EXAMINATION OF THE NITROGEN LIMITATION HYPOTHESIS IN POPULATIONS OF COTTON RATS (SIGMODON HISPIDUS)

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PREFACE

This thesis is comprised of a single manuscript formatted for submission to the journal Ecology or Ecological Monographs. This manuscript is complete as written and does not require additional material for support.

I would like to extend my thanks to my major advisor, Dr. Robert L. Lochmiller for his guidance throughout this research project and to my committee members, Drs. David M. Leslie, Jr. and David M. Engle for their valuable input. I would also like to thank Dr. Mark E. Payton for his statistical expertise. Thanks go to Brian Faulkner and all the other graduate and undergraduate students who helped with the field work, and to all the Lochmiller graduate students for their friendship and support. Special thanks go to my parents, Thomas E. and Jane R. Schetter and the rest of my family for their unending support, and to Troy Pierce and Anna Fallon for helping me make it through the final weeks of the project. Most of all I wish to thank my wife Amy for her love and patience and for giving me the inspiration to complete this thesis.

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Abstract Nitrogen-containing nutrients have long been considered to be a frequently limiting resource to the growth of herbivore populations. Although this heterogenous class of nutrients is represented by several essential amino acids which collectively determine overall quality of food proteins, few studies have actually attempted to relate demographic change to protein quality. We hypothesized that availability of essential amino acids (especially sulfur-containing amino acids) for reproduction is an important determinant of population density in herbivores.

To explore this hypothesis, we examined the relationships between availability of essential amino acids in the diets of cotton rats in central Oklahoma and the intrinsic characteristics of their populations. Cotton rat populations were censused by live-trapping at 3 month intervals on 2 sites supporting high-density populations and 5 sites supporting low-density populations. Stomach digesta were collected from cotton rats in similar habitats adjacent to these sites. Botanical composition of diets was determined using microhistological techniques. Amino acid composition of diets was determined using HPLC.

During the breeding season, concentrations of essential amino acids were as much as 40% greater in diets of cotton rats from high-density populations. During this same period, sulfur-containing amino acids may have been below requirements for optimum reproduction in low-density populations, but not in high-density populations. Dicots, typically higher in protein than monocots, were an important component of the diets of cotton rats and were preferred forages in all seasonal collections. Seeds (especially legume seeds) and arthropods were frequently utilized by cotton rats as

other important sources of essential amino acids. Cover in the habitat (more available in habitats supporting high-density populations), and total phenolics in the diet (greater concentrations in diets from low-density populations) were two other factors that showed consistent relationships to cotton rat population density.

Despite the lower concentrations of essential amino acids observed in diets of cotton rats from low-density populations during the breeding season, differences in measures of reproduction, survival, and condition of animals within populations showed no consistent pattern that was indicative of nutritional stress. We posit that dispersal and spacing behavior may have prevented low-density populations from reaching a threshold value where availability of essential amino acids in the habitat would become nutritionally limiting. Our data suggest that levels of essential amino acids during peek breeding seasons may dictate ultimate densities of cotton rats that can be supported in their habitat. Based on our results and those of previous studies, it appears that sulfur-containing amino acids are frequently the most limiting essential amino acids to reproduction in herbivores.

INTRODUCTION

Increasing evidence supports the hypothesis that availability of high quality food can limit the growth and size of many populations of wild herbivores (Hanson 1979, Keith 1983, Doonan and Slade 1995). Studies of rodent and lagomorph populations have demonstrated that relationships exist between availability of suitable forage and onset of breeding (Cole and Batzli 1979, Keith 1987), breeding intensity (Cole and Batzli 1978, Bomford and Redhead 1987), fecundity (Cole and Batzli 1978, 1979), growth rates (Cole and Batzli 1979, Batzli and Lesieutre 1991), juvenile and adult survival (Cole and Batzli 1979, Keith 1987), and home range size (Ostfeld 1985, Jones 1990). However, most of these studies have not identified specific nutrients that might be limiting and when these limitations occur at the population level.

White (1978, 1993) and Mattson (1980) have suggested that nitrogen-containing nutrients are frequently limiting in the habitats of many populations of wild herbivores. Animals do not have a dietary requirement for protein but require specific amounts of essential amino acids that cannot be synthesized in adequate amounts endogenously from dietary protein. Therefore, diet quality relative to nitrogenous compounds is largely determined by how well dietary proteins supply an animal with a proper balance of essential amino acids (Oser 1959). Despite the potential importance of essential amino acids to populations of wild herbivores, few studies have actually examined the relationship between their availability in the habitat and population fluctuations. Quality of proteins (amino acid composition) in the diets of waterfowl (Krapu and Swanson 1975, Thomas and Prevett 1980, Sedinger 1984), willow

ptarmigans (Lagopus lagopus - Steen 1988), primates (Oftedal 1991), northern bobwhite quail (Colinus virginianus - Peoples et al. 1994), and eastern cottontails (Sylvilagus floridanus - Lochmiller et al. 1995) have been described. Collectively, these studies suggest that levels of essential amino acids (especially the sulfur-containing amino acids) in the diet may be seasonally deficient relative to animal requirements.

We hypothesized that availability of sulfur-containing amino acids for reproduction and growth is an important determinant of population density in populations of wild herbivores. Cotton rats, Sigmodon hispidus (Rodentia: Cricetidae), are generalist herbivores that occur in grass dominated habitats in northern South America, Central America, and southeastern and southcentral North America (Cameron and Spencer 1981). In the tallgrass prairies of central Oklahoma, cotton rats are the dominant rodent species, exhibiting regular annual fluctuations in population density with peak densities occurring in early autumn and minimum densities occurring in early spring (Goertz 1964). This species also varies greatly in density from one year to another (Odum 1955) and from one habitat type to another (McMurry et al. 1994)

The primary objective of this study was to examine the dynamic relationships between availability of essential amino acids in the diet of hispid cotton rats and intrinsic characteristics of their populations. Our experimental approach was to compare seasonal changes in the botanical composition and protein quality of diets consumed by animals from replicated high-density and low-density populations. Our approach of examining correlations between diet quality and population density was

chosen over direct comparisons of dietary levels of nutrients to those levels required in the diet because information on the amino acid requirements of wild rodent species for growth and reproduction have not been determined (National Research Council 1995).

MATERIALS AND METHODS

Study Area

After conducting extensive surveys of potential tallgrass prairie study sites in August 1993, we identified five distinct habitats that supported low densities of cotton rats (peak densities of <25 animals / ha) in western Payne Co., Oklahoma (36°3'-36°7' N, 97°12'-97°13' W) and two habitats that supported high densities (peak densities of >80 animals per ha) in southern Caddo Co., Oklahoma (34°53'-34°54' N, 98°7'-98°11' W). Herbaceous ground cover on three low-density sites was dominated by the grasses little bluestem (Schizachyrium scoparium), big bluestem (Andropogon gerardii), tall dropseed (Sporobolus asper), and indiangrass (Sorghastrum nutans), and the forbs western ragweed (Ambrosia psilostachya), white sage (Artemisia ludoviciana), goldenrod (Solidago spp.), and serecia lespedeza (Lespedeza cuneata), an exotic legume. Woody plants occurring on these sites included smooth sumac (Rhus glabra), winged sumac (R. copallina), coral-berry (Symphoricarpos orbiculatus), sand plum (Prunus angustifolia), and eastern redcedar (Juniperus virginiana). The other two low-density sites occurred in an area that was subjected to wildfire three years previously and annual cattle grazing. Cotton rat populations on these sites were at very low densities (<3 animals / ha). Vegetation on these two sites was dominated by the grasses little bluestem, Muhlenbergia spp., purpletop (Tridens flavus), and Scribner's panicum (Panicum oligosanthes), the forbs western ragweed, white sage, and goldenrod, and the woody plants eastern redcedar and smooth sumac.

The two high-density study sites were located in heavily disturbed prairie dominated by johnsongrass (Sorghum halapense), which occurred in solid stands on ~50% of one site and ~25% of the second site reaching heights >2 m. Dominant forbs were western ragweed, white sage, and the legume prairie acacia (Acacia angustissima); smooth sumac was the most common woody plant.

Population Fluctuations

A live-trapping grid was established on each of the seven study sites, and consisted of 64 trap stations with one Sherman live trap (7.6 x 8.9 x 22.9 cm) per station. We used a 15-m spacing pattern between stations on low-density grids, with each grid arrayed in an 8 x 8 design. We used a 10-m spacing pattern arrayed in an 8 x 8 and 4 x 16 design on the two high-density grids. Each population was censused first in August 1993 and again in November 1993, and February, May, August, and November 1994. All traps were opened in late afternoon (1600-1800 hr), baited with rolled oats, provided with cotton for warmth during cold weather, and checked between 0600 and 1100 hr for three consecutive days during a census period. Traps were placed on the grids on the afternoon before the first day of sampling and were removed from the grids after the third day of sampling. Captured animals were toe-clipped with a unique number for identification and released immediately after data were recorded to include information on location of capture (station number), body mass (to the nearest 1 g), sex, reproductive condition (pregnant, lactating, or neither for females; scrotal or non-scrotal for males), and general condition (presence of

ectoparasites or wounds). Age was determined by body mass: ≤60 g = juvenile, 61-99 g = subadult, >100 g = adult (Stafford and Stout 1983).

Population size of cotton rats was estimated using program CAPTURE (Otis et al. 1978). Model M_0 was selected by CAPTURE as the best estimator of population size for most data sets in this study. Because Darroch's estimator (Model M_t) is always valid when Model M_0 is true and is a more robust estimator than M_0 (White et al. 1982), we used Darroch's estimator for all data sets except as follows. When the number of captures and/or recaptures was insufficient to estimate population size on a given grid using CAPTURE, we used the equation: $\underline{N} / 1-(1-\underline{p})^{\underline{t}}$, where $\underline{N}$ is the minimum number of animals known alive, $\underline{p}$ is the mean capture probability for animals on all other grids during the same trapping period, and $\underline{t}$ is the number of trapping occasions. If trap mortality occurred and was < 5% of the total animals captured on a grid during a three day trapping period, dead animals were removed from the data set, the population estimate were determined, and dead animals were added back to the population estimate. If trap mortality exceeded 5% of captures (this only occurred once), the generalized removal estimate (Model M_{bh}) was used. We calculated density by dividing the estimated population size by the effective trapping area for each grid; effective trapping area was calculated as the area of a grid after adding to its perimeter half the mean maximum distance moved by all cotton rats on the grid (McMurry 1993). Survival rate was calculated for populations on each live-trapping grid as the proportion of animals captured during a census period that were recaptured during any subsequent census periods.

Vegetation Sampling

Vegetation on each trapping grid was described during each census period. To estimate percent cover of individual plant species we used the Daubenmire canopy cover method (Bonham 1989) within each of 30 randomly placed quadrats (20 x 50 cm) on each grid. Cover of standing and fallen litter also was estimated using the Daubenmire method. After cover was estimated in each quadrat, all living herbaceous vegetation was clipped at ground level and sorted into monocots and dicots. Clipped vegetation was then dried at 55 C for 5 days, and mass was recorded to the nearest 0.01 g.

Collection of Stomach Digesta

To collect stomach digesta for diet analysis, we used snap-traps that were baited with the scent of peanut butter. Within 3 weeks of each census period, animals were removed from similar habitat >100 m from existing trapping grids (except during the last census period in November 1994 when they were collected directly from live-trapping grids). Snap traps were set near dusk, checked at night and again at dawn the following morning. Traps were checked every 3-4 hr during very hot weather to insure that trapped animals did not spoil. Variable numbers of animals were removed from each population due to fluctuating densities. It was especially difficult to obtain animals from low-density study sites despite intensive efforts during some collection periods when densities were extremely low. No cotton rats were caught on 2, 2, 3,

and 1 of the low-density sites during November 1993, February 1994, May 1994, and August 1994, respectively.

All animals trapped were returned to the laboratory within 1 - 2 hr where body mass, length, age, sex, reproductive condition, and general body condition were recorded. Stomach contents from each animal were removed, cleared of parasites, mucosa, and hair, and wet mass was determined before freezing. Animals were necropsied to measure mass of selected organs (liver, spleen, adrenal glands, seminal vesicles and testes for males, and uterus, ovaries and embryos, if present, for females.

Sample Preparation and Nutrient Analysis

We lyophilized individual stomach contents to dryness, determined dry mass, and ground contents to even consistency with mortar and pestle. We excluded from analysis any digesta samples with a dry mass < 0.1 g to minimize contributions of endogenous nitrogen (Peitz and Lochmiller 1993). To ensure adequate sample volume for all laboratory analyses (ca. 1 g dry mass), we composited stomach contents (1-4 rats per composite) from 222 cotton rats by season and trapping grid for a total of 104 composites following the procedure of Jenks et al. (1989).

We measured total phenolics in composited samples colorimetrically (absorbance read at 765 nm) with Folin-Ciocalteu reagent and gallic acid as a standard based on the procedures of Singleton and Rossi (1965). Lipid concentration was measured in composited samples using a soxlet apparatus and diethyl ether as a solvent (Williams 1984). We determined percent nitrogen and crude protein (6.25 x

%N) of composited samples using a Perkin Elmer 2410 Series II Nitrogen Analyzer calibrated with ethylenediaminetetracetic acid (EDTA). We used alfalfa (3.028% N) as an external standard (obtained from the Soil, Water and Forage Analytical Laboratory, Department of Agronomy, Oklahoma State University, Stillwater, OK).

For amino acid analysis, fat-extracted composited samples of digesta (ca. 40 mg of protein) were placed in 25 x 150 mm glass tubes with Teflon caps, purged with N gas for 4 min, and hydrolyzed in 15 ml 6N HCl at 110 C for 24 h. We filtered hydrolyzed samples through a 0.45-μm syringe filter (Acrodisc CRPTF, Fisher Scientific, Plano, TX) and added 50 μL internal standard (4 mM Norleucine in 0.1N HCl) to 150 μL of filtered hydrolysate prior to derivitization. Amino acids were derivitized (pre-column) with phenylisothiocynate to produce phenylthiocarbamyl amino acids using the procedure of Cohen et al. (1988). Samples were then refiltered through a 0.45-μm syringe filter. We determined concentrations of 9 essential (histidine, arginine, threonine, valine, methionine, isoleucine, leucine, phenylalanine, and lysine) and 8 nonessential (aspartic acid, glutamic acid, serine, glycine, alanine, proline, tyrosine, and cystine) amino acids using high pressure liquid chromatography (Waters Model 820 System Controller and Model 501 Pumps, Millipore Corporation, Milford, MA).

We used the following chromatographic conditions: Waters Pico-Tag Silica/C18 (150 mm x 3.9 mm) column and guard column (20 mm x 3.9 mm); column temperature, 37 C; flow rate, 1.0 mL/minute with pump back pressure of 16,095 kg/cm^2; system sensitivity, 489 mv/s (recorder) and 0.1 absorbance units full scale

(Waters Model 484 UV detector, set at 254 nm); injection volume, 12 µL; and run time, 27.5 min. We used solvents Eluent A and Eluent B (catalog no. 88208 and 88112, respectively, Millipore Corp., Milford, MA) under conditions and gradients described for separation of amino acids by Cohen et al. (1988). Two ground, ether-extracted feeds (A & M Complete Rabbit Pellets and A & M Quail Starter, Stillwater Milling Company, Stillwater, OK) of known amino acid composition (determined by a certified laboratory, University of Missouri Experimental Station Chemical Lab, Columbia, MO) were hydrolyzed and analyzed with samples for comparison of amino acid recovery. Concentrations obtained for methionine and cystine were combined as were phenylalanine and tyrosine because cystine and tyrosine may supply up to 50% of the requirement for their respective amino acid (National Research Council 1995). Tryptophan was destroyed during acid hydrolysis and therefore was not measured (Cohen et al. 1988). Nonprotein nitrogen was calculated as (crude protein nitrogen - amino acid nitrogen)/crude protein nitrogen.

Food Habits Analysis

Food items in composited digesta samples were identified through microhistological analysis. Dried, composited samples were cleared of pigments with 95% ethyl alcohol, bleached, stained using lactophenol blue solution, and permanently mounted on microscope slides using glycerin gel (Davitt and Nelson 1980).

For each composited sample, botanical composition of the diet was determined by randomly locating 25 microscope fields on each of three slides, identifying the

center most fragment in each field at 100x magnification, and counting the 0.25-mm^2 squares on a 10 x 10-mm ocular grid that were occupied by each fragment (McMurry et al. 1993). Identification of plant fragments was facilitated with reference slides of plant tissues prepared as above. Relative composition of plant species in the diet was estimated for each composite by dividing the total coverage of each plant species by the total coverage of all fragments.

For statistical purposes, items in the diet were placed into the following categories: monocot foliage (stems and leaves), dicot foliage (stems and leaves), non-legume seeds (monocots, woody and herbaceous dicots, gymnosperms), legume seeds (including pods), arthropods, and other (including fungi and unidentified fragments). A relative food preference index (PI = proportion of plant in diet / proportion of total plant cover in habitat) (Lindroth and Batzli 1984a) was calculated for categories of plants (monocots, forbes, legumes, woody plants), and all plants identified to genus or species in diets for each census period. PI values > 1.0 indicate preference and values < 1.0 indicate avoidance relative to the availability of plants in the habitat (for true avoidance, PI = 0).

Statistical Analyses

Initial analysis of amino acids using a two-way analysis of variance procedure (Proc GLM, SAS Institute, Inc. 1990) with grid and season as main effects indicated that there was significant grid by season interaction for concentrations of all amino acids, so all subsequent analyses were conducted within each season. One-way

analysis of variance (Proc GLM, SAS Institute, Inc. 1990) was used to test for differences in diet quality, diet composition, and vegetation cover among grids. Single degree of freedom contrasts were used in all analysis of variance procedures to test planned comparisons between low-density (Payne Co.) and high-density (Caddo Co.) populations. To correct for non-normality and heterogeneity of variance data were arcsine transformed or rank transformed (Kruskal-Wallis procedure) when necessary before data analysis (Conover and Iman 1981).

Demographic attributes (percent juveniles, subadults, and adults; percent reproductive adult males and females; sex ratios; survival rates) were analyzed within season between low- and high-density populations with chi-squared analysis or Fisher's exact test (Proc FREQ, SAS Institute, Inc. 1990). Due to small numbers of animals captured from low-density populations, these demographic parameters were analyzed within seasons after pooling animals from all low-density populations versus all animals from high-density populations. Body mass was analyzed using analysis of variance (Proc GLM, SAS Institute, Inc. 1990), and digesta mass, organ masses, and number of embryos per adult female were analyzed using analysis of covariance (Proc GLM in SAS, SAS Institute, Inc. 1990) with body mass as a covariate. Single degree of freedom contrasts were used as described above.

A multivariate approach was used to examine the relationship between population density and dietary concentrations of all nine essential amino acids within each season. Stepwise discriminant analysis (Proc STEPDISC, SAS Institute, Inc. 1990) was used to select a reduced set of discriminator variables (out of nine essential

amino acids) that would provide the best separation of population densities within each season. Discriminant function analysis (Proc DISCRIM, SAS Institute, Inc. 1990) was used to determine classification accuracy among low- and high-density populations using the reduced set of variables selected by stepwise discriminant analysis. Canonical discriminant analysis (Proc CANDISC, SAS Institute, Inc. 1990) was used to generate individual canonical variate scores (within each season) based on a linear combination of all nine essential amino acids. Data were rank transformed prior to multivariate analysis to correct for non-normality and heterogeneity of variance within the multivariate data set.

RESULTS

Habitat Composition

The composition of monocots and dicots varied considerably between low- and high-density study sites, but percent coverage and biomass of vegetation categories were not dramatically different between low- and high-density sites (Figs. 1 and 2). All sites showed considerable seasonal variation; standing crop biomass of monocots and dicots was over ten-fold greater in May and August 1994 than other months (Fig. 2). Legumes were only available from May to November 1994. Cool-season annual brome grasses (Bromus spp.) dominated high-density sites in November and February sampling periods after warm-season grasses matured and died, but brome grasses were less common on low-density sites.

Percent cover of forbs only differed between sites in May and November 1994 (greater on low-density sites, $P < 0.001$), and cover of legumes differed only between sites in November 1994 (greater on high-density sites, $P \leq 0.029$, Fig. 1). Coverage of warm-season grasses was similar among sites, but biomass estimates were 68% greater on high-density sites in August 1994 ($P = 0.010$). Cool-season grasses were consistently two to three times more abundant ($P \leq 0.023$) on high-density sites as measured by percent coverage (Fig. 1) and biomass (Fig. 2).

Vegetation litter provides an important source of cover to cotton rats and was consistently more abundant on high-density than low-density study sites (Fig. 1). Differences were most pronounced for fallen litter ($P \leq 0.001$), which averaged about 75% more on high-density than low-density sites. Standing litter also was more

abundant on high-density sites in November 1993 ($P = 0.007$) and August 1994 ($P < 0.001$) than low-density sites.

Population Characteristics

We observed considerable variation in small mammal community structure between the seven study sites (Appendix I). However, no consistent patterns in structure of community or small mammal population densities (other than cotton rats) were evident when comparing study sites supporting high- versus low-density cotton rat populations. Other than cotton rats, the most common small mammals occurring on the study sites were white-footed mice (Peromyscus leucopus - most numerous on one high-density site) and fulvous harvest mice (Reithrodontomys fulvescens - abundant on both high-density and three low-density sites).

Population densities of cotton rats were consistently greater on high-density census grids compared to the low-density grids, especially during August peaks (over 13-fold higher in August 1993 and 8-fold higher in August 1994; Fig. 3). With the exception of density, we failed to observe any consistent trends in other intrinsic demographic parameters between low-density and high-density cotton rat populations (Table 1). In August 1993, the proportion of juveniles was two-fold greater in high-density populations compared to low-density populations ($P = 0.013$). In February 1994, the proportion of juveniles was about two-fold greater in low-density populations ($P = 0.045$), but the proportion of subadults was nearly two-fold greater in high-density populations ($P = 0.031$). Other measures of age structure were similar

between low-density and high-density populations during other census periods ($\underline{P} \geq 0.082$).

In August 1993, the proportion of reproductively active (pregnant or lactating) females in combined live-trapped and snap-trapped census data was about seven times greater in high-density populations compared to low-density populations ($\underline{P} = 0.012$). The proportion of reproductively active (scrotal) males was two times greater in low- than high-density populations ($\underline{P} = 0.007$). No other significant differences in female or male reproductive activity (combined live-trapped and snap-trapped animals) were observed between low-density and high-density populations during any census period ($\underline{P} \geq 0.104$, Table 1). However, among animals that were snap-trapped, there was a greater proportion of reproductive females from high-density (75.0%, n = 12) than low-density (33.3%, n = 12) populations in August 1994 ($\underline{P} = 0.041$). This difference was likely due to the fact that palpating live-trapped females during pregnancy is only useful during late gestation. There was no significant difference ($\underline{P} = 0.163$) in the number of embryos per pregnant female (pooled across seasons) between high-density (5.27 ± 0.32, n=27) and low-density (6.19 ± 0.56, n=9) populations. We observed a two-fold greater ($\underline{P} = 0.045$, Table 1) survival rate in high-density populations compared to low-density populations from November to February; survival rates were similar for other census periods. Density was unrelated to the sex ratio of populations during all seasons ($\underline{P} \geq 0.308$), but we observed a disproportionately high ratio of males to females in all populations during February and May 1994 (Table 1).

Animal Condition

No consistent patterns in body mass were evident from seasonal comparisons between low-density and high-density populations of cotton rats (Table 2). Mean body mass of juveniles, reproductive females, and reproductive males was similar across all seasons of capture. The only differences in body mass that we observed were for animals >60 g. Females were about 35% heavier ($P = 0.001$) on low-density sites compared to high-density sites in November 1993 and males were about 20% heavier ($P = 0.009$) on high-density compared to low-density sites in February 1994. It was not possible to determine if these differences were the result of age structure or nutritional conditions that persisted in the populations.

Similar to body mass, no consistent trends in organ mass were apparent between high-density and low-density populations (Table 2). Liver mass was greater ($P = 0.035$) in cotton rats collected from low-density compared to high-density populations in August 1993. Significantly greater masses of livers ($P = 0.024$), spleens ($P = 0.048$), and paired adrenal glands ($P = 0.019$) were observed in cotton rats collected from low-density populations in November 1993, a period when body mass of females was also greater than on high-density sites. An opposite relationship was observed in February 1994 where the greater spleen mass ($P = 0.058$) in high-density populations was associated with greater body mass of males. Although paired adrenal mass was greater on low-density than high-density sites in November 1993 ($P = 0.019$), the opposite was observed in November 1994 ($P = 0.005$).

Diet Composition

Cotton rats from high-density sites consumed greater amounts of monocot foliage in November 1993, May 1994, and November 1994 ($P < 0.050$), but consumed less in August 1994 ($P < 0.050$) compared to low-density sites (Fig. 4). Monocot foliage was most abundant in diets of animals from high- and low-density sites in February 1994 ($\geq$44% of the diet), least abundant on high-density sites in May and August 1994 ($\leq$18% of the diet), and least abundant on low density sites in November 1993 and May 1994 ($\leq$3% of the diet). Of the monocot foliage fragments that were identified to genus or species, johnsongrass was most abundant in diets from high-density sites in May and August 1994, and annual brome was most abundant during other months. On low-density sites, Scribner's panicum was most abundant in February, tall dropseed and big bluestem were most abundant in August 1994, and brome was most abundant in November 1994.

Cotton rats from high-density sites consumed greater ($P < 0.050$) amounts of dicot foliage in February compared to low-density sites, while consumption of dicots did not differ between sites in other seasons (Fig. 4). Dicot foliage was most abundant in diets from high-density sites in February and November 1994 ($\geq$52 % of the diet) and least abundant in May and August ($\leq$33% of the diet). Dicot foliage was most abundant in diets from low-density sites in November 1994 (52% of the diet) and least abundant in February and August 1994 ($\leq$28% of the diet). Dicot foliage fragments most abundant in diets of cotton rats from high- and low-density sites were from the family Compositae (most fragments were not identifiable past family) in May

and August 1994, white sage in November 1994, and unidentifiable stems in November 1993, February, and November 1994.

Cotton rats from high-density sites consumed greater amounts of non-legume seeds in August 1994 ($P < 0.050$) compared to low-density sites, but consumption did not differ between sites in other seasons (Fig. 4). Non-legume seeds were most abundant in diets of animals from high-density sites in May and August 1994 (≥45% of the diet) and least abundant in February and November 1994 (≤7% of the diet). Non-legume seeds were most abundant in diets of animals from low-density sites in November 1993 and May 1994 (≥46% of the diet) and least abundant in November 1994 (13% of the diet). Of the seeds identified to genus or species, those from annual brome were most abundant in diets of cotton rats from high-density sites in November 1993, May 1994, and November 1994 (during November germinating seeds were consumed), johnsongrass in May and August 1994, smooth sumac in November 1994, and spurge (Euphorbia sp.) in May 1994. Non-legume seeds that were most abundant in diets of cotton rats from low-density sites were tall dropseed in November 1993 and November 1994, Scribner's panicum in May 1994, eastern redcedar in February 1994 and November 1994, and smooth sumac in February 1994. No single species dominated August 1994 diets on low density-sites, which consisted of a mixture of tall dropseed, brome, and lamb's quarter (Chenopodium album - found only on one site).

Cotton rats from high-density sites consumed greater amounts of legume seeds in May 1994, but less in November 1994 ($P < 0.050$), compared to those from low-density sites (Fig. 4). Legume seeds occurred in small amounts in diets of cotton rats

from high density sites in November 1993, May 1994, and August 1994 (≤3% of the diet), but did not occur at all in February and November 1994 diets. Legume seeds were abundant in diets of cotton rats from low-density sites in November 1993 and November 1994 (≥18 % of the diet), present in small amounts in February (2% of the diet), and absent in May and August 1994. The only legume seed fragments identified on low-density sites were from serecia lespedeza, a plant not found on high-density sites; no legume seed fragments were identified to genus or species in diets from high-density sites.

Arthropods were present in diets of cotton rats from high- and low-density sites in all seasons except November 1993 (all sites) and February (low-density sites) (Fig. 4). Consumption of arthropods was ≤5% of the diet during all seasonal collections and did not differ between sites ($P \geq 0.050$).

Preference index values for categories of plants (monocots, forbs, legumes, woody plants) indicated that cotton rats on high- and low-density sites generally preferred forbs and avoided monocots and woody plants. Legumes were preferred when seeds were available (May 1994 on high-density sites, November 1993-4 on low-density sites) (Appendix II). Preference for individual plant species in the diets of cotton rats changed seasonally on all study sites. On low-density sites, consumption of foliage of tall dropseed was similar to availability in spring and summer, but it became preferred forage as seeds matured in November. Annual brome was not abundant on low-density sites but was usually preferred when it was available (foliage in November 1993-4 and February 1994, seeds in May 1994). Scribner's panicum was

preferred in February 1994 (foliage) and May 1994 (seeds) but was usually avoided in other seasons. Big bluestem foliage was preferred in August on low-density sites but was not found in the diet during other seasons. Other plants that were sometimes preferred on low-density sites included sumac (seeds) in November 1993 and May 1994, goldenrod (foliage) in February 1994, lamb's quarter (seeds) in August 1994, and white sage (foliage) in November 1994. Serecia lespedeza seeds were highly preferred in November 1993-4.

On high-density sites, seeds and foliage of annual brome and johnsongrass were abundant in the diet of cotton rats when they were available (cool-season and warm-season, respectively), but neither species was preferred because they were both abundant in the habitat. Species that were sometimes preferred on high-density sites included spurge (seeds) in May 1994, Croton sp. (seeds) in August 1994, and white sage and plantain (Plantago sp.) (foliage) in November 1994. Other species of dicots likely were preferred by cotton rats on all sites, but this was not apparent due to the large percentage of stem fragments from dicots in the diet that we were not able to identify beyond class.

Diet Quality

Analysis of diet quality in high-density and low-density cotton rat populations showed considerable seasonal variation (Table 3, Figs. 5-8). Wet mass of stomach digesta from cotton rats was two-fold greater in animals collected from high-density populations compared to low-density populations in February 1994 ($P = 0.001$), but no

differences in dry mass of digesta were found ($P \geq 0.215$). This observation was reflected in the moisture content of diets which was 21% greater in February 1994 ($P < 0.001$) and 5% greater in May 1994 ($P = 0.009$) on high-density compared to low-density sites. Fat content in diets of cotton rats was three-fold greater in low-density compared to high-density populations in February 1994 ($P < 0.001$) but was similar during other census periods. Crude protein was 30% and 45% greater in diets of animals from high-density populations in May ($P = 0.045$) and August 1994 ($P = 0.004$), respectively, but was 27% less in November 1994 ($P = 0.028$) compared to low-density populations. Nonprotein nitrogen was over three-fold greater in diets from high-density populations in February 1994 ($P = 0.004$) and two-fold greater in November 1994 ($P = 0.012$) compared to diets from low-density populations. We also observed differences in concentrations of total phenolics in diets of cotton rats, which were two-fold greater in low-density populations November 1993 ($P = 0.005$) and August 1994 ($P < 0.001$) compared to those from high-density populations (Fig. 5). There were no significant differences in concentration of total phenolics between high- and low-density populations during other census periods ($P \geq 0.165$). Concentrations of non-essential amino acids were greater in diets of animals from low-density compared to high-density populations in February and November 1994, but concentrations in May and August 1994 were greatest in diets of animals from high-density sites (Table 3).

During the non-breeding seasons, concentrations of total essential amino acids in diets of cotton rats from low-density populations were 40% greater in February

1994 ($\underline{P}$ = 0.015) and 34% greater in November 1994 ($\underline{P}$ = 0.019) compared to those from high-density sites. The opposite was observed during the breeding seasons where concentrations of total essential amino acids in diets were 38% greater in May 1994 ($\underline{P}$ = 0.019) and 49% greater in August 1994 ($\underline{P}$ = 0.006) in high-density populations compared to low-density populations; no differences were observed in November 1993 ($\underline{P}$ = 0.496). In February 1994, concentrations of all essential amino acids but threonine, and in November 1994 all but valine, lysine and methionine + cystine were greater ($\underline{P}$ < 0.050) in diets from low-density populations compared to high-density populations; the same was true of lysine in November 1993 (Figs. 6-8). In May 1994, concentrations of all essential amino acids except lysine and histidine and in August 1994 all except lysine, histidine, and arginine were greater ($\underline{P}$ < 0.050) in diets of animals from high-density populations compared to those from low-density populations (Figs. 6-8).

Multivariate statistical analysis demonstrated that overall essential amino acid composition of diets was rather unique in low-density and high-density study sites during most seasons. Arginine, methionine + cystine, or leucine were selected at least once by stepwise discriminant analysis during each season as important discriminators of population density. Using these three variables, discriminant function analysis classified diets into their appropriate low-density or high-density categories with an overall accuracy rate of 79% in November 1993, 92% in August 1994, and 100% in February, May, and November 1994. Canonical discriminant analysis provided significant Mahalanobis distances between centroids of diets in

February 1994 ($P < 0.001$), August 1994 ($P = 0.012$), and November 1994 ($P < 0.001$) (Fig. 9). The canonical variate for each season (Table 4) was a linear combination of all nine essential amino acids.

DISCUSSION

Although other environmental factors may be involved in driving rhythmic fluctuations or cycles in herbivore populations, the abundance of quality food resources often dictates potential peak densities. Perhaps the most important factor in determining food quality for herbivores is the availability of nitrogen-containing nutrients (protein - White 1993). Previous studies of cotton rat populations have shown increases in density (Doonan and Slade 1995) and habitat affinity (Eshelman and Cameron 1996) in response to habitats supplemented with foods rich in protein. Prairie voles (Microtus ochrogaster), which are considered to be an ecological equivalent to cotton rats in the northern prairies of North America, have also responded to greater protein availability with increases in population density (Cole and Batzli 1978, 1979; Desy and Batzli 1989).

Seasonal changes and interpopulational differences in the botanical composition of diets consumed by cotton rats in this study clearly demonstrate the generalist foraging strategies utilized by this grassland herbivore (Randolf et al. 1991). These observations also demonstrate that cotton rats, like other small herbivores (Belovsky 1986), exercise considerable selectivity in making dietary choices. When availability in the habitat is considered, they portray a reliance on typically high-protein dicots (Mattson 1980) compared to monocots. As noted in several studies by Cameron and his associates (Kincaid and Cameron 1985, Randolf et al. 1991, Cameron and Eshelman 1996), cotton rats appear to rely heavily on dicots in their diet to obtain sufficient protein for life processes. We observed that seeds (especially legume seeds)

are an important item in their diet, and that dietary protein was >30% dry mass when legume seeds were consumed. It is also noteworthy that this herbivore consistently consumed a variety of arthropods (ca. 5%), which may be an extremely valuable source of essential amino acids (Peoples et al. 1994). The significance of this is readily apparent in the work of Campbell and MacArthur (1996), which showed that the herbivorous muskrat (Ondatra zibethicus) can meet its maintenance requirement for nitrogen by consuming diets containing as little as 3% animal tissue. Animal tissue is also a notable component of vole and lemming diets (Batzli 1985).

It is estimated that minimum protein levels in the diet necessary for reproduction in cotton rats is 11% (dry mass basis) when consuming natural forages (Randolph et al. 1995, Hellgren and Lochmiller in press); requirements for growth are unknown. Based on this estimate, cotton rats in our study from both high- and low-density populations appeared to consume sufficient dietary protein to support reproduction throughout the year. However, the 11% estimate assumes that animals are consuming a protein source that contains a proper balance of the required essential amino acids. Proteins in natural forages are known to be highly variable and frequently deficient in selected essential amino acids, especially the sulfur-containing nutrients methionine + cystine, relative to an animal's requirements for maximum growth and reproduction (Thomas and Prevett 1980, Sedinger 1984, Peoples et al. 1994). This also may be true of forages consumed by cotton rats in central Oklahoma.

Based on our earlier observations with cottontail rabbits (Lochmiller et al. 1995), we hypothesized that density of cotton rat populations is limited by the availability of essential amino acids, particularly the sulfur-containing amino acids methionine+cystine. It was our contention that an observation of greater levels of essential amino acids in the diets of cotton rats from high-density populations compared to those from low-density populations would be supportive of our original hypothesis. Cotton rats in central Oklahoma reproduce primarily between late spring and early fall and rarely breed at other times of year (Fig. 10). During the periods of intensive breeding activity in our study (May and August census periods), dietary concentrations of seven essential amino acids (including methionine + cystine) were greater by as much as 40% in high-density populations compared to low-density populations. Although this observation supports our initial hypothesis, it does not confirm that the levels of essential amino acids in diets of cotton rats from low-density populations were below the levels required to support optimum reproduction. Although caution must be exercised in doing so, one way to examine this question is to compare the essential amino acid requirements of laboratory animals with observed levels in the diets of cotton rats. A comparison of requirements for reproduction in laboratory rats (National Research Council 1995) to the dietary concentrations of essential amino acids of cotton rats in this study suggests that during the breeding season, methionine + cystine may have been limiting in low-density populations (Fig. 6), while other essential amino acids probably were not limiting (Figs. 6-8). Sulfur-containing amino acids have been found to be the most limiting essential amino acids

in diets of eastern cottontails (Lochmiller et al. 1995) and a variety of avian species (Murphy 1994).

There appeared to be a paradox between apparent limitations in essential amino acids during the breeding season and the lack of observed changes in population attributes. Protein restrictions (4% crude protein diet) imposed on female cotton rats in the laboratory have been shown to influence age at first estrus and pregnancy rate (Cameron and McClure 1988, Cameron and Eshelman 1996). Phenotypic plasticity in litter size of cotton rats across its range has been well documented (Cameron and McClure 1988). Reproductive performance also has been shown to vary with primary productivity of habitats (Doonan and Slade 1995, Slade et al. 1996). However, the demographic and physical condition parameters that we measured give us no convincing or consistent evidence that cotton rats from low-density sites experienced declines in fecundity or experienced remarkable nutritional stress by consuming a lower quality diet during the breeding season.

Data from August 1993 suggested that more females were reproductively active in high-density populations (also reflected in the greater proportion of juveniles in the population), but this pattern was not observed at any other time. Differences in body mass of females in November 1993 could be simply a reflection of differences in reproductive activity over the previous months: females on low-density sites bred less and conserved body reserves. However, another possible explanation is that an older age structure existed on low-density sites in November 1993 as a result of reproductive patterns the previous August (Cameron and Eshelman 1996). Of the

various internal organs measured to assess condition, liver mass was the most interesting. The greater mass of livers that we observed from August 1993 to February 1994 on low-density sites may have been related to phenolic levels in their diet (Jung and Batzli 1981, Bergeron and Jodoin 1989). Although Cameron and Eshelman (1996) have shown that dietary protein restriction of cotton rats can induce liver enlargement, we observed no differences in crude protein levels between low-density and high-density sites during this time period.

One possible explanation for the above paradox is that sulfur-containing amino acids in the diet may have been just above some threshold level below which declines in fecundity would occur in the low-density populations. In such a scenario, population densities may be maintained at low levels through the triggering of dispersal before sulfur-containing amino acids become severely limiting, similar to the pre-saturation dispersal hypothesis described by Lidicker (1975). A heterogenous habitat (a mixture of suitable and unsuitable habitat patches) plays an important role in maintaining low population densities by giving individual animals a place to disperse to (the unsuitable habitats) (Stenseth 1977). When dispersal is prevented using enclosures (Krebs et al. 1969, Boonstra and Krebs 1977) or in large uniform areas of good habitat (Klein 1970, Watson and Moss 1970), animal populations have been found to increase to the point where high-quality food resources are over-utilized and eventually exhausted.

Spacing behavior is an important mechanism of resource partitioning in cotton rats (Spencer and Cameron 1983, Cameron and Spencer 1985,) as it is in other small

mammals (Lidicker 1962, Ostfeld 1985). Spencer and Cameron (1983) found that dominant cotton rats are able to occupy preferred habitat patches and subordinates are forced to use less preferred habitats. Our low-density study sites were a mixture of suitable (tallgrass prairie) and unsuitable (oak forest) habitat patches; individuals dispersing into unsuitable habitats (poor cover and forage quality) would experience higher mortality risks. Such partitioning of resources would have three main consequences: populations would likely be more stable in habitats relative to the natural seasonal and climatic induced fluctuations in resource availability; individuals would be able to maintain fitness even if resource supplies diminished somewhat; and resources in the habitat would be more difficult to over-exploit.

Although we observed a relationship between density and protein quality of the diet, other relationships also existed with respect to phenolics and cover in the habitat. Cotton rats prefer habitats with dense overhead cover (Goertz 1964); numerous studies have found that availability of suitable cover influences population dynamics of cotton rats (Goertz 1964, Fleharty and Mares 1973, Kincaid et al. 1983). We observed considerably more fallen litter on high-density sites than on low-density sites during all seasons. Standing litter and biomass of monocots were also higher on our high-density sites in August during peak population densities. Eshelman and Cameron (1996) investigated the interaction between the effects of cover and protein availability on habitat use by cotton rats and found that both factors were important.

Another potential limiting factor to cotton rat populations is the presence of phenolic compounds in their forage. Phenolics act either as toxins or as digestive

inhibitors and thus decrease the quality of forage consumed by herbivores (Lindroth and Batzli 1984b). Phenolics influence forage selection (Jung and Batzli 1981, Bucyanayandi and Bergeron 1990) and have the potential to negatively influence growth and survival in voles (Jung and Batzli 1981, Lindroth and Batzli 1984b); they likely have the same effect on cotton rats. In our study, concentrations of total phenolics in the diet of cotton rats from low-density sites were over two-fold greater during the breeding season compared to high-density sites.

The results of this study support our hypothesis that the amount of high quality food (specifically, availability of essential amino acids) in the habitat is an important determinant of density in herbivore populations. The timing of nutrient limitations relative to life history events is also important. Our data suggest that although nutrient levels in diets were high throughout much of fall and winter, levels during peek breeding (spring and early fall) dictated ultimate densities that could be supported. It appears that the sulfur-containing amino acids (methionine + cystine) are frequently the most limiting amino acids in the diets of cotton rats in central Oklahoma.

The logical next step is to examine the relative impact of sulfur-containing amino acids and habitat cover to determining population densities of cotton rats. A test of this hypothesis could best be accomplished through the use of enclosures where supplemental methionine (breeding season supplements) and various levels of cover could be provided in a factorial design. Such a design could permit the exploration of interactions between these two resource factors across seasons. Because the use of enclosures would limit dispersal, we predict that nutrient-supplemented populations

would achieve greater densities as a result of improved rates of recruitment compared to unsupplemented populations.

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Table 1. Seasonal changes in selected demographic attributes of low- and high-density cotton rat populations in central Oklahoma from August 1993 to November 1994. The number in parentheses indicates sample size; the number in brackets below each set of numbers is the P value associated with comparisons between low-density and high-density populations.

Demographic parameter	Density (L = low H = high)	August	November	February	May	August	November
Juveniles (%)	L	16.9 (65)	33.3 (45)	46.4 (28)	11.8 (34)	22.5 (89)	29.3 (75)
	H	33.3 (177)	37.3 (83)	24.5 (53)	2.8 (72)	27.6 (116)	31.4 (70)
		[0.013]	[0.651]	[0.045]	[0.082]	[0.404]	[0.784]
Subadults (%)	L	47.7 (65)	33.3 (45)	39.3 (28)	14.7 (34)	30.3 (89)	34.7 (75)
	H	38.5 (177)	41.0 (83)	67.9 (53)	12.5 (72)	25 0 (116)	37.1 (70)
		[0.133]	[0.734]	[0.013]	[0.975]	[0.493]	[0.895]
Adults (%)	L	35.4 (65)	33.3 (45)	14.3 (28)	73.5 (34)	47.2 (89)	36.0 (75)
	H	28.2 (177)	21.7 (83)	7.5 (53)	84.7 (72)	47.4 (116)	31.4 (70)
		[0.284]	[0.230]	[0.334]	[0.277]	[0.917]	[0.706]
Females in reproductive condition (%)[1]	L	3.8 (26)	6.7 (15)	0 (7)	33.3 (9)	32.1 (28)	0 (23)
	H	27.8 (54)	0 (20)	0 (14)	55.6 (27)	37.8 (37)	0 (23)
		[0.012]	[0.429]		[0.443]	[0.634]	
Males in reproductive condition (%)[2]	L	77.8 (27)	6.7 (15)	0 (9)	85.7 (21)	81.7 (43)	0 (30)
	H	46.9 (64)	0 (32)	0 (25)	97.6 (42)	78.3 (46)	0 (24)
		[0.007]	[0.319]		[0.104]	[0.513]	
Survival rate (%)[3]	L	20.0 (50)	20.0 (35)	30.0 (10)	14.3 (21)	21.8 (55)	
	H	20.7 (135)	10.0 (60)	13.8 (32)	21.4 (42)	12.8 (86)	
		[0.912]	[0.045]	[0 490]	[0.735]	[0.157]	
Sex ratio (% female)	L	51.5 (66)	48.9 (43)	39.3 (28)	32.4 (34)	40.2 (87)	52.1 (73)
	H	48.6 (179)	47.6 (84)	38.0 (50)	39.4 (71)	47.4 (106)	52.9 (68)
		[0.686]	[0.891]	[0.911]	[0.472]	[0.308]	[0.916]

[1]Only females >60 g.
[2]Only males >60 g.
[3]Survival rate was calculated as the proportion of animals a during census period that were recaptured during any subsequent census period.

Table 2. Seasonal changes in body and organ masses (mean ± SE) from low- and high-density cotton rat populations in central Oklahoma from August 1993 to November 1994. The number in brackets below each set of numbers is the P-value associated with comparisons between low-density and high-density populations.

Condition parameter	Density (L = low H = high)	August	November	February	May	August	November
Body mass (g)							
Juveniles	L	34.2 ± 7.3	45.3 ± 0.4	48.7 ± 2.6		29.7 ± 4.1	48.9 ± 2.4
	H	36.2 ± 0.6	45.9 ± 1.5	51.3 ± 1.5		36.8 ± 10.3	48.4 ± 7.0
		[0.650]	[0.870]	[0.367]		[0.149]	[0.734]
Adult and subadult females	L	106.9 ± 5.9	111.8 ± 4.2	91.4 ± 6.6	115.8 ± 11.7	108.4 ± 5.3	104.0 ± 6.6
	H	101.6 ± 0.6	82.1 ± 1.9	77.6 ± 2.3	120.2 ± 2.0	113.8 ± 4.4	95.1 ± 0.8
		[0.676]	[0.001]	[0.084]	[0.313]	[0.525]	[0.268]
Adult and subadult males	L	116.0 ± 9.4	92.0 ± 4.9	74.3 ± 1.1	126.0 ± 4.4	120.7 ± 8.9	99.1 ± 9.3
	H	104.5 ± 2.0	101.6 ± 3.8	89.4 ± 1.8	123.9 ± 3.1	121.1 ± 6.4	99.7 ± 12.5
		[0.147]	[0.153]	[0.007]	[0.476]	[0.688]	[0.936]
Reproductive females	L				163.5 ± 36.1	127.4 ± 8.3	
	H				132.7 ± 9.7	132.7 ± 5.6	
					[0.206]	[0.763]	
Reproductive males	L	125.5 ± 7.9			125.5 ± 5.1	103.9 ± 5.0	
	H	118.8 ± 10.2			124.5 ± 3.6	111.7 ± 0.9	
		[0.413]			[0.560]	[0.752]	
Organ mass							
Liver (g)	L	3.60 ± 0.42	3.48 ± 0.13	3.00 ± 0.05	5.55 ± 0.34	4.12 ± 0.21	3.49 ± 0.16
	H	3.21 ± 0.12	3.21 ± 0.16	2.79 ± 0.21	5.72 ± 0.06	4.15 ± 0.23	3.77 ± 0.09
		[0.035]	[0.024]	[0.092]	[0.546]	[0.602]	[0.166]
Spleen (mg)	L	160.2 ± 23.8	156.0 ± 27.5	72.4 ± 10.3	296.6 ± 12.0	182.9 ± 14.0	124.4 ± 3.8
	H	198.7 ± 3.3	127.3 ± 20.3	97.0 ± 6.5	286.2 ± 36.9	236.1 ± 7.8	156.4 ± 9.6
		[0.713]	[0.048]	[0.058]	[0.835]	[0.085]	[0.249]
Adrenals (mg)	L	29.7 ± 2.8	34.0 ± 4.6	22.5 ± 2.8	49.6 ± 6.4	32.3 ± 3.1	24.8 ± 2.0
	H	30.5 ± 1.4	22.3 ± 0.3	21.1 ± 0.1	52.0 ± 0.7	38.2 ± 1.7	30.8 ± 0.1
		[0.275]	[0.019]	[0.679]	[0.646]	[0.139]	[0.005]
Testes (g)	L	2.00 ± 0.17	0.14 ± 0.04	0.28 ± 0.02	2.45 ± 0.05	2.24 ± 0.18	0.09 ± 0.02
	H	1.73 ± 0.05	0.10 ± 0.01	0.18 ± 0.05	2.30 ± 0.12	1.88 ± 0.15	0.15 ± 0.01
		[0.113]	[0.722]	[0.130]	[0.102]	[0.095]	[0.091]

Table 3. Seasonal changes in measures of diet quality (mean ± SE) from low- and high-density cotton rat populations in central Oklahoma from November 1993 to November 1994. The number in brackets below each set of numbers is the P-value associated with comparisons between low-density and high-density populations.

Nutrient category	Density (L = low H = high)	November	February	May	August	November
Wet mass (g)	L	2.79 ± 0.69	3.41 ± 0.83	3.21 ± 1.04	2.43 ± 0.24	3.94 ± 1.30
	H	3.08 ± 0.66	7.03 ± 0.19	3.81 ± 0.34	2.55 ± 0.17	2.67 ± 0.61
		[0.544]	[0.001]	[0.322]	[0.680]	[0.231]
Dry mass (g)	L	0.89 ± 0.26	0.83 ± 0.23	0.80 ± 0.34	0.60 ± 0.02	0.92 ± 0.20
	H	0.77 ± 0.17	1.17 ± 0.38	0.78 ± 0.07	0.75 ± 0.10	0.75 ± 0.27
		[0.971]	[0.637]	[0.803]	[0.569]	[0.215]
Moisture content (%)	L	73.0 ± 1.8	74.6 ± 1.3	77.0 ± 0.5	76.0 ± 2.6	77.3 ± 2.8
	H	74.4 ± 0.1	90.5 ± 1.4	81.4 ± 2.5	72.7 ± 0.7	78.5 ± 0.8
		[0.568]	[< 0.001]	[0.009]	[0.302]	[0.616]
Fat content (% dry mass)	L	5.7 ± 1.5	6.7 ± 3.4	5.3 ± 1.4	10.4 ± 2.3	10.1 ± 3.7
	H	5.5 ± 2.1	2.1 ± 0.6	8.2 ± 2.1	16.3 ± 2.4	8.5 ± 1.9
		[0.678]	[< 0.001]	[0.703]	[0.649]	[0.740]
Crude protein (% dry mass)	L	21.3 ± 6.5	17.6 ± 1.1	18.5 ± 2.8	18.7 ± 1.5	20.1 ± 2.3
	H	19.5 ± 3.3	16.2 ± 0.2	24.1 ± 0.8	27.2 ± 1.2	15.8 ± 0.7
		[0.636]	[0.402]	[0.045]	[0.004]	[0.028]

Table 3. (cont.)

Nutrient category	Density (L = low H = high)	November	February	May	August	November
Non-essential amino acids (% dry mass)						
Aspartic acid	L	2.27 ± 0.61	2.04 ± 0.14	1.90 ± 0.28	1.89 ± 0.21	2.25 ± 0.20
	H	2.19 ± 0.25	2.08 ± 0.05	2.61 ± 0.03	2.53 ± 0.04	1.79 ± 0.11
		[0.770]	[0.967]	[0.066]	[0.025]	[0.057]
Glutamic acid	L	3.43 ± 1.02	2.35 ± 0.25	2.61 ± 0.50	2.43 ± 0.18	3.08 ± 0.41
	H	3.17 ± 0.48	1.64 ± 0.05	3.65 ± 0.12	4.77 ± 0.20	2.11 ± 0.08
		[0.538]	[0.016]	[0.008]	[< 0.001]	[0.020]
Serine	L	0.93 ± 0.36	0.72 ± 0.04	0.92 ± 0.09	0.86 ± 0.08	0.87 ± 0.12
	H	0.79 ± 0.13	0.55 ± 0.00	1.17 ± 0.06	1.28 ± 0.05	0.65 ± 0.03
		[0.940]	[0.026]	[0.098]	[0.011]	[0.027]
Glycine	L	1.15 ± 0.25	0.87 ± 0.05	1.03 ± 0.16	1.01 ± 0.07	1.11 ± 0.16
	H	0.90 ± 0.18	0.73 ± 0.03	1.42 ± 0.05	1.49 ± 0.03	0.82 ± 0.07
		[0.054]	[0.140]	[0.037]	[0.154]	[0.003]
Alanine	L	1.05 ± 0.27	0.97 ± 0.13	1.09 ± 0.25	1.15 ± 0.16	1.05 ± 0.17
	H	1.09 ± 0.21	0.77 ± 0.01	1.45 ± 0.19	1.78 ± 0.23	0.92 ± 0.03
		[0.825]	[0.068]	[0.027]	[< 0.001]	[0.234]
Proline	L	1.40 ± 0.18	0.96 ± 0.06	1.29 ± 0.32	1.13 ± 0.12	1.22 ± 0.12
	H	1.23 ± 0.08	0.76 ± 0.02	1.41 ± 0.05	1.78 ± 0.17	0.92 ± 0.07
		[0.459]	[0.024]	[0.408]	[< 0.001]	[0.021]
Total essential amino acids (% dry mass)	L	9.77 ± 3.51	8.04 ± 0.40	8.84 ± 1.24	8.86 ± 0.90	9.37 ± 1.37
	H	8.51 ± 1.82	5.72 ± 0.09	12.25 ± 0.48	13.24 ± 0.68	7.00 ± 0.57
		[0.496]	[0.015]	[0.019]	[0.006]	[0.019]
Nonprotein nitrogen (% of total N pool)	L	5.5 ± 0.8	7.6 ± 1.6	5.2 ± 0.7	6.7 ± 1.3	5.9 ± 2.7
	H	11.9 ± 1.3	26.0 ± 0.3	2.9 ± 0.2	3.9 ± 0.1	11.1 ± 1.5
		[0.111]	[0.004]	[0.195]	[0.168]	[0.012]

Table 4. Coefficients used to calculate canonical variate scores for cotton rat digesta composites collected seasonally from low- and high-density populations.

	Canonical variate				
Variable	November	February	May	August	November
Lysine	0.232	-0.030	0.154	-0.120	-0.216
Phenylalanine + tyrosine	-0.229	0.701	-0 153	0.075	-0.241
Methionine + cystine	0.600	-0.256	0.272	0.057	-0 200
Valine	-0.574	0.750	-0.266	0.552	-0.177
Isoleucine	0.495	-0.506	-0.184	-0.175	0 628
Leucine	-0.088	-1.000	0.716	0.093	0 071
Histidine	-0.122	-0.194	-0.192	0.080	-0.144
Arginine	-0.114	1.412	0.130	-0.010	0.674
Threonine	0.158	-0.111	-0.199	-0.370	-0.170

Figure 1. Mean percent cover of categories of vegetation measured seasonally in habitats supporting low (white) and high (black) population densities of cotton rats. Within each season, statistically significant differences between low- and high-density sites are indicated by '+' = $\underline{P} < 0.10$, '$_{\star}$' = $\underline{P} < 0.05$, '$_{\star\star}$' = $\underline{P} < 0.01$

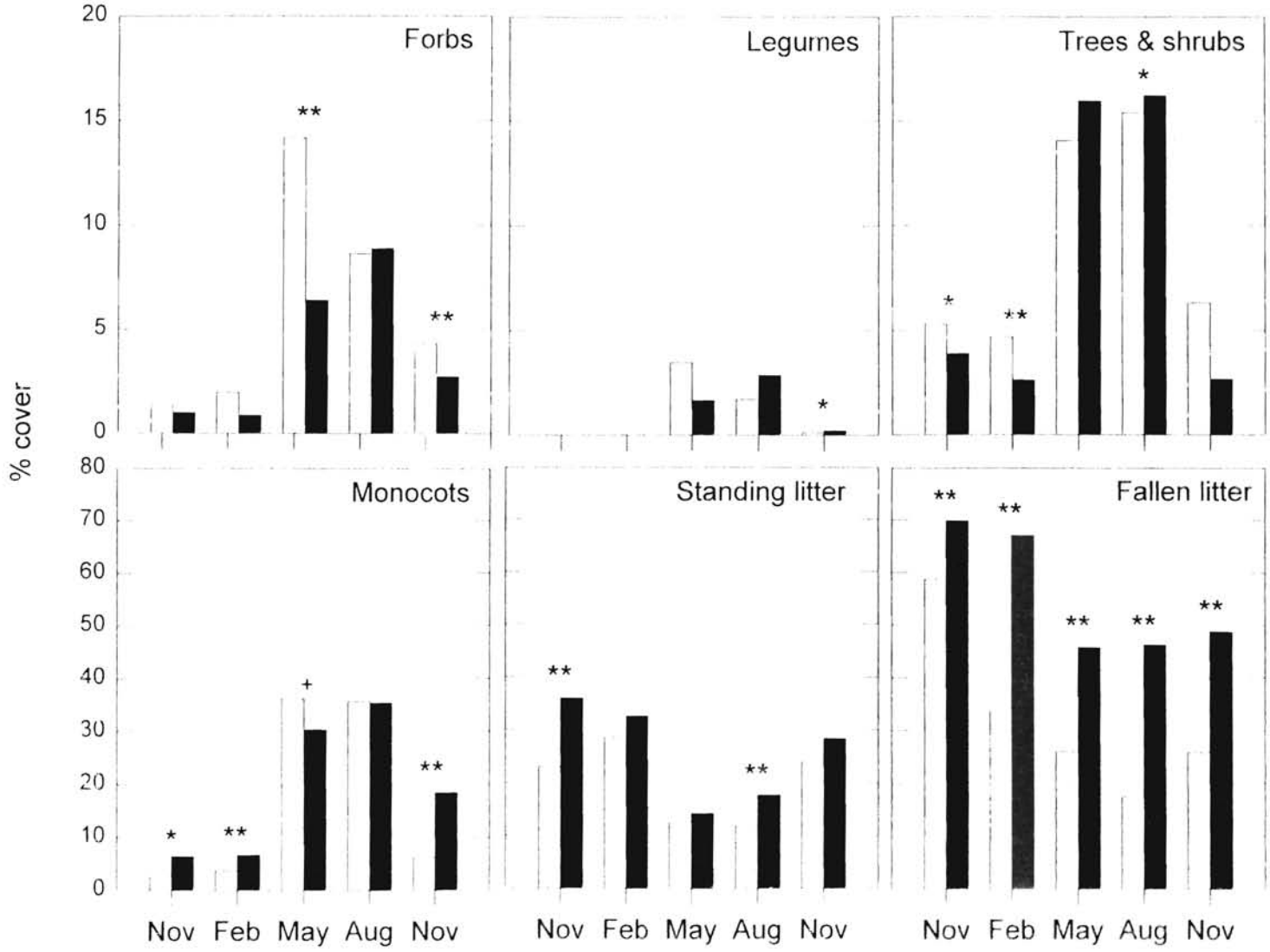

Forbs
Legumes
Trees & shrubs
Monocots
Standing litter
Fallen litter
% cover
Nov Feb May Aug Nov

Figure 2. Mean biomass of monocots and non-woody dicots in habitats supporting low (white) and high (black) population densities of cotton rats. Within each season, differences between low- and high-density sites are indicated by '+' = $\underline{P} < 0.10$, '$_{\star}$' = $\underline{P} < 0.05$, '$_{\star\star}$' = $\underline{P} < 0.01$

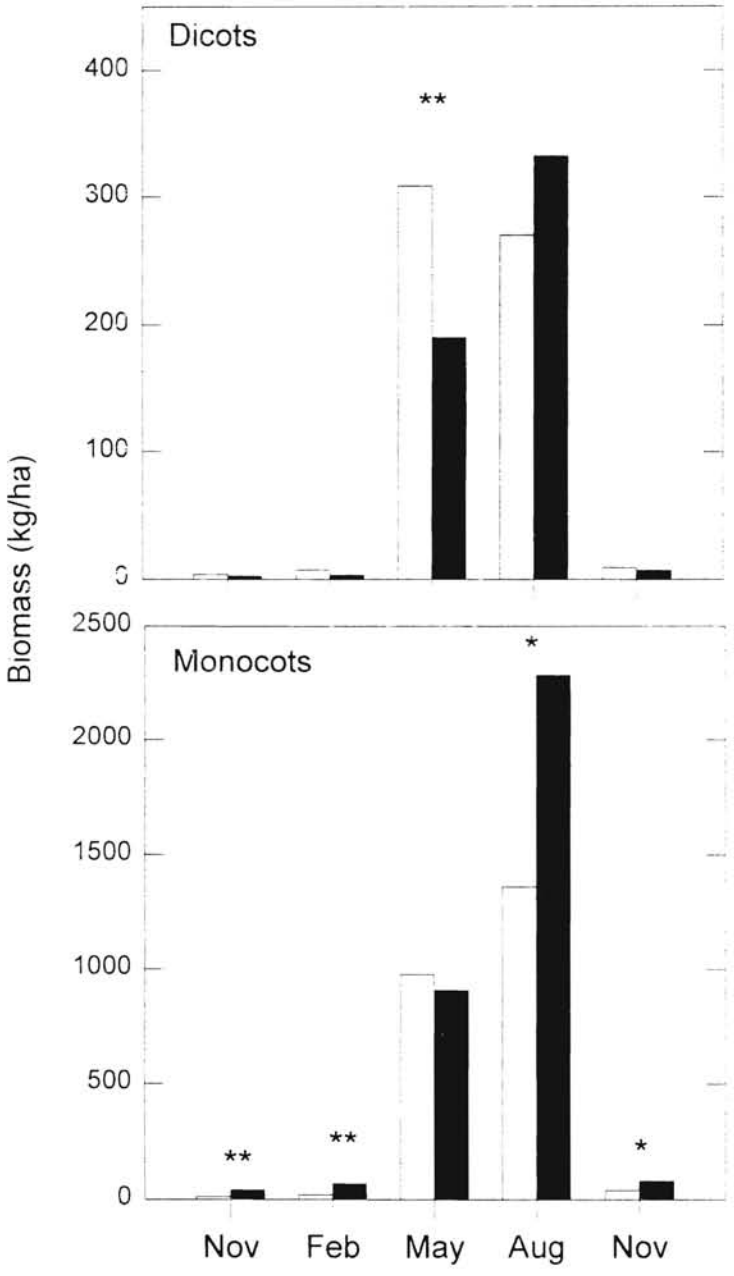

Dicots
400
300
200
100
0
**
Monocots
2500
2000
1500
1000
500
0
**
**
*
*
Biomass (kg/ha)
Nov
Feb
May
Aug
Nov

Figure 3. Seasonal fluctuations in density (± SE) of two high-density (■), and five low-density (○) cotton rat populations in central Oklahoma (a), and changes in mean density (± SE) of populations designated as high-density and low-density sites (b).

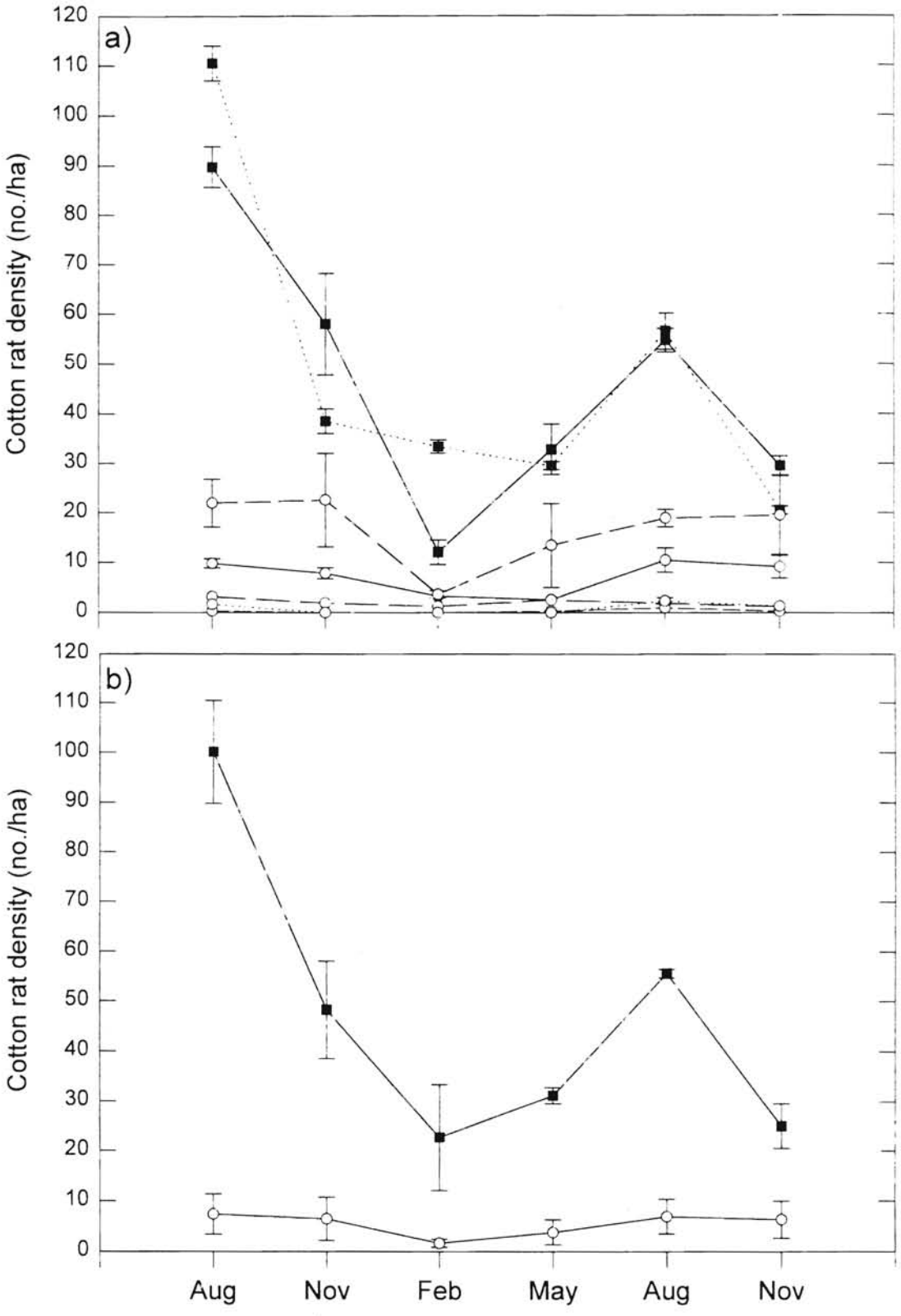

a)
b)
Cotton rat density (no./ha)
Cotton rat density (no./ha)
120
110
100
90
80
70
60
50
40
30
20
10
0
Aug
Nov
Feb
May
Aug
Nov

Figure 4. General composition of the diets of cotton rats collected seasonally from high density and low density populations in central Oklahoma. M = monocot vegetation, D = dicot vegetation, S = all seeds except legumes, L = legume seeds, A = arthropods, O = other (includes fungi and unidentified fragments). Within each season, differences ($P < 0.05$) between high- and low-density populations are indicated by '$\star$' above the value which is significantly greater.

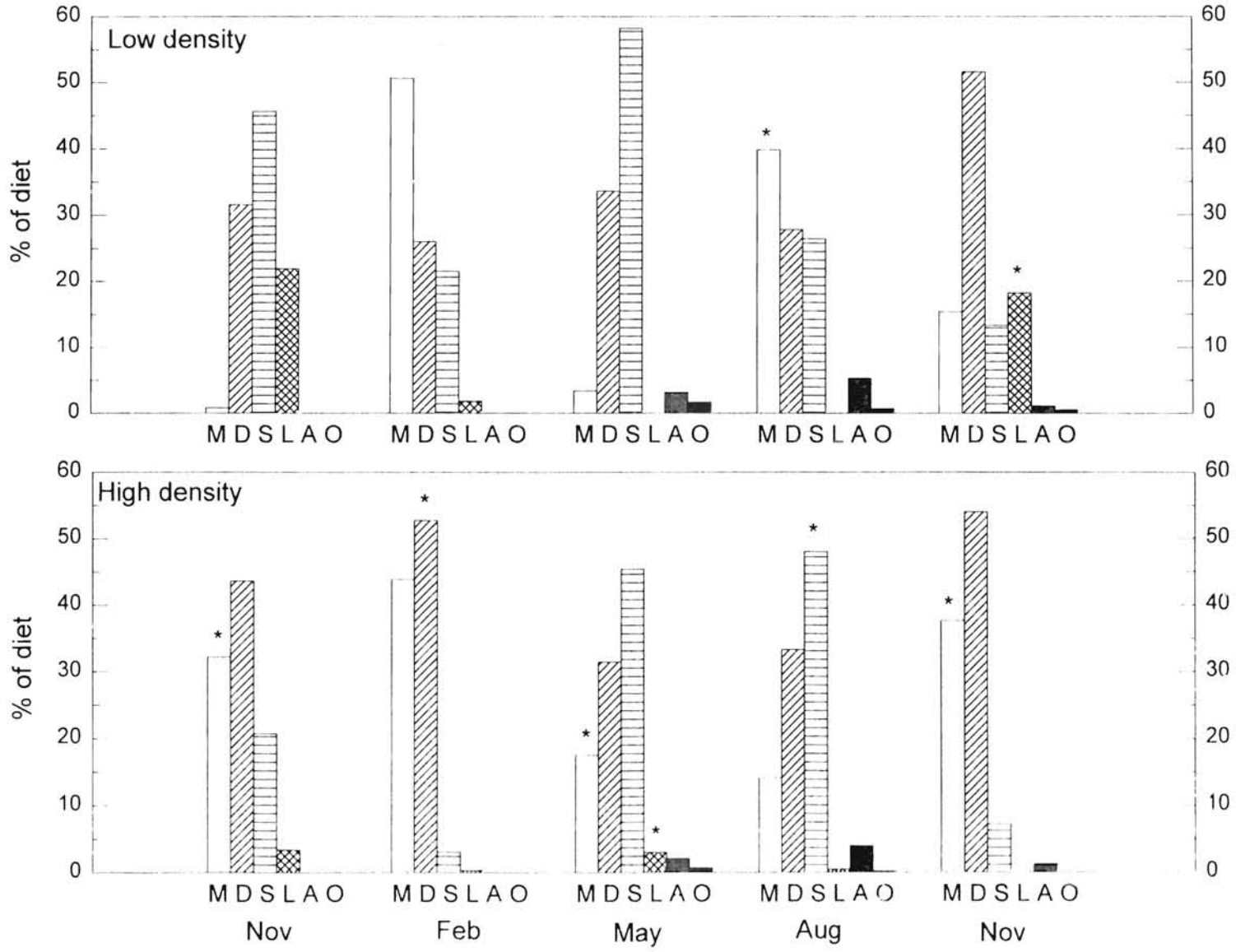

Low density
High density
% of diet
60
50
40
30
20
10
0
M D S L A O
Nov
Feb
May
Aug
Nov

Figure 5. Mean (± SE) concentrations of total phenolics (measured in gallic acid equivalents per gram) in diets of cotton rats collected seasonally from high density (■) and low density (○) populations in central Oklahoma. Within each season, differences ($P < 0.01$) between low and high density populations are indicated by '**'.

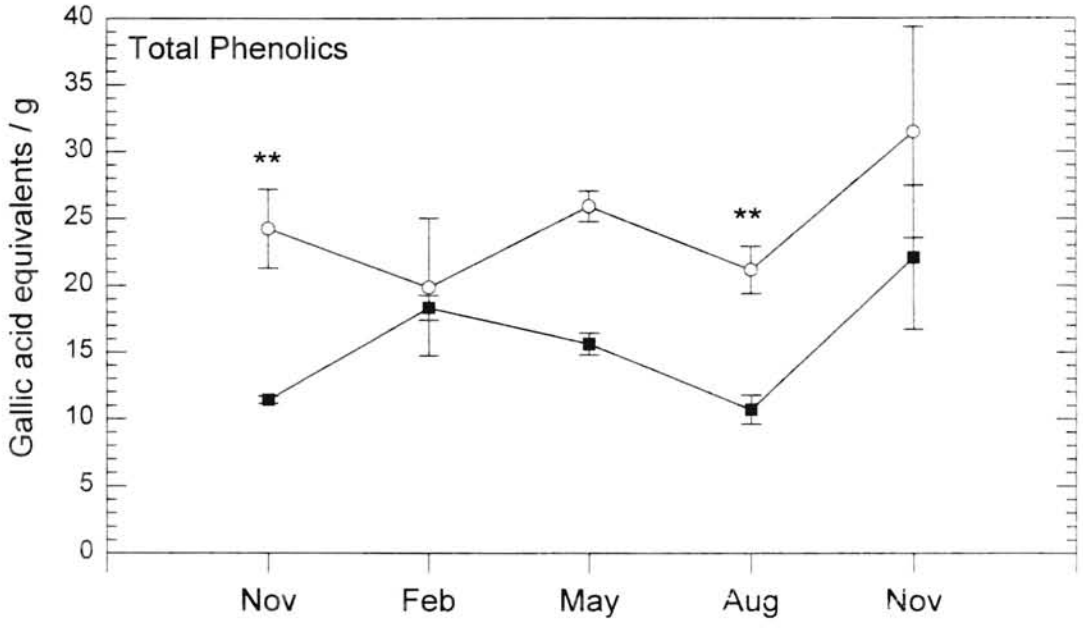

Total Phenolics
Gallic acid equivalents / g
40
35
30
25
20
15
10
5
0
**
**
Nov
Feb
May
Aug
Nov

Figure 6. Mean (± SE) concentrations of lysine, phenylalanine + tyrosine, and methionine + cystine in diets of cotton rats collected seasonally from high-density (■) and low-density (○) populations in central Oklahoma. Within each season, differences between high- and low-density populations are indicated by '+' = $P < 0.10$, '$_{\star}$' = $P < 0.05$, '$_{\star\star}$' = $P < 0.01$. The dotted line represents the level of nutrient concentration that meets the requirement for growth and reproduction in the laboratory rat (Natural Research Council 1995).

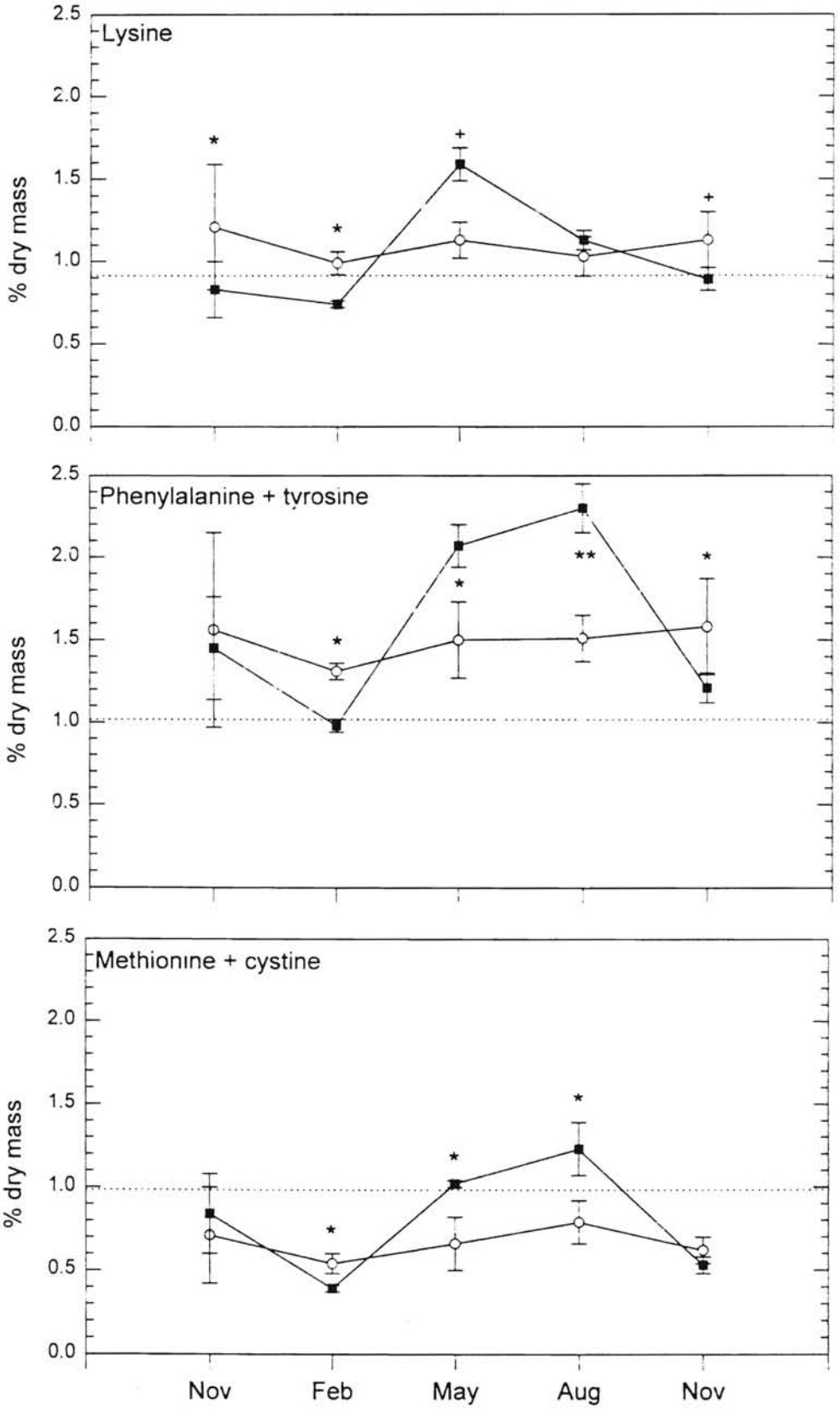

Lysine
Phenylalanine + tyrosine
Methionine + cystine
% dry mass
2.5
2.0
1.5
1.0
0.5
0.0
Nov
Feb
May
Aug
Nov

Figure 7. Mean (± SE) concentrations of valine, isoleucine, and leucine in diets of cotton rats collected seasonally from high-density (■) and low-density (○) populations in central Oklahoma. Within each season, differences between high- and low-density populations are indicated by '+' = $\underline{P} < 0.10$, '$\star$' = $\underline{P} < 0.05$, '$\star\star$' = $\underline{P} < 0.01$. The dotted line represents the level of nutrient concentration that meets the requirement for growth and reproduction in the laboratory rat (Natural Research Council 1995).

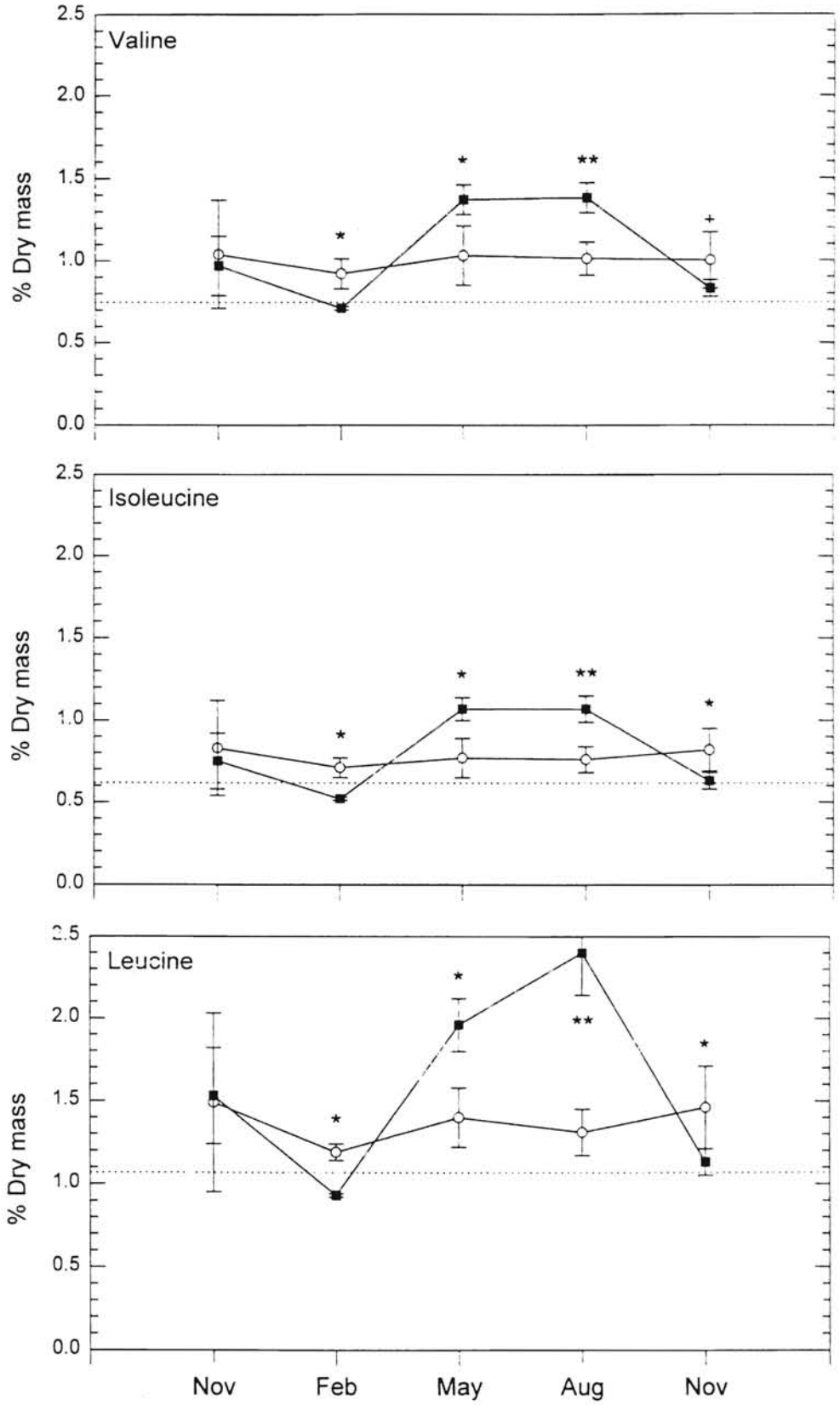

Valine
Isoleucine
Leucine
% Dry mass
2.5
2.0
1.5
1.0
0.5
0.0
Nov
Feb
May
Aug
Nov

Figure 8. Mean (± SE) concentrations of histidine, arginine, and threonine in diets of cotton rats collected seasonally from high-density (■) and low-density (○) populations in central Oklahoma. Within each season, differences between high- and low-density populations are indicated by '+' = $\underline{P} < 0.10$, '$_{\star}$' = $\underline{P} < 0.05$, '$_{\star\star}$' = $\underline{P} < 0.01$. The dotted line represents the level of nutrient concentration that meets the requirement for growth and reproduction in the laboratory rat (Natural Research Council 1995).

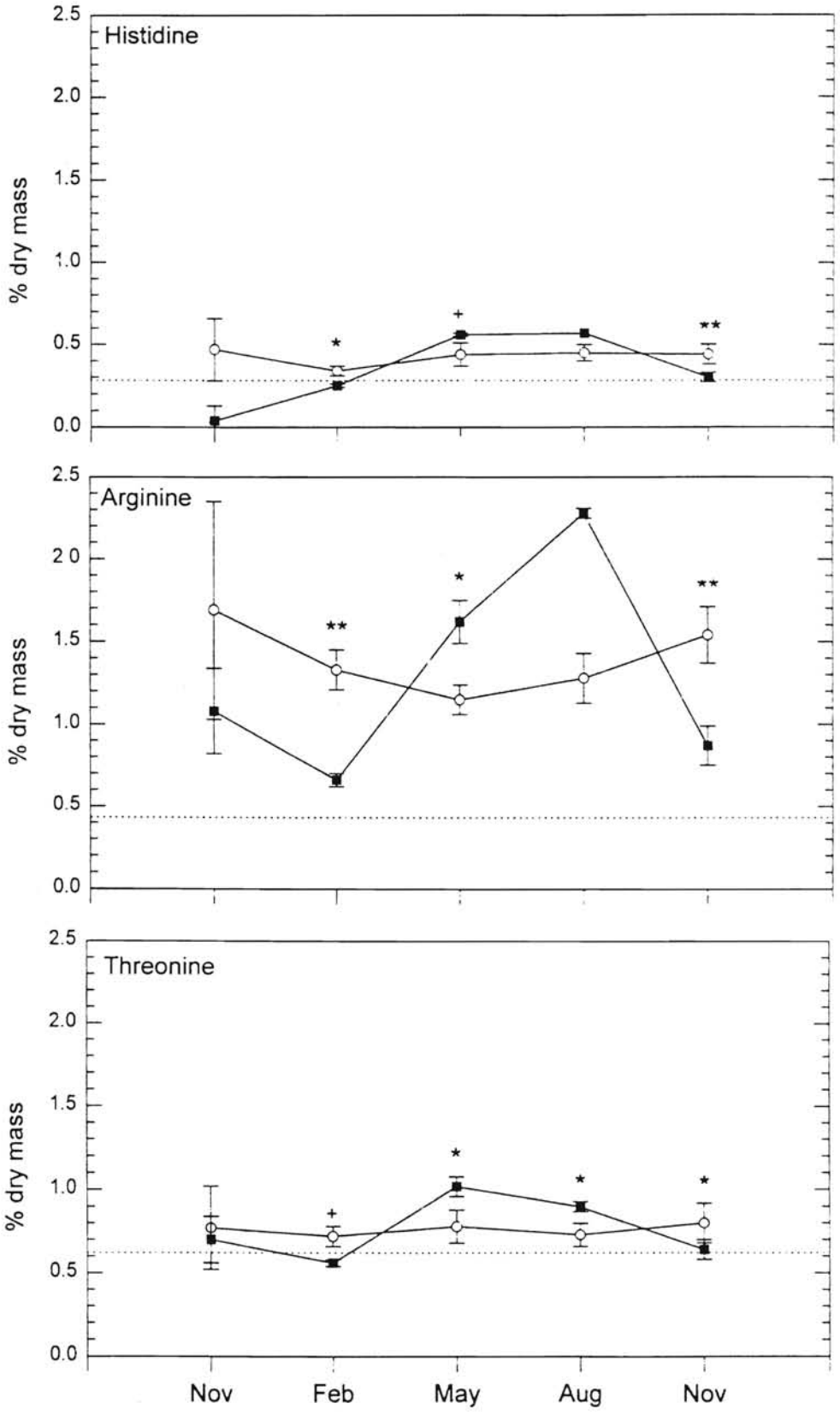

Histidine
Arginine
Threonine
% dry mass
2.5
2.0
1.5
1.0
0.5
0.0
Nov
Feb
May
Aug
Nov

Figure 9. Plot of canonical scores of amino acid composition in digesta composites from cotton rats collected seasonally from high-density (open triangle) and low-density (open circle) populations. The canonical variate is a linear combination of nine essential amino acids. P indicates statistical significance of Mahalanobis distances between centroids of digesta composites in high- versus low-density populations.

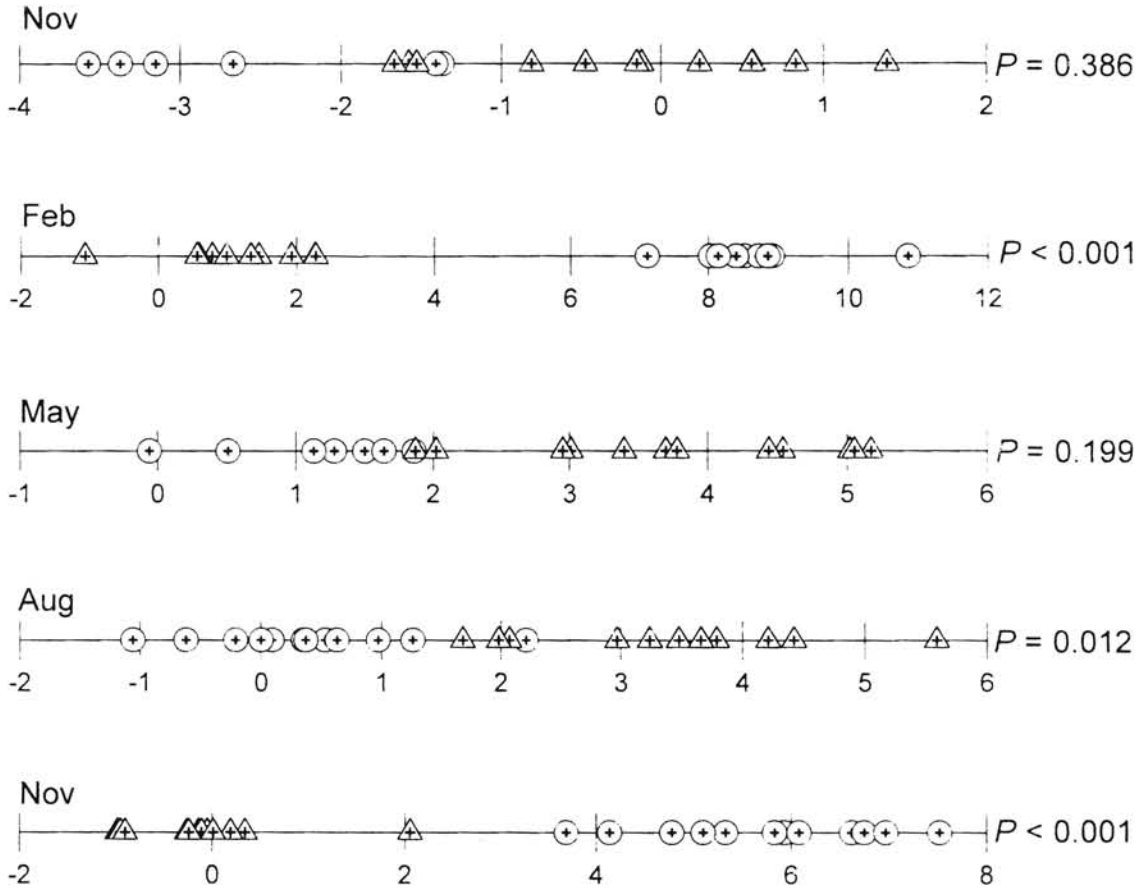
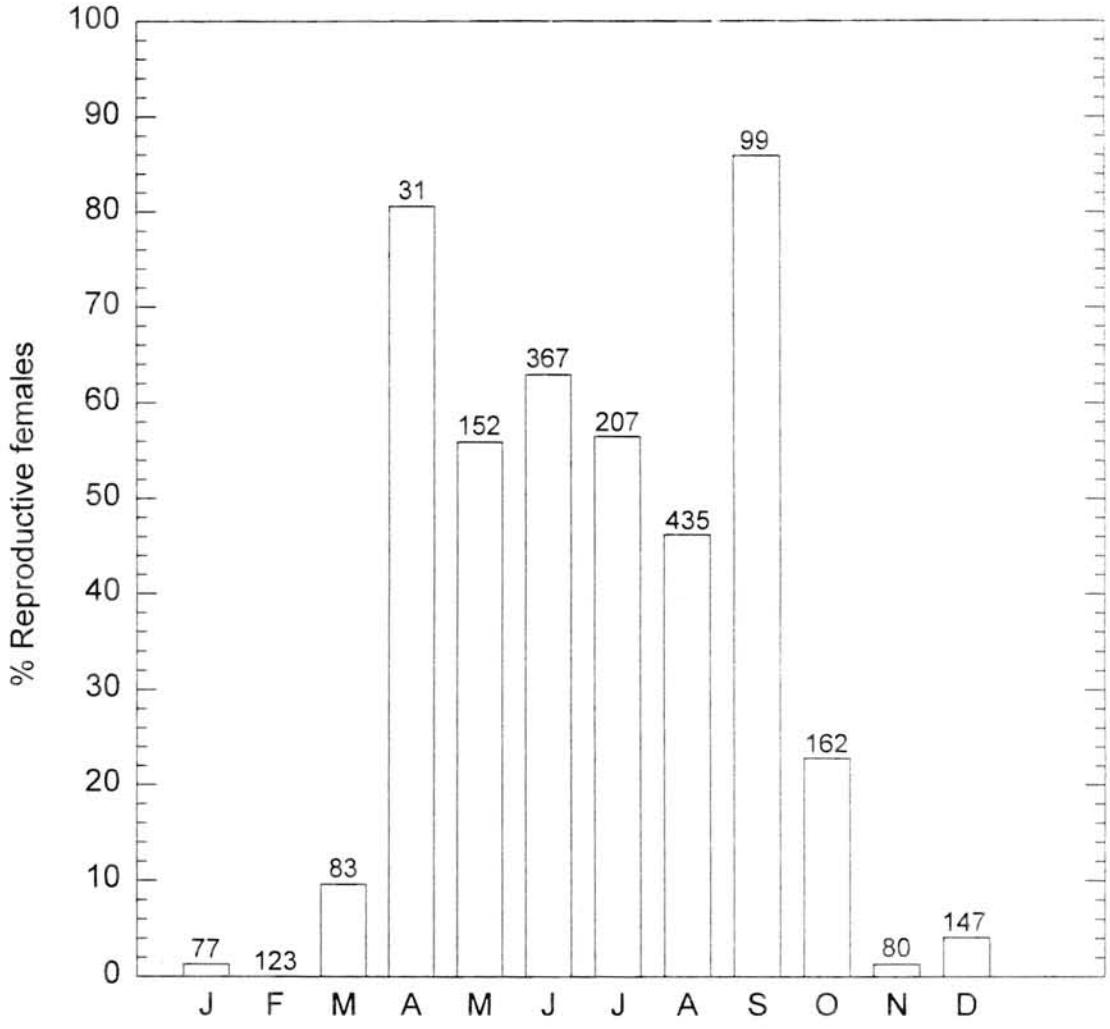

Nov
P = 0.386
-4
-3
-2
-1
0
1
2
Feb
P < 0.001
-2
0
2
4
6
8
10
12
May
P = 0.199
-1
0
1
2
3
4
5
6
Aug
P = 0.012
-2
-1
0
1
2
3
4
5
6
Nov
P < 0.001
-2
0
2
4
6
8
Canonical variate
Low density
High density

Figure 10. Annual cycle of reproductive activity for adult (> 60 g) female cotton rats. Females were considered reproductively active if pregnant or lactating. Animals were included from the present study, McMurry (1993), McMurry et al. (1994), and Lochmiller unpublished data. Numbers of females included during each month are indicated above the bars.


% Reproductive females
100
90
80
70
60
50
40
30
20
10
0
77
123
83
31
152
367
207
435
99
162
80
147
J
F
M
A
M
J
J
A
S
O
N
D

APPENDIX I

Seasonal fluctuations in small mammal populations (minimum number known alive) on live-trapping grids supporting low-density (grids 1-5) and high-density (grids 6 and 7) populations of cotton rats[1].

		Trapping grid						
		Low density					High density	
	Season	1	2	3	4	5	6	7
Reithrodontomys fulvescens	August	6	16	7	0	0	5	2
	November	2	15	7	0	2	13	16
	February	13	11	11	0	0	2	14
	May	8	10	10	0	1	9	7
	August	17	16	8	1	1	4	0
	November	29	7	12	1	3	16	17
Reithrodontomys montanus	August	0	2	1	0	0	0	0
	November	1	2	1	0	0	0	0
	February	3	2	2	0	2	0	0
	May	1	1	1	0	0	0	0
	August	2	5	0	0	0	0	0
	November	0	0	0	0	0	0	0
Peromyscus leucopus	August	0	0	0	2	0	0	0
	November	0	1	0	1	1	0	7
	February	0	0	1	0	0	0	17
	May	1	2	13	4	8	0	20
	August	0	0	7	4	4	1	16
	November	0	1	9	4	5	5	15
Peromyscus maniculatus	August	0	0	0	0	0	0	0
	November	0	0	0	0	0	0	0
	February	0	0	3	6	0	0	0
	May	0	0	0	1	0	3	8
	August	0	0	0	1	0	3	2
	November	0	2	1	1	1	5	6
Microtus spp.[2]	August	3	0	0	0	0	0	0
	November	1	0	0	0	0	1	0
	February	2	0	0	0	0	0	0
	May	1	0	0	0	0	2	0
	August	2	0	0	0	0	5	0
	November	3	0	0	0	1	0	0
Chaetodipus hispidus	August	0	0	0	1	0	0	2
	November	0	0	0	0	1	0	0
	February	0	0	0	0	0	0	0
	May	0	0	0	0	0	0	1
	August	0	0	0	0	0	1	4
	November	0	0	0	0	1	0	1

[1]Other small mammals captured during some seasons were Mus musculus (grids 1 and 7; 2 captures total), Neotoma floridana (grids 3 and 5; 8 captures total), Blarina hylophaga (grids 4, 6 and 7; 8 captures total), and Cryptotis parva (grid 7; 2 captures total).

[2]M. ochrogaster occurred on grid 1, M. pinetorum occurred on grids 5 and 6

APPENDIX II

Percent relative cover (± SE), percent (± SE) of diet and preference index (± SE) for categories, and genera and species of plants identified in the diets of cotton rats collected seasonally from low- and high-density populations. PI values for genera and species were only calculated for sites where they were found in the habitat.

	Low-density			High-density		
	% Cover	% Diet	P.I.	% Cover	% Diet	P.I.
November 1993						
Monocots	45.6 ± 15.1	42.8 ± 11.3	0.98 ± 0.12	55.1 ± 7.9	51.0 ± 1.4	0.95 ± 0.16
Forbs	19.6 ± 4.1	31.7 ± 16.7	1.48 ± 0.59	8.8 ± 0.5	45.3 ± 2.4	5.17 ± 0.54
Legumes[1]	3.6 ± 1.5	21.9 ± 21.9	14.62 ± 14.62	4.5 ± 1.7	3.8 ± 3.8	0.61 ± 0.61
Shrubs and trees	33.9 ± 12.4	3.6 ± 2.5	0.31 ± 0.28	36.1 ± 8.3	0 ± 0	0 ± 0
Achillea millefolium	2.1 ± 0.2	0.4 ± 0.4	0.18 ± 0.18	0.8 ± 0.2	0.2 ± 0.2	0.21 ± 0.21
Ambrosia psilostachya[1]	3.2 ± 1.6	0 ± 0	0 ± 0	3.7 ± 2.5	0.9 ± 0.9	0.14 ± 0.14
Bromus spp.	11.0 ± 3.7	0.4 ± 0.4	0.03 ± 0.03	46.3 ± 3.7	39.9 ± 1.5	0.87 ± 0.10
Juniperus virginiana	39.1 ± 2.4	1.2 ± 1.2	0.04 ± 0.04			
Lespedeza cuneata[1]	1.8 ± 0.3	21.9 ± 21.9	15.67 ± 15.67			
Panicum oligosanthes	21.1 ± 7.8	0.6 ± 0.6	0.04 ± 0.04	1.1	0	0
Rhus copallina	2.3 ± 0.4	4.3 ± 4.3	1.58 ± 1.58			
Sorghum halapense[1]				45.2 ± 2.5	0.5 ± 0.5	0.01 ± 0.01
Sporobolus asper[1]	12.5 ± 2.6	41.9 ± 11.6	3.26 ± 0.24			
February 1994						
Monocots	39.3 ± 2.7	51.3 ± 4.9	1.33 ± 0.23	79.2 ± 8.8	45.3 ± 12.8	0.56 ± 0.10
Forbs	16.0 ± 1.2	26.7 ± 4.6	1.48 ± 0.59	7.0 ± 0.5	52.2 ± 12.3	7.41 ± 1.29
Legumes	0 ± 0	1.8 ± 1.8		0 ± 0	2.4 ± 0.7	
Shrubs and trees	44.7 ± 2.9	20.2 ± 11.0	0.47 ± 0.24	13.9 ± 8.3	0.1 ± 0.1	0.02 ± 0.02
Achillea millefolium	3.5 ± 2.6	2.8 ± 2.8	0.46 ± 0.46	0.4 ± 0.2	0.8 ± 0.4	6.41 ± 5.80
Bromus spp.	12.4 ± 9.0	17.5 ± 12.7	1.93 ± 0.55	72.6 ± 4.7	41.1 ± 15.1	0.56 ± 0.18
Carex spp.	6.1 ± 1.9	2.1 ± 0.6	0.44 ± 0.18	1.5 ± 1.4	0.7 ± 0.7	7.15 ± 7.15
Geranium sp.	2.5 ± 1.8	0 ± 0	0 ± 0	1.1 ± 0.1	0.4 ± 0.1	0.32 ± 0.01
Juncus sp.	4.4 ± 4.3	0.4 ± 0.4	3.65 ± 3.65			
Juniperus virginiana	42.7 ± 6.0	18.9 ± 18.9	0.52 ± 0.52			
Lespedeza cuneata	0 ± 0	5.4				
Panicum oligosanthes	13.7 ± 3.8	37.0 ± 7.7	2.36 ± 1.10	0.1 ± 0	0.4 ± 0.2	4.35 ± 1.45
Rhus glabra	2.9 ± 1.5	11.5 ± 11.5	2.65 ± 2.65	13.3 ± 7.7	0.1 ± 0.1	0.02 ± 0.02
Solidago sp.	2.5 ± 1.8	7.0 ± 7.0	1.63 ± 1.63			
Sorghum halapense				0	1.4	
Sporobolus asper	12.5 ± 2.6	41.9 ± 11.6	3.26 ± 0.24			

APPENDIX II (cont.)

	Low-density			High-density		
	% Cover	% Diet	P.I.	% Cover	% Diet	P.I.
May 1994						
Monocots	60.4 ± 15.4	27.2 ± 15.1	0.55 ± 0.23	55.7 ± 0.3	47.2 ± 13.1	0.85 ± 0.24
Forbs	9.2 ± 0.4	67.8 ± 16.2	6.49 ± 2.23	11.5 ± 1.8	40.3 ± 5.4	3.53 ± 0.09
Legumes	4.6 ± 3.3	0.2 ± 0.2	0.03 ± 0.03	2.7 ± 2.1	9.9 ± 8.5	3.14 ± 0.67
Shrubs and trees	24.1 ± 10.7	0 ± 0	0 ± 0	30.1 ± 4.3	0 ± 0	0 ± 0
Artemisia ludoviciana	1.1 ± 0.8	0 ± 0	0 ± 0	3.5 ± 2.7	1.1 ± 1.1	0.18 ± 0.18
Bromus spp.	3.3 ± 2.0	7.4 ± 6.8	1.59 ± 1.11	13.9 ± 5.8	21.5 ± 0.6	1.84 ± 0.72
Croton sp.	0.1	3.9	38.60			
Euphorbia sp.				0.6 ± 0.5	11.9 ± 11.5	13.71 ± 9.71
Geranium sp.	0.1	1.2	12.10			
Panicum oligosanthes	2.6 ± 1.1	17.3 ± 10.8	10.22 ± 8.49	2.0	7.5	3.83
Sorghum halapense				29.8 ± 15.7	21.6 ± 17.0	0.59 ± 0.26
August 1994						
Monocots	59.3 ± 8.7	40.9 ± 13.7	0.61 ± 0.20	55.8 ± 1.1	39.4 ± 6.7	0.71 ± 0.14
Forbs	15.6 ± 1.7	52.7 ± 15.8	3.86 ± 1.67	14.0 ± 0.9	55.7 ± 8.1	4.03 ± 0.83
Legumes	3.5 ± 1.1	0.1 ± 0.1	0 05 ± 0.05	4.5 ± 1.7	0.9 ± 0.1	0.25 ± 0.10
Shrubs and trees	21.7 ± 10.4	0.3 ± 0.3	0.02 ± 0.02	25.7 ± 1.5	0 ± 0	0 ± 0
Andropogon gerardii	11.7 ± 4.7	24.1 ± 9.59	1.70 ± 0.59			
Artemisia ludoviciana	0.7 ± 0.5	0 ± 0	0 ± 0	4.9 ± 0.8	2.2 ± 2.2	0.54 ± 0.54
Bromus spp.	0 ± 0	0.8 ± 0.7		0 ± 0	0.8 ± 0.2	
Chenopodium album	0.6	23.8	39.68			
Croton sp.	0.2 ± 0.1	0 ± 0		0.9	2.8	3.21
Geranium sp.	0.1	0.4	3.60			
Rhus glabra	2.3 ± 0.4	4.3 ± 4.3	1.58 ± 1.58	21.2 ± 1.3	0 ± 0	0 ± 0
Sorghastrum nutans	6.1 ± 1.9	1.1 ± 0.6	0.12 ± 0.07	0.3 ± 0.1	0 ± 0	0 ± 0
Sorghum halapense				45.2 ± 2.5	0.5 ± 0.5	0.01 ± 0.01
Sporobolus asper	12.5 ± 2.6	41.9 ± 11.6	3.26 ± 0.24			

APPENDIX II (cont.)

	Low density			High density		
	% Cover	% Diet	P.I.	% Cover	% Diet	P.I.
November 1994						
Monocots	41.7 ± 8.5	25 2 ± 10.5	1.14 ± 0.77	76.1 + 2 3	39.8 ± 0	0 53 + 0.02
Forbs	31.4 ± 9.7	52.4 ± 16.1	2.64 ± 0 85	11.3 + 0.6	53.4 ± 4.4	4.77 ± 0.66
Legumes[1]	2.9 ± 1.0	18.9 ± 12.2	5.85 ± 3.54	4 5 ± 1 7	0.6 ± 0.6	0.09 ± 0.09
Shrubs and trees	28.1 ± 11.2	2.3 ± 2.3	0.28 ± 0 28	11.9 + 3 7	5.1 ± 5.1	0.62 ± 0.62
Artemisia ludoviciana	1.0 ± 0 5	6.0 ± 5.3	6.08 + 4.48	2.7 ± 2 2	4.9 ± 4.9	1.01 + 1.01
Bromus spp.	14.1 ± 6.4	6.3 ± 4.4	2.86 + 1.71	73.3 + 2.2	37.5 ± 1.6	0.52 ± 0.04
Juniperus virginiana	34.7 ± 13.2	3.9 ± 3.9	0.46 ± 0.46			
Lespedeza cuneata[1]	1.7 ± 0.3	31.5 ± 17.1	21.12 ± 11.64			
Panicum oligosanthes	10.2 ± 5.6	5.0 ± 5.0	2.64 ± 2.64	0.5 ± 0 1	0.1 ± 0.1	0.11 ± 0.11
Plantago sp.				0.4	1.2	2.74
Rhus glabra	3.3 ± 0.5	0 ± 0	0 + 0	11.7 + 3.4	5.1 ± 5.1	0.62 ± 0.62
Solidago sp.	10.0 ± 9.2	0.1 ± 0.1	0.06 ± 0.06			
Sorghastrum nutans	0 ± 0	1.7 ± 1.5				
Sorghum halapense				0	0.1	
Sporobolus asper[1]	12.5 ± 2.6	18.8 ± 4.0	1.84 ± 1.01			

[1]Percent cover from August 1994 was used to estimate available cover in November when seeds were consumed.

VITA

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