THE EFFECTS OF FOREST THINNING ON THE FOOD-BASED CARRYING CAPACITY OF A MIXED OAK FOREST FOR WHITE-TAILED DEER IN THE RIDGE AND VALLEY PROVINCE OF VIRGINIA

by

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INTRODUCTION

Timber harvest frequently is considered beneficial for white-tailed deer (*Odocoileus virginianus*). The benefits are attributed most commonly to increased yields of understory vegetation which occur after overstory reduction and increased potentially available food and cover. In the Ridge and Valley Province of Virginia, evaluation of the effects of timber harvest on deer habitat have emphasized forage production rather than cover. Moen (1966:88) suggests that cover becomes physiologically important only when the diet of deer does not supply sufficient metabolizable energy. The suggestion that cover is secondary to food may be particularly valid over the range of the Virginia subspecies of white-tailed deer, where climatic conditions are usually not as extreme as those of northern deer ranges.

In deciduous forests of Eastern North America, yields of deer forage provided by understory vegetation often increase for a period of time following timber harvest. The duration of the increases varies and eventually begins to decline (Crawford 1971, Harlow and Downing 1969, Patton and McGinnes 1964, Crawford and Harrison 1971). Patton and McGinnes (1964) determined the yields of species commonly consumed by deer in a mixed oak-pine stand in relation to elapsed time since and intensity of overstory reduction. This information was combined with data on daily forage consumption rates for deer to estimate the carrying capacity of this forest stand in deer days.

Calculation of nutrition-based carrying capacity for a species such as the white-tailed deer involves determination of the nutritional requirements, measurement of the availability of nutrients and energy on the range and division of the nutrient and energy availability by the animal's requirements over time (Robbins 1973:2). Intake rate is a crude measure of food requirements, since nutrients and energy are not measured directly. Likewise, measurement of standing crop of forage available or consumed is indirect. Wallmo et al. (1977) calculated higher carrying capacities for winter mule deer (_O. hemionus_) range, based on standing crop of forage and forage intake rates than when protein and energy requirements and availability were used.

Methods to evaluate the nutrient and energy requirements and availability of these requirements have been developed. Forage analysis systems designed initially for nutritive analysis of food for domestic animals are being used to determine nutritive values of food eaten by wildlife (Van Soest 1964, Hellmers 1940, Tilley and Terry 1963, Palmer et al. 1976, Short 1966, Ullrey et al. 1964). Information on the energy (Silver et al. 1959 and 1969, Ullrey 1969 and 1970) and nutrient (Magruder et al. 1957, Swift 1957, Ullrey et al. 1975) requirements of deer supplemented with information on requirements of domestic ruminants (Moen 1973) can be employed to estimate the nutritional requirements of deer throughout the annual cycle. This system is being employed to provide a refined method of calculating carrying capacity based closely on the animal's actual requirements and availability of the requirements (Whelan 1971, Wallmo et al. 1977).

This study employed nutritional concepts and collection and nutritional analysis of deer forage to estimate food-based carrying capacity of a southwestern Virginia mixed oak forest as a function of time elapsed since a commercial thinning operation.

STUDY AREA

School House Hollow is a secondary drainage which originates on the northwest slope of Johns Creek Mountain, in the Johns Creek watershed, Craig County, Virginia. This area lies within the Ridge and Valley Province of Virginia, described by Dietrich (1970:109).

School House Hollow typifies the small drainages which lie between the lateral ridges which extend from the main ridges. Dominant overstory vegetation on the study area includes scarlet oak (Quercus coccinea), chestnut oak (Q. prinus), black oak (Q. velutina), and some yellow poplar (Liriodendron tulipifera) associated with drainages. Midstory vegetation is dominated by red maple (Acer rubrum), sourwood (Oxydendrum arboreum), flowering dogwood (Cornus florida), sassafras (Sassafras albidum), blackgum (Nyssa sylvatica), and great rhododendron (Rhododendron maximum) along the drainages. Understory vegetation is dominated by mountain laurel (Kalmia latifolia), azalea (Rhododendron calendulaceum and R. nudiflorum), trailing arbutus (Epigea repens), galax (Galax aphylla), low-bush blueberry (Vaccinium vacillans), deerberry (V. stamineum), huckleberry (Gaylussacia baccata), and teaberry (Gaultheria procumbens).

An area of 184 acres (73.6 hectares), divided into four contiguous parcels, was commercially thinned over three consecutive years from September 1973 to October 1975. Parcels 1 and 2 were thinned from September 1973 to early January 1974. Parcel 3 was thinned from April to December, 1974 and Parcel 4 was thinned from April to October of 1975. A fifth parcel which had not been thinned was chosen as a control area. Parcel 2 was excluded from sampling since it was thinned at the same time as Parcel 1. Thus, the study design incorporated 3 thinned parcels which represent 1 to 4 years since thinning depending on season, compared to an unthinned area.

The thinned area was located east and south of county roads 601 and 632 respectively, approximately 1 km southeast of the intersection of the two roads (Fig. 1). School House Hollow bisects Parcel 4 near the eastern boundary of the thinned area. The unthinned control parcel was located south of county road 632, approximately 4 km east of the intersection of roads 601 and 632, and approximately 2 km east of the eastern boundary of the thinned area.

The parcels varied in elevation from 628 to 792 m along the toe of the slope. Slope inclination was approximately 13%.

Trees were removed from the thinned area over a network of skid trails and haul roads which were blocked with earthen barricades and seeded with a grass and forb seed

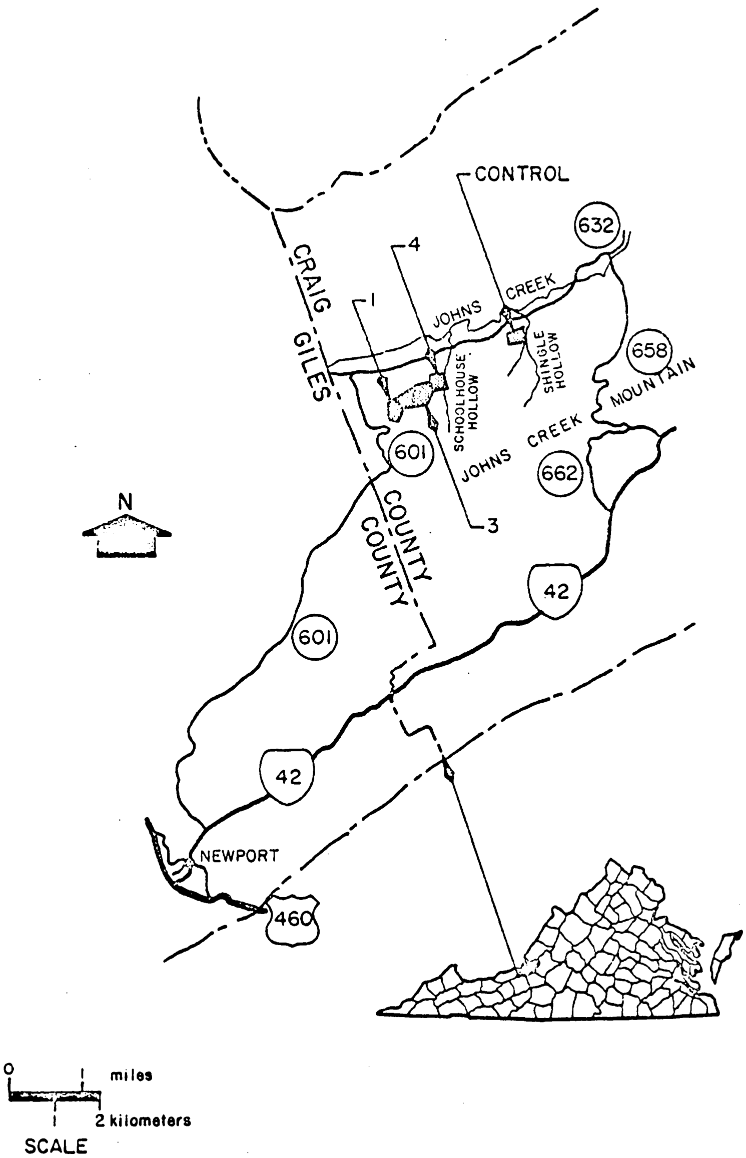

Fig. 1. Location of School House Hollow study area in Craig County, Virginia. Parcels 1, 3, 4 and the control are indicated by arrows.

mixture after cutting. Non-merchantable portions of harvested trees, such as branches, were left where the trees were felled.

MATERIALS AND METHODS

Stand Characteristics

Basal Area.

The residual basal area on each of the thinned parcels was calculated by measuring the diameter at breast height (DBH) of the unharvested trees within randomly located 0.10 acre (0.04 ha) plots.

Approximately 14% of the thinned parcels sampled for deer food were cruised to calculate basal area. Approximately 17% of the control (unthinned) parcel was cruised. Regression equations were developed to estimate the DBH of harvested trees from diameters of residual stumps (McClure 1968), in order to calculate the basal areas of thinned parcels prior to cutting. Tree measurement methods for predicting DBH of harvested trees from stump diameters followed McClure, except that only one stump diameter measurement was taken for each intact tree measured. Measurements were taken immediately above any butt swell, and the height of the measurement above ground was recorded to the nearest 3cm.

The diameters of some stumps of removed trees were greater than diameters of residual trees on the thinned area. Therefore, it was necessary to take stump diameter and DBH measurements of larger trees on an adjacent unthinned area to develop regression equations which would cover the complete range of stump diameters encountered on the harvested parcels . This allowed valid predictions of basal area from stump diameter. Basal area values calculated for removed trees, added to basal area values of the residual trees, yielded the basal area of the parcel prior to tree harvest.

__Canopy Cover__.

Percent canopy cover was measured with a spherical densiometer during early August (Lemmon 1956). Canopy cover in each parcel was measured at the same 20 randomly selected points sampled for wildlife food items. Canopy cover readings for points which fell within stump sprouts were taken a short distance away from the point to avoid inclusion of canopy formed by the stump sprouts. The values include cover from approximately 1m, where the instrument is held, to the top of the canopy.

__Forage Collection__

Current annual growth (CAG) of all plants within a m^2 and below 1.5m in height was clipped from randomly located sample points in both the thinned and the unthinned parcels. The 1.5m height was considered the average browse line for deer. Sample points for clipping were selected at random from a fixed number of potential sample points in each parcel. The number of m^2 plots sampled varied among treatments and seasons. Determination of summer sample size followed Harlow (1977), except that the number of plots required for a statistically valid sample was based on the ovendried rather than green weight of plants. The great variability of the fall sample did not allow application of this method of determining sampling intensity because of the large number of sample plots required and the necessity of confining the sampling to a discrete period of phenological development of understory. Consequently, the fall sample size was reduced below that of the summer, and the winter and spring sample sizes (no. of plots/parcel/season) were fixed, based on an estimate of the average amount of time required to clip the summer and fall plots. Potential sample points were located at 1 chain (20.1m) intervals along pre-established transect lines. The parallel transect lines in each parcel were oriented roughly perpendicular to the slope at 1.5 chain (30.2 m) intervals. The length of each transect line and the number of potential sample points varied, depending upon the shape and size of the parcel.

For some evergreen species it was not always possible to differentiate CAG from growth of previous years. In this case, all green plant tissue was collected, since it was available for consumption by deer.

After collection, the plants were weighed in the field or placed in plastic bags and weighed in a lab soon after returning from the field, to obtain fresh weights. All woody species except lowbush blueberry, deerberry, huckleberry, and azalea were further separated into plant parts (considered individual food items for deer). Leaves and stems of the excepted species were not seperated, due to the great time involved for seperation and relatively high leaf-to-stem ratio.

Plant part categories included leaves, browse (terminal three inches of current annual stem growth), nonbrowse (current annual stem growth minus browse), fruit, and flowers. Browse category for the summer sample was composed of the terminal 30 cm of CAG because a large portion of the summer sample was composed of long, succulent, rapidly-growing stems of stump sprouts. Dried samples were ground in a Wiley mill to pass a 40 mesh screen for later nutrient and energy analyses.

Plants were collected seasonally from the three thinned parcels and the unthinned control. Summer samples were collected from 29 June to 29 July 1976. Fall samples were collected between 18 October and 7 November 1976. Winter sampling was from 28 February to 23 March 1977. Spring samples were collected from 11 to 30 May 1977.

Oak Mast Availability

Oak mast, although not a consistently reliable food source, can comprise a substantial portion of the fall-winter diet of white-tailed deer during years of high acorn productivity (Harlow et al. 1975). To determine the potential contribution of oak mast to the fall-winter protein and energy balance of deer in the vicinity of School House Hollow, the amount of oak mast on the ground in each parcel was estimated using a modification of a technique developed by Forsythe (1978). Acorn counts were conducted at three different times during the 1976 fall-winter period. Acorns were collected in all 4 parcels from beneath 20 oak trees greater than 5 in. DBH near randomly selected points used for forage collection. At each count, fallen acorns were collected from within a m^2 sampling frame placed midway between the tree bole and the edge of the crown. The species of each tree sampled was recorded and the DBH of the tree was measured with a DBH tape.

Soundness of acorns was determined by external and internal examination. Acorns with less than 25% of the meat injured (infested with insect larvae, fungi, etc.) were considered "sound" acorns. Acorns which were not fully matured and/or with more than 25% injury were considered "unsound". Overall percent soundness was calculated for each species for the entire mast sampling period. The meat of all sound acorns was removed from the husk, oven-dried and weighed to the nearest 0.1g and average weights of acorns for each tree species were calculated. The total weight of acorns beneath each tree was estimated by applying the counts for the number of acorns/m^2 to the ground area beneath the canopy. However, Forsythe (ibid.) found that fallen acorns were not distributed uniformly beneath the canopy, but exhibited a radial distribution pattern in which acorn standing crop was generally maximal midway between the bole and crown perimeter. To account for this pattern in calculating standing crop of acorns, Forsythe developed radial production functions for each species. The count from the m^2 plots and the crown area measurements were incorporated into the radial mast production gradient functions to determine the number of acorns beneath the tree. Forsythe's species-specific radial production functions were employed in calculating the availability of acorns on the School House Hollow study area.

Estimates of total acorn yield were correlated with DBH for each oak species. The total number of acorns/ha for each parcel was then extrapolated from average basal area measurements of oak trees on each parcel. The product of the number of acorns/ha for each parcel and the average weight of acorn meat by species, yielded an estimate of the standing crop of the edible portion of oak mast.

Nutritive Quality of Food

Only plant food items which occurred commonly in the diet of white-tailed deer in the southern Appalachian mountains were analyzed for their nutritive value (Harlow et al. 1975, Harlow and Downing 1969, Crawford et al. 1975, Harlow and Hooper 1971). Collectively, these food items comprised the staple diet of white-tailed deer for specific seasons. Rationale for inclusion of food items based on frequency of occurence and percent volume of items in rumen analyses is discussed in the section on energy and protein availability. Samples of all food items were combined by season and thinned parcels for analysis of nutritive value.

In Vitro Digestibility.

Seasonally important food items were analyzed for digestibility using an *in vitro* micro-digestion technique. The technique was a modification of that used by Palmer et al. (1976). Rumen fluid from a fistulated steer fed a 50:50 concentrate:roughage diet was mixed in a 1:1 ratio with artificial saliva (McDougall 1948). The mixture was maintained in a water bath at a temperature of 38.5C and carbon dioxide (CO2) was bubbled continuously through the mixture. Fifty ml centrifuge tubes containing approximately

0.3g samples of food plants were inoculated with 30 ml of rumen-buffer solution, the remaining air space in the tubes filled with carbon dioxide (CO_2), and the tubes stoppered with one-way gas valves. Tubes were maintained in a water bath at 38.5 C and swirled 6 times at regular intervals during a 48-hour fermentation period. Following the fermentation period the tubes were centrifuged at approximatley 1200 X G for 20 minutes and the supernatant removed by aspiration. Twenty-five mls of 0.2% acid-pepsin mixture were then introduced into each tube and the tubes replaced unstoppered in the water bath at 38.5 C for a 24-hour acid-pepsin digestion. At the end of the 24-hour period, the tubes were centrifuged, the supernatant removed and the tubes containing the undigested residue were oven-dried for 24 hours and weighed to the nearest 0.1mg. Plant samples were analyzed in triplicate for digestibility. For every 6 tubes containing samples, an empty tube was inoculated with 30 ml of rumen-buffer solution to correct for the digesta already contained in the rumen fluid from the steer. Percent *in vitro* digestibility of samples was computed as the difference in sample weight before and after the digestion periods minus the average weight of residual digesta in the control tubes, divided by the weight of the undigested sample, multiplied by 100.

In addition to samples collected from the study area, 5 plant samples representing a range of digestibilities determined *in vivo* were included with each *in vitro* analyses. After determination of *in vitro* digestibility values for the five standards of known *in vivo* digestibility, regression equations were developed to correct all *in vitro* values to corrected *in vivo* values.

Gross Energy.

Staple food items were pressed into 0.3 to 0.4 g tablets and burned in a Parr adiabatic bomb calorimeter to determine gross energy of individual food items. One sample of each food item was analyzed.

Crude Protein.

A micro-Kjeldahl procedure was used to determine crude protein content of the staple food items. The technique used was a modification (Ellmore pers. comm.) of that described by McKenzie and Wallace (1954). Approximatley 0.2 g samples of preferred food items were digested in 50 ml test tubes until the samples were clear. Tubes were then transferred to a micro-Kjeldahl distillation apparatus and steam distilled into a flask containing boric acid indicator. The contents of the flask were then titrated with 0.05 N $KH(IO_3)_2$ to a lilac end-point. The volume of titrant required to reach the end point yielded a measure of percent nitrogen in the sample. This value was multiplied by 6.25 to calculate the percent crude protein in the staple food items.

Animal Requirements

The protein and energy requirements of deer are not static; they fluctuate in response to complex interactions between the deer and its environment. Generally these fluctuations are cyclic, associated with the seasons and attendant changes in the animal's habitat.

A valid estimate of carrying capacity must account for variations in body condition during the complete annual cycle (Verme and Ullrey 1972:282). Body weight is closely associated with the daily protein and energy requirements of deer. Requirements are customarily expressed on a per unit body weight basis or per unit of metabolic body weight (MBW) expressed as $kg^{.75}$. On an absolute basis, requirements increase with body weight but decrease per unit of body weight, with greater absolute body weight.

Deer experience a seasonal weight loss beginning in the fall and extending through winter into early spring (Wood et al. 1962, Taylor 1956, French et al. 1955). Weight losses range from as little as 4% up to 30% (Taylor 1956, Silver 1969, Wood et al. 1962). Verme and Ullrey (1972:277) indicate that overwinter weight losses greater than 30% can lead to rapid deterioration of the deer's health and result in death.

For the purpose of the current calculations, the mean total body weight of deer killed in the vicinity of Johns Creek Valley during the fall was reduced by 15% for the winter and spring determinations of nutrient requirements. Summer and fall weights were estimated from the average field-dressed body weight (FDBW) of 1.5 year old deer weighed at a deer check station in Johns Creek Valley during the 1976 fall hunting season (Va. Commission of Game and Inland Fisheries 1977). Mean total body weight (TBW) was estimated from the equation:

$$FDBW = 0.854TBW - 5.76$$

This equation was derived from the regression of FDBW on total body weight of deer collected in South Carolina (Urbston et al. 1976). FDBW of Johns Creek deer was 48.18 kg; estimated total body weight was 57.31 kg. With a 15 percent overwinter weight loss, winter and early spring weight was 48.71 kg.

Nutrient and energy requirements are also affected by the reproductive condition of the animal. Gestation and lactation, particularly, place increased demands on the nutrient pool of the doe. These additional requirements must also be accounted for in the carrying capacity calculations.

Portions of the nutritional requirement component for energy and protein have been determined from studies of captive deer during different seasons. However, data on protein and energy requirements of white-tailed deer are incomplete. Information is lacking on the requirements during certain seasons and for particular physiological and physical conditions of deer. In this study, values from similar ruminant animals were used to estimate these unknown requirements of deer. Requirements considered were those needed for daily maintenance of the doe alone, plus production associated with pregnancy in winter and spring, and lactation during summer.

Energy Requirements.

White-tailed deer exhibit a seasonal variability in fasting metabolic rate (FMR) which "may not be found in deer of other species, or in those maintained under conditions comparable to domestic stock (Silver et al. 1969:492)." Silver et al. (1969:497) further state, "it seems reasonable to assume that seasonal changes in metabolism represent a physiological response to seasons and/or weather; and further to assume that the molt, the abrupt change in FMR, and changes in endocrine activity are in some way interacting." These investigators measured the fasting metabolic rates of white-tailed deer by indirect calorimetry. FMR measured in this manner was approximately equal to the net energy requirement of the animal, assuming negligible physical activity (Thompson et al. 1973:303-304). They calculated an average FMR of 97.1 kcal/kg MBW and 143.6 kcal/kg MBW for adult deer in winter and summer coats, respectively. Since energy and protein availability in food items is most readily expressed in terms of digestible energy, net energy values were converted to digestible energy (kcal). Net energy is approximately 74% of metabolizable energy (Robbins 1973:140); therefore net energy values were converted to metabolizable energy values by multiplying net energy by 1.35. Since metabolizable energy values are rather consistently 80% of digestible energy (Moen 1973:352), digestible energy was calculated as the product of the metabolizable energy and the factor 1.25.

These values do not account for production related to reproductive condition, since the does in summer coat were not lactating and only 1 of 3 does in winter coat was pregnant. Ullrey et al. (1969 and 1970) determined the digestible energy requirements for maintenance of pregnant white-tailed does by conducting metabolism trials at various levels of feed consumption. In the seperate feeding trials they found comparable values of 158 and 160 kcal/kg MBW for the digestible energy requirements of pregnant does.

Energy requirements for maintenance of lactating deer have not been determined directly. However, a first approximation of additional energy requirements above maintenance may be computed based on the milk production necessary to meet the energy requirements of fawns, the caloric value of that milk and the energy increment above the caloric value of the milk required for the production of the milk, as determined for dairy cattle (Moen 1973:354-355). Moen provides an equation for calculation of milk production necessary to meet the energy requirements of fawns:

$$Qmp = ((Ima)(Imp)(70)(MBW))((RD)(1/Enet))/GEm$$

where

Qmp = milk production based on energy requirements

Ima = energy increment for activity of the fawn

Imp = energy increment for production by the fawn

RD = rumen development=(113.6-4.5wt. in kg)/100

Enet = net energy coefficient for milk=0.8

GEm = energy in milk

According to Moen, values of 2.0 to 3.5 for Ima will probably satisfy the requirements of a growing fawn. Moen (after Nordan et al. 1970) suggests a value of 2.5 for the Imp term.

Composition, and therefore caloric value, of milk (GEm) of lactating does changes with time over the period of lactation (Silver 1961:68). Generally, protein and fat content increases while sugar content decreases slightly. The GEm term in the milk production equation changes, depending on the stage of lactation. The caloric value of milk produced by a lactating doe for a 1 month old fawn was determined as the sum of the products of the caloric content of carbohydrates, fats, and proteins and their respective percentage composition in does milk at various stages of lactation. Energy requirements for lactation were added to the seasonal digestible energy requirements for maintenance to estimate total energy requirements during the summer.

The fawn weight used in the milk production equation was derived from the regression equation:

$$Y = (2.96) + (0.244X)$$

where

Y = body weight of the fawn (kg)

X = age of fawn in days (Robbins and Moen 1975:357)

The weight of the fawn was computed for the stage of lactation for which the composition, and therefore caloric value, of milk was determined.

The product of daily milk production and the caloric values of the milk is an estimate of the caloric content of the daily ration of milk needed to satisfy the energy requirements of a growing fawn.

Crampton and Harris (1969:151) estimated the caloric requirements for lactation in dairy cows as being equal to 1.6 times the caloric content of the milk. This coefficient was combined with the caloric content of milk to compute a first estimation of the additional energy above maintenance required for lactation by white-tailed does.

Protein Requirements.

Approximate protein requirements to sustain growth have been determined for fawns (Smith et al. 1975, Murphy and Coates 1966) and adult white-tailed deer (French et al. 1955). For optimal growth, 13 to 16% dietary crude protein is usually recommended (Verme and Ullrey 1972, Murphy and Coates 1966, French et al. 1955) although Smith et al. (1975) recommended a concentrate diet containing approximately 25% crude protein on a dry matter basis for maximal growth in fawns. A minimum of 6 to 7% dietary crude protein is recommended to maintain normal rumen function (Dietz 1965:276-277).

These values represent recommended requirements for growth. For comparative purposes maintenance requirements are more desirable than growth requirements, because growth rates can vary considerably. However, protein requirements necessary to maintain body weight of deer have not been determined directly. This requirement may be estimated based upon levels of endogenous urinary nitrogen (EUN) and metabolic fecal nitrogen (MFN) (Robbins 1973:334). The sum of these values is equal to maintenance requirements of the animal for nitrogen when the biological value (BV) of the nitrogen is 100%. At maintanence levels of protein intake, BV will always be 100%. According to Moen (1973:334, after Crampton and Harris 1969) EUN (g) may be calculated by the equation:

$$Qeun = 2 \text{ X } 70(MBW)/1000$$

MFN (g) is calculated according to the equation:

$$Qmfn = cFkg/6.25$$

where c equals protein loss in the form of catabolized protein contained in the feces (Moen 1973:336). For sheep and cattle on forage diets, c equals 5g/kg of dry matter intake/day (Moen 1973:336 after ARC 1965). The term Fkg is the dry matter intake in kg/day. Average Fkg for deer from Craig Co., Virginia was 0.074 kg/kg MBW /day (Whelan 1978).

Gestation requires an added increment of protein intake beyond that required by the doe to maintain body weight. This added increment was calculated according to the equation (Moen 1973:353):

$$Qpp = (e^{(-2.3623+0.0407td/1.428570)})/5.9$$

where

Qpp = the amount of protein required for pregnancy

td = days pregnant

The latter third of gestation is recognized as being most taxing on the nutrient pool of the pregnant doe. For this reason additional protein requirements for gestation were calculated only for the third trimester of pregnancy; specifically the midpoint of the period, or day 167 (td) in gestation. The protein increment (Qpp) then equals 3.778 g protein/day/kg fetal weight at term. The average weight of 26 fawns born at the captive deer facility at VPI & SU was 3.1 kg (Russell 1977:109); therefore the protein requirement for gestation at day 167 was approximately 11.7 g.

Protein requirements of the doe for lactation have not been determined directly. However, this requirement may be estimated based on the amount of nitrogen required for lactation, following the equation (Moen 1973:343):

$$Qnl = (Qmp)(N\%)(Imp)/100$$

where

Qnl = grams of nitrogen required for lactation

Qmp = quantity of milk produced in g/day

N% = percent nitrogen in milk

Imp = metabolic increment for milk production

The percent of nitrogen (N%) in milk will vary with the stage of lactation (Silver 1961). The value used for N% was chosen to correspond to the approximate stage of lactation at which a doe would have been at the time of the summer forage collections, about one month. Percent nitrogen in doe's milk at this stage is approximately 1.62 (Silver 1961). Metabolic increment for milk production (Imp) is approximately 1.5 (Moen 1973:344).

The Qmp value was calculated using the following equation (Moen 1973:355):

$$Qmp = (Wkg)(MD)(Qpf/6.25)/(.0162)(.85)$$

where

Qmp = quantity of milk produced (g) based on protein requirements

Wkg = weight of the fawn

MD = milk dependence=(113.6-4.5Wkg)/100

Qpf = quantity of protein required by fawn (mg/kg/day)

6.25 = protein:nitrogen ratio for body tissue

0.0162 = nitrogen fraction in deer milk at one month in lactation (Silver 1961)

0.85 = net protein coefficient for milk

The average weight of 18 one-month-old white-tailed fawns at the VPI & SU deer facility was 8.5 kg (Russell 1977); Wkg then was 8.5kg. This fawn weight provides an MD value of 0.7535. The quantity of protein required for maximum growth of white-tailed fawns is 6.6 g/kg/day (Moen 1973:343).

The quantity of milk produced (Qmp) at one month into lactation was 828.61g. The quantity of nitrogen required for lactation (Qnl) at 1 month was approximately 20.14g. This is converted to protein requirement by multiplying the nitrogen in the milk by 6.38. Additional protein requirement for lactation then was approximately 128.49g/day.

Protein and Energy Availability

The contribution of a food item to the nutrient and energy pool required for maintenance of deer is dependent in part on the consumption of the food item by deer. Consumption in turn is determined by the availability and palatability of the individual food items.

Relative consumption of various food items is reflected in the diet of the deer, which can be determined by analysis of rumen contents. All food items which make up the diet of a deer are not equally represented in the diet, again depending on the determinants of consumption. This variation in relative amounts of food items composing the diet must be accounted for in the requirement availability component of the carrying capacity calculation.

A weighting scheme which directly incorporates the availability of food items and indirectly the palatability of food items is applied to provide a refined estimate of contributions of food items to protein and energy content of the seasonal diets (Forsythe 1978).

For food items commonly found in the seasonal diets of white-tailed deer in the Ridge and Valley Province of Virginia, a relative utilization index (RUI) was calculated by the equation:

$$RUI = \frac{(\text{\% volume of food item in rumen contents})(\text{\% dry matter of food item})}{\text{standing crop of food item (kg/ha)}}$$

Rumen volume percentages for individual food items were obtained from rumen analyses of deer killed on the Broad Run Wildlife Management area (Harlow et al. 1975), and other locations in the Ridge and Valley Province of Virginia (Harlow and Hooper 1971). Seasonal dry matter percentages were determined for food items from the School House Hollow study area. Standing crop values for food items from Broad Run were used where available, supplemented with standing crop values for preferred food items from a similar area (Forsythe 1978).

Utilization indices for seasonal food items were ranked in descending order and a functional availability factor (FAF) was calculated for each food item by the equation:

$$FAFr = (r/n + RUIr/RUIn)(0.5)$$

with n equal to number of food items in a seasonal diet. The ranking (r) represents the absolute preference of each food item compared with the other food items, while the preference index indicates the relative degree of preference.

Total functional availability (TFA) of apparently digestible energy and true digestible protein to the animal was computed according to the equation:

$$TFA = [.50][\sum_{i=1}^{n} (FAFr)(Xr)]$$

where

Xr = apparent digestible energy/ha
or
true digestible protein/ha
for the rth food item

0.50 = maximum sustainable forage utilization (50%)
(Lay 1965)

Apparently digestible energy of individual food items was computed as the product of the gross energy and corrected IVDMD. True digestible protein of food items was considered 90% of the crude protein, based on discussions by Robbins et al. (1974) and Holter and Reid (1959).

Carrying Capacity

The values for total functional availability of digestible energy and protein represent the maximum amount of energy and protein available per ha. Depending on the intake rate and protein or energy density of the diet, the animal may or may not be able to satisfy its requirements from the available protein and energy pool. A diet with a given protein or energy density must be consumed in sufficient quantities during a 24 hour period to meet the animal's nutritional requirements, if the animal is to maintain body weight on that diet. The protein and energy density of the diet is determined by the seasonal selection of food items by the deer which make up the diet, and the the actual seasonal protein and energy densities of the food items. The intake rate is determined partially by the volume of the deer's digestive system and the turnover rate of the diet. Intake rate also fluctuates with the seasons, although the mechanics of this intake rate-season association are not well understood. The daily protein or energy supply in the diet was computed as the product of the average daily intake for a season and the protein or energy density of that diet (Wallmo et al. 1977:125). The protein and energy densities of seasonal diets were computed by weighting, with FAF, and summing the protein and energy densities of individual food items which comprised the seasonal diets.

When the combination of intake rate and protein or energy density do not provide the necessary requirements, the animal can not maintain body weight on the range regardless of the absolute levels of protein and energy. Thus, the potential carrying capacity of the range, based on immediate availability of digestible energy and protein, would be 0 ha/deer. If the protein and energy supplied in the diet surpass the daily requirements of the animal, potential carrying capacity is limited by the standing crop of staple food items. Under the circumstances, carrying capacity may be calculated by dividing the quotient of the total functionally available protein or energy per season over the number of days in the season, by the daily protein or energy requirement of the animal. This is an estimate of the area of range required to supply the animal with adequate protein or energy needs for maintenance.

Statistical Analysis

Standing crop data was analyzed by multiple comparisons tests on the ranked plot data to determine any differences in standing crop among parcels and seasons (Hollander and Wolfe 1973). Statistical analyses to determine significant differences in nutritional values were performed only for those species which were collected in sufficient quantities on the 4 parcels for most of the seasons. A block design was used in which the selected species were blocked according to season and then by parcel. The General Linear Models procedure (Barr et al. 1976) and Duncańs new multiple range tests (Steel and Torrie 1960:107) were used to discern any significant differences among parcels or seasons in protein or energy levels in selected plant species.

RESULTS

Basal Area

Residual basal areas among thinned parcels were similar, ranging from about 7.10 m^2/ha to 7.94 m^2/ha (Table 1). Original basal areas on the thinned parcels, computed from DBH-stump diameter correlations, ranged from 12.56 to 19.14 m^2/ha. The percentage reduction of basal area as a result of thinning ranged from 43 to about 62% among the thinned parcels. The average residual basal area of the three thinned parcels was approximately 54% of the basal area of the unthinned parcel.

Canopy Cover

Percent canopy cover over the thinned parcels differed significantly from canopy cover over the control (Table 2). There was no significant difference in canopy cover among the three thinned parcels ($P>0.05$). The percent canopy cover on the thinned parcels ranged from 74.6 to 78.8%. Canopy cover over the thinned parcels averaged 21.67% less than the unthinned parcel.

Standing Crop of Understory Forage

Total mean standing crop of food items on thinned parcels varied from approximately 2.5 to 18.5 times greater than on the unthinned parcel, depending on the season and parcel (Table 3). Standing crop on thinned parcels always

Table 1. Original and residual basal areas and basal area reduction by species on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Basal Area		
Parcel	Original (m^2/ha)	Residual (m^2/ha)	Reduction (%)
1+	19.14	7.34	61.66
3	14.02	7.94	43.41
4	12.56	7.10	43.44
unthinned	18.60	18.60	0.00

+Parcels are listed in order of decreasing time since thinning, from top to bottom.

Table 2. Canopy cover for thinned and unthinned parcels and reduction in canopy cover attributed to thinning. School House Hollow study area, Craig County, Virginia. 1976-77.

	Canopy Cover	
Parcel	After cut (%)	Reduction by cutting (%)
1	76.6	21.06
3	74.6	24.11
4	78.8	19.84
unthinned	98.3	0.00

Table 3. Seasonal mean standing crop (kg/ha) of the staple diet for white-tailed deer on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	571.70(51)≠ (±67.86)°	442.39(45) (±57.71)	321.70(38) (±76.78)	129.88(27) (±25.62)
Fall	200.32(29) (±37.44) (409.07)[3]	128.65(22) (±49.07) (258.90)	277.66(20) (±62.73) (382.81)	52.33(21) (±14.93) (358.91)
Winter	80.15(37) (±16.99)	79.98(35) (±35.78)	200.05(38) (±35.55)	10.72(36) (±2.70)
Spring	349.34(40) (±46.48)	283.92(35) (±70.06)	462.15(36) (±73.40)	98.72(36) (±23.01)

≠Sample size; number of plots/parcel for the season.

°Standard error.

+Values in parentheses are standing crops including oak mast in fall.

exceeded that on the unthinned parcel during a season. Only the summer values for standing crop reflected the usual production response where standing crop of understory increases consistently with time since overstory reduction. For the fall, winter and spring periods, Parcel 4, the youngest thinned parcel, had the greatest standing crop, followed by Parcels 1 and 3, the oldest and second oldest parcels, respectively. Standing crop of evergreen species was greatest on Parcel 4 during all seasons except spring (Table 4).

All parcels except Parcel 4 had the greatest standing crop of staple food items during the summer, followed by spring, fall and winter. For Parcel 4, spring and summer levels were reversed.

Based on the mean ranks of standing crop values, there were significant differences among seasons in standing crop of staple food items for all treatments (Table 5). For all parcels except 4, mean rank was greatest for summer followed by spring, fall and winter. In Parcel 4, the greatest mean rank was spring, followed by fall, winter, and summer.

Mean ranks of standing crop values differed significantly among parcels for all four seasons (Table 6). Highest mean rank in summer was Parcel 1, the oldest parcel, followed by 3, 4 and the unthinned parcels. For the other

Table 4. Contribution (%) of 4 evergreen species+ to the total standing crop of staple diet for white-tailed deer on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	17.49	9.46	33.62	27.36
Fall	27.24	48.88	61.91	46.92
Winter	34.25	53.81	77.47	37.61
Spring	7.63	9.87	21.84	34.18

+Galax, mountain laurel, teaberry, trailing arbutus.

Table 5. Seasonal mean ranks of the standing crops of staple diets for white-tailed deer on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	106.45a+	89.74a	57.96a	81.33a
Fall	69.43b	52.77bc	68.12ba	60.00a
Winter	42.64c	45.91c	61.08ba	35.70b
Spring	84.58b	75.61ab	80.33b	72.33a

+Within columns, means with same letter not significantly different at 15% level.

Table 6. Parcel mean ranks of the standing crops of staple diets for white-tailed deer on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Season			
Parcel	Summer	Fall	Winter	Spring
1	101.69b+	56.88b	87.47bc	84.18b
3	88.27b	36.16a	65.74b	70.60ba
4	64.34a	57.85b	102.56c	91.00c
unthinned	53.26a	32.19a	39.00a	49.00a

+Within columns, means with the same letter are not significantly different at the 15% level.

three seasons, Parcel 4 had the greatest mean rank, followed by Parcels 1, 3 and the unthinned.

<u>Standing Crop of Oak Mast</u>

Standing crop of oak mast was greatest in the unthinned parcel (Fig. 2). Standing crop of oak mast among thinned parcels increased with time since thinning. However, acorn yields among parcels also paralleled total basal areas of oaks in the parcels.

Chestnut oak had the highest overall production of sound acorns among parcels, followed by scarlet and black oak (Table 7). Although chestnut oak had the greatest acorn yields, basal area was lower than for scarlet oak. Chestnut oak had the lowest R^2, 0.374, when acorn yield was regressed on DBH. Regression coefficients for scarlet and black oak were 0.605 and 0.517, respectively. Numbers and standing crop of scarlet oak acorns were greater than black oak on the thinned parcels, although this pattern was reversed on the unthinned parcel.

<u>In Vitro Digestibility</u>

There were no significant differences in mean <u>in vitro</u> dry matter digestibility (IVDMD) for the combined values for mountain laurel, galax and teaberry, associated with time since thinning ($P>0.05$) (Table 8). There were significant differences in mean IVDMD values for combined values of

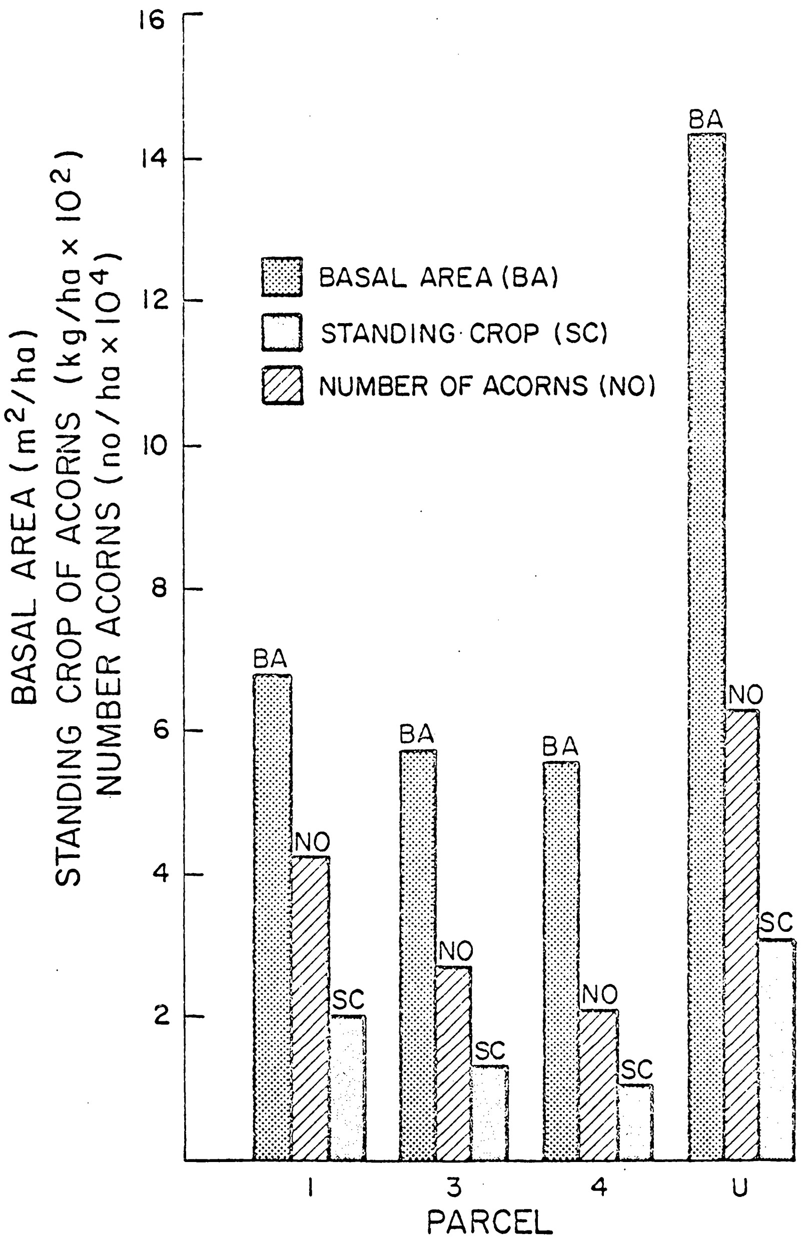

Fig. 2. Total oak basal areas and mast yields by parcel. School House Hollow study area, Craig County, Virginia. Fall-winter 1976-77.

Table 7. Oak basal areas (m^2/ha) and mast yields (no. acorns/ha and kg/ha) for thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. Fall-winter 1976-77.

	Parcel			
Oak spp.	1	3	4	unthinned
Chestnut				
basal area	8.22	5.19	2.58	25.70
no. acorns	31,437	16,800	9,984	46,117
wt. acorns	154.67	82.66	49.12	226.89
Scarlet				
basal area	20.95	15.74	13.74	12.40
no. acorns	10,551	7,335	5,975	2,748
wt. acorns	50.65	35.21	28.68	13.19
Black				
basal area	0.29	4.10	7.92	23.96
no. acorns	641	3,231	5,112	13,854
wt. acorns	3.43	12.28	27.35	66.50
TOTAL				
basal area	29.46	25.03	24.24	62.06
no. acorns	42,629	27,366	21,071	62,719
wt. acorns	208.75	130.15	105.15	306.58

Table 8. Parcel mean crude protein (%), gross energy (kcal/g) and *in vitro* dry matter digestibility (%), for a composite of staple food items.≠ School House Hollow study area, Craig County, Virginia. 1976-77.

	Nutritive component		
Parcel	Crude protein (%)	Gross energy (kcal/g)	IVDMD (%)
1	7.84a+	4.72a	43.91a
3	7.33a	4.74a	41.76a
4	7.10a	4.78a	41.15a
unthinned	7.33a	4.67a	40.00a

+Within columns, means with the same letter are not significantly different at the 5% level.

≠Trailing arbutus, galax, teaberry, mountain laurel, chestnut oak and sassafrass leaves.

Table 9. Seasonal mean crude protein (%), gross energy (kcal/g) and *in vitro* dry matter digestibility (%), for composite of staple food items.≠ School House Hollow study area, Craig County, Virginia. 1976-77.

Season	Crude protein	Gross energy	IVDMD
	Nutritive component		
Summer	6.93ab+	4.62a	41.67a
Fall	5.52b	4.67a	46.97b
Winter	6.60ab	4.66a	49.05b
Spring	7.94a	4.71a	46.63b

+Within columns, means with same letter are not significantly different at the 5% level.

≠Galax, teaberry, mountain laurel and chestnut oak leaves. Chestnut oak leaves were excluded from IVDMD analysis.

these three species among seasons ($P < 0.05$) (Table 9). Summer values were significantly lower than values for the other three seasons. There were no significant differences among fall, spring and winter values for IVDMD. Mean IVDMD values for the three species were highest in winter followed by fall, spring and summer. Values for IVDMD among all staple food items for all seasons ranged from 9.54 to 75.58%.

Generally the deciduous species from School House Hollow followed a trend of declining digestibility with advancing maturity (Figs. 3 and 4). However, the evergreen species exhibited a tendency toward higher digestibility values during the fall and winter, normally the period at which most plants have matured and become senescent or dormant (Figs. 5 and 6). Mean IVDMD values for individual food items are summarized in Appendix II.

Energy

Means of combined gross energy values for 6 staple food items did not differ significantly among parcels (Table 8). Parcel 4 had the highest mean gross energy value followed by Parcels 3 and 1, and the unthinned parcel. Gross energy of all food items varied from 3.24 to 6.22 kcal/g. Mean gross energy values for individual food items from all 4 parcels are listed by season in Appendix III. Combined gross energy

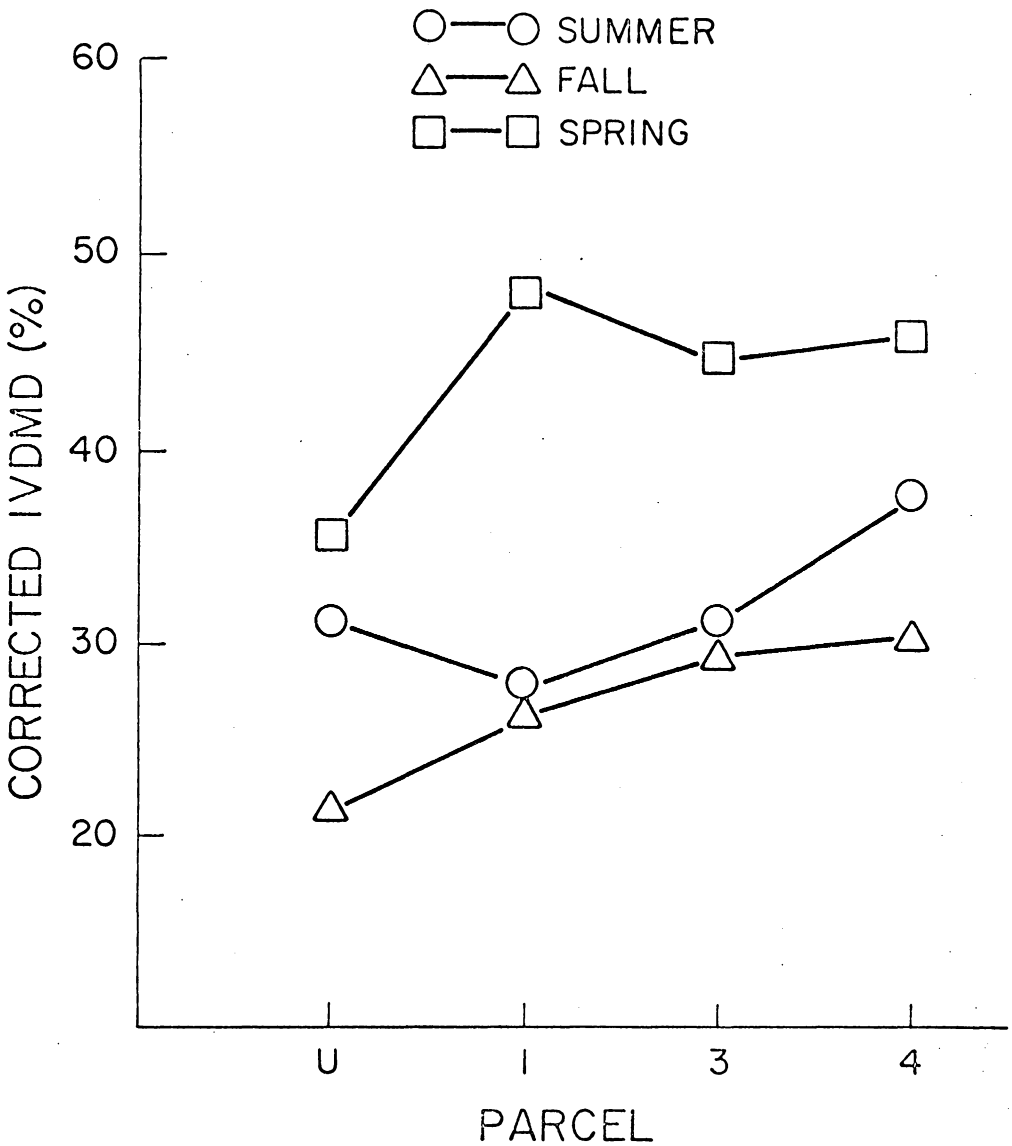

Fig. 3. Seasonal *in vitro* dry matter digestibility of chestnut oak leaves. School House Hollow study area, Craig County, Virginia. 1976-77.

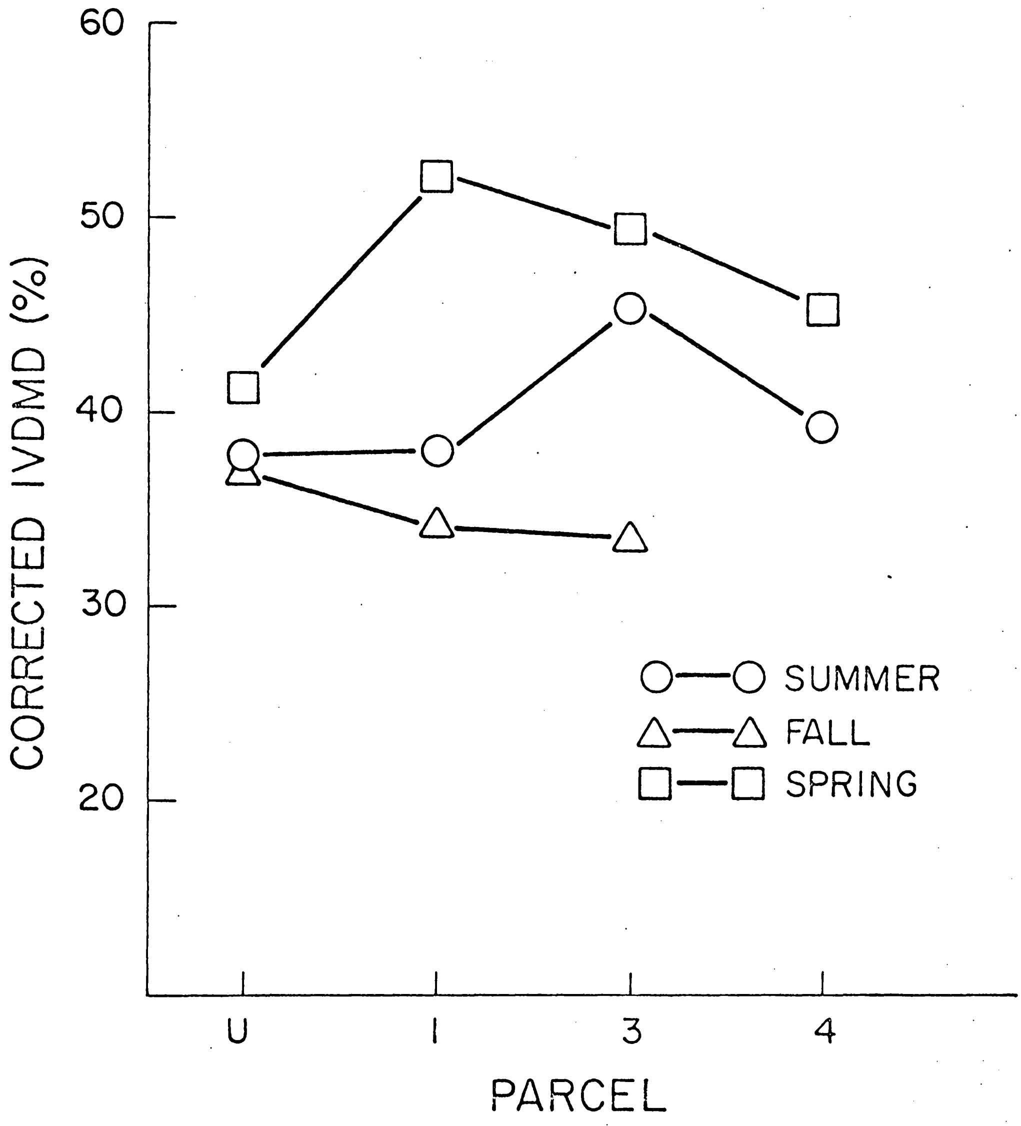

Fig. 4. Seasonal *in vitro* dry matter digestibility of of sassafrass leaves. School House Hollow study area, Craig County, Virginia. 1976-77.

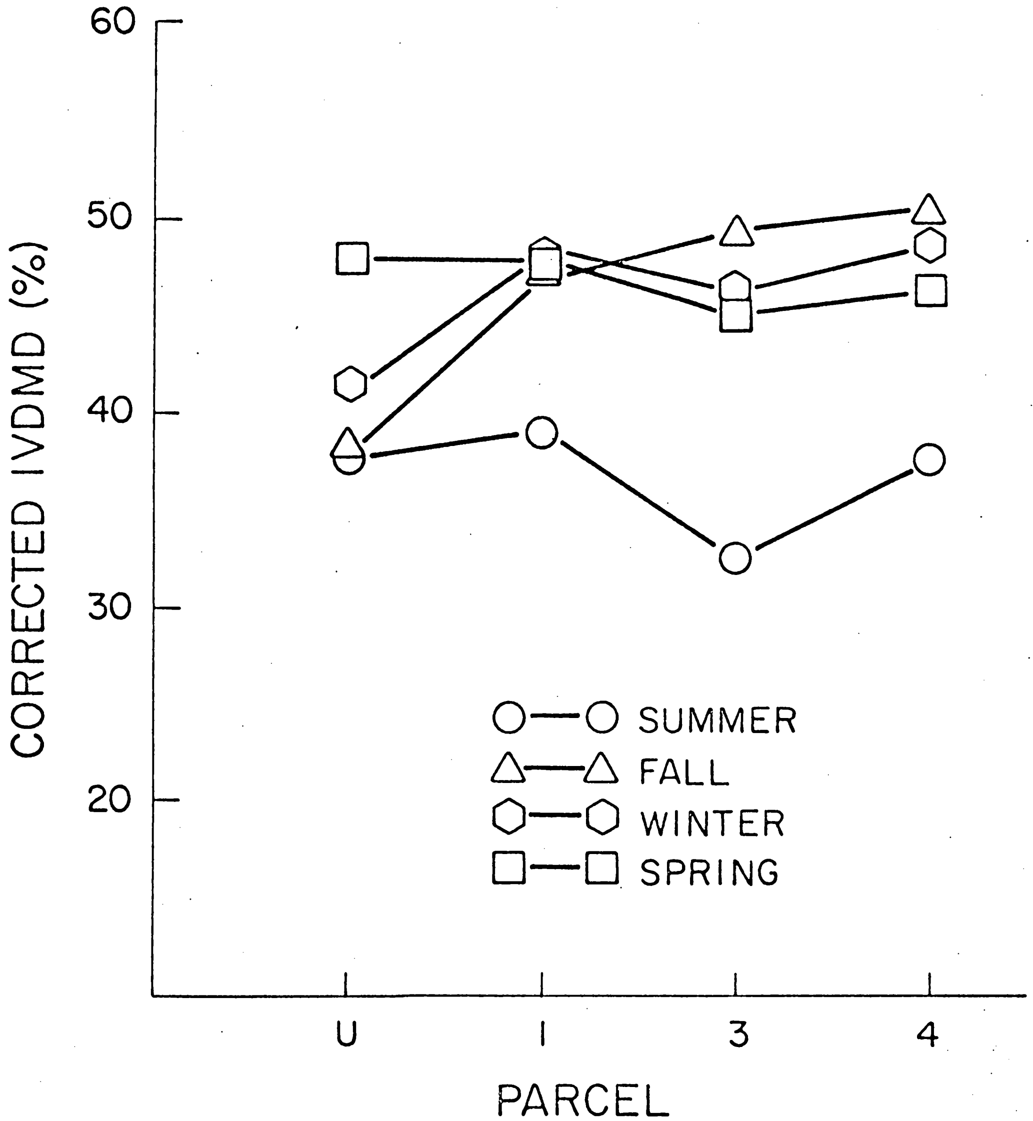

Fig. 5. Seasonal *in vitro* dry matter digestibility of teaberry. School House Hollow study area, Craig County, Virginia. 1976-77.

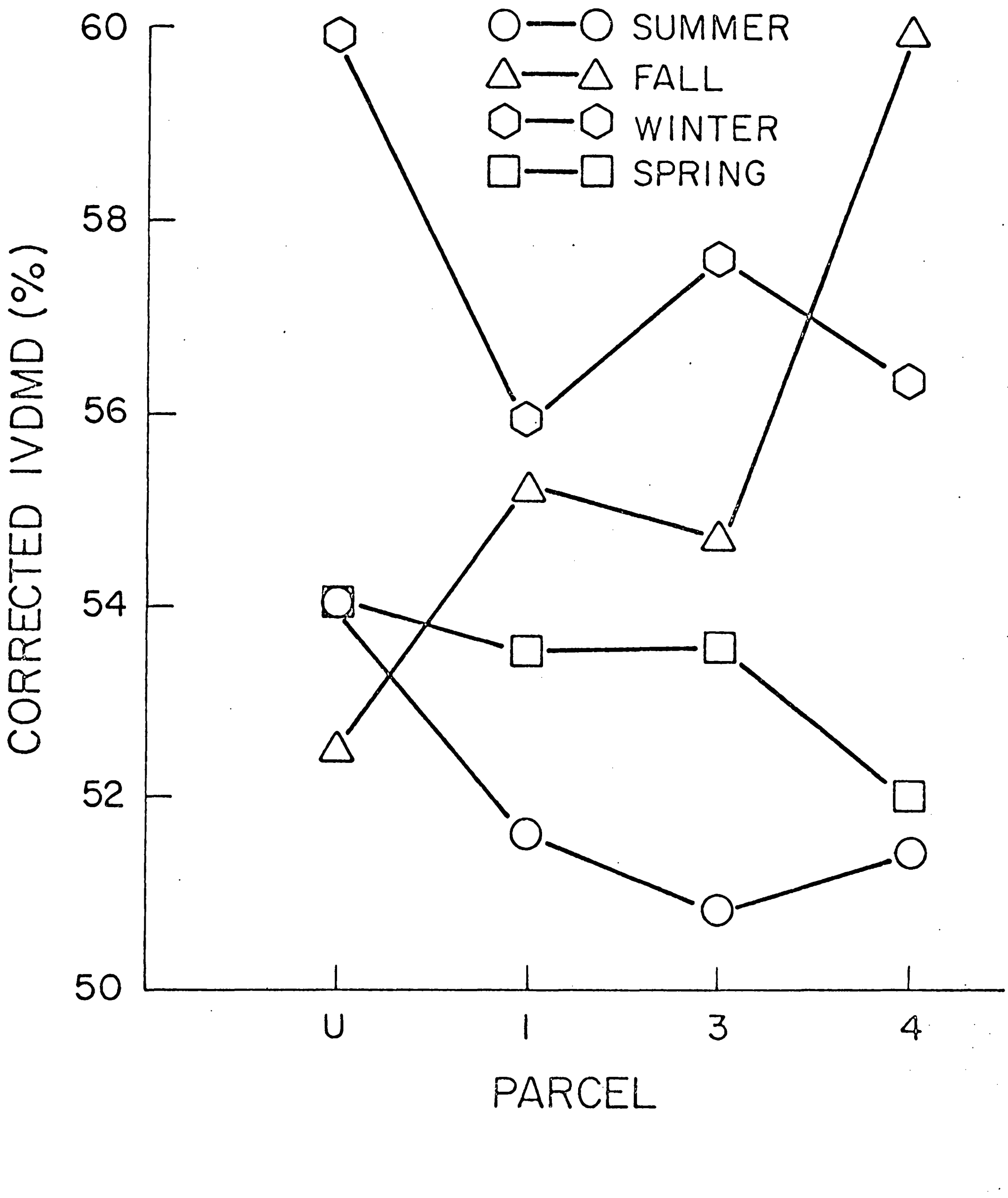

Fig. 6. Seasonal *in vitro* dry matter digestibility of galax. School House Hollow study area, Craig County, Virginia. 1976-77.

values for 4 staple food items did not differ significantly (P>0.05) among seasons (Table 9). Mean gross energy for the four food items was highest in spring, followed by fall, winter and summer. Seasonal functionally available apparently digestible energy in staple diets are summarized in Table 10.

Protein

Means of combined crude protein values of 6 staple food items did not differ significantly among thinned parcels (Table 8). However, Parcel 1 had the highest mean crude protein value followed by Parcels 3 and the unthinned, with equal mean levels and Parcel 4. Among the 6 food items, spring food items had the highest mean crude protein content followed by summer, winter, and fall. Only spring and fall differed significantly (P<0.05) (Table 9). Crude protein content of all staple food items ranged from 1.85% for panic grass (*Panicum* spp.) in fall, to 18.05% in chestnut oak leaves during spring.

Mean crude protein content for all plant parts was highest during spring, declined in summer and reached the lowest levels during the fall and winter. Generally, mean protein levels of woody stems were slightly higher in winter than fall. Mean seasonal crude protein levels are listed in Appendix IV.

Table 10. Seasonal functionally available apparently digestible energy (kcal/ha) in the staple diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	139,383.82 (1,302.65)+	126,391.55 (1,181.23)	60,318.64 (563.73)	40,952.82 (382.74)
Fall (mast excluded)	20,870.37 (274.61)	17,231.11 (226.71)	23,555.31 (309.94)	9,694.61 (127.56)
Fall (mast included)	579,140.37 (7,620.27)	382,301.11 (5,030.28)	320,225.31 (4,213.49)	774,164.61 (10,186.38)
Winter	15,624.63 (129.13)	11,835.25 (97.81)	27,169.32 (224.54)	1,672.50 (13.82)
Spring	187,752.36 (1,551.67)	69,834.23 (577.14)	94,220.81 (778.68)	11,866.41 (98.07)

+Values in parentheses are functionally available apparently digestible energy on a daily basis. Season lengths of 107, 76, 121 and 46 days were assigned to summer, fall, winter and spring respectively.

Leaf tissue during spring and summer had higher mean levels of crude protein than the terminal 3 in. of woody stem tissue. There was no consistent trend among parcels in absolute mean crude protein levels for any plant parts. Among thinned parcels for spring and summer, dietary true digestible protein densities (calculated using FAF) were maximal for Parcel 1 and minimal for Parcel 4 (Table 11). During fall, the reverse was true. Parcel 4 had the highest and 1 the lowest protein densities. For the winter diet, Parcel 4 had the highest level of true digestible protein, followed by Parcels 1 and 4. For all seasons, true digestible protein levels of the unthinned parcel was intermediate compared to the thinned parcels.

Protein and Energy Requirements

Seasonal apparent digestible energy and true digestible protein requirements of a doe white-tailed deer are listed in Table 12.

Carrying Capacity

Energy-based.

Digestible energy densities were insufficient to provide the energy requirements of the doe during some seasons (Table 13). Thus carrying capacity of all parcels during summer, winter and fall was 0 when oak mast was excluded from the fall diet (Table 14, Figs. 7-11). The low

Table 11. Seasonal functionally available true digestible protein (g/ha) in the staple diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	7441.86 (69.55)	6001.34 (56.09)	4230.52 (39.54)	1834.48 (17.14)
Fall (mast included)	12017.94 (158.13)	1548.38 (20.37)	5794.29 (76.24)	17822.65 (234.51)
Fall (mast excluded)	424.54 (5.59)	406.70 (5.35)	486.26 (6.40)	225.22 (2.96)
Winter	315.35 (2.61)	280.55 (2.32)	545.04 (4.50)	44.64 (0.37)
Spring	6691.01 (109.69)	2742.46 (44.96)	4230.52 (69.35)	423.54 (6.94)

+Values in parentheses are functionally available true digestible protein on a daily basis. Seasons lengths of 107, 76, 121 and 46 days were assigned to summer, fall, winter and spring respectively.

Table 12. Body condition, forage intake rates and energy and protein requirements of doe, white-tailed deer as influenced by season and physiological condition.

Season	Doe condition	Body wt. (kg)	Forage Intake rate (kg/kg$^{.75}$)	Energy requirement (kcal/day)	Protein requirement (g/day)
Summer (July)	summer coat; lactating; 1 fawn.	57.31 (20.83)+	0.088	7178.39	86.68
Fall (Nov.)	winter coat.	57.31 (20.83)	0.074	3413.20	25.93
Winter (Feb.-March)	winter coat; mid-pregnancy.	48.71 (18.44)	0.088	2913.52	24.25
Spring (May)	summer coat; late pregnancy	48.71 (18.44)	0.102	2913.52	37.23

+Values in parentheses are metabolic body weights (kg$^{.75}$).

Table 13. Apparently digestible energy densities (kcal/kg) in the seasonal diets of white-tailed deer from thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

Season	Parcel 1	Parcel 3	Parcel 4	Parcel unthinned
Summer	1801.04	1800.92	1842.36	2031.19
Fall (mast excluded)	1633.05	1878.23	1773.17	1749.71
Fall (mast included)	2269.79	2469.30	2301.11	2406.45
Winter	1601.21	1576.54	1636.06	1579.50
Spring	2335.96	2211.06	1920.19	2164.44

Table 14. Seasonal energy-based carrying capacities (ha/deer) of thinned and unthinned parcels. School Hollow study area, Craig County, Virginia 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	0 (0.50)+	0 (0.50)	0 (0.47)	0 (0.52)
Fall (mast included)	0.45 (1.02)	0.68 (1.12)	0.81 (1.04)	0.34 (1.09)
Fall (mast excluded)	0 (0.74)	0 (0.85)	0 (0.80)	0 (0.79)
Winter	0 (0.89)	0 (0.88)	0 (0.91)	0 (0.88)
Spring	1.88 (1.51)	5.05 (1.43)	3.74 (1.43)	29.71 (1.40)

+Values in parentheses are ratios of dietary energy availability to dietary energy requirements.

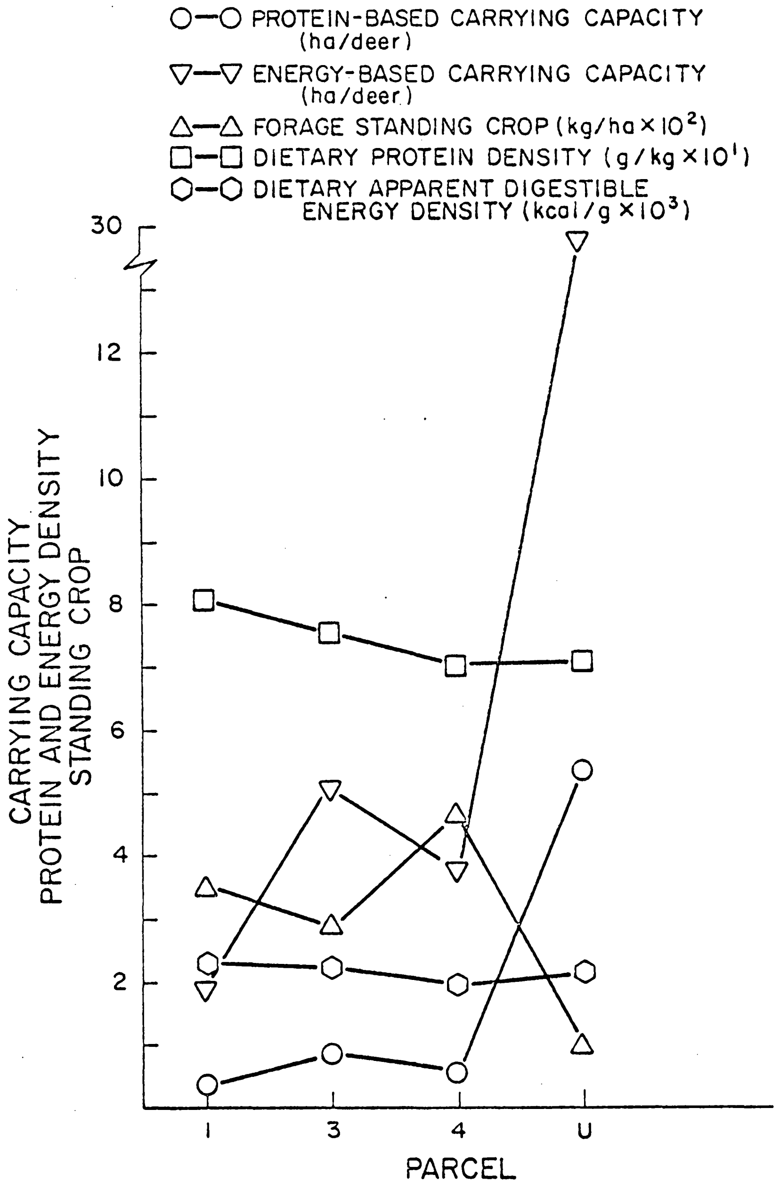

Fig. 7. Spring dietary digestible energy and protein density, forage standing crop and carrying capacities on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

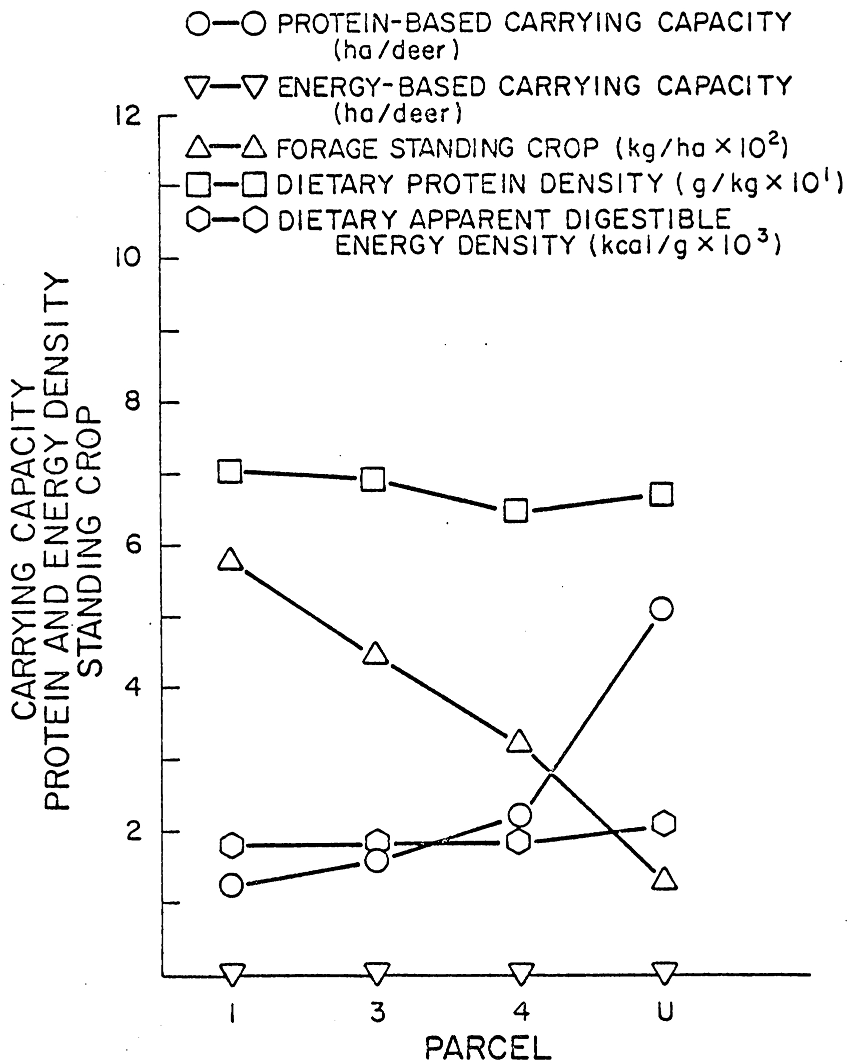

Fig. 8. Summer dietary digestible energy and protein density, forage standing crop and carrying capacities on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

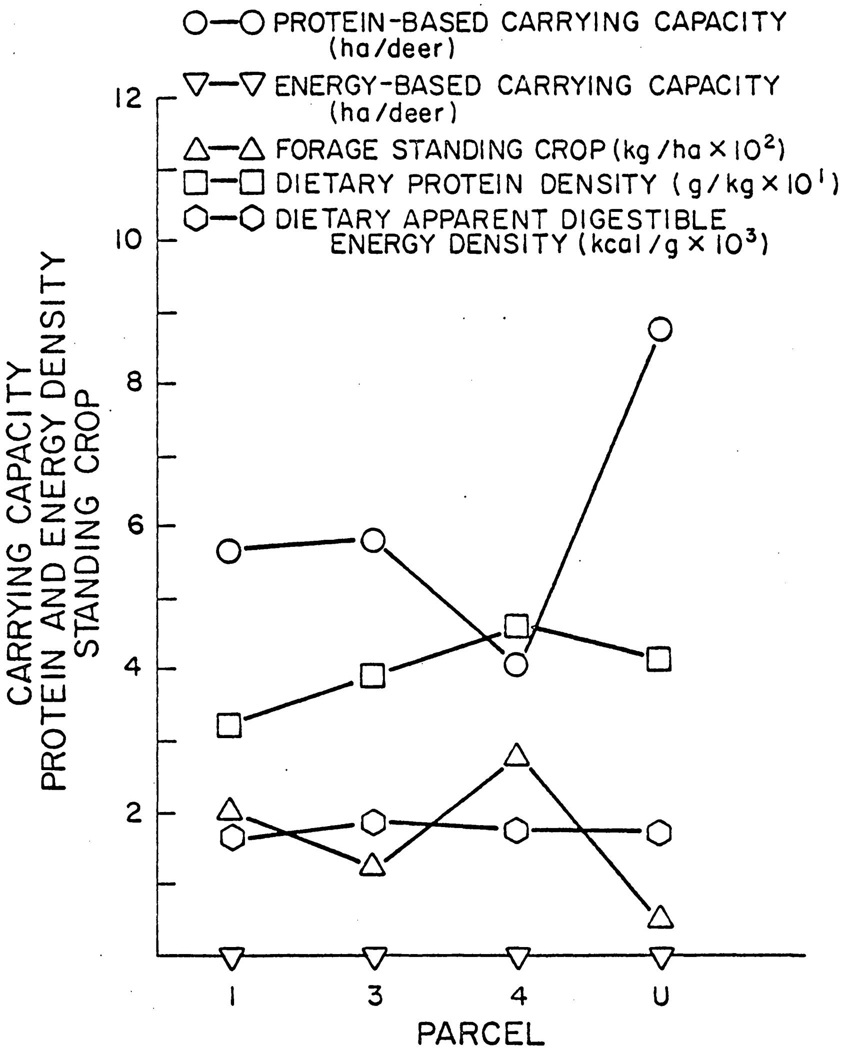

Fig. 9. Fall dietary digestible energy and protein density, forage standing crop and carrying capacities without acorns, on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

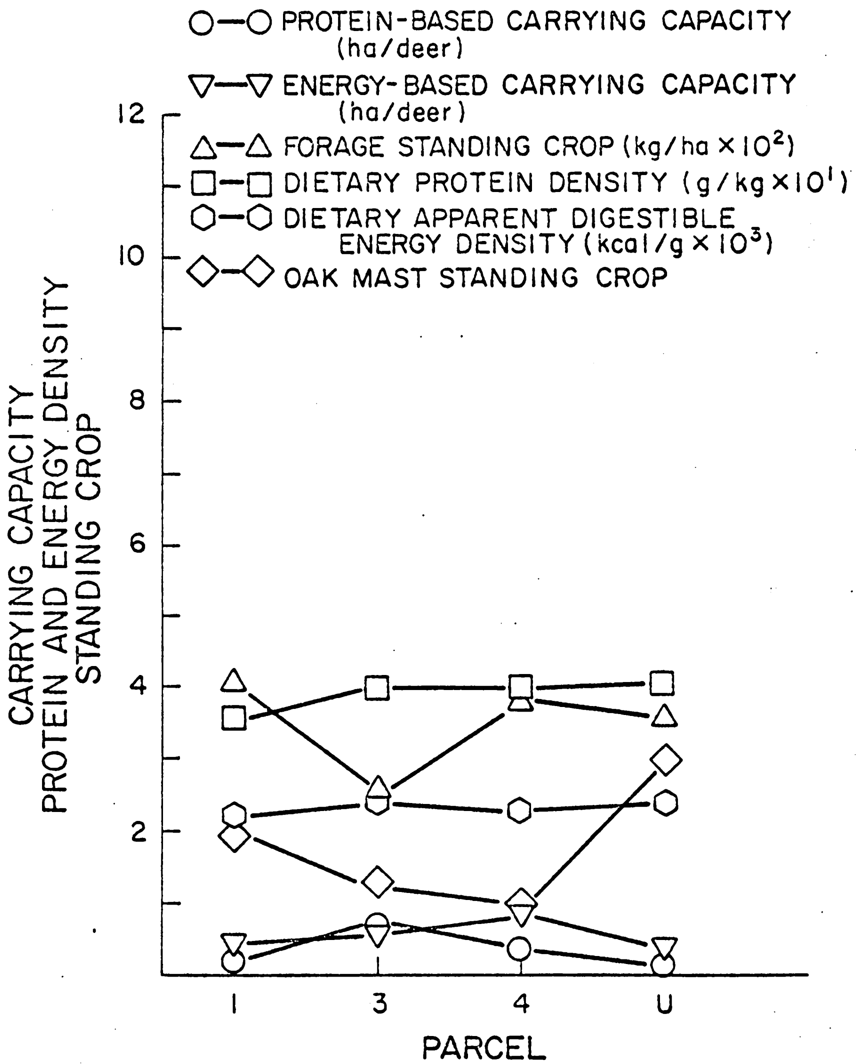

Fig. 10. Fall dietary digestible energy and protein density, forage standing crop and carrying capacities with acorns, on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

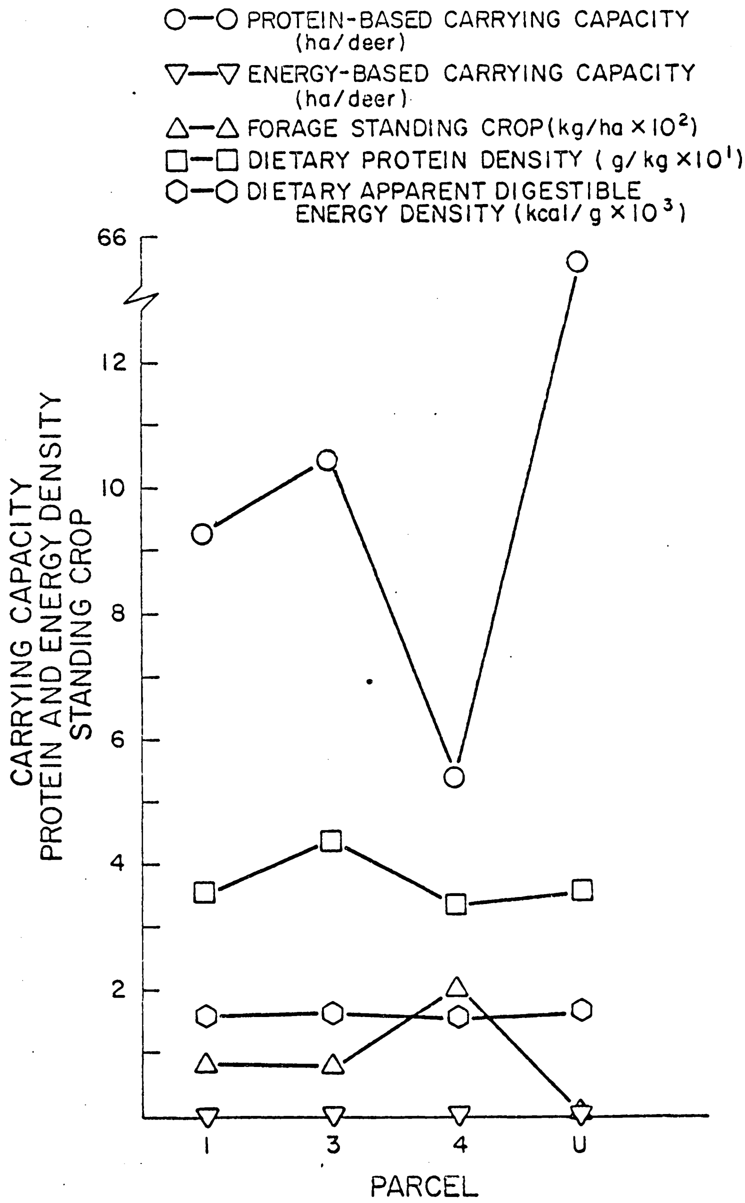

Fig. 11. Winter dietary digestible energy and protein density, forage standing crop and carrying capacities on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

energy density diets at these seasons did not provide the minimum daily requirements of energy for maintenance. For spring, Parcel 1 had the highest carrying capacity, followed by Parcels 4, 3 and the unthinned parcel. If oak mast is included in the fall diet, the dietary energy density is adequate to meet the daily energy requirements of the doe for maintenance (Table 13, Figs. 7-11). With mast included, the unthinned parcel had the greatest carrying capacity, followed by Parcels 1, 3, and 4.

Protein-based.

Protein densities of diets for all parcels and seasons provided the doe with sufficient digestible protein for maintenance (Table 15). Protein-based carrying capacity among parcels increased in the same order as standing crops of parcels for all seasons except spring. (Table 16). For spring, this pattern was reversed in Parcels 1 and 4. Parcel 1 had lower standing crop of staple food but a greater protein-based carrying capacity, while Parcel 4 had a greater standing crop, but lower carrying capacity (Table 14, Figs. 7-11). For fall, when oak mast is included in the diet, protein-based carrying capacities were more closely aligned with standing crop of oak mast rather than with total standing crop of forage (Fig. 9).

Table 15. True digestible protein densities (g/kg) in the seasonal diets of white-tailed deer on thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	70.2	69.4	64.5	66.7
Fall (mast excluded)	32.3	39.6	46.2	41.4
Fall (mast included)	35.5	39.9	39.9	40.6
Winter	35.5	43.2	33.6	35.4
Spring	81.0	75.6	70.1	70.8

Table 16. Seasonal protein-based carrying capacities (ha/deer) of thinned and unthinned parcels. School House Hollow study area, Craig County, Virginia. 1976-77.

	Parcel			
Season	1	3	4	unthinned
Summer	1.25 (1.48)+	1.55 (1.47)	2.19 (1.36)	5.06 (1.41)
Fall (mast included)	0.16 (2.11)	0.79 (2.37)	0.34 (2.37)	0.11 (2.41)
Fall (mast excluded)	4.64 (1.92)	4.85 (2.35)	4.05 (2.75)	8.76 (2.46)
Winter	9.29 (2.38)	10.45 (2.89)	5.39 (2.25)	65.54 (2.37)
Spring	0.34 (6.28)	0.83 (5.86)	0.54 (5.44)	5.36 (5.49)

+Values in parentheses are ratios of protein availability to dietary requirements.

DISCUSSION

Standing Crop of Understory Forage

Increased standing crops of understory vegetation have been associated with time since reduction of canopy coverage by tree harvest (Crawford 1971, Crawford and Harrison 1971, Patton and McGinnes 1964, Knierim et al. 1971, Wood 1971, Baskett et al. 1957, Cook 1939, and others). Variations of standing crop following timber harvest have also been associated with percent reduction of overstory (Knierim 1971:167, Patton and McGinnes 1964 :461, Leak and Solomon 1975:6, Ehrenreich and Crosby 1960:564, Crawford 1971:277), forest type (Knierim et al. 1971:167) and quality of the site (Crawford 1971:284, Crawford and Harrison 1971:535). In this study, total standing crop of preferred food items exhibited the common production pattern expected for time since thinning, only for the summer sample. For the summer sample, standing crop was greater with time since thinning of the parcel, and was lowest for the unthinned parcel.

The regular pattern of increased standing crop with time since thinning was not as evident during fall, winter or spring. The greater standing crop of staple forage on Parcel 4 during these seasons may be due in part to the interaction of species composition and season. At each season, Parcel 4 had the greatest percentage representation of evergreen species in the seasonally available diet on thinned parcels. With higher proportions of evergreen phytomass in the available forage, the standing crop of forage would not be expected to decline as much as it would on those parcels with higher composition of deciduous species which shed their leaves in the fall.

The greater proportion of mountain laurel leaves, galax, teaberry and trailing arbutus on Parcel 4 for all seasons suggests somewhat drier conditions on this parcel. Crawford and Harrison (1971:535) noted increased mean dry matter vegetation weights on poor and intermediate sites but not on the best sites of clearcut Missouri Ozarks. Increased yields of shrub and herbaceous phytomass have also been related to more xeric conditions in undisturbed deciduous forests (Whittaker 1966, Mowbray and Oosting 1968, Whittaker and Woodwell 1968).

The departure of Parcel 4 from the common seasonal pattern of standing crop distribution may be a result of the drier site condition of that parcel, coupled with the beginning of an additional growing season at the time of the spring sample. During spring sampling, Parcel 4 was beginning it's second growing season, whereas during summer, fall and winter sampling the Parcel had undergone only a single growing season since thinning.

Since residual basal area and canopy cover on all thinned parcels was essentially the same, the differences in standing crop probably cannot be attributed to these factors.

Standing Crop of Oak Mast

Standing crop of oak mast on the thinned parcels was positively associated with time since thinning. However, it seems more plausible that standing crop was affected most by residual basal area of oaks, since standing crop was also positively associated with oak basal area for all parcels. Yield from chestnut oak was greater than scarlet and black oak. However, the estimated number and weight of acorns based on basal areas of chestnut oak is open to more question than for the other two species because of the low R^2 value, and the relatively low absolute number of chestnut oak acorns used to derive the polynomial regression equation used as a predictor. Field observations suggested lower yields from chestnut oaks than from other species.

Downs and McQuilken (1944:340) reported similar relative standing crops among the three oak species considered here. Beck (1977:5), working in one of the areas considered by Downs, reported greatest yields from scarlet oak followed by chestnut and black oak for a 12-year period. During certain years, acorn yield followed the sequence noted in the present study. Both authors noted yearly and species variations in oak mast yield.

In Vitro Dry Matter Digestibility

Digestibility of food items for ruminant animals has frequently been associated with plant maturity and growth rate (Klein 1965:273, Dietz 1965:279, Hellmers 1940:318, Fuller 1976:108, and others). Generally, as the plant matures, the proportion of less digestible cell wall constituents (CWC) increases and contributes to a decline in the overall digestibility of the plant. Klein (1965:273) indicated that the increased fiber and lignin in cell walls renders the cell contents less available, thereby decreasing the overall digestibility and therefore nutritive value of the forage. Consequently digestibility of most plants is greatest during spring and summer months and lowered digestibility during fall and winter (Wallmo et al. 1977:123, Dietz 1965:279).

However, Regelin (1971:34) observed no decline in *in vitro* dry matter digestibility of understory vegetation in spruce-fir and lodgepole pine types with advancing plant maturity.

Steinhubel and Halas (1969) have noted instances in which evergreen plants experience net gains in dry matter weights of leaves during winter. It is possible that the evergreen species actually experience a slightly accelerated growth during the fall-winter months, in response to the reduction of overstory canopy and consequent increase in solar insolation on lower forest strata. If their growth is accelerated during the normally dormant period, evergreen species might contain relatively lower levels of structural carbohydrates. Thus, digestibility of the evergreen fraction of the diet consumed by deer would be greater during the fall and winter than during spring and summer.

The overall digestibility of a seasonal diet depends on the relative proportions of various food items in the diet, their growth forms, the maturity of the plants, and the rate of growth. These are all related factors which affect the energy and protein composition of the diet. Factors which increase the growth rates of plants should cause increased digestibility. Growth rates of vegetation in lower forest strata would tend to increase with reduction of canopy cover. This increase can be attributed to increases in solar insolation in lower strata as well as increased soil moisture availability. Increases in soil moisture would be attributable to greater precipitation throughfall and reduced evapotranspiration losses from overstory vegetation. Evergreen species on the thinned parcels displayed no consistent tendency toward greater digestibility over those on the unthinned parcel. However, it is probable that the amount of solar insolation reaching three of these evergreen species, teaberry, galax and trailing arbutus, was not much greater than on the unthinned parcel during spring and summer. This is due to the dense midstory canopy formed by the proliferation of stump sprouts soon after thinning, and the very low growth form of these species. Digestibilities of leaves from at least three woody species, scarlet and chestnut oak, and sassafrass, had a tendency to increase on the thinned parcels. Leaves of these three species were primarily from stump sprouts, which formed a midstory canopy. Thus, solar insolation on these leaves was probably greater than on the ground strata, or understory leaves on the unthinned parcel. This would tend to accelerate the growth, and thus digestibility, of the leaves early in the growing season. In addition, the existing root systems of harvested trees provide abundant nutrients and moisture to stump sprouts, which further increases the growth rate of predominantly sprout origin leaves over those leaves on the unthinned parcel.

Gross Energy

There were no significant differences in gross energy of four species among parcels and seasons. The results concur with other research findings which indicate only minor variations in gross energy values of forage. Wallmo et al. (1977) computed averages of 4.5 and 4.3 kcal/g for the gross energy content of summer and winter deer forage respectively. Treichler et al. (1946:14) determined an average gross energy of 4.5kcal/g for 6 food items of ruffed grouse during the winter.

Crude Protein

Vegetative food items generally exhibited maximum crude protein levels in spring, declined through summer and reached the lowest levels in fall and winter. This fluctuation in crude protein levels with seasons has been documented for a wide variety of plant species consumed by deer (Fuller 1976, Blair and Epps 1969. Short 1971, Dietz 1965, Wallmo et al. 1977, Hellmers 1940 and others). Higher levels of crude protein in individual plant food items during spring and summer have been attributed to rapid growth of new plant tissue at these seasons (Blair and Epps 1967:10, and 1969:8, Klein 1965:273, Dietz 1972:291).

The slight trend toward higher mean crude protein levels in woody stems in winter over fall, is possibly associated with translocation of nitrogen from leaves to stems during fall. Dietz (1972:291) discusses the process whereby nitrogen in the leaves of deciduous species is translocated into stem tissue prior to leaf abscission.

Thinning may cause fluctuations in levels of crude protein in staple diets through changes in protein levels of individual food items and/or changes in plant species composition of the staple diet. Crawford et al. (1975:8) found variable crude protein levels in the same plant species from select and clearcut oak-pine stands. They noted differences between select and clearcuts in the availability of certain species, with some species found in one type cut and not the other. Overall, they found higher levels of crude protein in the staple diet from the select cut. In at least one case, plants growing in shade were found to have higher percentage of protein than the same species growing in the sun (McEwen and Dietz 1965). Although variations in crude protein levels of diets and diet components were found in the present study, the variations were not consistently associated with thinning or time elapsed since thinning. Therefore, it would be difficult to attribute differences in crude protein levels to thinning or a particular characteristic of thinning.

Carrying Capacity

Nutrition-based carrying capacity can be determined by the energy or protein density of a diet, the standing crops of the items which comprise the diet, and the energy and protein requirements of the animal. Since nutritional requirements for a particular phase of the year are assumed to be the same from year to year, any variations in seasonal carrying capacity among parcels for a particular phase can be attributed largely to the standing crops of food items and the energy and protein levels in the diets. Variations in carrying capacity among seasons may result from seasonal variations in animal requirements as well as fluctuations in energy and protein density of diets, and standing crop of food items.

For this study, calculations of carrying capacity were based on animal requirements, and the availability of those requirements during relatively short periods of the year. Strictly interpreted, these calculations are a measure of the degree to which a seasonal diet satisfies the animal requirements during periods when dietary components were collected. They do not account directly for accumulation and depletion of energy or protein reserves during periods of dietary excess and deficiency, respectively. Thus, carrying capacity of the range, using this method, may be calculated as 0 ha/deer when the population may be thriving, because of energy and protein stores accumulated when availability surpassed requirements. Based on metabolizable energy, Wallmo et al. (1977) calculated carrying capacities of 0 for early and late winter mule deer (O. hemionus) range in Middle Park, Colorado. They calculated adequate forage in both energetic quality and quantity to support the estimated population of this range during the summer.

Energy-based

Results of carrying capacity calculations emphasize the importance of forage quality as well as quantity. Despite increased standing crops associated with the thinned parcels, the energy density of at least 2 of 4 seasonal diets was insufficient to supply the daily energy requirements of a doe at the estimated average seasonal intake rates. Based on energy densities of diets composed only of vegetative food items, only the spring diet was sufficiently rich in energy to supply a deer with maintenance requirements, at the estimated average intake rates. For other seasons, a doe could not obtain enough digestible energy regardless of the distance she travelled or the standing crop of staple food items.

Although the standing crop of forage in Parcel 4 was greater than that of Parcel 1, the energy density of the diet in Parcel 1 was greater than in 4, and this probably contributed to the greater carrying capacity of Parcel 1. For the other parcels, relative carrying capacity was associated more closely with standing crop.

If the fall diet is augmented with oak mast, an energy-rich food item, the caloric density of the diet is increased to the point where the animal's energy requirements are satisfied in the daily fall diet. In this case, carrying capacity during fall is most closely associated with standing crop of oak mast.

Carrying capacity of deer is not determined strictly by the immediate quality and quantity of food items. Throughout the annual cycle, deer probably experience energy deficiencies and excesses depending upon fluctuations in the animal's requirements and the ability of the range to supply the required food energy. At certain times in the annual cycle the animal may not acquire the necessary energy to meet it's requirements strictly from the current standing crop of forage. Verme and Ullrey (1972) discuss the inability of deer to satisfy energy requirements in winter. This may result from increased energy demands, as during lactation or from limitations in the range supply, as in winter. At other times, the animal may acquire energy beyond immediate needs for growth and activity and this can be accumulated as energy stores, primarily in the form of fat, and secondarily as protein. During periods when energy needs of the animal are not supplied by the daily diet, these energy stores are catabolized to supplement the daily caloric intake, and thus contribute to daily energy requirements.

Lactation is a particularly energy-demanding stage in the annual cycle of the doe (Verme and Ullrey 1972, Moen 1973:6, Robbins 1973:374). It is conceivable that at some stages of lactation the doe may not be able to satisfy her own requirements, plus those of lactation, strictly from dietary energy. When this happens, energy stores accumulated in spring may be mobilized to help provide the needed energy. The suggested deficiency is substantiated by the much reduced weight gains in lactating does (Verme 1967), and the frequent observation that the body weights of does reach the nadir during lactation (Moen 1973:415). The amount of energy derived from milk by fawns is maximal when the fawn weighs about 10 kg (Moen 1973:355). Thereafter, the amount of energy derived from milk declines, as the fawn relies more on forage. The summer forage sample and estimation of requirements coincided with this period of predicted maximal energy demand from milk. This apparently is a stage in the annual cycle when dietary energy does not meet maintenance requirements and must be supplemented with energy stores accumulated during the spring. The energy demand for lactation declines toward fall and the doe probably is able to obtain required energy from available food items during declining stages of lactation.

Similar accumulations of energy stores in the fall may contribute to meeting demands during the winter, when forage alone usually cannot supply adequate energy for maintenance.

Calculations indicate that during fall and early winter of 1976, inclusion of oak mast in the diet increased the energy density of the diet sufficiently to provide an excess of the daily requirements of the doe. When oak mast was excluded from the calculations, the doe was unable to meet it's energy requirements. The accumulation of energy reserves during the fall, derived largely from oak mast, may help offset energy deficiencies experienced by the doe during winter, when diet alone does not provide sufficient energy for mainteinance. During years of oak mast failure or scarcity, deer may be hard-pressed to satisfy caloric requirements during fall and early winter and experience critical energy deficiency in the late winter.

During two years of oak-mast abundance on the Broad Run Wildlife Management area, the fall-winter diet of white-tailed deer provided daily digestible energy in excess of the daily requirements of the deer (Whelan 1978). During three years of oak-mast scarcity, the fall-winter diet was deficient in digestible energy (Whelan 1978). Harlow et al. (1975:335) noted a similar instance of insufficient energy availability when mast yield was low.

Comparisons of energy requirements and availability during various stages of the annual cycle of white-tailed deer help to clarify the probable nature of energy dynamics in the species. Over the course of a year, deer can be expected to experience periods of dietary energy deficiencies and excesses. During periods of excess, the animal accumulates energy in the form of fats and protein. When the diet is deficient in energy, these stores are catabolized to supplement dietary energy. When energy deficiencies equal energy excess, the animal will maintain weight. However, for an animal to grow and be active, the amount of surplus energy must exceed energy deficiencies. A balanced energy pool during the year will not necessarily assure maintenance of body weight. There undoubtedly exists a threshold below which an energy deficiency leads to irreversible degeneration of body function and results in death of the animal. Overwinter weight losses in excess of 30% of body weight result in collapse of the animal's defense mechanism and the deer will die (Verme and Ullrey 1972:277). During periods of energy deficiency, survival of the deer depends upon the magnitude of the negative energy balance, length of time on the diet that is energy deficient, and the amount of accumulated energy stores which can be drawn upon during the deficient period (Ammann et al. 1973:196).

Energy-based calculations of carrying capacity tend to support Verme and Ullrey's (1972:282) contention that "...it is now clear that the year-round nutritional plane is far more important in controlling dynamics and welfare of a herd than is the influence of winter conditions alone."

Protein-based

The reversed pattern of carrying capacities and standing crops of Parcels 1 and 4 may be largely attributed to the relative protein densities for the diets, 8.1 and 7.0% for Parcels 1 and 4, respectively.

Differences in protein-based carrying capacity between the unthinned and thinned parcels were determined largely by differences in standing crops of staple food items. This association is expected since the levels of standing crop are incorporated into the carrying capacity calculation.

The great potential contribution of oak mast to the fall and winter well-being of white-tailed deer is again evident in protein-based estimates of carrying capacity for diets with and without acorns. The carrying capacity of the unthinned parcel in fall, when acorns are a part of the diet, indicates the positive effects of dense overstory of oak species on the nutrition of white-tailed deer in fall and winter. The substantial increase in carrying capacity of the range with mast included is largely a result of the great contribution of mast to the standing crop of available food. Where inclusion of oak mast in the diet elevated the overall protein density of the diet, the increase was slight, and in half of the parcels the protein density of the diet was actually reduced when acorns were included, yet carrying capacity increased. (Figs. 7 and 8).

Like estimates of carrying capacity based on energy availability, the estimates based on protein are calculated from requirements for maintenance. Although protein is generally not required for activity, it is necessary for growth, and this increment is not accounted for by the carrying capacity calculations. Adding this increment to the requirements would decrease the carrying capacities of the various parcels through the seasons.

Calculations of protein requirements based on EUN and MFN, plus the increments for gestation and lactation indicate ample protein availability for maintenance throughout the year. However, only the spring and summer diets closely approximate the percentage dietary levels of protein commonly accepted as the minimum for maintenance, around 7% (Murphy and Coates 1966, Dietz 1965). Protein levels in fall and winter diets fall below the 5% level at which negative nitrogen balance occurs as a result of a constant loss of MFN (Robbins 1973:197), and below the 6-7% level, which impairs proper rumen function (Dietz 1965:276-277). However, white-tailed deer apparently have the ability to select food items with high protein levels, and may consume a diet with a higher protein content than forage analysis would indicate (Blair and Epps 1969:13, Wallmo et al. 1977:124, Swift 1948:10).

Although carrying capacity based on protein is high at all seasons, relative to energy-based carrying capacity, requirements for the two nutritional components cannot be easily segregated in considering carrying capacity. Robbins (1973:147) points out that nitrogen utilization is dependent on energy intake. The amount of dietary nitrogen converted to microbial protein declines with a decrease in the available energy in the diet. Therefore, energy availability may limit the carrying capacity directly, or indirectly by depressing the metabolism of protein.

Like energy, protein may be mobilized to supply nitrogen for production purposes at times when the animal is in negative nitrogen balance (Moen 1973:366). However, calculations indicate that even during the nitrogen-demanding period of lactation the doe would not be experiencing a protein deficit, based solely on dietary protein availability.

As with energy-based calculations, protein-based calculations of carrying capacity account only for the ability of the current diet to supply the necessary requirements at a time coincidental with the animal's requirements. There is no direct consideration or adjustment for protein excesses or deficiencies from earlier diets which may have an effect on the animal at a particular stage of the annual cycle. This possible discrepancy between animal requirements and availability of requirements may not be as crucial as it is for energy, since protein availability exceeded the doe's requirements during the seasons considered in these calculations.

Calculations of carrying capacity based on protein indicate the importance of quality and quantity of forage. If the protein density of the daily diet exceeds the daily requirements of the doe for protein, as it does for all parcels and seasons on the School House Hollow study area, then food-based carrying capacity of the area seems to be determined primarily by the standing crop of the diet. Generally, protein-based carrying capacity increased with time since thinning although the relationship diverged somewhat for Parcel 4 as a result of the drier nature of this site. Working in an oak-pine habitat type, in the Ridge and Valley Province of Virginia, Patton and McGinnes (1964:461) calculated increased carrying capacities for deer with the number of years after forest cutting. Carrying capacity also increased with percent basal area removed.

The lack of distinct variations in dietary protein levels associated with variation in parcel characteristics, notably time since thinning, suggest a relatively minor contribution of intra-seasonal variation of protein levels in the diet among parcels to the relative carrying capacities of the parcels. Protein levels of diets displayed a much more evident and consistent inter-seasonal variation for all parcels, and this, coupled with standing crop of food items through the seasons, contributed to the more striking inter-seasonal variation in protein-based carrying capacity.

SUMMARY AND CONCLUSIONS

The objective of this study was to evaluate the effects of a commercial thinning operation on the protein- and energy-based carrying capacity of a mixed oak forest for white-tailed deer in the Ridge and Valley Province of Virginia. Calculation of carrying capacity was based on the ability of a white-tailed doe to obtain sufficient energy and protein from the daily diet. When the ratio, energy or protein density of the daily diet: daily energy or protein requirements of the doe was less than 1, the doe was unable to meet her requirements. Thus, carrying capacity was determined to be 0 ha/deer. When this ratio equalled or exceeded 1, carrying capacity was calculated by dividing the daily standing crop of protein or energy by the daily protein or energy requirements of the doe. Emphasis was placed on carrying capacity as a function of time elapsed since thinning.

During summer, fall without mast and winter, a doe white-tailed deer would be unable to maintain her body weight in the mixed oak forest of the study area. The nutrition-based carrying capacity for these periods was calculated to be 0 ha/deer because the energy density of the forage was too low, assuming a forage intake rate that is constant. In spring and mast-supplemented fall seasons, energy availability was greater and the computed carrying capacity was well above 0. These relationships held for the unthinned and thinned parcels. Carrying capacity estimates based on protein availability yielded positive values for all seasons and parcels. Although protein availability increased with time elapsed since thinning, protein availability alone is an inadequate measure of carrying capacity. Kirkpatrick (1975) suggests that dietary energy levels may be more important than protein in limiting deer abundance in southeastern forests.

The findings of this study suggest that energy availability should be used routinely in evaluation of deer habitat. Further, the finding that this mixed-oak stand provided insufficient energy to sustain a lactating doe in summer suggests that deer managers overemphasize winter carrying capacity. Year-round information on energy and other nutrient yields is needed.

The potential carrying capacity of a mixed oak forest for deer in the Ridge and Valley Province of Virginia can be influenced by commercial thinning operations. Minor variations in protein and energy levels of foods indicate that this influence is related primarily to changes in the standing crop of food items, rather than variations in protein and energy levels of the food items. When a standard diet of understory species possesses sufficient energy and protein, carrying capacity can be expected to increase following thinning, for at least four years, based on this study. This is primarily a result of increased understory production following thinning. When diets contain oak mast, thinning may reduce potential carrying capacity because of the removal of mast-producing trees. The total availability of energy and protein for deer in commercially thinned mixed oak forests would be expected to decline after several years when understory vegetation grows beyond the reach of deer and production decreases.

The time after thinning considered in this study was four years. No decline in understory yield with time elapsed since thinning was noted. However, the expected decline in understory yields with time can be monitored by periodic sampling of the thinned and unthinned areas at periodic time intervals of 2 to 4 years, up to the point that yields on thinned and unthinned areas are similar. This would provide valuable information on the magnitude and duration of increased carrying capacities resulting from thinning. A schedule such as this should also be employed to monitor changes in mast yields among the thinned and unthinned parcels.

From the standpoint of longer-term production of deer forage, commercial thinning would seem more advantageous than clearcutting. This advantage is a result of increased yields of understory species plus maintenance of mast-producing oaks on a common site. This combination would tend to supply valuable food items throughout the year. Understory species on a commercially thinned stand would probably have a slower growth rate than the same species on a clearcut area due to competition from residual overstory species for light and moisture. Therefore, more understory vegetation would probably remain within reach of deer for a longer period of time on a thinned versus a cleacut.

All habitat types which a deer can potentially use to obtain life requirements must be considered in a comprehensive program of deer management. Winter diets from thinned and unthinned mixed oak stands which were energy defficient suggest the possibility that deer might select food items from other habitat types, such as pasture, along forest edges to increase the energy density of the daily diet. In this way deer might be able to avoid or reduce the magnitude of a dietary energy deficiency during winter.

Evaluations of silvicultural practices such as commercial thinning are most useful when incorporated into a comprehensive evaluation of the total land area used by deer. When inherent variations in habitat conditions might confound analysis and evaluation of habitat manipulation, stratified sampling should be used.

The validity and applicability of the habitat evaluation procedure employed is determined largely by the accuracy and completeness of the the data on requisite variables. Our information on nutrient and energy requirements and availability is limited. Knowledge of intake rates of deer for different seasons and physiological conditions is incomplete. Since my calculations of potential food-based carrying capacity were quite sensitive to intake rates, further research on this variable is desirable. The protein and energy requirements of deer subjected to various habitat, climatic and physiological conditions have not been delineated fully. For some seasons and conditions this study employed data from ruminants other than deer to estimate requirements during certain stages of the annual cycle. Truly accurate determinations of food-based carrying capacity will require information on protein and energy requirements of deer under all conditions experienced by free-ranging animals. Since wildlife habitat evaluation is inextricably tied to knowledge of habitat requirements, valid evaluations can advance no further than knowledge of the animal requirements.

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APPENDIX I

Appendix I. Procedure used to calculate seasonal energy- and protein-based carrying capacity of and unthinned parcels for white-tailed deer. parcels for white-tailed deer.

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1. If $\dfrac{\text{seasonal dietary digestible energy or protein density (Tables 13 or 15).}}{\text{seasonal dietary digestible energy or protein requirements of a doe white-tailed deer (Table 12).}}$

   a.) <1, then potential carrying capacity = 0 ha/deer. (insufficient protein or energy to satisfy maintenance requirements of the doe regardless of standing crop of forage or cruising radius of the doe).

   b.) ≥1, then go to 2.

2. $\dfrac{\text{seasonal standing crop of dietary digestible energy or protein (Tables 10 or 11).}}{\text{seasonal dietary digestible energy or protein requirements of doe white-tailed deer (Table 12).}}$

   = potential carrying capacity (ha/deer).

APPENDIX II

Appendix II. Mean (±SE) seasonal *in vitro* dry matter digestibility of staple food items in the seasonal diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77.

	Season			
Species	Summer	Fall	Winter	Spring
Acer rubrum				
leaves	42.39(1.11)	---	---	50.93(2.19)
stems	---	38.29(0.50)	41.57(0.88)	43.41(1.55)
Cornus florida				
leaves	44.90(1.55)	47.70(1.19)	---	45.20(1.99)
stems	---	38.83(0.50)	40.39(0.48)	42.86(1.02)
Kalmia latifolia				
leaves	36.65(0.43)	38.61(0.80)	43.06(1.55)	39.45(0.91)
Nyssa sylvatica				
leaves	50.71(0.57)	---	---	53.52(1.47)
stems	35.02(0.88)	---	---	59.34(0.16)
Oxydendrum arboreum				
leaves	52.82(2.72)	63.61(0.56)	---	57.83(3.50)
stems	---	26.43(0.88)	---	33.15(1.20)

Appendix II. Mean (±SE) seasonal *in vitro* dry matter digestibility of staple food itmes in the seasonal diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77 (continued).

Species	Summer	Fall	Winter	Spring
	Season			
Quercus coccinea				
leaves	36.10(0.85)	34.28(1.18)	---	45.33(1.76)
stems	---	20.96(0.39)	20.12(1.07)	36.53(1.37)
fruit	---	61.66(0.25)	---	---
Q. prinus				
leaves	32.57(1.73)	26.95(1.09)	---	41.09(1.50)
stems	---	28.34(0.44)	25.97(0.68)	32.38(1.32)
fruit	---	---	---	---
Q. velutina				
leaves	34.21(1.73)	34.38(0.40)	---	39.15(1.07)
stems	---	26.45(0.42)	26.08(1.32)	31.30(1.11)
fruit	---	57.56(1.16)	---	---
Sassafrass albidum				
leaves	40.65(1.97)	32.80(1.28)	43.06(0.85)	46.58(1.66)
stems	---	36.03(0.95)	---	39.58(1.95)
Smilax glauca	39.83(1.41)	34.74(3.28)	19.33(2.10)	42.69(0.96)
Smilax rotundifolia	---	---	12.36(0.30)	62.06(0.57)

Appendix II. Mean (±SE) seasonal *in vitro* dry matter digestibility of staple food itmes in the seasonal diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77 (continued).

	Season			
Species	Summer	Fall	Winter	Spring
Vaccinium vacillans	33.39(0.87)	23.85(0.81)	22.36(0.58)	41.10(0.46)
Coreopsis major	44.89(0.10)	---	---	---
Desmodium nudiflorum	50.60(0.88)	29.33(0.68)	---	51.36(0.54)
Dioscorea villosa	---	---	---	52.95(0.91)
Epigea repens	26.65(0.51)	30.18(0.46)	29.67(0.58)	22.11(0.90)
Galax aphylla	52.07(0.56)	55.29(0.83)	57.20(0.59)	53.24(0.43)
Gaultheria procumbens	36.77(1.28)	47.54(0.87)	46.23(1.23)	47.00(1.59)
Panicum spp.	51.74(2.32)	34.77(0.35)	---	58.14(1.19)

APPENDIX III

Appendix III. Mean (±SE) seasonal gross energy levels (kcal/g) in the diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77.

	Season			
Species	Summer	Fall	Winter	Spring
Acer rubrum				
leaves	4.71(0.02)	4.68(--)+	---	4.72(0.04)
stems	---	4.64(0.00)	4.68(0.04)	4.40(0.04)
Cornus florida				
leaves	4.25(0.05)	4.28(0.05)	---	4.35(0.12)
stems	---	4.49(0.01)	4.45(0.02)	4.36(0.01)
Kalmia latifolia				
leaves	5.09(0.04)	5.14(0.02)	5.14(0.02)	5.19(0.03)
Nyssa sylvatica				
leaves	4.45(0.02)	4.62(--)	---	4.39(0.01)
stems	---	4.58(0.01)	---	4.12(0.01)
Oxydendrum arboreum				
leaves	4.17(0.35)	4.45(0.04)	---	4.73(0.02)
stems	---	4.63(0.01)	4.45(0.02)	4.66(0.03)

+Values without standard errors (SE) represent analysis of a single sample.

Appendix III. Mean (±SE) seasonal gross energy levels (kcal/g) in the diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77 (continued).

Species	Summer	Fall	Winter	Spring
	Season			
<u>Quercus coccinea</u>				
leaves	4.71(0.07)	4.70(0.11)	---	4.68(0.01)
stems	---	---	---	---
fruit	---	5.56(0.50)	---	---
<u>Q. prinus</u>				
leaves	4.62(0.05)	4.70(0.05)	---	4.62(0.03)
stems	---	---	---	---
fruit	---	---	---	---
<u>Q. velutina</u>				
leaves	4.99(0.06)	4.63(0.07)	---	4.62(0.05)
stems	---	4.45(--)	---	---
fruit	---	5.21(0.10)	---	---
<u>Sassafrass albidum</u>				
leaves	4.81(0.05)	4.75(0.05)	---	4.80(0.06)
stems	---	4.70(0.04)	4.48(0.01)	4.31(0.10)
<u>Smilax glauca</u>	4.70(0.01)	4.77(0.01)	4.74(0.05)	4.85(0.13)
<u>Smilax rotundifolia</u>	4.84(--)	---	4.58(--)	4.78(0.84)

Appendix III. Mean (±SE) seasonal gross energy levels (kcal/g) in the diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77 (continued).

Species	Season			
	Summer	Fall	Winter	Spring
Vaccinium vacillans	4.68(0.12)	4.90(0.03)	5.00(0.02)	4.84(0.02)
Coreopsis major	4.26(00)	---	---	---
Desmodium nudiflorum	4.56(0.05)	---	---	---
Dioscorea villosa	---	---	---	---
Epigea repens	4.83(0.11)	4.88(0.04)	4.93(0.01)	4.98(0.06)
Galax aphylla	4.11(0.09)	4.30(0.06)	4.28(0.05)	4.31(0.07)
Gaultheria procumbens	4.61(0.20)	4.77(0.03)	4.68(0.04)	4.68(0.02)
Panicum spp.	4.33(0.04)	4.26(0.10)	4.06(--)	4.36(--)

APPENDIX IV

Appendix IV. Mean (±SE) seasonal crude protein levels in staple food items in the diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77.

Species	Summer	Fall	Winter	Spring
Acer rubrum				
leaves	6.97 (0.36)	2.73 (--)+	---	8.48 (0.49)
stems	---	5.26 (0.27)	5.31 (0.37)	5.31 (1.04)
Cornus florida				
leaves	8.64 (0.48)	5.16 (0.56)	---	10.65 (1.42)
stems	3.39 (--)	6.06 (0.38)	6.45 (0.16)	6.89 (0.83)
Kalmia latifolia				
leaves	4.15 (0.30)	5.09 (0.47)	4.89 (0.21)	4.70 (0.21)
Nyssa sylvatica				
leaves	12.78 (0.36)	4.04 (--)	---	15.20 (1.30)
stems	---	4.09 (0.61)	---	7.06 (0.96)
Oxydendrum arboreum				
leaves	7.97 (0.50)	3.22 (0.60)	---	11.41 (0.46)
stems	---	4.08 (0.15)	2.95 (0.32)	4.37 (1.02)

+Values without standard errors (SE) represent analysis of a single sample.

Appendix IV. Mean (±SE) seasonal crude protein levels in staple food items in the diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77. (continued).

	Season			
Species	Summer	Fall	Winter	Spring
Quercus coccinea				
leaves	10.27 (0.35)	5.41 (0.07)	---	9.30 (1.69)
stems	---	3.17 (0.44)	5.13 (0.31)	7.41 (1.54)
fruit	---	3.82 (0.28)	---	---
Q. prinus				
leaves	13.45 (1.10)	5.69 (0.21)	---	16.14 (1.12)
stems	---	4.86 (0.23)	5.09 (0.30)	5.45 (0.50)
fruit	---	---	---	---
Q. velutina				
leaves	9.39 (0.87)	5.24 (0.66)	---	11.87 (1.19)
stems	---	3.79 (0.22)	4.54 (0.23)	6.04 (0.32)
fruit	---	5.18 (0.71)	---	---
Sassafrass albidum				
leaves	13.80 (0.54)	7.03 (0.71)	---	17.20 (1.48)
stems	---	4.17 (0.31)	3.06 (0.25)	10.30 (1.37)
Smilax glauca	7.03 (0.24)	4.72 (0.41)	4.07 (0.42)	9.56 (0.36)
Smilax rotundifolia	12.48 (--)	---	4.59 (0.56)	12.78 (2.19)

Appendix IV. Mean (±SE) seasonal crude protein levels in staple food items in the diet of white-tailed deer. School House Hollow study area, Craig County, Virginia. 1976-77. (continued).

Species	Summer	Fall	Winter	Spring
Vaccinium vacillans	5.97(0.64)	1.59(0.30)	4.32(0.20)	8.44(0.47)
Coreopsis major	4.05(--)	---	---	---
Desmodium nudiflorum	9.61(0.61)	4.91(--)	---	11.82(0.33)
Dioscorea villosa	6.90(--)	---	---	---
Epigea repens	6.50(0.99)	4.85(0.18)	5.36(--)	5.83(1.11)
Galax aphylla	5.37(0.31)	5.86(0.35)	5.47(0.56)	5.86(0.44)
Gaultheria procumbens	4.15(0.10)	4.02(0.34)	3.77(0.17)	4.32(0.14)
Panicum spp.	6.75(0.38)	3.46(0.86)	6.40(1.15)	10.39(3.50)

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THE EFFECTS OF FOREST THINNING

ON THE FOOD-BASED CARRYING CAPACITY OF A MIXED OAK FOREST

FOR WHITE-TAILED DEER

IN THE RIDGE AND VALLEY PROVINCE OF VIRGINIA

by

David W. Carlile

(ABSTRACT)

The ability of a mixed oak forest in the Ridge and Valley Province of Virginia to provide the seasonal digestible protein and energy requirements of a white-tailed doe following a commercial thinning operation was evaluated. The element of time elapsed since thinning was emphasized and was represented by three contiguous forested parcels thinned over 3 consecutive years and an unthinned parcel. Digestible protein and energy requirements of a doe, white-tailed deer in four different physiological conditions associated with four seasons were obtained directly from the literature or calculated from data in the literature. Availability of dietary digestible energy and protein coincident with the requirement periods were determined by clipping, weighing and analyzing for digestible protein and energy content food items commonly used by white-tailed deer. Calculation of carrying capacity was based on the ability of a white-tailed doe to obtain sufficient energy

and protein from the daily diet. When the ratio, energy or protein density of the daily diet: daily energy or protein requirements of the doe was less than 1, the doe was unable to meet her requirements. Thus, carrying capacity was determined to be 0 ha/deer. When this ratio equalled or exceeded 1, carrying capacity was calculated by dividing the daily standing crop of protein or energy by the daily protein or energy requirements of the doe. Summer, winter and mast-supplemented fall diets were deficient in energy . Thus, potential carrying capacity, based on immediately available dietary digestible energy, was estimated as 0 ha/deer during these periods. Spring and mast-supplemented fall diets provided adequate digestible energy for maintenance of the doe. Diets from all parcels and seasons provided sufficient protein for maintenance. For those periods when dietary protein and energy were sufficient, carrying capacity exceeded 0 ha/deer and was greater with increased standing crop of the seasonal diets. Standing crop of seasonal diets tended to be larger with increased time since thinning, although this pattern was confounded by the drier nature of one parcel. The role of seasonal energy and protein excesses and deficiencies in the annual nutrition of white-tailed deer are discussed. The necessity of considering dietary quality as well as quantity and the year-round nutritional plane of deer are emphasized for forage-based evaluations of deer habitat. Calculations suggest that dietary energy is a more important limiting factor than protein on the abundance of white-tailed deer in this forest stand.