ENERGETIC PRODUCTION BY SOFT AND HARD MAST FOODS OF AMERICAN BLACK BEARS IN THE SMOKY MOUNTAINS

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Abstract: We measured caloric production by 19 species of vegetation used as food by American black bears (*Ursus americanus*) in Great Smoky Mountains National Park to determine the significance of production by mast type, season, and species. Mean annual production by all species was 351,209 cal/ha. Hard mast produced 74.5% (16.0 billion cal) of total calories available on the study area; soft mast produced 25.5% (5.5 billion cal). Gross energetic content of soft and hard mast did not differ ($P = 0.488$, $n = 19$). Mid-summer was the lowest period of production. Northern red oak (*Quercus rubra*) produced 65.7% of calories; squawroot (*Conopholis americana*) produced 15.8%, and huckleberries (*Gaylussacia spp.*) produced 5.1%. A white oak (*Q. alba and Q. prinus*) mast failure occurred, and white oaks produced only 5.1% of calories. Oaks are likely the single most influential genera affecting bear ecology in the southern Appalachians. However, availability of soft mast likely has a substantial impact on bear populations because of the timing of production, nutrients available, and its function as a surrogate during hard mast failure. Further study is needed to determine the effects of soft mast abundance on age of primiparity, litter interval, recruitment, and density. Once the roles of major foods are well understood, appropriate habitat compositions and silvicultural prescriptions may be defined.

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Nutritional condition of American black bears affects age of primiparity (Jonkel and Cowan 1971, Eiler et al. 1989), litter interval (Rogers 1976, Eiler et al. 1989), litter size (Beecham 1980, Elowe and Dodge 1989), cub survival (Rogers 1976, Eiler et al. 1989), and yearling survival (Jonkel and Cowan 1971; Rogers 1976, 1987). Nutritional condition may also influence fertility (Noyce and Garshelis 1994). Thus, habitats with adequate food sources are essential for effective bear management.

Because of the importance of energy storage for the denning period, previous southern Appalachian bear studies were designed to determine the relationship between fall oak mast availability and reproduction. Bear reproduction was found to be highly correlated with hard mast indices by Eiler et al. (1989), Pozzanghera (1990), and McLean (1991). However, Coley (1995) found no significant positive correlations between hard mast indices and bear population size. Coley (1995) analyzed 20 years of black bear population data to determine the influence of hard mast production on black bear population dynamics in Great Smoky Mountains National Park (GSMNP). Coley (1995) correlated hard mast indices from GSMNP with various population estimates for periods up to 5 years after recorded hard mast data, a broad approach that should account for the influence of recruitment in addition to reproduction. Because soft mast availability was not documented during the 20-year period that Coley (1995) studied, the variation in population estimates that could be explained by soft mast availability is unknown.

Soft mast may also be an important nutritional component of black bear habitats in the southern Appalachian region. Soft mast composed a greater percent than hard mast in both annual volume index (45% vs. 14%, Beeman and Pelton 1980) and relative percent density (37% vs. 10%, Eagle and Pelton 1983) of scats collected in GSMNP. Gypsy moth (*Lymantria dispar*) infestations in Virginia resulted in complete acorn crop failures, yet bear reproduction and survival in those areas did not decrease immediately after the infestation and subsequent failure of the mast crop (Kasbohm et al. 1996). The amount of shrub soft mast available in an area influences the seasonal and annual home range sizes of bears and their activity patterns (Garshelis and Pelton 1980, Quigley 1982). Bears with abundant black cherry (*Prunus serotina*) in their home range displayed delayed movement to areas of abundant oak mast (Garshelis and Pelton 1981). Abundant grape (*Vitis* spp.) crops reduced the impacts of a severe oak mast failure on bear reproductive effort (Eiler et al. 1989).

Managing bear habitats requires identification of important habitat components and determination of the optimal, or at least minimal, habitat mix necessary for maintaining populations at desired levels (Schoen 1990). Policies regarding natural disturbances in national parks and silvicultural practices on multiple-use lands influence food availability for bears. Bear habitat management in the southern Appalachians currently emphasizes the importance of the fall hard mast component (Eiler et al. 1989, Pelton 1989). A better understanding of the influence of soft mast on bear population dynamics in the southern Appalachians may lead to more effective management strategies. In this study, we examined food availability by measuring the calories produced by the majority of

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vegetative bear foods in GSMNP (59% annual volume index of scat; Beeman and Pelton 1980). Our objectives were (1) to test for differences in caloric production per hectare between mast types and among seasons, and (2) to estimate total calories produced on the study area seasonally, by mast type, and by species.

STUDY AREA

GSMNP is located along the border of Tennessee and North Carolina (Fig. 1). This study was limited to the northwestern quadrant of GSMNP (613 km^2). Elevations within the study area ranged from 270 m to 2,025 m. Soils are thin and poorly developed with medium to high acidity, low water storage capacity, and low to moderate fertility (Soil Survey 1945, 1953). Climate of the area has been classified as a warm–temperate rain forest (Thornthwaite 1948). Annual precipitation ranges from 140 cm at lower elevations to 230 cm at higher elevations (Stephens 1969). GSMNP's microclimatic diversity represented site potentials for much of the federally owned land in the southern Appalachians, and management goals of the Park are intended to maintain an absence of human alteration. Thus, GSMNP afforded a unique opportunity to study habitat use of wildlife populations in a relatively controlled setting.

METHODS

We selected 19 plant species for this study that had been identified as primary foods for black bears during previous studies in the southern Appalachians (Beeman and Pelton 1980, Eagle and Pelton 1983, Brody and Pelton 1988). All plants were common in GSMNP (Whittaker 1956, Stupka 1960, Golden 1974).

Sampling Scheme

We stratified the study area to select 275 sample points by (1) vegetation type, (2) elevational range of each vegetation type, (3) aspect, and (4) distance from trails. We used the vegetation classification by MacKenzie (1993; Table 1). To stratify by vegetation type we overlaid topographic maps with Landsat Thematic Mapper satellite imagery that was remotely sensed during 1984 (MacKenzie 1993). This vegetation data layer had a pixel resolution of 90 x 90 m, with each pixel classified as 1 of 14 vegetation types. We sampled 9 of 14 vegetation types: cove hardwood, xeric oak, mesic oak, mixed mesic hardwood, pine, pine–oak, tulip–poplar, northern hardwood, and spruce–fir. The 5 unsampled types (treeless, grassy bald, grape thicket, heath bald, and water) comprised 2.4% of the study area. We did not record stand age, but it was generally >60 years. Thus, forests in most vegetation types were relatively mature and undisturbed. An exception to this was the spruce–fir type, in which over 70% of the Fraser fir (*Abies fraseri*) had been killed by the balsam wooly adelgid (*Adelges piceae*) during the past 30 years (National Park Service [NPS] personnel, Gatlinburg, Tennessee, USA, personal communication, 1995). We classified elevation ranges for each vegetation type as low or high, and aspects as northeastern (315–134°) or southwestern (135–314°). We distributed 30–33 sample plots

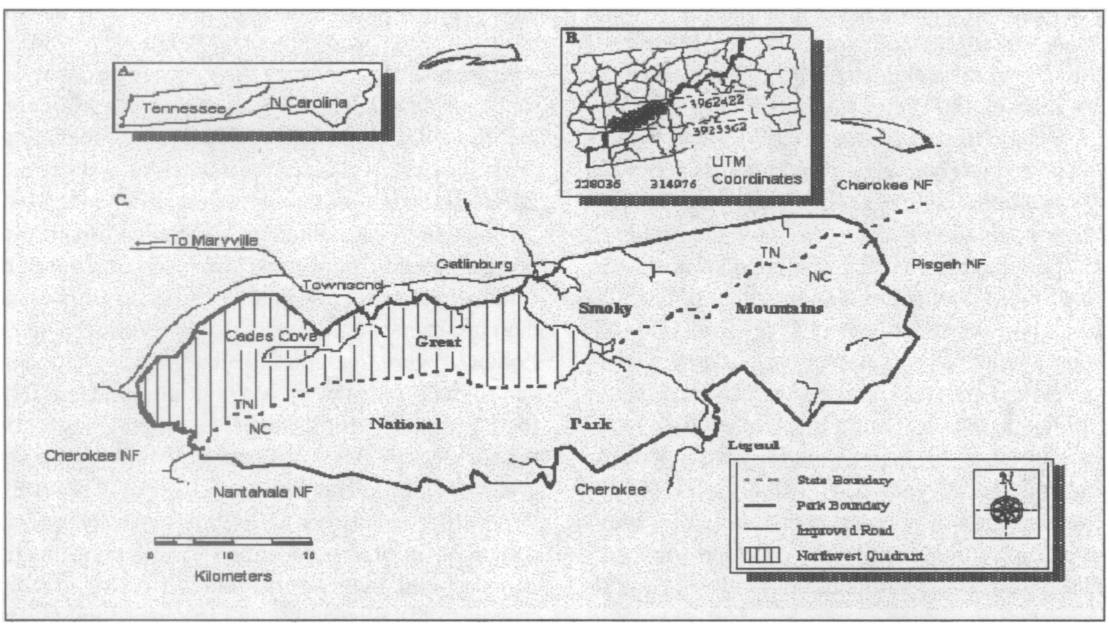

Fig. 1. Location of study area in Great Smoky Mountains National Park, Tennessee (TN) and North Carolina (NC), USA. Much of surrounding area is national forest (NF).

Table 1. Vegetation types as classified by MacKenzie (1993), including dominant tree species, area, and percent of northwest quadrant of Great Smoky Mountains National Park, North Carolina and Tennessee, USA.

Vegetation type	Dominant tree species [a]	Hectares	Area (%)
Cove hardwood	Eastern hemlock (*Tsuga canadensis*)	14,710	24%
	Sweet birch (*Betula lenta*)		
	Red maple (*Acer rubrum*)		
	Carolina silverbell (*Halesia carolina*)		
	Tulip-poplar (*Liriodendron tulipifera*)		
	Northern red oak (*Quercus rubra*)		
	Basswood (*Tilia heterophylla*)		
	Yellow birch (*Betula alleghaniensis*)		
Pine	Table-mountain pine (*Pinus pungens*)	13,476	22%
	Pitch pine (*Pinus rigida*)		
	Virginia pine (*Pinus virginiana*)		
	Scarlet oak (*Quercus coccinea*)		
Xeric oak	Chestnut oak (*Quercus prinus*)	13,235	22%
	Red maple		
	Tulip-poplar		
	Sourwood (*Oxydendrum arboreum*)		
	Scarlet oak		
Mixed mesic hardwood	Tulip-poplar	8,017	13%
	Red maple		
	Eastern hemlock		
	Chestnut oak		
Northern hardwood	Yellow birch	3,363	6%
	American beech (*Fagus grandifolia*)		
	Sweet birch		
	Eastern hemlock		
	Red maple		
	Northern red oak		
	Red spruce (*Picea rubens*)		
Tulip–poplar	Tulip-poplar	3,045	5%
	Red maple		
	Carolina silverbell		
Mesic oak	Northern red oak	1,770	3%
	Red maple		
	Chestnut oak		
Pine–oak	Scarlet oak	1,542	3%
	Table-mountain pine		
	Blackgum (*Nyssa sylvatica*)		
	Red maple		
	Chestnut oak		
Spruce–fir	Yellow birch	693	1%
	Red spruce		
	Red maple		
	Fraser fir (*Abies fraseri*)		

[a] Species within each vegetation type are ordered according to dominance, based on a mean of species basal area >2.0 m^2/ha, from MacKenzie (1993).

within each of 9 vegetation types as equally as possible among the elevation and aspect combinations where that vegetation type was found. If field inspection indicated that the vegetation had been incorrectly classified by MacKenzie (1993), that plot was discarded and a new plot sampled. All sample points were constrained to be >90 m from the nearest trail.

Distribution and Abundance of Food Species

At each sampling point we used a square plot of 0.04 ha (400 m^2) to measure crown volume (m^3) of relevant tree species and percent cover (m^2) of relevant shrub and vine species. To estimate crown volume we made 3 measurements on each tree within the plot: (1) crown width from east–west, (2) crown width from north–south, and (3) crown height. We used a clinometer to estimate crown height. We subsequently converted m^3 of tree crown volume and m^2 of shrub coverage into caloric production per hectare for each sample point, using information describing the average number of calories produced per m^3 or m^2 by each food species. We estimated the timing of that production as described below.

Phenology

For each species of bear food, 5–45 individual trees or patches of shrub were marked along 4 transects that passed through a variety of watersheds and elevational ranges: (1) Forge Creek–Parson's Branch–Gregory Bald Trails (549–914 m elevation), (2) Lead Cove–Bote Mountain–Schoolhouse Gap–Turkeypen Ridge Trails (518–945 m), (3) Jake's Creek–Miry Ridge Trails (671–1,372 m), and (4) Appalachian–Sugarland Mountain Trails (1,524–1,829 m). Individual trees or shrubs for each food species were selected and permanently marked so that each species was represented at various elevations and in different watersheds. We surveyed each transect bi-weekly from 20 March 1995 to 11 December 1995 and recorded the phenological condition of each tree or shrub patch. Individuals were recorded as ripe when fruits were mature, edible, and present (including on the ground). If an individual tree or shrub patch was the same condition during consecutive surveys, that condition was also assigned for the intervening week when no survey occurred. If consecutive weeks differed, an entry of no observation was recorded for the intervening week. Thus, all species and individuals had an equal possibility of having been ripe 1 week more or less than observed. Measures of fruiting periods were thus imprecise. We defined peak production as the period when >50% of individuals had ripe fruits available.

Fruit Production

When the majority of fruits of an individual tree or shrub patch were ripe, we estimated total fruit production from that individual. To estimate fruit production for trees, we counted the fruit seen within a measured volume of tree crown using a spotting scope (Inman 1997). We took 2 samples at random locations from within each tree crown and averaged the 2 samples to estimate production for that individual. To estimate fruit production by shrubs, we sampled the number of fruits within a 0.5 m^2 area of shrub coverage. We sampled by randomly tossing a square 0.5 m^2 sampling grid into the patch of shrubbery and counting all fruits within the grid. Fruits were counted from the top of the plant crown to the ground. Two 0.5 m^2 samples were taken at each individual patch, and the mean of the 2 samples was used as the estimate of production for that patch.

Fruit Weight and Gross Energetic Content

We collected fruits during 1995 and prepared samples for bomb calorimetery in a Parr Oxygen Calorimeter (Parr Instrument Company, Moline, Illinois, USA). For fruits with large, indigestible seeds (black cherry and blackgum) or hulls (hickories [*Carya* spp.]), we removed the seed or hull and analyzed only the fleshy part of the fruit. Species with minute seeds were left intact (huckleberries, blueberries [*Vaccinium* spp.], blackberries [*Rubus* spp.], grapes). One composite sample of each species was oven dried at 60°C until no weight change was detected. The weight of the entire sample was divided by the number of fruits in the sample to obtain the mean dry weight/individual fruit for a species. Samples were then measured for caloric value per gram dry weight. We required a variation in caloric value of <3% over at least 2 tests (Johnson and Robel 1968, Golley 1961).

Data Analysis

We estimated gross caloric production per unit area (m^2 of shrub coverage) or volume (m^3 of tree crown) by each species during 1995 as the mean number of fruits produced per m^2 (shrubs) or m^3 (trees) x mean dry weight/fruit (g) x energetic content per g dry weight. To estimate the temporal availability of calories, we pooled all phenological observations for a species and assigned each week a portion of the total caloric production. The assigned portion of production was based on that particular week's percent of the total number of ripe observations recorded for the species. For example, if a species had 50 observations of ripe, and 5 of those occurred in week 1, then week 1 received 10% of the total caloric production for that species. Dates used to separate seasonal periods were spring (1 Apr–15 Jun), summer (16 Jun–15 Sep), and fall (16 Sep–15 Dec; Beeman and Pelton 1980, van Manen 1994).

We used analyses of variance to compare caloric production/ha between mast types and among seasons. Although sample points were located using a stratified sampling scheme, analyses were based on a random design. Differences in mean production/ha between mast types and among seasons were analyzed using a completely random design with repeated measures. Each plot was sampled for cal/ha by soft mast and by hard mast, and during spring, summer, and fall seasons. This repeated measures design effectively blocked out the variation due to vegetation type. We tested the null hypotheses that mean caloric production per hectare did not differ between mast types ($P = 0.05$) and among seasons ($P = 0.05$).

We also estimated total caloric production within the entire study area for the year 1995, for each defined season, for both mast types, and for each species. We estimated species coverage within the study area by multiplying the mean areas of coverage by each food species within each vegetation type by the total area of each vegetation type (from McKenzie's [1993] GIS coverage). We estimated total caloric production by applying cal/ha values (above) to the acreage figures and phenological categorizations. Thus, we estimated the average number of calories produced by each food species, within each vegetation type, for the entire study area through the growing season, 1995.

During 1995 there was a mast failure by 2 species of white oaks and an extremely abundant mast crop by northern red oak. We developed differing scenarios of mast production by increasing or reducing the levels of oak mast production (cal/m^3) to the maximum or minimum levels recorded in 1995. We estimated total annual and mast type production for 2 scenarios: (1) the production of all oak species was set at 30.3 cal/m^3 (level of northern red oak's abundant crop during 1995), and hickory production was increased to half (15 cal/m^3) of the oak production (1995 hickory levels represented near total crop failure); and (2) we set production of all oaks at the mean of the 2 lowest producers during 1995 (mean = 1.6 cal/m^3). The first scenario represented a high mast year for all species and the second scenario a total mast failure.

RESULTS

Distribution and Abundance of Food Species

Oaks occurred in 8 of 9 vegetation types and accounted for 85.7% tree crown volume among species producing bear foods (Tables 2, 3, Fig. 2). White oaks were found in fewer vegetation types than red oaks, but accounted for more (45.4%) crown volume than did red oaks (40.3%). Hard mast trees occurred in 8 of 9 vegetation types and accounted for 97.2% of the tree crown volume, whereas soft mast trees occurred in only 5 of 9 vegetation types and accounted for <3%. Black cherry occurred in only 3 vegetation types. Blueberries, greenbriers (*Smilax* spp.), and huckleberries each occurred in at least 7 of 9 vegetation types whereas blackberries, grapes, and squawroot occurred in relatively few. Huckleberries accounted for 58.1% of shrub coverage and were the most abundant shrub in 7 of 9 vegetation types. Area of coverage by blueberries was <15% of coverage by huckleberries.

Phenology

Shrub fruits were ripe earlier (summer and early fall) than tree fruits (fall; Inman 1997). Squawroot was at peak production for 6 weeks (22 May–2 Jul). Peak production by blueberries was earlier (Jul) than huckleberries (Jul–Aug) with the exception of the high elevation southern

Table 2. Shrub coverage (m^2/ha) within 9 vegetation types in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

Overstory vegetation	Shrub species[a]	Mean (m^2/ha)	SD
Spruce–fir	Thornless blackberry (Vaccinium canadensis)	1,880	2,531
	S. mountain cranberry (Vaccinium erythrocarpum)	68	270
	N. highbush blueberry (Vaccinium corymbosum)	54	296
Northern hardwood	Thornless blackberry	743	1,914
	Allegheny blackberry (Rubus allegheniensis)	358	1,187
	N. highbush blueberry	100	326
	Greenbriers	4	23
Cove hardwood	Huckleberries (Gaylussacia sp.)	1,028	2,466
	Greenbriers	332	805
	Grapes	168	551
	Squawroot	88	259
	N. highbush blueberry	17	63
	Upland low blueberry (Vaccinium pallidum)	10	55
	Deerberry (Vaccinium stamineum)	4	23
Mesic oak	Huckleberries	1,383	2,634
	Allegheny blackberry	200	779
	Greenbriers	312	523
	Thornless blackberry	3	18
	Upland low blueberry	1	5
Mixed mesic hardwood	Huckleberries	2,385	3,351
	Greenbriers	461	1,144
	Grapes	197	754
	Deerberry	4	23
	Squawroot	6	24
Tulip–poplar	Huckleberries	339	904
	Greenbriers	323	613
	Grapes	275	1,194
	Squawroot	4	23
Xeric oak	Huckleberries	1,587	2,337
	Upland low blueberry	566	1,372
	Greenbriers	385	450
	Deerberry	96	247
	N. highbush blueberry	4	22
Pine–oak	Huckleberries	2,946	3,500
	Hairy blueberry (Vaccinium hirsutum)	279	1,064
	Greenbriers	235	347
	Upland low blueberry	225	855
	Deerberry	129	418
Pine	Huckleberries	1,434	2,244
	Greenbriers	403	1,075
	Upland low blueberry	162	464
	Grapes	8	44
	Squawroot	3	15

[a] N. = northern, S. = southern

Table 3. Tree crown volume (m^3/ha) for bear food producing trees in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

Overstory vegetation	Tree species[a]	Mean (m^3/ha)	SD
Spruce–fir	Fire cherry (*Prunus pennsylvanica*)	449	1,958
Northern hardwood	American beech	6,066	2,634
	Black cherry (*Prunus serotina*)	1,704	631
	N. red oak	1,417	7,759
	Fire cherry	47	255
Cove hardwood	N. red oak	14,325	30,669
	Chestnut oak	5,563	5,881
	Hickories	2,048	7,916
	White oak	1,598	4,387
	Scarlet oak	1,085	3,675
Mesic oak	N. red oak	9,903	12,087
	Chestnut oak	3,536	15,143
	Black cherry	2,173	11,904
	White oak	2,118	8,429
Mixed mesic hardwood	N. red oak	11,753	17,390
	Hickories	7,984	27,480
	Chestnut oak	7,534	12,911
	White oak	6,523	26,509
Tulip–poplar	Chestnut oak	5,850	18,713
	N. red oak	3,519	8,118
	Hickories	219	1,200
Xeric oak	Chestnut oak	19,645	17,402
	N. red oak	4,295	8,856
	Scarlet oak	3,207	5,940
	White oak	1,646	5,450
	Hickories	1,620	2,420
	Blackgum	809	2,943
Pine–oak	Chestnut oak	14,210	11,371
	N. red oak	3,773	6,329
	Scarlet oak	2,468	2,383
	Hickories	1,107	5,084
	White oak	1,066	2,364
Pine	N. red oak	4,889	10,982
	Chestnut oak	4,366	13,817
	Hickories	3,334	7,715
	Scarlet oak	3,055	10,378
	White oak	2,365	3,565
	Blackgum	725	1,806
	Black cherry	529	2,992

[a] N. = northern, S. = southern

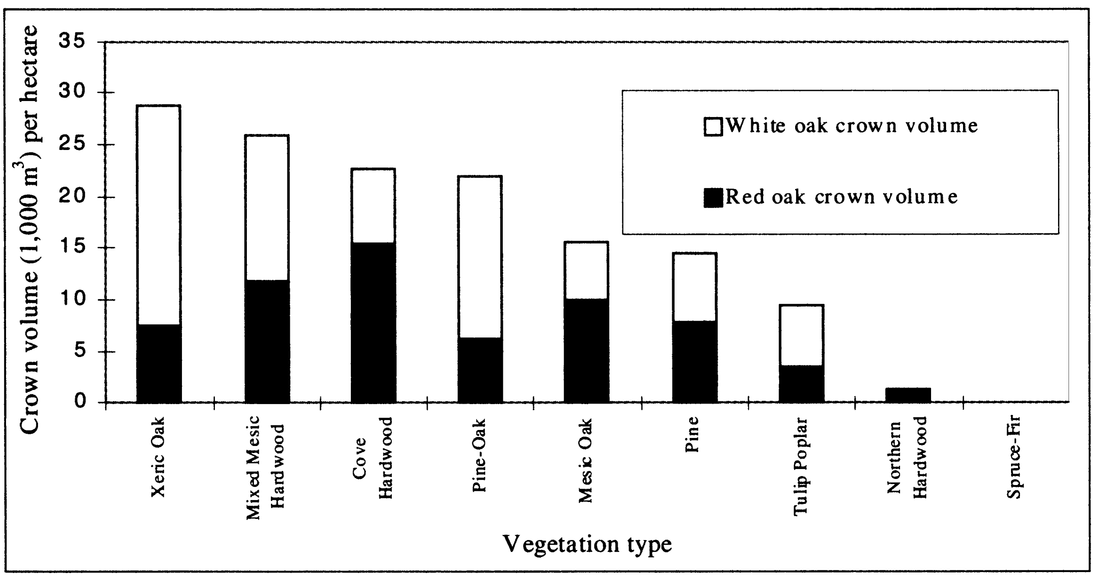

Fig. 2. Mean red and white oak crown volume per hectare, by vegetation type, in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

mountain cranberry (*Vaccinium erythrocarpum*), which peaked during September. Black cherry was at peak production from late August through early October. Oaks were ripe and available from late August through late December when we ceased sampling. Peak production occurred during the last week of September for red oaks and early October for white oaks.

Fruit Weight and Gross Energetic Analysis

Although not quantified, we considered acorn sizes during 1995 typical of most years, with the exception of white oak (*Q. alba*) which was less than ½ normal size. Gross energetic content ranged from 5.27 cal/g for thornless blackberry to 3.44 cal/g for hairy blueberry (Table 4). The 7 highest values were soft mast species; however, mean cal/g of soft ($\bar{x} = 4.47$ cal/g) and hard ($\bar{x} = 4.36$ cal/g) mast species did not differ ($P = 0.488$, $n = 19$).

Fruit Crop Production

The number of tree fruits produced per m3 of crown volume ranged from 0.14 for chestnut oak to 80.20 for black cherry (Table 5). Fruit production by red oaks was 8 times greater than that by white oaks. Shrub fruits produced per m^2 ranged from 21.5 (greenbriers) to 109.5

Table 4. Gross energetic content and single dried fruit weight of black bear foods in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

Fruit species	Sample type	Cal/g	SD	weight (g)	*n* [a]
Thornless blackberry	whole fruit	5.27	0.01	0.17	160
Blackgum	seed removed	4.98	0.01	0.08	142
Fire cherry	whole fruit	4.94	0.09	0.04	66
Grapes	whole fruit	4.90	0.01	0.09	245
Squawroot	entire stalk	4.66	0.03	9.23	8
Allegheny blackberry	whole fruit	4.66	0.04	0.06	11
Huckleberries	whole fruit	4.65	0.07	0.03	83
Northern red oak	whole fruit	4.60	0.07	2.22	35
Hickories	meat only	4.53	0.01	0.15	50
Greenbriers	whole fruit	4.44	0.04	0.09	178
Scarlet oak	whole fruit	4.26	0.07	0.67	30
Upland low blueberry	whole fruit	4.24	0.00	0.03	662
Chestnut oak	whole fruit	4.19	0.07	2.99	57
Northern highbush blueberry	whole fruit	4.18	0.03	0.06	218
Southern mountain cranberry	whole fruit	4.17	0.07	0.04	57
Deerberry	whole fruit	4.17	0.06	0.04	389
White oak	whole fruit	4.05	0.07	0.67	33
Black cherry	seed removed	3.95	0.01	0.04	100
Hairy blueberry	whole fruit	3.43		0.05	5

[a] Number of fruits in composite sample that was weighed to estimate individual fruit weight.

Table 5. Fruits and calories produced per square meter of shrub coverage or cubic meter of tree crown volume in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

Species	Fruits/m^3	Fruits/m^2	SD	*n*	Cal/m^3	Cal/m^2
Trees						
Northern red oak	2.97		5.1	84	30.33	
Black cherry	80.17		115.0	90	12.99	
Scarlet oak	2.69		5.5	86	7.63	
Fire cherry	21.64		46.6	48	4.49	
Chestnut oak	0.14		0.4	92	1.73	
White oak	0.59		1.3	80	1.59	
Blackgum	2.76		16.9	78	1.13	
Hickories	0.20		1.5	78	0.14	
White oaks	0.35					
Red oaks	2.83					
Shrubs and vines						
Squawroot		57.33	38.5	6		2,467.33
Thornless blackberry		67.96	72.1	90		59.46
Grapes		66.36	62.1	14		30.25
Northern highbush blueberry		70.00	38.7	4		16.66
Huckleberries		109.54	105.8	78		13.23
Upland low blueberry		106.96	155.7	50		13.15
Southern mountain cranberry		74.71	119.6	102		11.84
Allegheny blackberry		32.77	65.6	26		9.46
Greenbriers		21.50	80.7	50		9.08
Hairy blueberry		28.50	31.5	8		5.09
Deerberry		25.50	40.3	8		4.14

(huckleberries; Table 5). Standard deviations of fruit samples were high relative to means.

Caloric Production by Area and Volume

Caloric production by tree species ranged from 0.1 cal/m^3 for hickories to 30.3 cal/m^3 for northern red oak (Table 5). Caloric production by shrub species (excluding squawroot) ranged from 4.1 cal/m^2 for deerberry to 59.5 cal/m^2 for thornless blackberry (Table 5). Squawroot was by far the most productive shrub species on a per area basis.

Energetic Productivity

Mean production on the study area was 351,209 cal/ha (SE = 49,834). We estimated that annual production during a year of hard mast failure would be 122,963 cal/ha and 690,344 cal/ha during a year of high hard mast production.

Calories produced per hectare were greater for hard mast ($\bar{x}$ = 204,475, SD = 592,775, n = 275) than for soft mast ($\bar{x}$ = 75,275, SD = 74,550, n = 275, 1 df, F = 32.16, P = 0.0001). Although production by mast types differed, variance was less for soft mast, indicating less patchy distribution. Hard mast produced 74% of the calories within the study area, and soft mast produced 26%. However, in our scenario of hard mast failure, soft mast accounted for 72% of all caloric production. We noted a 17-fold difference in annual cal/ha contributed by hard mast in comparing our maximum hard mast scenario with our mast failure scenario (Fig. 3). In these scenarios, differences in annual production levels of hard mast greatly affected total annual production, but maximizing annual production levels of soft mast did not (Fig. 3).

Calories produced per hectare were greatest during fall ($\bar{x}$ = 167,600, SD = 455,525, n = 275) and lowest during spring ($\bar{x}$ = 22,300, SD = 164,950, n = 275, 2 df, F = 284.92, P = 0.0001). Summer production was intermediate ($\bar{x}$ = 89,850, SD = 168,200, n = 275). Summer and fall production did not differ (P = 0.8896), but spring production differed from both summer (P = 0.0001) and fall (P = 0.0001). Estimates of production over the entire study area indicated that 12.5% of all calories were available during spring, 28.2% during summer, and 59.3% during fall. However, 63% of the calories available during summer were hard mast, typically considered fall food. There was a period of low energetic availability during mid-summer (Fig. 4).

Northern red oak produced 65.7% of annual bear food calories; squawroot ranked second, producing 15.8% (Table 6). Although white oaks accounted for 45.4% of the tree crown volume on the study area among bear food producers, they produced only 6.7% of the calories available from trees. Red oaks accounted for 40.3% of the tree crown volume and produced 91.7% of tree calories. White oaks produced only 5.1% of all calories, which was equivalent to production by huckleberries (5.1%). Excluding

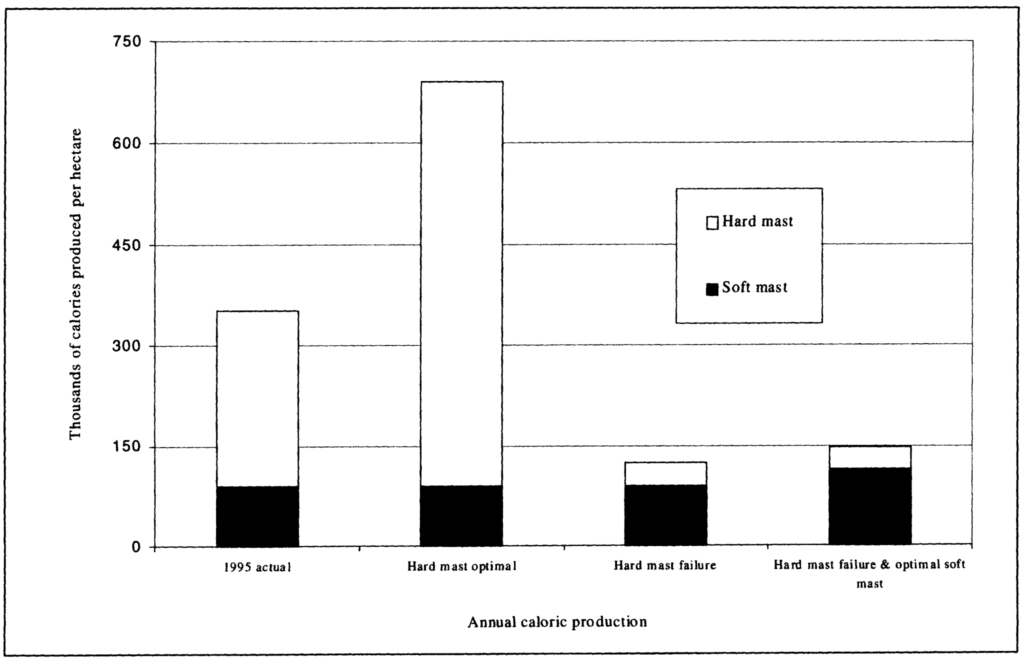

Fig. 3. Contributions of soft and hard mast to annual caloric production per hectare under 4 mast production scenarios in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

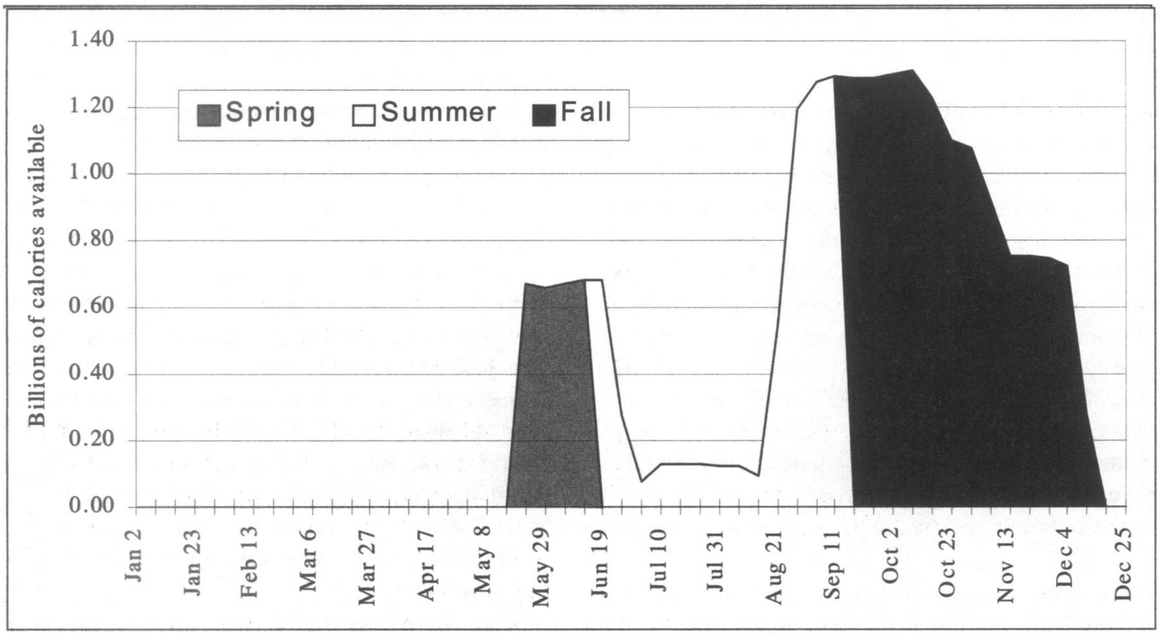

Fig. 4. Total calories available/week (1 Apr–15 Dec) of hard and soft mast species used as food by bears in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

Table 6. Estimates of total calories produced, percent of study area production, and caloric production per hectare for 19 species of vegetation used as food by black bears in the northwest quadrant of Great Smoky Mountains National Park, USA, 1995.

Species	Mast type	Total calories	% of area production	SE	Cal/ha	SD
N. red oak	H	14,147,184,151	65.70	648,797,209	230,711	10,581
Squawroot	S	3,413,293,121	15.80	551,769,040	55,664	8,998
Huckleberries	S	1,093,165,414	5.10	643,004,494	17,827	10,486
Chestnut oak	H	877,345,427	4.10	643,004,494	14,308	10,486
Scarlet oak	H	789,142,618	3.70	602,264,335	12,869	9,822
Thornless blackberry	S	226,337,206	1.10	99,365,195	3,691	1,620
Black cherry	S	217,041,793	1.00	349,561,350	3,539	5,701
White oak	H	214,239,731	1.00	638,217,240	3,494	10,408
Greenbriers	S	190,784,595	0.89	648,797,209	3,111	10,581
Blueberries (all *Vaccinium* spp.)	S	154,101,237	0.72		2,513	
Grapes	S	151,090,557	0.70	551,769,040	2,464	8,998
Upland low blueberry	S	133,703,304	0.62	603,982,343	2,180	9,850
Blackgum	S	23,085,653	0.11	466,902,036	376	7,614
Hickories	H	22,494,795	0.10	641,391,018	367	10,460
Allegheny blackberry	S	14,723,375	0.07	97,751,627	240	1,594
Northern highbush blueberry	S	11,151,068	0.05	506,272,716	182	8,256
Deerberry	S	6,494,296	0.03	540,935,436	106	8,822
Hairy blueberry	S	2,191,760	0.01	39,668,758	36	647
Fire cherry	S	2,103,400	0.01	88,323,839	34	1,440
Southern mountain cranberry	S	560,809	0.00	17,834,274	9	291
Total		21,536,133,072	100		351,209	
Oaks					261,381	41,296
Berries (*Rubus* spp., *Vaccinium* spp., and *Gaylussacia* spp.)					24,271	41,566

squawroot, huckleberries produced 60% of shrub calories. All 5 blueberry species combined produced <1% of all calories, whereas blackberry species produced 1.2% of all calories. Soft mast species ranked as 2 of the top 3 producers (Table 6). Caloric production per hectare was 261,381 cal/ha by oaks and 24,271 cal/ha by berries (blackberries, blueberries, and huckleberries; Table 6, Inman 1997).

DISCUSSION

We believe our measurements of energetic availability fairly represented the average annual level on our study area. Major alterations likely occur during years of complete hard mast failure or during extreme weather conditions such as severe drought. Oaks accounted for 74% of calories available to bears during this study, and have likely been the most influential genera affecting bear ecology in the recent past. Inherent productive ability of the red and white oak groups is not represented well by this data. If measurement had occurred during 1996, white oaks would have produced a larger crop. Hard mast surveys conducted by NPS on the Tennessee side of GSMNP during 1995 resulted in index values of 1.35 mast units for white oaks and 4.05 mast units for red oaks; index values for 1996 were 4.07 mast units for white oaks and 1.99 mast units for red oaks (Bill Stiver, National Park Service Biologist, Great Smoky Mountains National Park, Gatlinburg, Tennessee, USA, personal communication, 1997) Production by northern red oak during 1995 was the highest recorded level in NPS mast survey history (1979–97).

Our analyses determined gross energy rather than digestible energy. The amount of energy available for bear use will be different, depending on the chemical composition of the food and its digestibility by black bears. However, we used gross energy as an acceptable representation because trials to determine the digestibility of each food species would require captive facilities and great expense.

Results of this study strengthen the hypothesis that oak productivity has been of foremost importance in providing energy for bears in the Smoky Mountains. However, soft mast was responsible for 26% of the energy available to bears and may provide even more resources to bears during years of medium to low hard mast production. Soft mast may affect population dynamics of bears in the Smoky Mountains because it has different physiological usage than hard mast and provides an abundance of energy when hard mast is not available. Squawroot, a parasitic plant that grows on the roots of oaks, was the second most productive species on the study area, yielding almost 16% of available energy. Squawroot generates a surge of carbohydrate energy (Seibert and Pelton 1994) during late spring and early summer. After 4–5 months with no energy intake, bears, especially females with young, are in great need of metabolizable energy. This may be of particular importance after years of medium to low hard mast production and the resultant lack of remaining fat stores. Females with cubs are the most active sex–age group (Garshelis and Pelton 1980, Villarrubia 1982), and this increased activity is likely in response to increased nutritional demands in support of lactation. Because squawroot is usually abundant in the habitats where it does occur, it is a food that may be acquired with relatively little effort. We recorded the presence of squawroot in 3 of the top 4 vegetation types used by female bears in spring (van Manen 1994) in GSMNP. Although fall mast crops can be good enough to result in high reproduction (Eiler et al. 1989), survival, particularly of cubs, could be affected by the presence of sufficient sources of energy during late spring and summer. We speculate that squawroot abundance affects cub survival and other important population parameters, such as age of primiparity and litter interval. Increasing bear population size within GSMNP (Coley 1995) could be in part due to increasingly abundant squawroot in a maturing oak forest.

Huckleberry was the third most productive species on our study area, and may be of importance to the bear population as a source of both protein and carbohydrate energy. The protein found in huckleberries and other soft masts is available during a period when bears are physiologically focused on assimilating proteins for growth and muscular maintenance (Eagle and Pelton 1983, Nelson et al. 1983, Brody and Pelton 1988). Insects available during this period have a high protein content (Eagle and Pelton 1983) and constituted 11% of annual volume index of scat in GSMNP (Beeman and Pelton 1980). However, huckleberry and other soft masts constituted 37% of scat volume (Beeman and Pelton 1980), and although soft mast species generally have moderate protein contents (Eagle and Pelton 1983, Inman 1997), increased intake can offset deficiencies in nutritional content (Crampton and Harris 1969). Thus huckleberry and other soft masts are likely to be significant contributors to the annual protein intake of bears.

Because soft and hard mast fruits have different methods of seed dispersal, production by soft mast crops may be less variable than that of hard mast crops. Acorns and hickory nuts are destroyed by consumption. Hard mast producers have gained selective advantage by occasionally producing large crops that saturate seed predators (Silvertown 1980, Sork et al. 1993). Soft mast species, on the other hand, have seeds that are scarified and dispersed when fleshy fruits are eaten; therefore, consumption enhances reproductive potential. From an evolutionary perspective, hard mast producers have selective advantage by investing in production of occasional large crops whereas soft mast producers gain advantage with relatively stable, high production. Soft mast, therefore, may provide a relatively stable source of energy for bears, whereas hard mast fluctuates.

Black bears are large carnivores whose diet consists mostly of vegetation. Consequently, they have a relatively low basal metabolism that results in low fecundity, long generation time, and altricial young (McNab 1989). Constraints on carrying capacity may be determined during the period of lowest energetic availability. Bears have adapted to low caloric availability during winter with fall hyperphagia and winter hibernation, effectively increasing the energetic availability during winter via fat storage and inactivity. We found an additional period of relatively low caloric production during summer. More vertebrate species consume fleshy fruits than consume hard mast (Martin et al. 1951), and inter-specific competition may be most intense during summer. Nuisance bear activity in GSMNP typically begins when squawroot availability decreases, is highest during mid-summer when we found lowest energetic availability, and decreases with the onset of fall food availability (Singer and Bratton 1977, Stiver 1991). In years when fall mast crops are average-to-good, such as 1995, caloric availability far exceeds what the bear population can consume (Inman 1997). Thus, availability of food in fall may limit the population only during years of severe mast failure. A threshold level of low fall mast availability may negatively affect the survival and reproduction of bears.

Both hard and soft masts serve necessary functions for bears and are important components of bear habitat. Differences in usefulness of soft and hard masts result from the timing of production in conjunction with nutritional content and bear physiological needs. Inherent differences in annual fluctuations of productivity may also influence the utility of each mast type for bears. It is likely that southern Appalachian bear populations with access to ample carbohydrate energy and protein during spring and summer have a lower median age of primiparity and inter-birth interval as well as higher rates of cub survival, breeding success, and sub-adult survival than those populations that rely solely upon fat stores from the previous fall.

MANAGEMENT IMPLICATIONS

Effective habitat management for black bears in the southern Appalachians requires abundant oak stands that are mature and composed of both red and white oak species (Pelton 1989). This study further confirms that oaks and oak habitats are of great importance for bears in the southern Appalachians. Our results also indicate that the abundance of energy found in squawroot and the low energetic availability during mid-summer have the potential to significantly influence bear population dynamics. Further study is needed to determine the effects of squawroot abundance upon survival, recruitment, age of primiparity, and litter interval. The relationship of mid-summer food abundance and bear density also warrants further investigation. Defining the role of soft mast will be a positive step toward effective habitat management for bears of the southern Appalachians. Once the roles of major foods are well understood, appropriate habitat compositions and silvicultural prescriptions may be defined.

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