# MINERAL METABOLISM BY WHITE-TAILED DEER FED DIETS OF GUAJILLO

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ABSTRACT—Seasonal scarcity of forbs in southern Texas often requires white-tailed deer (*Odocoileus virginianus*) to subsist on browse. Deer might seek minerals during periods of high browse consumption as buffers or as precursors to conjugate-based detoxification of plant secondary compounds (PSCs) contained in many browse species. To determine importance of plant secondary compounds on mineral consumption, we fed diets of 0, 25, 50, and 75% guajillo (*Acacia berlandieri*), a browse species high in PSCs, to 4 male white-tailed deer in a Latin square design experiment, and we compared mineral metabolism and determined how well guajillo met mineral requirements for maintenance and productive processes as described in the literature. Concentrations of calcium, phosphorus, and sodium in the diet decreased with increases in guajillo, whereas magnesium concentration did not change. Losses of calcium, phosphorus, and magnesium occurred largely via fecal excretion, whereas sodium losses occurred via urinary excretion. Calcium, magnesium, and sodium intake rates from diets up to 100% guajillo exceeded requirements. Adult males met summer and fall phosphorus requirements with diets of 100% guajillo and their spring and annual requirements were met with diets of <75 and 97% guajillo, respectively. Phosphorus supplementation during periods of low rainfall and high guajillo consumption might reduce the phosphorus deficit in reproducing females.

RESUMEN—La escasez temporal de vegetación herbácea en el sur de Texas requiere que el venado cola blanca (*Odocoileus virginianus*) frecuentemente subsista a base de una dieta arbustiva. Es probable que los venados busquen minerales durante periodos de alto consumo de arbustos para que estos sirvan como reguladores o precursores para formar conjugados en la desintoxificación de compuestos secundarios contenidos en muchas de las especies arbustivas. Para determinar la importancia de los compuestos secundarios en el consumo de minerales, se utilizó un diseño experimental en cuadrado Latino. Se alimentó a 4 venados machos con dietas que consistían de 0, 25, 50 y 75% de "guajillo" (*Acacia berlandieri*), el cual es un arbusto que contiene gran cantidad de compuestos secundarios. Se comparó el metabolismo de minerales y se determinó si el guajillo satisface las necesidades de minerales para los procesos productivos y de mantenimiento descritos en la literatura. La concentración en la dieta de calcio, fósforo, y sodio disminuyó con el incremento en el consumo de guajillo, mientras que la concentración de magnesio no varió. Las pérdidas de calcio, fósforo, y magnesio ocurrieron mayormente a través de las heces fecales, mientras que las pérdidas del sodio ocurrieron por la vía urinaria. Las tasas de consumo de calcio, magnesio, y sodio en dietas que consistían de hasta 100% de guajillo excedieron lo requerido. Durante el verano y otoño, el macho adulto obtuvo el fósforo requerido con dietas que consistían en 100% de guajillo y obtuvo lo necesario durante la primavera y a través del año, con dietas de <75 y 97% de guajillo, respectivamente. El suplemento de fósforo durante periodos de baja precipitación y alto consumo de guajillo puede reducir el déficit de fósforo en hembras en periodo reproductivo.

White-tailed deer (*Odocoileus virginianus*) in southern Texas prefer diets of nutrient-rich forbs (Chamrad and Box, 1968; Davis, 1990). However, because of uncertain precipitation and seasonal scarcity of forbs, deer often subsist on diets predominantly of browse (Davis, 1990). Guajillo (*Acacia berlandieri*) occurs on 2.4 million ha in southern Texas (Scifres,

1980) and is browsed by both domestic and wild ruminants (Varner and Blankenship, 1987). However, guajillo might be deficient in some minerals (Barnes, 1988) and contains high levels of plant secondary compounds (PSCs), including amines, alkaloids, and tannins (Clement et al., 1997).

Herbivores can exhibit mineral appetites when ingesting large quantities of PSCs (Freeland et al., 1985; Launchbaugh et al., 2001). Freeland et al. (1985) found that mineral supplements greatly reduced the acute and chronic consequences of tannin ingestion in mice. Minerals often function as buffers to organic acids produced from ingested PSCs (Foley et al., 1995). Consequently, herbivores might seek minerals to buffer acidic metabolites when limited to diets high in PSCs (Freeland et al., 1985; Kreulen, 1985) or as precursors to conjugate-based detoxification (Launchbaugh et al., 2001). Although benefits are unproven (Schultz and Johnson, 1992), supplementing white-tailed deer diets with minerals is a common practice in southern Texas intended to increase antler size. An indirect consequence of mineral supplementation might be increased ability of deer to detoxify PSCs in browse, such as guajillo.

Our objectives were to compare mineral metabolism among diets containing varying quantities of guajillo and to determine the effectiveness of guajillo at meeting mineral requirements for maintenance and productive processes as identified from the literature.

METHODS—Research was conducted at the captive wildlife research facility of Texas A&M University-Kingsville, located 1.5 km north of Kingsville, Texas. Research procedures were approved by the Texas A&M University-Kingsville Institutional Animal Care and Use Committee. In June 1998, deer were placed into individual pens (3.0 × 3.7 m) where food and water were available ad libitum. Deer were maintained on 56A3 Kleberg Custom Deer Feed Hi-P (Purina Mills, Inc., St. Louis, Missouri) and provided alfalfa hay (*Medicago sativa*) until the experiment began.

We collected guajillo growing in Webb and Duval counties in Texas from 11 June through 2 July 1998. Growth from the current year <1.5 m in height was collected to reduce inclusion of physically unavailable forage. Herbaceous guajillo stems and leaves were removed with hand clippers and allowed to air-dry for 5 days (90% dry matter). Alfalfa hay was used as control forage because its nutritive value is similar to native forbs, it has low PSC concentrations, and it requires minimal preparation. Guajillo and alfalfa were ground with a hammer mill to pass a 1-cm screen. Before each trial (see below), guajillo and alfalfa forages were thoroughly mixed into 4 diets containing guajillo to alfalfa ratios (dry mass:dry mass) of 0:100, 25:75, 50:50, and 75:25. Four experimental diets containing different portions of guajillo were used because deer diets seldom consist of a single plant species, and deer perform poorly on diets consisting entirely of guajillo (Barnes et al., 1991).

In vivo metabolism trials were completed on 4 adult (≥5 yr old) males in a 4 × 4 Latin square design. For each of 4 trials, 4 deer were assigned randomly to the 4 diets such that 1 deer received each diet. For each successive trial, randomization was restricted to ensure that each individual received a diet it had not received previously. Four 17-day trials were conducted from 12 July through 18 September 1998. Each trial consisted of a 10-day acclimation period and a 7-day collection period. The first 5 days of each trial were completed in 3.0 × 3.7 m individual pens, and the final 12 days were completed in 3.375-m$^3$ metabolism crates. Food, double-distilled water, and a mineral supplement (Record Rack Deer and Game Mineral, Cargill, Inc., Minneapolis, Minnesota) were available ad libitum throughout each trial as required by the institutional Animal Care and Use Committee. Unconsumed rations and intake of food and minerals were recorded daily on a dry-matter basis.

Feces and urine were collected, quantified, and sampled daily during the collection phase of the trial (Hellgren and Pitts, 1997). We pooled a 10% sample of daily fecal excretion by individual deer and stored it at −20°C. At the conclusion of the collection period, the composited fecal sample was dried for 24 h at 50°C and ground with a Wiley mill to pass a 1-mm screen for subsequent chemical analysis. Daily fecal excretion that was not retained for analysis was oven-dried at 100°C for 24 h to determine dry matter. Urine was acidified with 150 mL of 0.1 N HCl and a 10% daily aliquot by volume was pooled and stored at −20°C. At the conclusion of the collection period, urine was thawed and mixed, and a 400-mL sample was stored at −20°C for subsequent chemical analysis. A 200-g sample of each diet during each trial was ground with a Wiley mill to pass a 1-mm screen, and a 200-g sample of the mineral supplement was stored at −20°C for analysis.

Samples of feed, feces, and mineral supplements were ashed in a muffle furnace between 550°C and 600°C, then digested in sequential treatments of 50% and 10% NHO$_3$ as described by Fick et al. (1979). The solubilized ash was filtered and stored following the procedure of Hellgren and Pitts (1997). Contents of the feed, feces, urine, and min-

eral supplements were determined by atomic absorption spectrophotometry (calcium and magnesium), atomic emission spectrophotometry (sodium), and calorimetry (phosphorus) as described by Fick et al. (1979). Phosphorus was analyzed at the Texas A&M University-Kingsville Forage Lab, and calcium, magnesium, and sodium were examined at the Texas Agricultural Experiment Station–Uvalde Nutrition Lab. Calcium, phosphorus, magnesium, and sodium balance were calculated as input (food plus mineral supplement) minus output (feces plus urine) and reported on a mg·kg body mass$^{-0.75}$·day$^{-1}$ basis (Grasman and Hellgren, 1993; Hellgren and Pitts, 1997).

Mineral compositions of the 4 diets collected from each trial were analyzed with a 1-way ANOVA, and data from metabolism trials were analyzed with a 3-way ANOVA without interaction effects (SAS Institute, Inc., 1994). Class variables in the model were diet, trial, and individual deer. Because a Latin square design was used, $P$ values generated on row (trial) and column (deer) variables were not reported (Kuehl, 1994). If significant dietary effects were detected, pairwise comparisons were completed with Tukey's honestly significant difference test (SAS Institute, Inc., 1994). Statistical significance was determined at $P < 0.05$.

Mineral intake from feed (excluding supplement) was plotted as a function of dietary guajillo concentration. Data were subjected to stepwise polynomial regression. The linear equation was used because higher order polynomials did not improve the relationship. Published mineral requirements were used to assess diets. Calcium requirements for white-tailed deer were assumed to be 206.4 mg·kg$^{-0.75}$·day$^{-1}$ (Robbins, 1993; our calculation). Phosphorus requirements for adult male white-tailed deer on an annual basis, during spring, during summer, and during fall were assumed to be 72.2, 94.4, 57.4, and 59.6 mg·kg$^{-0.75}$·day$^{-1}$ (Grasman and Hellgren, 1993). Sodium requirements for adult male white-tailed deer were assumed to be 8.8 mg·kg$^{-0.75}$·day$^{-1}$ (Hellgren and Pitts, 1997; our calculation). Free-ranging wildlife rarely experience magnesium deficiencies (Robbins, 1993). Magnesium requirements of 0.06% of dry matter for mammals in general have been reported (Maynard et al., 1979). Our experimental diets contained 5 times more magnesium than this and did not vary (Table 1); consequently, requirement comparisons were not included for magnesium.

RESULTS—Dry matter intake and change in body mass did not vary with diet, as previously reported by Campbell (1999). Deer consuming diets greater in guajillo did not voluntarily consume more of the mineral supplement (Table

TABLE 1—Mineral supplement intake (mg·kg$^{-0.75}$·day$^{-1}$) and mineral composition for diets fed to captive male white-tailed deer from July through September 1998 in Kingsville, Texas. Means in a row with different letters were different at α = 0.05; $n$ = 4 for all diets.

| Nutritional parameter | Percent guajillo in diet[a] | | | | | | | | P-value[b] |
| | 0 | | 25 | | 50 | | 75 | | |
| | Mean | SE | Mean | SE | Mean | SE | Mean | SE | |
|---|---|---|---|---|---|---|---|---|---|
| Mineral supplement intake | 187.2 A | 110.9 | 227.0 A | 133.4 | 188.4 A | 108.4 | 481.0 A | 339.1 | 0.442 |
| Calcium (% dry matter) | 2.16 A | 0.07 | 1.88 B | 0.02 | 1.70 C | 0.03 | 1.58 C | 0.03 | <0.001 |
| Phosphorus (% dry matter) | 0.25 A | 0.01 | 0.22 B | 0.00 | 0.17 C | 0.00 | 0.14 D | 0.00 | <0.001 |
| Magnesium (% dry matter) | 0.31 A | 0.03 | 0.30 A | 0.02 | 0.29 A | 0.01 | 0.29 A | 0.00 | 0.751 |
| Sodium (% dry matter) | 0.23 A | 0.02 | 0.21 AB | 0.01 | 0.16 BC | 0.02 | 0.13 C | 0.01 | 0.003 |

[a] Percent guajillo in diets based on alfalfa hay to guajillo ratio (dry mass:dry mass).
[b] P-values are for an ANOVA test for differences among diets.

1). However, mineral supplement use was highly variable (Table 1), particularly for deer receiving the 75% guajillo diet.

Dietary calcium decreased with increases in guajillo (Table 1). No dietary differences occurred for calcium intake from mineral supplement, fecal and urinary calcium excretion, or calcium balance (Table 2). Total (feed + mineral supplement) calcium intake did not vary between diets ($P = 0.077$). Mean (*SE*) total calcium intakes (mg·kg$^{-0.75}$·day$^{-1}$) for 0% guajillo, 25% guajillo, 50% guajillo, and 75% guajillo diets were 1,416.5 (112.8), 1,307.5 (92.0), 1,214.9 (140.1), and 1,070.9 (157.6), respectively.

Phosphorus concentrations were greater in alfalfa than in guajillo (Table 1), causing lower phosphorus intake from feed with increased dietary guajillo (Table 2). No dietary differences occurred for phosphorus intake from mineral supplement, fecal and urinary phosphorus excretion, or phosphorus balance (Table 2). Total phosphorus intake did not vary between diets ($P = 0.306$). Mean (*SE*) total phosphorus intakes (mg·kg$^{-0.75}$·day$^{-1}$) for 0% guajillo, 25% guajillo, 50% guajillo, and 75% guajillo diets were 187.7 (23.5), 176.8 (16.3), 144.2 (17.2), and 152.8 (52.4), respectively.

Dietary magnesium did not vary among diets (Table 1). No differences occurred between diets for magnesium intake from feed and mineral supplement, fecal and urinary magnesium excretion, or magnesium balance (Table 3). Total magnesium intake did not vary between diets ($P = 0.761$). Mean (*SE*) total magnesium intakes (mg·kg$^{-0.75}$·day$^{-1}$) for 0% guajillo, 25% guajillo, 50% guajillo, and 75% guajillo diets were 203.2 (27.4), 207.3 (9.2), 201.0 (27.1), and 187.2 (22.2), respectively.

Dietary sodium decreased with increased dietary guajillo (Table 1), resulting in lower sodium intake from diets with increased guajillo (Table 3). No dietary differences occurred for sodium intake from mineral supplement, fecal and urinary sodium excretion, or sodium balance (Table 3). Total sodium intakes did not differ ($P = 0.065$). Mean (*SE*) total sodium intakes (mg·kg$^{-0.75}$·day$^{-1}$) for 0% guajillo, 25% guajillo, 50% guajillo, and 75% guajillo diets were 165.9 (27.3), 156.5 (15.3), 128.4 (24.7), and 119.7 (31.4), respectively.

Calcium and sodium requirements were met by all experimental diets (Fig. 1 and 2). Diets

TABLE 2—Calcium (Ca) and phosphorus (P) balance data (mg·kg$^{-0.75}$·day$^{-1}$) for male white-tailed deer fed 4 diets from July through September 1998 in Kingsville, Texas. Means in a column with different letters were different at $\alpha = 0.05$; $n = 4$ for all diets.

| Mineral parameter | Percent guajillo in diet[a] | | | | | | | | P-value[b] |
|---|---|---|---|---|---|---|---|---|---|
| | 0 | | 25 | | 50 | | 75 | | |
| | Mean | SE | Mean | SE | Mean | SE | Mean | SE | |
| Ca intake from feed | 1,386.0 A | 99.4 | 1,270.5 AB | 95.7 | 1,184.2 AB | 141.3 | 992.4 B | 118.5 | 0.042 |
| Ca intake from mineral supplement | 30.5 A | 18.1 | 37.0 A | 21.8 | 30.7 A | 17.7 | 78.5 A | 55.3 | 0.422 |
| Fecal Ca loss | 1,157.5 A | 66.5 | 1,232.7 A | 91.5 | 1,083.0 A | 85.4 | 945.5 A | 126.3 | 0.066 |
| Urinary Ca loss | 20.2 A | 8.4 | 18.3 A | 3.1 | 22.8 A | 7.3 | 16.6 A | 2.4 | 0.772 |
| Ca balance | 238.9 A | 87.8 | 156.6 A | 103.5 | 109.2 A | 85.4 | 108.5 A | 43.3 | 0.442 |
| P intake from feed | 163.2 A | 10.8 | 147.1 AB | 10.7 | 119.6 BC | 13.5 | 89.9 C | 11.8 | 0.001 |
| P intake from mineral supplement | 24.5 A | 14.5 | 29.7 A | 17.5 | 24.7 A | 14.2 | 62.9 A | 44.4 | 0.422 |
| Fecal P loss | 125.6 A | 12.7 | 127.3 A | 13.7 | 118.7 A | 13.2 | 125.8 A | 25.2 | 0.951 |
| Urinary P loss | 10.4 A | 0.9 | 10.7 A | 1.6 | 8.3 A | 1.6 | 7.6 A | 2.1 | 0.149 |
| P balance | 51.7 A | 15.1 | 38.8 A | 24.2 | 17.2 A | 13.6 | 19.4 A | 31.8 | 0.095 |

[a] Percent guajillo in diets based on alfalfa hay to guajillo ratio (dry mass:dry mass).
[b] P-values are for an ANOVA test for differences among diets.

TABLE 3—Magnesium (Mg) and sodium (Na) balance data (mg·kg$^{-0.75}$·day$^{-1}$) for male white-tailed deer fed 4 diets from July through September 1998 in Kingsville, Texas. Means in a column with different letters were different at $\alpha = 0.05$; $n = 4$ for all diets.

| | Percent guajillo in diet[a] | | | | | | | | |
| | 0 | | 25 | | 50 | | 75 | | |
| Mineral parameter | Mean | *SE* | Mean | *SE* | Mean | *SE* | Mean | *SE* | *P*-value[b] |
|---|---|---|---|---|---|---|---|---|---|
| Mg intake from feed | 201.6 A | 26.8 | 205.3 A | 24.3 | 199.4 A | 27.2 | 183.0 A | 20.2 | 0.701 |
| Mg intake from mineral supplement | 1.6 A | 1.0 | 2.0 A | 1.2 | 1.6 A | 0.9 | 4.2 A | 2.9 | 0.422 |
| Fecal Mg loss | 178.4 A | 16.4 | 184.0 A | 17.1 | 174.8 A | 21.4 | 148.7 A | 22.9 | 0.160 |
| Urinary Mg loss | 14.8 A | 1.7 | 18.7 A | 2.5 | 20.7 A | 5.2 | 25.0 A | 1.2 | 0.160 |
| Mg balance | 10.1 A | 10.9 | 4.5 A | 8.8 | 5.6 A | 5.7 | 13.5 A | 4.1 | 0.818 |
| Na intake from feed | 151.8 A | 20.8 | 139.5 A | 15.5 | 114.3 AB | 22.0 | 83.7 B | 8.2 | 0.013 |
| Na intake from mineral supplement | 14.0 A | 8.3 | 17.0 A | 10.0 | 14.1 A | 8.1 | 36.1 A | 25.4 | 0.422 |
| Fecal Na loss | 34.4 A | 8.1 | 23.7 A | 4.8 | 27.1 A | 8.8 | 30.9 A | 9.2 | 0.615 |
| Urinary Na loss | 144.7 A | 15.4 | 125.6 A | 11.8 | 106.1 A | 8.9 | 89.7 A | 23.8 | 0.051 |
| Na balance | −13.2 A | 12.9 | 7.2 A | 5.3 | −4.8 A | 12.8 | −0.9 A | 5.3 | 0.433 |

[a] Percent guajillo in diets based on alfalfa hay to guajillo ratio (dry mass:dry mass).

[b] *P*-values are for an ANOVA test for differences among diets.

$$y = 1398.30 - 5.0681\,x$$
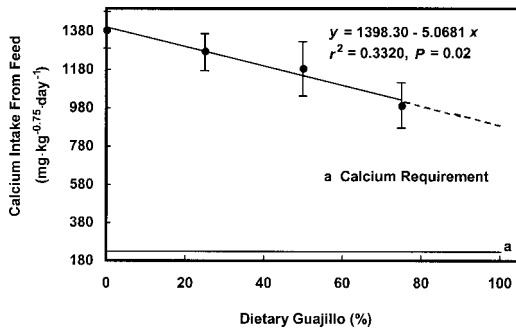$$r^2 = 0.3320, \ P = 0.02$$

FIG. 1—Calcium intake from feed as a function of percent guajillo in 4 diets of adult male white-tailed deer from July through September 1998 in Kingsville, Texas ($n = 16$, $y = 1398.30 - 5.0681x$, $r^2 = 0.3320$, $P = 0.02$). The calcium requirement for mammals (a) from Robbins (1993) is displayed. Hashed line represents extrapolation of equation to 100% dietary guajillo.
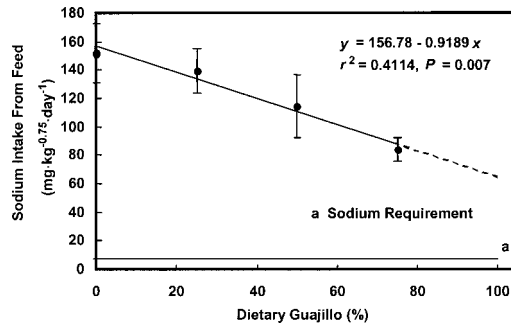


$$y = 156.78 - 0.9189\,x$$
$$r^2 = 0.4114, \ P = 0.007$$

FIG. 2—Sodium intake from feed as a function of percent guajillo in diet for adult male white-tailed deer fed 4 diets from July through September 1998 in Kingsville, Texas ($n = 16$, $y = 156.78 - 0.9189x$, $r^2 = 0.4114$, $P = 0.007$). The sodium requirement for adult male deer (a) from Hellgren and Pitts (1997) is displayed. Hashed line represents extrapolation of equation to 100% dietary guajillo.

comprised of 100% guajillo exceeded estimated requirements for calcium and sodium (Fig. 1 and 2). Phosphorus requirements for adult males during summer and fall were met even when diets were comprised of 100% guajillo. Phosphorus requirements for adult male white-tailed deer during spring were met with diets containing <75% guajillo (Fig. 3). Annually, adult males require 72.2 mg phosphorus·kg$^{-0.75}$·day$^{-1}$, which was met with diets of <97% guajillo (Fig. 3). Reproducing females require more phosphorus, which was met with diets <55% guajillo (Fig. 3).

DISCUSSION—To maintain acid-base homeostasis, herbivores consuming diets with absorbable PSCs might exhibit increased urinary mineral loss (Foley et al., 1995). The lack of treatment effects for urinary mineral loss and balance data suggested that guajillo intake did not alter the metabolism of minerals and that deer met their mineral requirements regardless of the amount of guajillo consumed (Tables 2 and 3). The only differences in mineral use occurred in calcium, phosphorus, and sodium intakes from feed, which can be explained by the varying mineral concentrations of the diets. Calcium, phosphorus, and magnesium losses occurred largely via fecal excretion, whereas sodium losses occurred via urinary excretion (Tables 2 and 3). Deer did not exhibit sodium wasting when fed diets high in guajillo.

In fact, there was a negative relationship ($P = 0.051$) between urinary sodium excretion and guajillo concentration and no difference in sodium balance among diets. This, coupled with the lack of differences in urinary ammonium excretion and pH values (Campbell, 1999), suggested that guajillo does not initiate metabolic acidosis in deer.



$$y = 167.05 - 0.9897x$$
$$r^2 = 0.6421, \ P < 0.001$$

a Adult Males - Annual
b Adult Males - Spring
c Adult Males - Summer
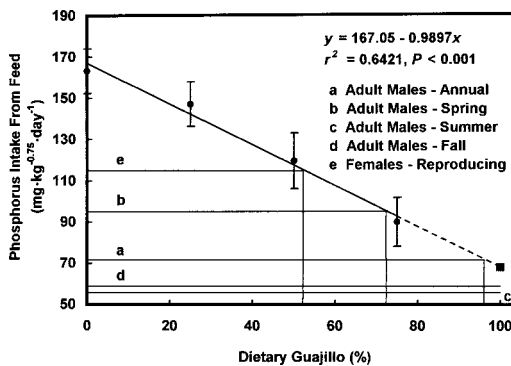d Adult Males - Fall
e Females - Reproducing

FIG. 3—Phosphorus intake from feed as a function of percent guajillo in diet for adult male white-tailed deer fed 4 diets from July through September 1998 in Kingsville, Texas ($n = 16$, $y = 167.05 - 0.9897x$, $r^2 = 0.6421$, $P < 0.001$). Phosphorus requirements for adult male deer annually (a), during spring (b), summer (c), fall (d), and for reproducing females (e) from Grasman and Hellgren (1993) are displayed. Hashed line represents extrapolation of the equation to 100% dietary guajillo and the square represents phosphorus intake of white-tailed deer fed 100% guajillo (calculated from Barnes, 1988).

Barnes (1988) reported negative phosphorus absorption coefficients (more phosphorus lost in feces than ingested) for diets of 100% guajillo, which suggested that guajillo was a poor forage. Our data indicated that deer fed 75% guajillo maintained a positive phosphorus balance. However, 3 of 4 deer on the 75% guajillo diet displayed negative phosphorus balance, and the only deer with positive balance consumed 189.0 mg phosphorus$\cdot$kg$^{-0.75}\cdot$day$^{-1}$, which was 9 times the mean of the 3 deer in negative balance.

Mineral appetites have been observed in herbivores consuming forages with elevated PSCs (Freeland et al., 1985). Kreulen (1985) suggested that herbivores ingest mineral-rich soil to defend against anti-quality components of forages and acidosis. Freeland et al. (1985) hypothesized that some PSCs might deplete mineral reserves, thus creating a demand for minerals. The mechanism whereby PSC ingestion resulted in mineral appetites depended upon the ability of the PSCs to deplete mineral reserves within the herbivore, thus creating a demand for minerals not already available in excess (Freeland et al., 1985). Contrary to the PSC-mineral appetite hypothesis, deer consuming the experimental diets did not vary in intake of mineral supplements (i.e., deer ingesting more PSCs did not have greater mineral appetites; Table 1). This is possibly due to the lack of alteration in mineral use by deer (Tables 2 and 3), and therefore, deer were not challenged from a mineral standpoint. White-tailed deer and other cervids regulate mineral metabolism efficiently and can deposit and reabsorb minerals from their skeletal system (Brown, 1990; Grasman and Hellgren, 1993). This ability makes it difficult to experimentally alter mineral metabolism and antler development in deer (Grasman and Hellgren, 1993; Hellgren and Pitts, 1997). For instance, Campbell and Hewitt (2000) found that metabolic acidosis, a result of PSC ingestion in some herbivores, resulted in elevated urinary calcium excretion, but did not alter antler development in adult white-tailed deer.

Recent balance studies by Grasman and Hellgren (1993) and Hellgren and Pitts (1997) have increased our understanding of white-tailed deer mineral requirements. For all diets, calcium, magnesium, and sodium intake rates greatly exceeded requirements (Maynard et al., 1979; Robbins, 1993; Hellgren and Pitts, 1997). We also suggest that the requirements for these minerals were met with diets of 100% guajillo (Fig. 1 and 2) and concur with Barnes et al. (1990), who determined that browse species in southern Texas provide adequate calcium and magnesium. However, Barnes et al. (1990) suggested that sodium deficiencies might occur during the summer in response to elevated browse consumption. Furthermore, Barnes et al. (1990) recommended sodium supplementation as a simple solution to sodium deficiencies, a management practice not supported by our results.

In southern Texas, phosphorus is the mineral most likely to limit white-tailed deer populations (Barnes et al., 1990). Phosphorus intake requirements were met by all experimental diets for adult males during summer and fall (Grasman and Hellgren, 1993; Fig. 3). Traditional thought suggested that male deer have the greatest phosphorus deficit during summer, when they are forming antlers and consuming a greater portion of browse (Barnes et al., 1990). However, use of natural mineral licks often peaks during spring (Weeks and Kirkpatrick, 1976), suggesting white-tailed deer experience a mineral deficit during this period. For adult males during spring, diets containing ≤74% guajillo exceeded phosphorus requirements (Grasman and Hellgren, 1993; Fig. 3).

The annual phosphorus requirement is a more important measure than seasonal requirements because white-tailed deer have the ability to conserve, store, and mobilize minerals during periods of mineral excess and scarcity (Grasman and Hellgren, 1993). Annually, diets of ≤96% guajillo met the phosphorus requirement for adult male deer (Grasman and Hellgren, 1993; Fig. 3). Varner and Blankenship (1987) reported maximum browse intakes in southern Texas during dry summers as ≤97%. Phosphorus concentrations of brazil (*Condalia hookeri*) and blackbrush (*Acacia rigidula*), 2 other browse species commonly consumed by deer in southern Texas, were 0.13 and 0.18%, respectively (Barnes, 1988), which exceed the phosphorus concentration of guajillo (Table 1). Consequently, it is unlikely that male white-tailed deer will experience a cumulative annual phosphorus deficit in southern Texas, even during years of low rainfall.

Reproducing females have phosphorus requirements that exceed males due to the demands of gestation and lactation. Our data suggested that reproducing females consuming >54% guajillo would not meet these demands (Fig. 3). In dry years, when females are forced to consume diets high in guajillo, they might experience a seasonal phosphorus deficit. This shortage might be compensated by increasing forage intake (Parker et al., 1999) or by employing mechanisms of phosphorus conservation, storage, and mobilization similar to the responses of males during antler development (Grasman and Hellgren, 1993). Because of the highly negative energy balance of reproducing females consuming guajillo diets (Campbell, 1999), we consider that the seasonal phosphorus deficit to be of secondary importance. In severe droughts, it is likely that female deer would cease reproduction for energetic reasons rather than deficiencies of phosphorus.

Our phosphorus intake values (Fig. 3) represented liberal estimates of what was available to deer because we did not consider the antiquality components of guajillo. Barnes (1988) suggested that phosphorus in browse species might not be available because of elevated PSCs and lignin that reduce digestibility. In our study, 2 deer consumed little phosphorus from the mineral supplement ($<3$ mg·kg$^{-0.75}$·day$^{-1}$), and these deer were in negative phosphorus balance when fed diets of 50 and 75% guajillo. Other deer on low phosphorus diets (0.19%) during summer were in positive balance (53.5 mg·kg$^{-0.75}$·day$^{-1}$, calculated by adding antler loss to balance; Grasman and Hellgren, 1993). Data from Barnes (1988) and Grasman and Hellgren (1993) indicated that phosphorus availability in guajillo is low. Consequently, our phosphorus requirements (Fig. 3) were overestimated, and free-ranging deer consuming natural forages are more likely to be challenged from phosphorus deficiency than deer in our study.

Despite the widespread use of mineral supplements as a management tool among private land managers (Thackston, 1991), there are no data suggesting that mineral supplements increase body growth, body size, or antler characteristics. In fact, Schultz and Johnson (1992) found no differences in these parameters between supplemented and unsupplemented deer. From a nutritional standpoint, we do not support the practice of mineral supplementation for white-tailed deer in southern Texas during periods of forb abundance. However, during periods of low rainfall, when deer subsist on diets high in guajillo, phosphorus might limit reproduction within females, and phosphorus supplementation might be justified. Land managers should weigh the benefits with the negative consequences of supplementation (Williamson, 2000) and the impacts of artificial mineral sources on deer movements (Campbell et al., in press).

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