SEASONAL FOOD SELECTION AND DIGESTIBILITY BY TAME WHITE-TAILED DEER IN CENTRAL MAINE

HEWLETTE S. CRAWFORD, USDA Forest Service, Northeastern Forest Experiment Station, University of Maine, Orono, ME 04469

Abstract: Seasonal food selection and digestibility by tame white-tailed deer (*Odocoileus virginianus*) were studied in the white pine (*Pinus strobus*)–Canada hemlock (*Tsuga canadensis*) and lowland conifer types, areas representative of important deer habitat in the northeastern United States. Deer selected highly digestible late spring, summer, and autumn diets. Winter and early spring food were less digestible. Forbs and newly grown leaves of hardwood plants were the most commonly selected late spring and summer foods; mushrooms and hardwood leaves were selected during autumn. Winter foods consisted largely of green and dry leaves of conifers and hardwoods gleaned from the snow surface. Early growth of grasses and sedges and dried red maple (*Acer rubrum*) leaves were selected as soon as the snow left the ground in early spring. Lignaceous woody twigs, ferns, and trailing-arbutus (*Epigaea repens*) also were consumed during this period, reducing the overall digestibility of the diet.

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Traditionally, deer habitat has been evaluated by the quality of winter cover and the quantity of woody twigs available for winter browsing. The quantity of herbaceous foods during spring, summer, and fall were considered less important. Many biologists now recognize that food availability and quality each season are important for deer, and that food quantity during the tranditional "pinch-period" is probably no more important than during other seasons (Snider and Asplund 1974, Mautz 1978). Spring foods condition the animal, and the fetus, for the important time of parturition (Moen 1973). Summer foods nourish the lactating doe and provide important alternate foods for the growing fawn. Late summer and fall foods condition the animal, particularly the young animal, for the climatic stress of winter. To determine the importance of deer range for food production and to recommend useful improvements, it is necessary to determine year-long habitat values based on food availability and ingestion, and digestion, which is related to food quality.

Deer foods generally have been determined by rumen analysis, counts of browsed twigs, or direct observation of wild deer. All 3 methods give a biased estimate of total deer foods because they underestimate the use of herbaceous material. Herbaceous material breaks down rapidly in the rumen and is difficult to identify in rumen samples. Browsed twig counts give no estimate of use of herbaceous plants. Observations made at a distance often overlook the smaller herbaceous material consumed by deer while they are actively feeding.

Close observation of selection of plants and plant parts by tame deer can give reliable information on food selection (Dunkeson 1955, Healy 1971, Crawford et al. 1975). The use of small herbaceous plants and fruits can be easily seen. Healy (1971), McMahan (1964), and Wallmo and Neff (1970) compared forages selected by tame and wild deer and found that similar plants were used. Regelin et al. (1976) found that tame mule deer (*O. hemionus*) with unlimited access to concentrated feed selected forages similar to those selected by deer subsisting on native forage. The assumption of similarity of natural diets for wild and tame free-ranging deer with supplemental feed seems acceptable.

The objectives of this study were to

quantify plant parts selected by tame white-tailed deer during spring, summer, and autumn in the white pine–Canada hemlock forest type and during winter in the red spruce (*Picea rubens*)–balsam fir (*Abies balsamea*) and northern white cedar (*Thuja occidentalis*) lowland types (SAF 1954), and to determine the digestible dry matter of the mixed diets.

D. H. Hankinson, P. M. O'Neil, W. A. Wright, M. M. Genthner, and L. P. Rogacki assisted with data collection and animal training and handling. Hankinson determined the digestible dry matter of the mixed diets. C. F. Banasiak, D. L. Marston, and D. W. Seegrist reviewed drafts of the manuscript.

STUDY AREA

Central Maine is near the northern limit of the range of white-tailed deer. I selected the white pine–hemlock forest type as representative of important deer range in this area. It contains a mixture of intolerant pioneer hardwoods, tolerant northern hardwoods, spruce, and fir and represents a transition from northern hardwood to spruce-fir zones. The study area, approximately 50 ha, near Bradley, Maine contained a small clear-cut, a shelterwood cut, a selection cut, and a "logger's choice" unregulated stand, in about equal proportions. Soils were stony loams and silt loams. The stony loams were deep and well drained, forming undulating small knolls. The silt loams were poorly drained and level with a high water table and slow runoff and absorption.

The winter portion of the study area was in 2 nearby active deer wintering areas in the spruce-fir and northern white cedar types. The stands were primarily coniferous with a scattering of intolerant hardwoods in small openings and wet areas. Soils were deep, very poorly drained silt loams, forming level flats.

METHODS

Two tame deer, raised in captivity at the University of Maine Deer Facility, were used during the winter and winter–spring transition periods in 1977. One animal was used during the last 2 years of the study (1977–78). The animals were 6 months old at the beginning of the study and weighed approximately 27 kg.

The tame deer were kept at the deer facility and transported in a truck to the study area each day. In the initial phases of the study, they were released in the study area and allowed to roam without constraint. After the dominant animal, a buck, was killed by poachers a long lead was used on the remaining deer, a doe, to ensure tractability. Light restraint was used and the animal was allowed to roam at will until it was time to return to the truck. Feeding bouts lasted approximately 1 hour and were conducted between 0800 and 1000 hours during spring through autumn, and 0900 and 1100 hours during winter when loading problems, adverse weather, or poor roads occasionally caused later starts. The animals were fed a pelleted dairy ration (Agway 620 T) ad libitum, upon return to the deer facility. No food was offered before the animals were taken to the field. The animals were trained on the Bradley study area for 4 months and made at least 5 2-hour visits to the winter study areas prior to data collection. The animals were thoroughly familiar with the plots. The doe escaped early in the study and spent several days and nights on the Bradley area. She was recaptured in the same locality where she escaped.

The sampling crew consisted of a handler and an observer. The observer dictated into a portable tape recorder the estimated weight in grams, and by species and plant part, all of the material con-

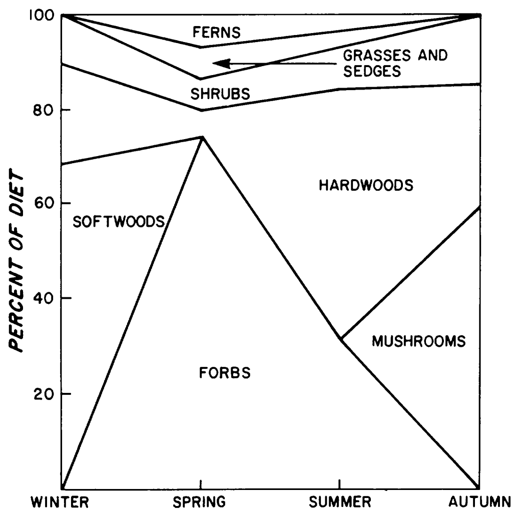

Fig. 1. Seasonal importance of major food groups based on top three-fourths of white-tailed deer diets in central Maine (pooled data for 2 years).

sumed by the deer. Observers were trained in weight estimation before sampling and were checked throughout the sampling period. The handler carried a scale sensitive to 0.1 g and served as a control for the weight estimation procedures by occasionally weighing unit samples similar to the plant material consumed.

Data were summarized daily. Three or 4 daily samples were averaged each week and then a representative sample was hand picked in the study area, oven-dried at 65 C to a constant weight, ground in a Wiley mill through a 1-mm mesh screen, and stored in sealed jars for determinations of in vitro digestible dry matter (DDM).

Weekly samples were prepared by combining individual plant parts—representing approximately the top three-fourths, by weight, of foods selected—in a mixture representing the mixed diet of the deer for that week. Seasonal samples were determined from 3 weekly samples. Digestible dry matter was determined using bovine rumen fluid by a 2 stage in vitro technique with a neutral detergent fiber extraction (Goering and VanSoest 1970). This technique was selected after comparing its accuracy with DDM values determined by 2 other digestibility techniques and in vivo standards (Hankinson and Crawford, unpubl. data). True digestibility standard reference forages were provided by R. L. Cowan of Pennsylvania State University (Palmer and Cowan 1980). The forages were used to correct in vitro DDM values determined by regressions computed by Hankinson and Crawford (unpubl. data).

RESULTS

Food Selection

Our tame deer were highly selective while feeding in the wild. Often, plant species or parts were nuzzled or held in the mouth and rejected. When available, easily digested plants or parts were selected over less digestible portions. Healy (1971) and Willms et al. (1979) found that tame deer were selective when feeding. Short (1963) indicated the dietary need for deer to select easily-digestible foods.

Food selection varied by season (Fig. 1). Softwood species were eaten only during winter while hardwood tree and shrub species were eaten throughout the year. Grasses or sedges were selected during all seasons except winter. Ferns were taken in trace amounts during winter and in more abundance through summer in 1977 but only in spring in 1978. Forbs were taken during spring and summer and mushrooms only during autumn.

Green Canada hemlock shoots gleaned from the snow surface accounted for the greatest proportion of winter food consumed (Table 1). Green needles of white pine, green and dried shoots of northern white cedar, and dried red maple leaves

Table 1. Contribution (%) of principal plants to white-tailed deer diets in central Maine by season. Computed from seasonal means of daily field weight consumption; 3 weekly samples comprise a season.

Species	Winter (Jan–Feb)	Early spring (Mar–Apr)	Late spring (May–Jun)	Summer (Jul–Aug)	Autumn (Sep–Oct)	Late autumn (Nov–Dec)
Allegheny blackberry, leaves and twigs						3.6
American beech, twigs		3.8				
American elm, green leaves				3.5		
Balsam fir, shoots	4.8[a]					
Beaked filbert, green leaves				1.5		
Bigtooth aspen, dried leaves						2.6
Blue beadlily, leaves			30.4	11.6		
berries				6.5		
Bracken fern				2.0		
Bunchberry dogwood						3.2
Canada beadruby			24.9	2.7		
Canada hemlock, green shoots	33.0					
Common cattail				1.3		
Graceful sedge				3.0		
Grasses spp. (Gramineae)		3.0				
Gray birch, green leaves				1.5		
Gilled mushroom Agarics					45.2	
Interrupted fern (*Osmunda claytoniana*)			5.3			
Kalmia lambkill, leaves		4.7				2.6
Northern red oak, green leaves				1.3	2.1	
Northern white cedar						
green shoots	5.2	13.7				4.6
dried shoots	6.5					
Paper birch, leaves				9.3	4.3	
Quaking aspen, green leaves				3.6		
Red raspberry, leaves			4.8	2.6	9.6	1.39
Red maple						
twigs	11.1	9.1	4.1			6.4
green leaves				20.5	6.1	
dried leaves	4.9	4.1			1.4	15.5
colored leaves					5.8	
Sedge (*Scirpus* spp.)			5.2			
Sedges		8.6				9.0
Speckled alder						
leaves				2.4	1.4	
twigs	7.8					
Swamp dewberry, dried leaves		3.3				
Trailing-arbutus, leaves		4.8				5.3
Violet, green leaves				1.6		
White pine, leaves	2.6					
Wintergreen, leaves		6.1				
Woodfern, evergreen frond		17.8				7.9
Total, %	75.9	79.0	74.7	74.9	75.9	74.6
Total weight, g	756.6	450.7	822.0	1,648.8	1,524.3	426.2

[a] Changes in food choice are continuous, thus discrete seasonal variability data would be misleading.

also were gleaned from the snow surface or where they could be reached by the deer. Green balsam fir shoots were taken both from the snow surface and from the plant. Red maple and speckled alder (*Alnus rugosa*) twigs made up the remainder of the important foods consumed. Minor amounts of white ash (*Fraxinus americana*) and red osier dogwood (*Cornus stolonifera*) twigs and dried bracken fern

(*Pteridium aquilinum*) fronds were consumed. Herbaceous plants were not important as a source of deer food during winter.

As the snow left the ground in early spring, the animals began to eat ferns, sedges, green leaves of lambkill kalmia (*Kalmia angustifolia*), wintergreen (*Gaultheria procumbens*), and trailing-arbutus, dried leaves of swamp dewberry (*Rubus hispidus*), American beech (*Fagus grandifolia*) twigs, and other species in small amounts, while continuing to eat red maple twigs and dried leaves and northern white cedar green shoots (Table 1).

During late spring, forbs accounted for nearly three-fourths of the diet (Fig. 1). Blue beadlily (*Clintonia borealis*) and Canada beadruby (*Maianthemum canadense*) accounted for more than 50%, by weight, of all plants eaten during late spring (Table 1). Sedges, ferns, red maple twigs, and red raspberry (*Rubus idaeus*) shoots also were important components of the diet. Numerous other species were consumed in minor amounts.

Consumption of forbs decreased from spring to summer (Fig. 1, Table 1). The use of blue beadlily leaves remained constant and the ripening fruits were consumed during summer. Canada beadruby was eaten but not as much as during spring. Violet (*Viola* spp.) and common cattail (*Typha latifolia*) leaves also were eaten. Other important herbaceous summer foods included graceful sedge (*Carex gracillima*) and bracken fern.

Leaves of hardwood plants comprised the most important class of summer foods. Red maple leaves accounted for more than 20%, by weight of the total summer diet and paper birch (*Betula papyrifera*) leaves nearly 10%. Quaking aspen (*Populus tremuloides*), American elm (*Ulmus americana*), speckled alder, beaked filbert (*Corylus cornuta*), northern red oak (*Quercus rubra*), and gray birch (*Betula populifolia*) leaves also were selected by the deer. Conversely, the use of red raspberry decreased from spring to summer.

During autumn, deer continued to select hardwood leaves (Fig. 1, Table 1). Red maple leaves—green, colored, and dried—and green leaves of paper birch, speckled alder, and red oak were eaten. Red raspberry leaves were the 3rd most important autumn food. The most important food was gilled mushrooms, which accounted for nearly one-half of the total autumn diet.

After a hard freeze eliminated mushrooms and green leaves in late autumn, deer continued to eat dead leaves of red maple, bigtooth aspen (*Populus grandidentata*), red raspberry, and Allegheny blackberry (*Rubus allegheniensis*) (Table 1), but also consumed leaves of low growing green plants such as sedge (*Carex* spp.), trailing-arbutus, bunchberry dogwood (*Cornus canadensis*), lambkill kalmia, and wood fern (*Dryopteris* spp.) until snow covered these plants. They also began to eat northern white cedar and hardened woody twigs of red maple.

The rate of consumption was similar for all seasons except winter (Table 2). During winter, the deer consumed less food while spending more time searching. Snow depths were moderate, approximately 30–50 cm, each winter.

Digestibility by Season

Percent DDM in mixed diet differed by season. Autumn diets were the most digestible, followed by summer diets, with winter and spring diets the least digestible. Percent DDM as a function of day of the year was estimated by

$$Y = -1.82 - 0.21X + 121.91 \cdot \exp\{-[\mathrm{abs}(X/283 - 1)]^{1.4}/0.67\}$$

Table 2. Seasonal white-tailed deer feeding rates in central Maine, 1977–79.

Season	No. deer	Minutes of feeding	Food consumed (g)	Feeding rate (g/minute)
Winter	2	2,732	998	0.37
Spring	1	1,187	1,100	0.93
Summer	1	2,344	2,204	0.94
Autumn	1	1,730	2,008	1.16

where $Y = \%$ DDM and $X =$ day of the year (Fig. 2).

DISCUSSION

Rumen microflora and microfauna interact within a mixed diet in the digestion process in the rumen. We simulated those natural conditions to determine DDM by using diets mixed in proportions comparable to the amounts of food ingested in the field. These values should be preferable to values determined by averaging DDM of individual plants or by basing DDM on a few plants.

The number of tame animals used to determine diets of wild animals may affect study results. Crawford et al. (1975) and Stormer and Bauer (1980) used 3 deer for 1 season. McMahan (1964) used 1 animal. I used 2 animals, a male and a female, during 2 seasons, and 1 animal, the female, for the 8 remaining seasonal sampling periods. The female consumed more forage than the male. In winter there was no difference in the plant species selected by the 2 deer. During the transition from winter to spring, the female selected more plant species than the male.

The white pine–hemlock forest type is capable of producing a variety of summer and autumn foods that are palatable and highly digestible for deer. Summer foods consisted of growing succulent plant parts, largely turgid leaf and some fruit cells high in cell plasma and digestible cellulose. As was true for aspen stands

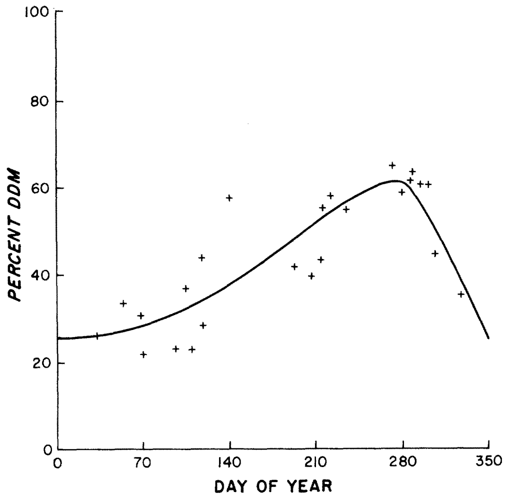

Fig. 2. In vitro digestible dry matter (DDM) as a function of day of the year.

(Stormer and Bauer 1980), deer selected leaves of regenerating hardwood trees, forbs, and shrubs. These summer diets provide deer with a highly digestible source of food to build energy reserves for the following winter (Torgerson and Pfander 1971), and to withstand the energy drain of nursing young.

Autumn diets in this forest type also provide a highly digestible food source to build winter energy reserves. Autumn foods were more digestible than summer foods in our study due in large part to the high proportion of succulent mushrooms and lack of hardened woody material in the diet. Mushrooms are rich in protein and phosphorus (Miller and Halls 1969) and yield high proportions of volatile fatty acids in the rumen (Short 1971). These conditions favor increased plant digestibility (Rice et al. 1962, Short 1963). Green and colored hardwood leaves comprised nearly one-half of the autumn diet. Studies in the south showed that digestibility of leaves in autumn is less than in summer (Short 1971). Apparently, digestibility of dried leaves was greater when eaten in mixture with mushrooms, perhaps due to the increased proportions of volatile fatty acids or dietary protein in the rumen. Digestibility of leaves in mesic northern forests also may be greater than that of leaves in xeric southern forests because there is less cuticular development in mesic forests. Harshbarger and McGinnis (1971) found that energy levels in leaves increased from summer through autumn until after abscission; thus, they may be an important source of energy.

Woody browse was not abundant in the wintering areas studied. Availability of winter foods was dependent on strong winds and heavy snow to remove leaves and limbs from the tops of trees and bring them to the ground. The animals had to feed approximately 3 times longer than in other seasons to get as much food. The material from the tree crowns was more abundant and more digestible than woody browse, but the lignaceous dietary component disproportionately decreased the DDM content of the mixed diet. Mautz et al. (1976) found relatively high apparent DDM of hemlock and balsam fir shoots and low DDM of red maple twigs.

The DDM of the early spring diet was less than that of the summer and autumn diets and similar to that of the winter diet. Dried maple leaves, northern white cedar and sedges and grasses—the digestible components of the diet—were counterbalanced by lignaceous, hardened woody twigs that were poorly digested. Other poorly digested plants that contributed to overall lower digestibility were ferns and trailing-arbutus. Individually, the poorly digested items ranged from 8 to 27% DDM.

The energy reserves accumulated by the animals during the summer and autumn are depleted through the long winter period of food scarcity and reach a low point in early spring. Also, in early spring the lowered metabolic rate of winter increases (Silver et al. 1969), causing a greater need for food. Developing embryos impose additional nutritional stress. The growth of palatable, digestible plants has just begun during early spring and the animals do not have the selection found during summer and autumn. Consequently, less-digestible foods are consumed, which lowers the total digestibility of the diet. In this study, foods high in DDM were not available in sufficient supply to be reflected in the diet until late April or early May.

MANAGEMENT IMPLICATIONS

Management to improve deer habitat in the white pine–hemlock type should be directed at providing more palatable early spring foods without decreasing the abundance of summer and autumn foods or the quality of deer wintering areas. Plant growth is delayed in spring because slowly drained silty soils with conifer overstory are wet from snowmelt and slow to warm. Cool-season plants, green, succulent and adapted to actively grow during snowmelt, should be encouraged. The native cool-season grasses and sedges are highly digestible. Several species of forbs have prostrate basal rosettes that enable the plant to receive enough radiant heat from the surface of the ground to grow as soon as the snow melts. Adapted cool-season species that are highly nutritious and digestible might be introduced successfully.

Small clear-cuts can provide nutritious forage. These cuts should be designed to enhance early spring snowmelt and include cool-season plants. Short strip clearcuts, oriented east and west and 3 times as wide as the height of trees on the south side of the cut, will provide a sunlit edge that is free of snow early in spring and not subjected to severe winds from the north. The same type of opening, seeded to palatable cool-season plants or burned and allowed to revert to native plants, also should provide suitable foods. Where more intensive management is justified, properly oriented openings can be cleared, burned, seeded with cool-season grasses and forbs, and fertilized. The same plants can be sowed on abandoned logging roads, especially where sunlight can easily reach the ground. Wide distribution of bedded and seeded roads distribute animals so that they have access to other early-maturing plants. Establishment of cool-season plants also benefits other wildlife species.

Although openings will provide an increase in early spring foods, it is important to maintain areas of forest overstory within a deer's home range. Important summer and autumn foods were found in the forest understory. Many of the late spring and summer forbs are understory species. Mushrooms are common in the moist litter of the forest floor, where organic content is high (Miller and Halls 1969). They do not require sunlight, and the moist conditions under the dense forest overstory are favorable for their growth. Deer wintering areas require dense forest stands to protect the animals from excessive snow depth, wind, and cold (Gill 1957).

Providing an abundance of habitat suitable for only 1 or 2 seasons will result in a decrease in the deer herd. Ideally, a variety of habitats suitable for year-long use should be provided within an area equivalent to the average home range for mature does. This translates into cutting units of approximately 10 ha with a balance of other age classes within the range.

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