Influence of Acorn Use on Nutritional Status and Reproduction of Deer in the Southern Appalachians

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Abstract: We examined the influence of acorn abundance on fall and winter diets and on nutritional and reproductive status of white-tailed deer (*Odocoileus virginianus*) in the Southern Appalachians from 1983 to 1988. When acorns were abundant, they dominated the diet; when they were scarce, leaves of broadleaf evergreen species, primarily rosebay rhododendron (*Rhododendron maximum*), largely replaced acorns in the diet. When acorn production was poor, kidney fat indices in winter were significantly lower for most sex and age classes. Also, reproductive rates of yearling does were significantly lower, and conception dates were significantly later when acorns were scarce. Reproductive rates of adults were not appreciably affected by acorn abundance. Because acorn abundance is largely independent of deer density, the important role of acorns in deer nutrition presents special problems in deer management.

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Acorns are an important food of white-tailed deer over much of the eastern United States (Duvendeck 1962, Korschgen 1962, Harlow and Hooper 1971). When available, acorns comprise a significant portion of the diet throughout the fall and winter. However, acorn production varies greatly from year to year (Downs and McQuilkin 1944, Beck 1977), and in some years the supply is depleted by early winter.

There have been no comprehensive studies of the effects of seasonal and annual abundance of acorns on deer nutrition, reproduction, and population dynamics. The few studies dealing with the subject have involved only data from the fall months

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before effects of varying acorn abundance are clearly manifested. For example, Harlow et al. (1975) observed significant differences in both dietary composition and nutritional quality of foods eaten by deer between years of acorn abundance and scarcity in the Ridge and Valley province of Virginia. However, their study revealed no significant difference in the physical condition of the deer related to the mast crop. The authors concluded that any effects of acorns in the diet on condition would not be evident until late in the winter, and all the deer they examined were killed in fall. We examined the relationship of acorn abundance to diet, nutritional status, and reproduction of deer taken at intervals throughout the fall and winter during a 5-year period in the Southern Appalachians.

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Methods

Deer were examined from 12 state wildlife management areas in the 4 national forests of eastern Tennessee, western North Carolina, and northern Georgia. The management areas included the Tellico unit of the Cherokee Wildlife Management Area in Tennessee; the Pisgah Game Land in Haywood, Henderson, and Transylvania counties, the Pisgah Game Land in Yancey County, and the Nantahala Game Land in Macon County, all in North Carolina; and the Blue Ridge, Chattahoochee, Chestatee, Coleman River, Cooper's Creek, Lake Burton, Swallow Creek, and Warwoman Wildlife Management Areas in Georgia. The study region lies within the Blue Ridge physiographic province and is characterized by mountains with steep slopes and sharp crests. Elevations range from <300 m to 2,037 m. Annual precipitation averages 130 to 140 cm region-wide, with extremes in specific localities ranging from 100 to 200 cm (U.S. Dep. Commerce 1968). Average length of the frost-free period is between 150 and 210 days; snow is common at the higher elevations during winter. Soils are generally acidic and relatively infertile. Ultisols and Inceptisols are the dominant soil orders of the region (U.S. For. Serv. 1969). The major forest type is oak-hickory (*Quercus* spp.-*Carya* spp.). Dominant oak species include northern red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), white oak (*Q. alba*), and chestnut oak (*Q. prinus*). Common associates other than hickory include yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*), and sourwood (*Oxydendrum arboreum*). Other major forest types include oak-pine (*Quercus* spp.-*Pinus* spp.) and loblolly-shortleaf pine (*P. taeda-P. echinata*). Deer population densities on the study areas were 5–10/km^2 (estimates provided by the state wildlife agencies, derived from population models based on harvest data).

Samples were obtained from deer killed during public hunts and from supplementary collections between November 1983 and February 1988. Samples collected included 1 liter of rumen contents, the kidneys and associated perirenal fat, and the female reproductive tract. Rumen contents were mixed thoroughly before sampling. In addition, femurs were removed from deer taken during supplementary collections. All samples were immediately placed on ice and stored frozen until analyzed. Ages of deer were estimated from tooth eruption and attrition.

For food habits analysis, rumen contents were washed through 3 sieves with mesh sizes of 5.66, 3.35, and 1.41 mm. Materials retained in the largest mesh sieve were separated, identified macroscopically, and measured volumetrically by water displacement to the nearest 1 ml (Harlow and Hooper 1971). This material was then recombined with the material retained in the 2 smaller mesh sieves, dried at 80 C, and ground in a Wiley mill with a 20-mesh screen. Crude protein levels of the ground rumen contents (RP) were determined by semi-micro Kjeldahl techniques (Horwitz 1980).

Three samples of each of the dominant food items (species) in the fall and winter diet (fruit and evergreen leaves as revealed in rumen contents) were collected for nutritional analysis. Each sample was collected in a different area and was a composite from several plants. Samples were prepared and analyzed for crude protein content as described for the rumen contents. Dry-matter digestibility (DDM) was determined by a standard *in vitro* digestion procedure (Tilley and Terry 1963) with rumen fluid obtained from a fistulated steer maintained on a hay-grain diet. Samples were run in quadruplicate. Gross energy (GE) was determined with a Parr bomb calorimeter. Digestible energy (DE) was calculated by multiplying DDM by GE. Crude protein (including RP) and GE values were averaged for 2 replicates not differing by >5%.

Kidney fat indices (KFI) were determined as described by Riney (1955). Femur marrow fat levels (FMF) were determined by ether extraction (Warren and Kirkpatrick 1978). Ovaries were fixed and examined macroscopically for the presence of corpora lutea. Uteri were inspected to determine the number and sex of fetuses present. Fetal age was established based on the regression equation and development key of Hamilton et al. (1985). Conception date was calculated by backdating fetal age from the date of collection.

Acorn crops were rated as good or poor each year (1983–1987) based on quantitative scores derived from pre-drop mast surveys conducted annually by the 3 state wildlife agencies. The surveys involved counts of acorns on sample branches of trees systematically selected along standard routes (Whitehead 1969). Each area was rated independently. Hereafter, all references to acorn abundance or scarcity relate to production on specific areas in specific years (area-year combinations).

Data from all areas were combined and grouped into 3 seasonal periods: fall (1 Nov to 21 Dec), early winter (3 Jan to 3 Feb), and late winter (25 Feb to 27 Mar). (No deer were taken between these periods.) For statistical analysis, food items were combined into 11 categories: acorns, soft mast, agricultural crops, broadleaf evergreen leaves, deciduous green leaves, dead leaves, woody twigs, grasses, forbs, fungi, and miscellaneous. Pearson product-moment correlations were used to examine the relationships among categories, and between categories and rumen protein levels within each season. Volumetric percentages by food category were transformed (arc sine-square root) before analysis. Differences in RP, KFI, and FMF between conditions of acorn abundance and scarcity were analyzed with *t*-tests. Rumen protein levels were compared within seasons, and fat levels were compared within sex, age class, and season. Seasonal differences in RP and KFI between the 2 categories of acorn abundance, and nutritional differences among the selected food items were analyzed with 1-way analysis of variance and Tukey's Studentized range tests (Steel and Torrie 1980). All analyses for KFI and FMF were performed with log-transformed (base 10) values because the F (folded) statistic (Ray 1982) revealed unequal variances between groups.

Because many deer were collected before the peak of the breeding season, only reproductively active does were used in estimating reproductive rates. Differences in ovulation incidence (corpora lutea/ovulated doe) and counts of fetuses (fetuses/visibly pregnant doe) between conditions of acorn abundance and scarcity were analyzed with Fisher's exact test (Steel and Torrie 1980). Number of corpora lutea and number of fetuses were classified as either 1 or ≥ 2 for this analysis. Data for yearling and adult does were analyzed separately. Mean conception dates and fetal sex ratios each were compared between conditions of good and poor acorn production with a *t*-test and Fisher's exact test, respectively. All analyses were made with the Statistical Analysis System (Ray 1982). Statistical significance was indicated at $P \leq 0.05$.

Results

Acorn production was good on all areas in 1985 and on 1 area (Tellico) in 1983. Acorn production was low for other area-year combinations. Rating of the acorn crop on 1 area in 1 year was changed from good (based on the mast survey index) to poor after post-survey observations showed that most acorns dropped prematurely and were unsound.

In years when acorns were abundant, they were the dominant food throughout the fall and winter (Table 1). The proportion of the diet comprised of acorns increased from fall to early winter as other forage groups such as soft mast and fungi became less available. When acorns were scarce, they never comprised >5% of the diet in any season. In the absence of acorns, the bulk of the diet was made up of the leaves of broadleaf evergreen shrubs and vines, primarily rosebay rhododendron.

Table 1. Fall and winter deer diets in the presence of good and poor acorn crops, Southern Appalachians, 1983–88.

	Fall				Early winter				Late winter			
	Good (N = 37)		Poor (N = 144)		Good (N = 97)		Poor (N = 119)		Good (N = 12)		Poor (N = 41)	
Food category	V[a]	F[b]	V	F	V	F	V	F	V	F	V	F
Acorns	49.6	78	5.0	19	65.2	89	3.8	10	44.1	83	0.0	0
Soft mast	12.0	35	10.9	38	2.4	27	0.3	5	5.0	17	0.0	0
Agricultural crops	2.3	3	3.7	8	0.4	2	0.2	1	0.0	0	0.0	0
Broadleaf evergreen leaves	15.2	89	33.5	93	16.3	97	69.4	99	24.7	100	73.2	100
Deciduous green leaves	2.3	76	16.8	83	1.0	75	0.7	37	tr[c]	58	tr	17
Deciduous dead leaves	2.7	81	7.2	83	2.6	86	5.1	78	1.5	83	1.3	63
Woody twigs	0.9	41	1.6	35	1.0	42	2.7	42	2.7	50	6.6	46
Grasses	0.2	27	2.6	45	0.9	47	5.3	50	10.4	92	17.3	95
Forbs	0.8	46	4.0	47	1.1	57	0.3	28	8.6	83	tr	32
Fungi	13.2	81	12.0	77	7.4	82	8.0	61	2.7	58	1.4	32
Miscellaneous	0.9		2.7		1.6		4.2		0.3		0.2	

[a] Aggregate percent volume.
[b] Frequency of occurrence (%).
[c] <0.05% by volume.

Volumetric percentages (fall, early winter, late winter) for important individual species in this category were: rosebay rhododendron (21, 41, 53), mountain laurel (3, 11, 6), and galax (*Galax aphylla*) (6, 9, 6). Other species used less were doghobble (*Leucothoe axillaris*), dwarf rhododendron (*Rhododendron minus*), and Japanese honeysuckle (*Lonicera japonica*). Use of evergreen leaves increased 2- to 4-fold during acorn scarcity and was inversely correlated with acorn use in all seasons (fall: $r = -0.34$, $P < 0.001$; early winter: $r = -0.61$, $P < 0.001$; late winter: $r = -0.46$, $P < 0.001$). Other minor food groups used more intensively when acorns were scarce were green and dead leaves of deciduous woody plants, grasses, and woody twigs.

Rumen protein levels were strongly influenced by acorns. In fall, early winter, and late winter, RP values were significantly lower when acorn crops were good ($\bar{x}$ = 7.5, 9.1, and 8.8, respectively) than when crops were poor ($\bar{x}$ = 9.7, 10.8, and 10.3, respectively). Rumen protein levels were inversely correlated with acorn use (fall: $r = -0.31$, $P < 0.001$; early winter: $r = -0.51$, $P < 0.001$; late winter: $r = -0.40$, $P < 0.001$). Nutritional analyses indicated that acorns were low in protein but relatively high in digestible energy (Table 2). The DE content of rosebay rhododendron, the dominant non-mast food item, was significantly lower than for any of the other foods examined.

Stratification of the kidney fat data by sex and age classes resulted in inadequate sample sizes for many comparisons during the fall and late winter periods (Table 3). Generally, acorn crops appeared to have little influence on kidney fat indices in fall. In early winter, KFI's for all sex and age classes except yearling males were significantly higher when acorn production was high. In late winter, only adult does were sampled adequately, and they had significantly higher KFI's when acorn crops were good. For most sex and age classes, abrupt declines in KFI occurred later when acorn production was good. Adequate numbers of FMF samples were available only from adult does in winter. At this time, FMF levels were significantly higher with good acorn crops ($\bar{x}$ = 98%). But, even when acorns were scarce, FMF levels were high ($\bar{x}$ = 96%) in late winter.

During the 5-year study, fetal rates averaged 1.09 and 1.47 for yearling and adult does, respectively. Ovulation incidence of yearling does was significantly less when acorn production was low than when acorns were abundant (Table 4). Numbers of fetuses followed a similar trend but the difference was not significant, likely because of the smaller sample sizes. Also, when acorn crops were poor, 7 of the 31 (23%) yearling does examined after 16 January (date of the latest observed conception) had not ovulated. When acorn crops were good, only 3 yearling does were collected after 16 January, but all 3 had ovulated. Ovulation incidence and numbers of fetuses of adult does were not significantly different between conditions of good and poor acorn production. Throughout the study, no evidence of reproductive activity was observed in doe fawns.

Fetal sex ratios were not influenced by acorn availability ($P = 0.93$). However, when acorns were abundant, the mean conception date was approximately 9 days

Table 2. Nutritional quality of the dominant fall and winter foods of deer in the Southern Appalachians, 1983–88.

Species	% Crude protein		% Digestible dry matter		Gross energy[a]		Digestible energy[a]	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Acorns								
Quercus prinus	5.79ABC[b]	0.96	53.34A	1.57	4.37B	0.03	2.33AB	0.06
Quercus alba	5.31BC	0.68	51.27A	3.56	4.53B	0.05	2.32AB	0.14
Quercus coccinea	4.01C	0.35	38.26B	2.30	5.05A	0.02	1.93BC	0.12
Leaves								
Leucothoe axillaris	7.80AB	0.32	50.94A	0.57	4.93A	0.04	2.51A	0.01
Galax aphylla	7.69AB	0.48	52.52A	2.46	4.42B	0.02	2.32AB	0.11
Kalmia latifolia	7.99A	0.33	34.74BC	0.50	5.08A	0.02	1.77C	0.02
Rhododendron maximum	6.02ABC	0.24	25.85C	0.79	4.91A	0.05	1.27D	0.05

[a] Kcal/g.
[b] Within a column, means followed by the same letter are not significantly different ($P > 0.05$).

Table 3. Kidney fat indices of deer in the presence of good and poor acorn crops, Southern Appalachians, 1983–88.

Age class	Crop	Fall				Early winter				Late winter			
		N	$\bar{x}$	SE	P[a]	N	$\bar{x}$	SE	P[a]	N	$\bar{x}$	SE	P[a]
						Male							
0.5	Good	4	60.15A[b]	28.23	0.064	15	38.00A	7.00	<0.001	0			
	Poor	17	23.66A	4.09		40	12.59B	1.40		8	7.43B	1.04	
1.5	Good	10	26.48A	6.01	0.010	11	28.51A	6.38	0.116	0			
	Poor	49	49.73A	5.29		22	17.92B	2.16		0			
≥2.5	Good	24	66.51A	10.02	0.659	23	20.47B	3.18	0.048	2	15.85B	3.45	
	Poor	78	66.85A	5.13		14	12.01B	1.99		1	4.10B		
						Female							
0.5	Good	0				14	38.06A	8.73	<0.001	2	5.95B	0.75	0.077
	Poor	12	20.56A	4.33		52	13.24A	1.64		8	11.24A	1.48	
1.5	Good	0				14	71.83	17.72	0.013	0			
	Poor	6	45.40A	7.32		39	39.01A	6.24		8	13.54B	3.02	
≥2.5	Good	4	70.93AB	28.45	0.733	68	84.87A	5.94	<0.001	8	44.30B	11.15	0.004
	Poor	24	52.15A	6.87		106	39.82A	2.66		16	18.64B	2.60	

[a] Probability values refer to comparisons between good and poor acorn crops.
[b] Within rows, means followed by the same letter are not significantly different ($P > 0.05$).

Table 4. Reproductive performance of does in the presence of good and poor acorn crops, Southern Appalachians, 1983–88.

Variable	Age class	Good			Poor			
		N	$\bar{x}$	SE	N	$\bar{x}$	SE	P[a]
Ovulation incidence	1.5	13	1.31	0.13	41	1.07	0.04	0.049
	≥2.5	82	1.68	0.06	137	1.59	0.05	0.261
Fetuses/pregnant doe	1.5	6	1.33	0.21	27	1.04	0.04	0.078
	≥2.5	48	1.42	0.08	96	1.50	0.05	0.375

[a] Probability values refer to comparisons between good and poor acorn crops within age classes.

earlier than when acorns were scarce ($P < 0.001$) (Fig. 1). Fetal sex ratios and conception dates of yearling and adult does were not different ($P > 0.05$).

Discussion

Rumen protein levels declined as consumption of acorns increased. Although low in crude protein, acorns are high in digestible fats and carbohydrates and thus are an important source of energy. Depending on the species of oak, the estimated

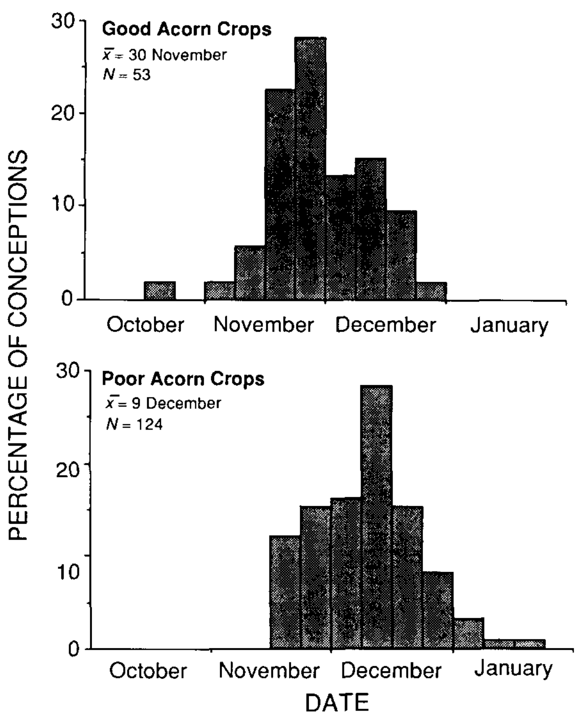

Figure 1. Conception dates of deer in the presence of good and poor acorn crops, Southern Appalachians, 1983–88.

digestible energy content of acorns was 1.5 to 1.8 times greater than that of rosebay rhododendron. Doghobble and galax had DE levels comparable to acorns, but these species did not comprise a significant portion of the fall and winter diet. These findings generally support other studies involving comparisons of various measures of dietary quality related to acorns in the diet (Kirkpatrick et al. 1969, Harlow et al. 1975, Pekins and Mautz 1988). However, our results should be interpreted with caution because standard methods of forage analysis may not accurately predict nutritional quality of complex native forages (Nastis and Malechek 1988). The high content of tannins and other secondary chemical compounds characteristic of some of the forages we studied (Servello et al. 1987) reduce digestibility of protein and interact with the temperature at which forage samples are dried before analysis (Robbins et al. 1987, Nastis and Malechek 1988). The relatively high temperatures at which our samples were dried may have affected different forages in different ways, depending upon their phenolic content and other factors.

When acorns comprise a substantial portion of the fall diet, dietary energy appears to be elevated and available protein is depressed. Verme and Ozoga (1980) concluded that energy was more important than protein for fawn growth in autumn. Fawns provided with low levels of protein still experienced excellent growth rates as long as dietary energy levels were adequate. Ovulation rates and fawning rates generally are affected by dietary energy level but not protein (Verme 1969, Vogelsang 1977). Similarly, fat deposition is strongly influenced by energy intake and not dietary protein (Verme and Ozoga 1980, Warren and Kirkpatrick 1982). Thus in the fall and winter, dietary energy appears to be more critical than protein. Ruminants, including deer, can conserve nitrogen through the recycling of urea which is utilized in protein synthesis by rumen microorganisms (Robbins et al. 1974). Therefore the reduction in protein intake on the high acorn diets is likely more than offset by the benefit of higher digestible energy. However, when energy supply is adequate, increased protein levels would be valuable in reaching optimal development (Ullrey et al. 1967, Verme and Ozoga 1980). All major winter foods of deer in the Southern Appalachians are relatively low in protein.

We found, as did Harlow et al. (1975), that deer examined in the fall generally had moderately high fat levels regardless of the availability of acorns. Generally, even when acorn production is poor, some mast is available, resulting in moderate fat accumulation in early fall. By early winter, the higher energy content of the diets containing acorns was reflected in KFI's. When acorn production was high, mean KFI's were significantly greater for all sex and age classes except yearling males. Adult does were able to retain substantial levels of body fat even in late winter.

The influence of acorns on patterns of fall and winter fat deposition and loss differed among sex and age classes. Regardless of acorn abundance, fat levels of adult does (the only female age class with adequate samples) did not change significantly from fall to early winter but dropped sharply between early and late winter. Fat levels of fawn and yearling males declined significantly from fall to early winter only when acorns were scarce. Condition of adult bucks declined significantly from fall to early winter even when acorns were abundant. Mature bucks reduce food consumption and lose weight during the rut, even when provided with a high-quality diet (Long et al. 1965, Short et al. 1969, Warren et al. 1981). Therefore, condition of adult bucks during and immediately following the breeding season may not be influenced appreciably by the acorn crop. However, availability of acorns after the breeding season may affect late winter condition of bucks.

The influence of the acorn crop on reproduction was reflected most strongly in the yearling age class. Ovulation rates, and presumably fetal rates, were lower when acorn production was low. The proportion of yearlings breeding also seemed to be reduced when acorns were scarce, although sample sizes were small. Young animals are generally more responsive to nutritional deficiencies than prime-aged animals (Verme 1967, Verme 1969, Vogelsang 1977). Apparently the nutritional quality of the fall diet when acorn crops were poor was adequate to produce normal ovulation rates in adults because ovulation and fetal rates of older does did not differ with acorn abundance. However, factors other than dietary quality, including reproductive performance in the previous year and stress associated with lactation, also can influence subsequent productivity in adult does (Verme 1967). Any influence of the acorn crop on adult productivity may be obscured by these confounding effects.

Management Implications

This study demonstrated the nutritional importance of acorns to deer in the Southern Appalachians. Acorn production varies greatly from year to year, independent of deer density. Therefore, the effectiveness of management practices (e.g. increased harvest) directed at inducing density-dependent responses in size, condition, and reproduction of deer may be severely reduced. Further refinement in the knowledge of the effects of acorn abundance on recruitment rates is needed so that this relationship can be incorporated into recruitment models, and the size of recent acorn crops can be used more confidently in setting harvest goals. Annual mast surveys provide very useful data and should be refined and continued.

Literature Cited

Beck, D. E. 1977. Twelve-year acorn yield in Southern Appalachian oaks. U.S. For. Serv. Res. Note SE–244. 8 pp.

Downs, A. A. and W. E. McQuilkin. 1944. Seed production of Southern Appalachian oaks. J. For. 42:913–920.

Duvendeck, J. P. 1962. The value of acorns in the diet of Michigan deer. J. Wildl. Manage. 26:371–379.

Hamilton, R. J., M. L. Tobin, and W. G. Moore. 1985. Aging fetal white-tailed deer. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 39:389–395.

Harlow, R. F. and R. G. Hooper. 1971. Forages eaten by deer in the Southeast. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 25:18–46.

———, J. B. Whelan, H. S. Crawford, and J. E. Skeen. 1975. Deer foods during years of oak mast abundance and scarcity. J. Wildl. Manage. 39:330–336.

Horwitz, W., ed. 1980. Official methods of analysis of the Association of Official Analytical Chemists. Thirteenth ed., Assoc. Off. Anal. Chem., Washington, D.C. 1018 pp.

Kirkpatrick, R. L., J. P. Fontenot, and R. F. Harlow. 1969. Seasonal changes in rumen chemical components as related to forages consumed by white-tailed deer in the Southeast. Trans. North Am. Wildl. Nat. Resour. Conf. 34:229–238.

Korschgen, L. J. 1962. Foods of Missouri deer, with some management implications. J. Wildl. Manage. 26:164–172.

Long, T. A., R. L. Cowan, G. D. Strawn, R. S. Wetzel, and R. C. Miller. 1965. Seasonal fluctuations in feed consumption of the white-tailed deer. Pa. Agric. Exp. Sta. Prog. Rep. 262. 5 pp.

Nastis, A. S. and J. C. Malechek. 1988. Estimating digestibility of oak browse diets for goats by in vitro techniques. J. Range Manage. 41:255–258.

Pekins, P. J. and W. W. Mautz. 1988. Digestibility and nutritional value of autumn diets of deer. J. Wildl. Manage. 52:328–332.

Ray, A. A., ed. 1982. SAS user's guide: statistics. SAS Inst. Inc., Cary, N.C. 584 pp.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. New Zealand J. Sci. Tech. 36(B): 429–463.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98–107.

———, R. L. Prior, A. N. Moen, and W. J. Visek. 1974. Nitrogen metabolism of white-tailed deer. J. Anim. Sci. 38:186–191.

Servello, F. A., R. L. Kirkpatrick, and K. E. Webb, Jr. 1987. Predicting metabolizable energy in the diet of ruffed grouse. J. Wildl. Manage. 51:560–567.

Short, H. L., J. D. Newsom, G. L. McCoy, and J. F. Fowler. 1969. Effects of nutrition and climate on southern deer. Trans. North Am. Wildl. Nat Resour. Conf. 34:137–146.

Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. Second ed. McGraw-Hill Book Co., New York, N.Y. 633 pp.

Tilley, J. M. A. and R. A. Terry. 1963. A two-stage technique for the *in vitro* digestion of forage crops. J. Br. Grassl. Soc. 18:104–111.

U.S. Forest Service. 1969. A forest atlas of the South. U.S. For. Serv. South. and Southeast. For. Exp. Stas. 27 pp.

U.S. Department of Commerce. 1968. Climatic atlas of the United States. U.S. Dep. Commerce, Environ. Sci. Serv. Adm., Environ. Data Serv. 80 pp.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, and B. L. Bradley. 1967. Protein requirement of white-tailed deer fawns. J. Wildl. Manage. 31:679–685.

Verme, L. J. 1967. Influence of experimental diets on white-tailed deer reproduction. Trans. North Am. Wildl. Nat. Resour. Conf. 32:405–420.

———. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildl. Manage. 33:881–887.

——— and J. J. Ozoga. 1980. Influence of protein-energy intake on deer fawns in autumn. J. Wildl. Manage. 44:305–314.

Vogelsang, R. W. 1977. The effect of energy intake and reproductive state on blood urea nitrogen, cholesterol, and progestin levels in captive and free-ranging white-tailed deer. M.S. Thesis, Va. Polytech. Inst. and State Univ., Blacksburg. 100 pp.

Warren, R. J. and R. L. Kirkpatrick. 1978. Indices of nutritional status in cottontail rabbits fed controlled diets. J. Wildl. Manage. 42:154–158.

——— and ———. 1982. Evaluating nutritional status of white-tailed deer using fat indices. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 36:463–472.

———, ———, A. Oelschlaeger, P. F. Scanlon, and F. C. Gwazdauskas. 1981. Dietary and seasonal influences on nutritional indices of adult male white-tailed deer. J. Wildl. Manage. 45:926–936.

Whitehead, C. J., Jr. 1969. Oak mast yields on wildlife management areas in Tennessee. Tenn. Wildl. Resour. Agency, Nashville. 11 pp.