the characteristics of plant communities and the profile of ungulate food quality and quantity available in an annual cycle (DeYoung 2011, Cook et al. 2016). Characteristics of the forage plants and the environment can influence ungulate density dependence independent of animal demography. Some plant communities are very resistant to ungulate grazing or have other characteristics that make density-dependent behavior of large mammal populations weak or rare (Gann et al. 2019*b*).

All populations at times display density dependence (McCullough 1999, DeYoung et al. 2008). DeYoung et al. (2008) described a gradient of frequency or strength of density dependence in white-tailed deer populations from east to west across South Texas. They found density dependence more likely in the wetter, eastern side of the region near the Gulf of Mexico. However, they were not able to detect density dependence on the Faith Ranch, one of our study areas (DeYoung et al. 2019*a*), in western South Texas. Although there occasionally may be density effects in free-ranging populations on our study areas, the stochastic environment and the characteristics of the plant communities prevent deer populations in western South Texas from commonly building to densities where density dependence is apparent.

We conducted a 9-year study of vegetation and white-tailed deer dynamics in the western part of South Texas. We replicated the study in 12, 81-ha enclosures on 2 large ranches under both natural and enhanced nutrition and at 3 levels of deer density (DeYoung et al. 2019*a*). We examined deer diet composition, intake rate, and forage quality using bite counts of tractable deer at low and high deer density under natural nutrition (Gann et al. 2019*a*; Fig. 3A) and enhanced nutrition and natural nutrition at low deer density (Darr et al. 2019; Fig. 3D). Gann et al. (2019*b*; Fig. 3B,E) analyzed effects of deer density under natural and enhanced nutrition on vegetation composition. Finally, Cook et al. (2019) examined deer density and nutrition effects on deer population dynamics (Fig. 3C,F). Our objective is to integrate the results of these studies, draw overall conclusions, and discuss the implications in relation to past ungulate research (Table 21).

NATURAL NUTRITION

Our study was not of deer populations varying with the stochastic South Texas environment. Rather, we forced deer populations to stay relatively constant at low, medium, and high density for the region by adding and harvesting deer through 9 years of study (DeYoung et al. 2019*a*). Our high-density treatment averaged 46.7 deer/km^2, slightly above the highest published estimates of deer density and carrying capacity in the region (DeYoung et al. 1989, DeYoung 2011). Cook et al. (2019) detected density-dependent effects on fawn:adult female ratios, adult deer body mass, and population growth rate, whereas Gann et al. (2019*a*) found only minor effects of density on diet composition and nutrient intake. Similarly, Gann et al. (2019*b*) found relatively minor and indirect effects of deer density on vegetation composition. There was an unexpected density effect on canopy cover of preferred forbs, whereby cover was not reduced in the high-density treatment over 9 years. This result raises the question of why density-dependent effects were detected by Cook et al. (2019).

In untangling ungulate density-dependent behavior from other factors impinging on a population, McCullough (1990) framed the problem in terms of signal-noise. Density-dependent responses are the signal. Alpha noise is the usually small variation seen from repeating an experiment in the absence of other noise. Beta noise is that caused by environmental factors, and in a South Texas context, this would primarily be seasonal and interannual rainfall variation. Finally, gamma noise is variation resulting from measurement error in sampling a population.

Relative to beta noise, there is no question about the significant impact of rainfall flux on our enclosure deer populations and the plant communities on which they depended. Drought

Table 21. Summary of effects from varying deer density and nutrition on deer diets, vegetation, and population dynamics of white-tailed deer in 81-ha enclosures, Dimmit County, Texas, USA, 2004–2012.

Chapters	Metric	Density effect	Nutrition effect	Density × nutrition interaction	Source table or text
Gann et al. (2019*a*)	Shrubs in natural nutrition diets	0[a]			2
	Forbs in natural nutrition diets	0			2
	Mast in natural nutrition diets	0			2
	Cacti in natural nutrition diets	0			2
	Grass in natural nutrition diets	+[b]			2
	Subshrubs in natural nutrition diets	0			2
	Other in natural nutrition diets	0			2
	Metabolizable energy in natural nutrition diets	0			Text
	Digestible protein in natural nutrition diets	0			Text
	Bite rate for natural nutrition diets	0			3
	Bite size for natural nutrition diets	0			3
	Dry matter intake for natural nutrition diets	0			3
	Digestible protein intake rate for natural nutrition diets	0			3
	Metabolizable energy intake rate for natural nutrition diets	0			3
Darr et al. (2019)	Shrubs in enhanced versus natural nutrition diets at low density		0		6
	Forbs in enhanced versus natural nutrition diets at low density		0		6
	Mast in enhanced versus natural nutrition diets at density		–[c]		6
	Cacti in enhanced versus natural nutrition diets at low density		0		6
	Grass in enhanced versus natural nutrition diets at low density		+		6
	Subshrubs in enhanced versus natural nutrition diets at low density		0		6
	Flowers in enhanced versus natural nutrition diets at low density		–		6
	Dead leaves in enhanced versus natural nutrition diets at low density		+		6
	Fungi in enhanced versus natural nutrition diets at low density		0		6
	Digestible protein in vegetation portion of diet		0		7
	Metabolizable energy in vegetation portion of diet		0		7
	Bite rate of vegetation		–		8
	Bite size of vegetation		0		8
	Dry matter intake rate of vegetation		0		8
	Digestible protein intake rate from vegetation		0		8
	Metabolizable energy intake rate from vegetation		0		8
Gann et al. (2019*b*)	Canopy cover of preferred forbs	0	+	+	10
	Canopy cover of other forbs and grasses	0	0	0	10
	Canopy cover of preferred and other shrubs	0	0	0	10
	Shannon's diversity index (forbs)	0	+	0	11
	Forb evenness	0	+	0	11
	Forb species richness	0	0	0	11
	Relative standing crop of forbs	0	0	0	12
	Awnless bushsunflower density	0	0	0	13
	Hairy wedelia density	–	+	+	13
Cook et al. (2019)	Fawn:adult female ratio (ANOVA)	0	+	0	14
	Fawn:adult female ratio (1-tailed test, natural nutrition)	–			14
	Fawn:adult female ratio (1-tailed test, enhanced nutrition)	0			14
	Fawn growth rate (ANOVA)	0	+	0	15
	Fawn growth rate (1-tailed test)	0			15
	Yearling growth rate (females, ANOVA)	0	0	0	16
	Yearling growth rate (females, 1-tailed test)	0			16
	Yearling growth rate (males, ANOVA)	0	+	0	16
	Yearling growth rate (males, 1- tailed test, enhanced nutrition)	0[d]			
	Adult body mass (ANOVA)	0	+	+	17
	Adult body mass (males, natural nutrition, 1-tailed test)	–			17
	Adult body mass (females, natural nutrition, 1-tailed test)	–			17
	Adult body mass (males, enhanced nutrition, 1-tailed test)	–[e]			17
	Adult body mass (females, enhanced nutrition, 1-tailed test)	0			17
	Adult body mass (males, winter, 1-tailed test)	–			17
	Adult body mass (females, winter, 1-tailed test)	0			17
	Annual survival (deer > 14 months old, ANOVA)	0	+	0	18
	Annual survival (males > 14 months old,1-tailed test)	0			18
	Annual survival (females > 14 months old, natural nutrition, 1-tailed test)	–[f]			18
	Annual survival (deer 6–14 months old, ANOVA)	0	+	0	19
	Annual survival (deer 6–14 months old, natural nutrition, 1-tailed test)	0			19
	Annual survival (deer 6–14 months old, enhanced nutrition, 1-tailed test)	0			19

(*Continued*)

Table 21 (Continued)

Chapters	Metric	Density effect	Nutrition effect	Density × nutrition interaction	Source table or text
	Population growth rate (λ apparent, ANOVA)	0	+	0	20
	Population growth rate (λ apparent, natural nutrition, 1-tailed test)	–			20
	Population growth rate (λ apparent, enhanced nutrition, 1-tailed test)	+			20

ANOVA = analysis of variance.

[a] Denotes no effect ($P > 0.10$).

[b] Denotes positive effect ($P \leq 0.10$).

[c] Denotes negative effect ($P \leq 0.10$).

[d] There was a positive effect of enhanced nutrition on yearling males in 2006 but not other years.

[e] Mass increased from low to medium density then declined at high density to a level higher than low density (Fig. 31).

[f] Survival increased from low to medium density then declined at high density to a level higher than low density (Fig. 32).

and non-drought years had a much larger effect on deer diets than did deer density (Gann et al. 2019*a*). Forbs, especially cool-season annuals and perennials, were preferred by deer when available. However, forbs were much reduced during drought, and absent during the severe drought of 2011 (Gann et al. 2019*b*). When forbs were reduced by drought, deer ate more mast, flowers, and browse, which reduced digestible protein intake in tame adult females (Gann et al. 2019*a*).

Periods of high rainfall during 2007 and 2010 resulted in abundant herbaceous vegetation (Gann et al. 2019*b*). Lack of a strong influence of herbivores on vegetation may have occurred in part because the likelihood of excessive use of preferred forbs or preferred shrubs was low during wet years owing to the abundance of food. Cool-season forbs senesce during early summer from heat stress (Bryant et al. 1979), thereby abrogating effects of selective foraging. Selective foraging by deer, consequently, had little effect on preferred forbs or other forbs during our study because forbs were unavailable during droughts and seasons other than late winter and spring, and senesced from heat before deer could deplete them during wet years. Extremely moist years and drought years combined accounted for 8 of the 9 years of our study (Gann et al. 2019*b*).

Work with livestock suggests that herbivores and vegetation are weakly linked in semi-arid environments with high inter-annual variation in precipitation (Ellis and Swift 1988, Vetter 2005, Derry and Boone 2010). For example, most of the research on the influence of environmental stochasticity on herbivore-plant interactions has focused on livestock in semi-arid pastoral systems in Africa and Australia (McLeod 1997, Vetter 2005, Derry and Boone 2010). In these systems, frequent droughts keep herbivore populations low and variation in precipitation has a much stronger influence on vegetation dynamics than do herbivores (Vetter 2005, Derry and Boone 2010). Livestock numbers are held in check by mortality resulting from starvation during periodic drought. Essentially, livestock numbers rarely build up to densities high enough to influence vegetation dynamics. Because drought constrains population densities, herbivores in these systems are unlikely to cause degradation of vegetation (Vetter 2005).

Investigators have recognized that episodic disturbances such as drought may alter interactions between vegetation and wild ungulates as well (Wisdom et al. 2006). White-tailed deer populations in South Texas may be constrained by environmental stochasticity in a similar manner to livestock in pastoral systems in Africa except that in the case of white-tailed deer, high mortality is largely restricted to neonates (Fig. 1). Fawns in South Texas are born in July, and survival is commonly low during years when low precipitation limits forb abundance. Browse is consumed when forbs are unavailable; however, browse from shrubs that dominate the region is generally too low in quality to support reproduction (Campbell and Hewitt 2004, 2005; Timmons et al. 2010). Consequently, the high inter-annual variation in precipitation limits white-tailed deer populations to levels that are less likely to affect vegetation dynamics by constraining fawn recruitment.

Relative to McCullough's (1990) gamma noise, what may be more relevant to discerning causes for density dependence found by Cook et al. (2019) is what we did not sample. For the diet study in natural-nutrition enclosures (Gann et al. 2019*a*), we used adult female deer. Therefore, we do not know if there were density effects on diets of fawns and adult males. Fawn diets could be influenced through milk production by mothers, and adult female mass did decline with density (Cook et al. 2019). Kie and Bowyer (1999) studied sexual segregation in white-tailed deer in eastern South Texas, where average annual precipitation is roughly 60% higher than on our study areas. They compared deer densities of 39 deer/km^2 versus 77 deer/km^2 and found differences between adult males and adult females in diet and use of space at the lower density that diminished at higher density. However, it is difficult to see how different adult male diets in our natural-nutrition enclosures could have contributed to the density effects identified by Cook et al. (2019). Both adult males and adult females lost mass at higher density, but male survival was not affected by density. Therefore, adult males were unlikely to have contributed to the observed density effects on λ_{APP} (Cook et al. 2019).

Commonly, all animals in a population do not have access to the same resources (Bonenfant et al. 2009) and this variation could have contributed to density effects in our natural-nutrition enclosures. Clark (2015) analyzed adult female home ranges during spring and summer in our enclosures in a follow-up study. He found that adult female home range size decreased 25% from low- to high deer density in the enclosures. Adult males and adult females also commonly did not use the entire 81 ha of an enclosure but established smaller home ranges (C. A. DeYoung, Texas A&M University–Kingsville, unpublished data). Constraints of the high fences, reduced coyotes, and absence of large herbivore competitors could have had effects on home range size. Thus, home-range quality in our enclosures may have varied across individual deer and the effects could have been stronger at high density. With smaller home ranges, density effects would likely be greater because of reduced habitat heterogeneity (Wang et al. 2006).

Environmental variation has been widely documented as an important influence on ungulate dynamics (Bonenfant et al. 2009) and was a strong influence on our enclosure populations with natural nutrition. However, the profile of food quantity and quality through an annual cycle and its influence on ungulate density dependence has not been widely addressed (Hobbs and Swift 1985, DeYoung 2011, Cook et al. 2016). This profile is especially important for ungulates like white-tailed deer that depend on both food quality and quantity (Owen-Smith 1990). For a density-dependent response to occur, there needs to be a gradient of good-quality to poor-quality food, and in some cases, a limited quantity of food. As more animals eat the better-quality forage and its abundance declines, deer productivity suffers. In South Texas, drought takes away the best-quality food (preferred forbs; Gann et al. 2019*b*) and leaves a large quantity of mediocre and poor-quality food (browse; Gann et al. 2019*b*). During these stress times, deer eat more flowers and mast (Gann et al. 2019*a*). Also during drought, many of the preferred browse species drop their leaves (Gann et al. 2019*b*), providing only lower-quality stems. This nutritional regime generally provides adequate nutrition for survival of adult deer but not enough for survival of fawns (Gann et al. 2019*a*). However, density-dependent effects are subtle or non-existent because population density is usually lower than our high-density treatment, or even medium density (DeYoung 1985, DeYoung et al. 1989), where Cook et al. (2019) found the strongest density effects. If deer density in an unsupplemented population is near our low-density treatment level, lowering deer numbers, as through harvest, does not help the remaining deer. There is still a large amount of medium-quality food, regardless of the number of deer. This profile is similar to that found by Cook et al. (2016) for elk in forests at low to moderate elevation composed of mid- and late-seral stages in western Oregon and Washington, USA.

The seasonal rhythm of plant availability in our natural-nutrition enclosures provided resistance against deleterious grazing effects on plant communities (Gann et al. 2019*b*; Fig. 28). During non-drought, most foods in deer diets were forbs in spring, mast in summer, and browse in autumn and winter. This rhythm protected different classes of deer food because none were being grazed heavily year around. During drought, deer diets were lower in digestible protein because deer ate more flowers, mast, and browse (Gann et al. 2019*a*). However, these foods were frequently available in abundance, buffering plants from extended heavy use, even at high deer densities. Additionally, some of the preferred shrubs exhibited compensatory growth (Gann et al. 2019*b*) and once wet periods followed drought, they sometimes grew more tissue than was present before the heavy browsing.

ENHANCED NUTRITION

We found that enhanced nutrition significantly boosted deer population productivity and resulted in no measurable harm to plant communities over 9 years at the deer densities used in our experiments (Cook et al. 2019, Darr et al. 2019, Gann et al. 2019*b*). However, it is important to remember that we removed potential large-herbivore competitors from enclosures. The pelleted supplement that we provided in enhanced-nutrition treatments made up >50% of the diet of most deer (Darr et al. 2019). This diet dominance may have reduced grazing pressure on plant communities, although we had no direct evidence. However, the plant composition in the diet changed for enhanced-nutrition deer and contained less mast and more dead leaves (Darr et al. 2019). Furthermore, browse use did not decline; rather, there was some evidence of increased browse use. Canopy cover of preferred forbs increased in enhanced-nutrition enclosures (Gann et al. 2019*b*). Browse use was generally on abundant species, some of which were capable of compensatory growth (Gann et al. 2019*b*). Our results contradict Murden and Risenhoover (1993), who reported that giving a high-quality supplement to deer caused them to forage more selectively.

Enhanced nutrition resulted in increases in fawn:adult female ratios, fawn growth rate, adult survival and mass of both sexes, survival of fawns 6–14 months of age, pregnancy rate of female fawns, and population growth rate as measured by λ_{APP} (Cook et al. 2019). Productivity of deer in enhanced enclosures was not affected by deer density and was comparable to productivity in productive areas in the upper midwestern United States (Cook et al. 2019). We found λ_{APP} averaged >1.3 over 9 years at all density levels in enhanced-nutrition enclosures. However, λ_{APP} in medium- and high-density enclosures with natural nutrition was <1 during the same period. The difference between natural- and enhanced-nutrition treatments (Cook et al. 2019) showed the stochastic environment limited natural-nutrition deer populations over time. Providing free-choice supplement would likely have similar effects in other areas where deer are nutritionally limited.

MANAGEMENT IMPLICATIONS

White-tailed deer are an adaptable species with a large geographic range. Managers should not expect techniques useful in one region to always apply in others. Managers of ungulates should consider the characteristics of plant communities in stochastic environments and their influence on density-dependent population behavior. In regions like western South Texas, where density-dependent population behavior may be less apparent, ungulate populations cannot withstand much harvest pressure because of the lack of compensatory mortality. Density-dependent models that are useful in temperate climates are not applicable to South Texas thornshrub environments (DeYoung et al. 2008). In addition to conservative harvest rates, managers in such environments should be cautious about including adult females in harvest prescriptions, unlike other environments. During drought times in South Texas, reducing populations is not an effective management strategy to make conditions better for surviving deer. Because high-quality vegetation is absent during drought and mediocre and poor-quality browse remains available at such times, all that is accomplished by this practice is fewer deer with no benefit to the remaining population. However, it appears that our low-density treatment of about 13 deer/km^2 is sustainable under natural nutrition in western South Texas thornshrub communities similar to our study areas.

Managers in South Texas feed deer because the stochastic environment limits deer productivity and food plots are difficult to farm during frequent drought years when supplemental nutrition is most needed by deer. Most managers are interested in producing larger antlers on mature males, but additional benefits are increased recruitment of fawns (Zaiglin and DeYoung 1989) and survival of adults (Cook et al. 2019). McBryde (1995) analyzed costs of feeding pellets, such as in our study (DeYoung et al. 2019*a*), versus farming food plots. He found that under most circumstances, food plots were the more expensive way to supplement deer if initial cost of equipment is considered. Also, food plots may fail during drought for all but the most expert farmers. White (2014) analyzed hunting lease prices and economics of feeding supplemental pellets in South Texas and found that, based on increased adult male numbers and antler size, a 225-day annual feeding program could be more profitable versus a property that did not supplement. However, he projected that a 365-day feeding program would not be profitable. Our results (Cook et al. 2019, Darr et al. 2019, Gann et al. 2019*b*) are based on 1 feed site per 81 ha and year-around feeding. Managers may experience different deer productivity increases with differing feeder density and only periodic availability of supplement.

Providing enhanced nutrition to deer is controversial. Some writers have criticized the practice on ethical grounds (Brown and Cooper 2006, Knox 2011). These arguments revolve around domestication and loss of wildness for fed deer, and the definition of hunting. Feeding deer results in concentration of animals and concerns about spread of disease (Williams et al. 2002, Inslerman et al. 2006). Recently, Foley et al. (2016) demonstrated how chronic wasting disease could cause decline in South Texas deer populations because of the stochastic environment and frequent density-independent behavior of deer populations. Certainly if this disease became widespread in the region, feeding deer would be discouraged.

Up to a sustained density of 58 deer/km^2, managers providing enhanced nutrition in a way similar to our study can expect significant productivity increases in individual deer and deer populations in western South Texas (Cook et al. 2019, DeYoung et al. 2019*a*). At this deer density, populations will not have measureable impacts on plant communities over a several-year time scale (Gann et al. 2019*b*). We do not know if deleterious effects on plants will occur over longer time periods. Our results apply to diverse thornshrub communities in western South Texas, and managers should be cautious in applying them to less diverse communities that can result from intensive thornshrub control methods. Another consideration is that our results were in the absence of other grazers such as domestic livestock, feral pigs, and collared peccary and the absence of coyotes, a key predator. We also do not know how applicable our results with enhanced nutrition will be in other regions with different plant communities.

Because we found enhanced nutrition populations with $\lambda_{APP} > 1$ over several years, managers may have to employ significant deer harvest over time to keep populations from continuing to increase beyond levels we studied. Feeding deer is expensive and managers will have to assess the costs and benefits for individual populations. Finally, if a malady such as chronic wasting disease becomes established in South Texas (Foley et al. 2016), feeding deer would not be recommended.

SUMMARY

Deer Density Under Natural Nutrition

- We evaluated effects of low, medium, and high deer density on deer diets, vegetation, and deer demographics in western South Texas.
- Evidence supporting our hypothesis that density dependence is weak in the stochastic environment of our study areas included:
    - A 3.4-fold difference in deer density with natural nutrition caused negligible differences in botanical composition of deer diets and failed to influence diet quality or foraging behavior.
    - Percent canopy cover of preferred forbs and shrubs, density of awnless bushsunflower and hairy wedelia, and forb species diversity were similar among deer densities during 9 years of study.
    - Variation in precipitation was a more influential driver of deer diet composition, diet quality, vegetation canopy, and forb diversity than variation in deer density.
    - The annual cycle of forage use across plant classes buffered effects of increasing deer density because no 1 class was used year around.
- Evidence not supporting an absence of density dependence included declines in fawn:adult female ratios, adult body mass, and population growth rate with increasing density under natural nutrition.
- Evidence that environmental stochasticity has a strong effect on white-tailed deer and their habitat in western South Texas included:
    - Deer diets shifted to more flowers and shrubs during drought and dietary digestible protein of deer declined; forbs composed a greater proportion of deer diets during wet conditions.
    - Dietary digestible protein and bite rate were greater and bite size was smaller during wet conditions than during drought.
    - Canopy cover of vegetation, forb species diversity, and density of 2 plant species preferred by deer varied dramatically among years depending on precipitation. Forbs were essentially absent during severe drought.
- We recommend that managers in stochastic environments such as South Texas thornscrub, recognize that density-dependent population behavior is not as strongly expressed as it is in more mesic environments. Populations may act in a density-independent manner without several years of above-average rainfall.
- In South Texas thornscrub, harvest pressure on deer populations should be limited because of the lack of compensatory reproduction and mortality. Reducing deer populations is unlikely to result in a corresponding increase in preferred forage plants. Increased harvest during drought, for example, will only result in fewer deer and will not reduce damage to vegetation because only medium- and poor-quality woody vegetation is available during those times.

Enhanced Nutrition

- We evaluated effects of low, medium, and high deer density under enhanced nutrition on deer diets, vegetation, and deer demographics, and compared effects to natural nutrition.
- Supplemental feed composed 50–70% of deer diets.
- Our hypothesis that enhanced nutrition would not result in increased foraging pressure on palatable plants and increased quality of the vegetation portion of deer diets was supported. Deer with enhanced nutrition foraged for 20% shorter time periods and consumed more low-quality forages, including browse and dead leaves, than deer with natural nutrition.
- Nutrition is a limiting factor to white-tailed deer populations in the thornscrub vegetation of South Texas because providing enhanced nutrition increased deer diet quality, fawn:adult female ratios, fawn growth rates, fawn productivity, population growth rate, and survival of fawns and adult females.
- Enhanced nutrition may have reduced foraging pressure on palatable plants because >50% of deer diets are composed of supplemental feed rather than vegetation.
- We recommend that managers consider the pros and cons of supplemental feeding when making decisions. Providing supplemental feed may benefit white-tailed deer productivity and reduce foraging impacts on native vegetation. However, supplemental feeding is costly, may increase spread of disease, and is controversial because of philosophical issues regarding wildness of deer.

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