VARIABLE ACORN CROPS: RESPONSES OF WHITE-TAILED DEER AND OTHER MAST CONSUMERS

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We examined movements and behavior of female white-tailed deer (*Odocoileus virginianus*) relative to the acorn mast-fall from 1986 through 1989 in a mature deciduous forest in Front Royal, Virginia. Ten white-tailed deer with radiotransmitters increased their home range to incorporate acorn-producing areas during mast-fall. Consumption of acorns by deer constituted ca. 50% of foraging time during peak mast-fall; average consumption rate was 0.75 acorns/min searching. Although the number of acorns eaten by deer was correlated with mast-fall, a prolonged time was spent searching for acorns after mast-fall. Deer consumed 70% of marked acorns placed out during mast-fall, while medium-sized animals (e.g., *Tamias striatus, Sciurus niger, Sciurus carolinensis*) consumed 61% of acorns placed out later in autumn. We hypothesize that high densities of deer may limit populations of more mast-dependent species, particularly at low acorn-crop densities.

Key words: ***Odocoileus virginianus*, white-tailed deer, acorns, Virginia, sciurids**

Mast crops, particularly acorns, are a seasonally-limited food resource and influence overwinter survival of many forest animals in North America (Goodrum et al., 1971; Johnson et al., 1989; Martin et al., 1951). Hard mast is a major source of fat stores in large mammals (Eiler et al., 1989; Mautz, 1978; McCaffery, 1984), and constitutes the bulk of winter larders for many small mammals (Abbott and Quink, 1970; Hamilton, 1941; Wolff et al., 1985) and some birds (DeGange et al., 1989; Stacey, 1979).

For hand-raised deer, hard mast can constitute 50% of the diet during autumn (Pekins and Mautz, 1987). Analysis of rumen contents of wild deer indicated that acorns were a substantial portion of the autumn diet (76–90%) when available (Harlow et al., 1975; McCullough, 1985). Birth weights and survival of fawns of white-tailed deer in deciduous forests is positively correlated with abundance of hard-mast crops (Feldhamer et al., 1989; Wentworth et al., 1989).

Although analyses of rumen and fecal samples and observations of hand-raised deer indicate that acorn consumption occurs, these data do not address questions concerning the dynamic behavior of free-ranging deer. Failure to shift home ranges into oak (*Quercus* sp.) stands during acorn-fall, or switching to alternate foods when acorn densities are still above that necessary to support other species, would reduce the importance of acorn consumption by deer relative to other mast-dependent species. We tested the hypotheses that high population densities of deer consume a significant portion of the acorn crop, and that spatial and temporal variability in the acorn crop is correlated with the behavior of deer and other mast consumers.

METHODS

Our study site was the Natural Studies Area within the Conservation and Research Center, a 1,100-ha research facility of the National Zoological Park, located 2 km SE Front Royal, Virginia (38°54′N, 78°09′W), and contiguous with Shenandoah National Park. The Natural Studies Area is a 456-ha site that is ca. 80% wooded, 50% (174 ha) of which is mature (60–80 years of age) oak and hickory (*Carya* sp.) overstory, with an understory dominated by dogwood (*Cor-*

nus sp.) and spicebush (*Lindera benzoin*). The Natural Studies Area is surrounded by a fence 1.5–1.9 m in height; the fence is only 50% effective in restricting movements of deer (Seidensticker, 1983) and gates spaced every 500 m along the fence were open during our study. Hunting was not permitted in either the Shenadoah National Park or the Conservation Center. Densities of deer are ca. 35 deer/km^2 (Seidensticker, 1983) and have been at these levels since the 1970s, with the exception of a population crash in 1983–1984 (Stuewe, 1986). This density of deer was comparable to other state and federal lands where hunting is not permitted (Healy et al., 1987; Wilcox, 1976) suggesting this population was at, or near, carrying capacity. The study period encompassed mast-falls (August–November) from 1986 through 1989.

Mast production (kg/ha) in 1987 through 1989 was estimated by establishing two grids of mast collectors in two oak-hickory stands (Posey Hollow and Bear Hollow) that were 2 km apart. Each grid was composed of 100 collectors in a 10 by 10 configuration at 20-m intervals. Mast collectors were wire funnels (collecting surface = 2,910 cm^2) attached to tin cans and fastened to 1-m stakes, making collected acorns inaccessible to foraging animals. Mast production in 1986 was obtained from only 18 of these collectors at each of the two sites. We observed no difference in response of deer to acorns of the three common species of oak in the area (*Quercus rubra, Q. alba,* or *Q. prinus*), so all species were pooled for analyses. Hickory (*Carya* sp.) nuts were excluded from analyses because they were not consumed by deer. During 1988 and 1989, mast collectors were checked weekly to determine mast-fall. Seed cups were removed from acorns collected, and nuts were air-dried for 1 month and weighed to the nearest gram. After weighing, all acorns were cut open to determine if the seed was whole or infested with larvae of curculionid beetles. We estimated the synchrony in timing and amount of mast-fall between the two disjunct oak stands in Posey and Bear hollows. The peak of mast-fall for each grid during 1988 and 1989 was determined by fitting a quadratic equation to the amount of mast collected each week. All radiotracked deer used in the study were captured within 1 km of the Posey Hollow grid; consequently mast production at that site was used to identify good and poor mast years. Acorn-falls of <100 kg/ha were considered poor (French, 1985; Goodrum et al., 1971).

To estimate acorn availability on the ground, 10 randomly selected 20 by 20-m plots within the mast grids were systematically searched for acorns at ca. 2-week intervals during 1988 and 1989. To allow comparison with the mast collectors (kg/ha), the number of acorns seen/m^2 was multiplied by the mean weight of acorns (3.2 $\pm$ 0.52 g), obtained by weighing 30 groups of 30 acorns each randomly collected from the Posey Hollow study area during the peak of the mast-fall in 1989. While searching for acorns within the 20 by 20-m plots, all groups of fecal pellets also were counted. Distributions of pellets should reflect relative use of habitat (Edge and Marcum, 1989; Leopold et al., 1984).

Deer were captured using clover traps (Clover, 1956), drop-nets (Holzenbein et al., 1989), and rocket-nets (Hawkins et al., 1968), and adult females were fitted with radiocollars. A minimum of 10 separate matrilines were radiotracked throughout the study, with 12–17 females radiotracked each year. During each week of the study, three locations were obtained for every radiocollared deer. Each of the weekly locations was obtained during a separate time period (within 1 h after dawn, within 1 h before dusk, and the remainder of the daylight period), and animals were approached until visually located (Holzenbein and Schwede, 1989). The Spatial Ecology Analysis System (Cary, 1990) was used to calculate minimum-convex polygons of home ranges by month. The convex polygon for each deer was based on the 13 locations taken each month of the study. Significant ($P < 0.05$) changes in monthly size of home range for radiotracked deer were determined with ANOVA for repeated measures (Winer, 1971). During 1986, 1987, and 1988, we recorded in which of five habitat types, based on overstory composition (field, *Robinia-Ailanthus,* dogwood-*Celtis,* cove hardwood, oak-hickory, or *Liriodendron*), each radiocollared deer was located.

Each week, 10–25 h of observations were conducted on focal radiocollared deer (Altmann, 1974), which were habituated to humans and could be approached to within 20 m. The number of focal deer varied each year, with 3 deer followed in 1987, 10 deer followed in 1988, and 7 deer followed in 1989. Focal deer observed in 1987 were included in each year's sample. Observations of feeding were made from dawn to dusk in 1987 and 1988, and 5 h after dawn and 5 h before dusk in 1989. Only observation periods in which the observer was close enough to

determine the forage types consumed were included. During each observation period, a foraging event was considered the length of time between the first bite of a food type and the first bite of a different food type, or the cessation of foraging. The unique posture assumed by deer while searching for acorns (neck stretched, head down and swinging slowly in an arc) allowed us to estimate search time. Acorns were taken singly, with the nut cup expelled, nut cracked and swallowed while the head was in an upright position. Analysis of consumption rates for deer (number of acorns eaten/min of search behavior) included ANOVA with weighted values, because longer foraging bouts (>20 min) were considered more accurate than shorter feeding bouts.

During 1989 and 1991, acorns were marked with water-based White-out (LHB Industries, St. Louis, MO) and placed within 1-m plots to assess the consumption rate of acorns on the ground. Ten acorns were placed within each of 30 plots, which were spaced at 20-m intervals within a stand of mature oak-hickory. For 3 weeks during the peak of mast-fall in 1989 and 1991, plots were examined weekly and missing marked acorns replaced, whereas unmarked acorns within the plots were removed. Following the end of mast-fall, 2 weeks of additional trials were conducted each year. Marking the acorns did not influence their consumption, because marked (n = 36) and unmarked (n = 36) acorns placed at 1-m intervals along a forest transect 14–21 September 1991, were not consumed at different rates ($\chi^2 = 0.78$, $P > 0.10$).

The 30 experimental plots were divided into three groups; 10 randomly selected plots were covered with poultry wire (2.5-cm diameter mesh) across the top to prevent consumption of acorns by large animals; 10 plots had poultry wire stretched across the top and sides, and staked along the ground, to prevent access by both large and medium-sized animals; and the remaining 10 plots were controls. Consumption rates for medium-sized animals were estimated by subtracting the number of acorns consumed in closed plots from the number of acorns consumed in plots that excluded large animals. Consumption rates for large animals were estimated by subtracting the number of acorns consumed within plots that excluded only large animals from the number of acorns consumed in open plots. Consumption rates for small mammals were estimated as the number of acorns removed from closed plots. Potential large animals within the study area were white-tailed deer, wild turkeys (*Meleagris gallopavo*), and black bears (*Ursus americanus*). There was no evidence of disturbance at the sites to indicate foraging by either turkeys or bears, so all consumption by large animals was attributed to deer, which frequently were seen at the site. Medium-sized mammals captured at the nearby Posey Hollow grid include gray and fox squirrels (*Sciurus carolinensis, S. niger*), southern flying squirrels (*Glaucomys volans*), eastern chipmunks (*Tamias striatus*), raccoons (*Procyon lotor*), and eastern woodrats (*Neotoma floridana*). White-footed mice (*Peromyscus leucopus*) were the only mast-consuming small mammal captured on the Posey Hollow grid.

Results

At the Posey Hollow site, acorn production was variable; poor in 1987 (81 kg/ha), intermediate in 1988 (165 kg/ha), and good in 1986 and 1989 (320 and 356 kg/ha, respectively). Although acorn production at the Bear Hollow grid was not significantly correlated with the acorn production at Posey Hollow ($r^2 = 0.69$, $n = 4$, $P > 0.10$), variability in annual production was similar, with poor acorn crops in 1987 and 1988 (3 and 28 kg/ha, respectively), an intermediate acorn crop in 1989 (123 kg/ha), and a good acorn crop in 1986 (396 kg/ha).

For 1988 and 1989, when mast was collected each week, the timing of the mast-fall was relatively consistent; most acorns (range, 81–92%) fell 14 September–14 October. Peak mast-fall occurred within 3 days (25–27 September) for each of the four samples, with three of the quadratic equations providing a good fit of the data (Posey Hollow 1988, $F = 5.6$, $d.f. = 2,7$, $r^2 = 50.6$; Bear Hollow 1989, $F = 5.0$, $d.f. = 2,7$, $r^2 = 46.8$; Posey Hollow 1989, $F = 5.9$, $d.f. = 2,7$, $r^2 = 52.1$). Densities of acorns on the ground coincided with the amount of acorns in the collectors ($r^2 = 0.89$, $n = 21$, $P < 0.001$), with densities of acorns on the ground dropping an average 4.4 fold during the 2 weeks following peak (range, 2.24–7.26 fold). This rapid decrease in densities of acorns occurred regardless of the size of the mast crop; there was no significant correlation between production of acorns and

TABLE 1.—*Percent of acorns not infected with curculionid larva for acorns collected in mast traps (August, September, October) and on the ground (November, March), National Zoological Park, Front Royal, Virginia.*

		August		September		October		November[a]		March	
Area	Year	%	(*n*)	%	(*n*)	%	(*n*)	%	(*n*)	%	(*n*)
Posey Hollow	1988	20	(25)	55	(56)	57	(66)	14	(62)	2	(50)
Bear Hollow	1988	0	(5)	45	(40)	56	(50)	8	(48)	0	(50)
Posey Hollow	1989	0	(17)	56	(169)	81	(128)	6	(100)	0	(50)
Bear Hollow	1989	0	(9)	41	(83)	53	(34)	8	(54)	2	(50)

[a] For each sample, the proportion of infected acorns was higher in November than for acorns collected during mast-fall (χ^2 = 57, 43, 58, and 400, respectively, $P < 0.01$).

the number of acorns on the ground in November ($r^2 = 0.01$, $n = 4$, $P > 0.10$). The percentage of acorns infected by curculionid larvae was significantly higher in November and March, compared to acorns collected in September and October (Table 1). Of the acorns remaining on the ground by November, >90% were infected by larva.

Mean size of home ranges for female deer increased from summer to autumn during years with good mast: 1986, 1988, and 1989 (Fig. 1; ANOVA, $F = 11.2$, $d.f. = 4,32$, $P < 0.01$; $F = 7.31$, $d.f. = 3,33$, $P < 0.01$; $F = 11.31$, $d.f. = 4,32$, $P < 0.01$). During the poor mast year of 1987, no monthly increases in the size of home ranges were detected during mast-fall, and mean size of home range (Fig. 1) was significantly smaller than during years of good acorn crops (ANOVA, $F = 11.07$, $d.f. = 1,41$, $P < 0.02$).

We do not have information on use of habitat by deer for 1989, but during the other years of good mast-fall (1986 and 1988) significant shifts in use of oak-hickory habitat occurred during autumn (Fig. 1; ANOVA, $F = 22.5$, $d.f. = 4$, $P < 0.001$, and $F = 7.56$, $d.f. = 3$, $P < 0.01$, respectively) that were not evident during the poor-mast year of 1987 ($F = 0.74$, $d.f. = 4$, $P > 0.10$). For 1986, 1987, and 1988, use of oak-hickory habitat during mast-fall varied significantly with year ($F = 7.74$, $d.f. = 2$, $P < 0.01$).

Use of oak-hickory habitat during the mast-fall also was reflected by the increase in fecal groups located on plots within the stands. The mean ($\pm$ *SE*) number of fecal groups located during the peak of the mast-fall was significantly higher than those occurring outside of that period (8.4 $\pm$ 0.8, and 2.5 $\pm$ 0.6 fecal groups, respectively; Kruskal-Wallis $H = 12.15$, $P < 0.01$, $n = 9, 25$). During autumn (15 August–30 November), a significant correlation existed between number of acorns on the ground and number of fecal groups located during each survey ($r^2 = 0.56$, $P < 0.01$, $n = 34$).

During 856 h of direct observation on 12 deer, 501 h of foraging was recorded. The rate of acorn consumption (acorns/min foraging) of deer was positively correlated with the timing of the acorn-fall ($F = 31.01$; $d.f. = 1,31$; $P < 0.001$). Nonetheless, because of the persistence of searching for acorns after the peak of availability, the amount of time spent looking for acorns was not significantly correlated with acorn-fall ($F = 0.34$; $d.f. = 1,31$; $P > 0.10$).

The mean rate of consumption of acorns during the mast-fall was 0.75 acorns/min ($\pm$0.09 *SE*) foraging ($n = 33$). This consumption rate multiplied by the estimated daily time spent feeding on acorns approximates 340 acorns (e.g., 1 kg day^{-1} deer^{-1}), which agrees with estimated consumption of mast by hand-raised deer (Pekin and Mautz, 1987). Because all radiotracked deer and their family groups moved into the oak stands during mast-fall, we estimate ca. 160 kg/day was consumed, assuming a density

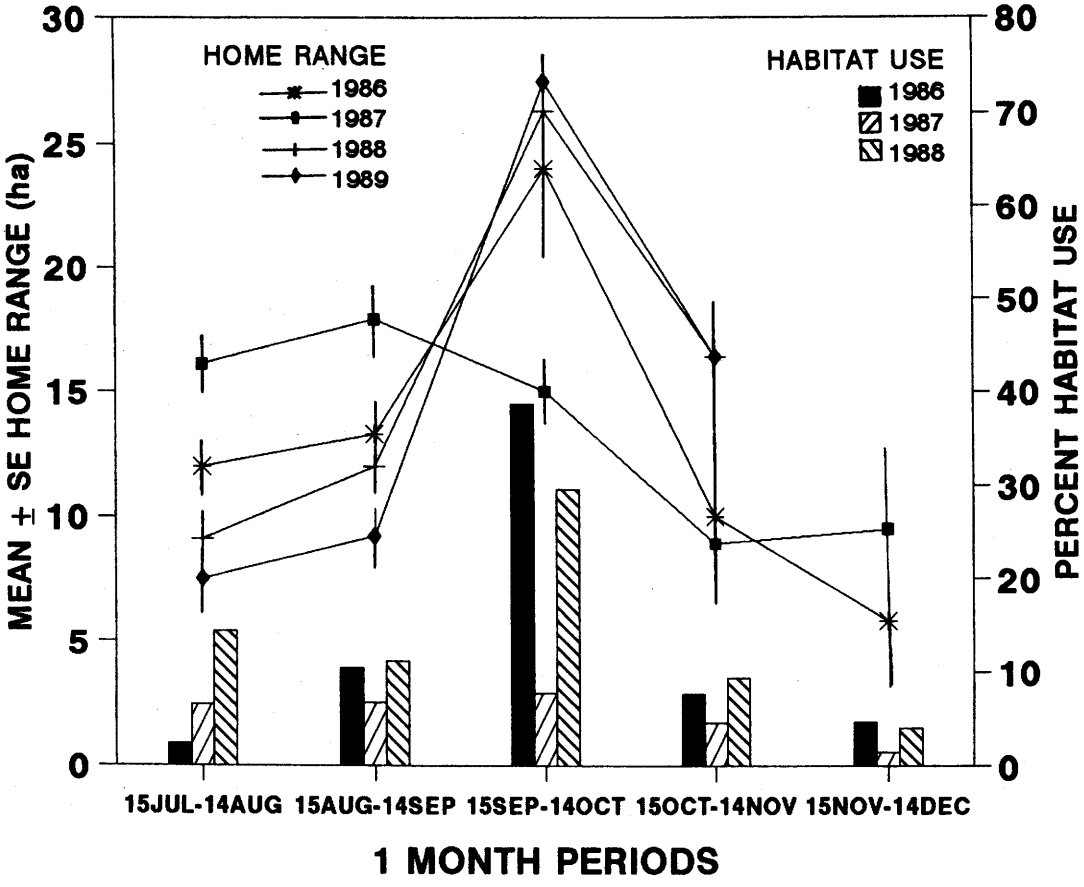

FIG. 1.—Size of home range ($\bar{X} \pm$ SE) of female white-tailed deer with radiotransmitters for 1986 (n = 10), 1987 (n = 17), 1988 (n = 13), and 1989 (n = 10). Deer were included only if radiotracked for all periods of the year; each 1-month period includes 13 locations for each animal. For 1986, 1987, and 1988, percent of radiolocations in oak habitat are given for each period. Each year the peak of the mast-fall was 15 September–14 October, National Zoological Park, Front Royal, Virginia.

of 35 deer/km^2 within our 456-ha study area. With ca. 174 ha of oak-hickory forest within the study area, deer feeding for 40 days would have consumed between 10 (based on Posey Hollow grid estimate) and 30% (based on Bear Hollow grid estimate) of the 1989 acorn crop.

Comparison of rates of larval infestation between acorns collected in mast traps and those collected on the ground in November indicate selection for noninfested acorns (Table 1). If estimates of acorn production are reduced based on infestation by curculionid larva during peak acorn-fall, the estimated percentage of acorn crop consumed by deer increases to 16 and 67% for each of the two oak stands.

Marked acorns placed within plots that excluded animals based on size were removed at variable rates during mast-fall (total number of marked acorns eaten = 601). Deer consumed 70% (n = 274) of the acorns during the peak of the mast-fall. Medium-sized mammals (e.g., squirrels and chipmunks) consumed more acorns (61%, n = 327) after the mast-fall, when the availability of acorns throughout the area was low. Small mammals consumed the least

amount of acorns (12–19%) throughout the study.

Discussion

Our observations on the consumption of mast by white-tailed deer support previous reports (Harlow et al., 1975; McCullough, 1985; Pekins and Mautz, 1987, 1988) that, when available, acorns form a significant portion of the autumn diet of deer. The shift in activity of deer into oak-hickory stands, and the continued search for acorns after they become scarce, demonstrate the importance of the acorn crop to white-tailed deer and the potential for deer to reduce availability of acorns for other vertebrate species. The high percent of marked acorns removed by deer during the peak of the mast-fall underscores the ability of deer to exploit high densities of seeds prior to leaf-fall. Only after leaf-fall (i.e., after 1 November) were marked acorns more often consumed by smaller mammals, but densities of acorns within the study area declined substantially prior to leaf-fall each year.

Estimates of mast needs for wildlife range from 100 to 200 kg/ha (French, 1985; Goodrum et al., 1971; Johnson et al., 1989). Acorn production was >150 kg/ha for four of our eight measurements, but the amount of acorns on the ground declined rapidly after both good and poor acorn crops. Our results agree with other reports of rapid decreases in density of acorns within forests of the southern Appalachians (Downs and McQuilikin, 1944; French, 1985) and not with studies reporting the persistence of acorns through winter during bumper crops of >200 kg/ha (Dunkeson, 1955; Goodrum et al., 1971).

Consumption of alternate foods enables deer to survive mast failures (Harlow et al., 1975), but persistent mast failures may reduce population sizes of mast-dependent species, such as *Sciurus* (Nixon et al., 1975). With storage of acorns by small mammals and birds, a proportion of the caches are not retrieved and potentially increase recruitment of mast-producing species (Abbott and Quink, 1970; Barnett, 1977; Cavers, 1983). Consumption of acorns by large species, however, does not allow for the escape of captured seeds and may result in reduced rates of regeneration within the forest.

This study measured only the portion of the acorn crop that reached the ground; some portion was consumed or cached by other species (i.e., sciurids, blue jays *Cyanocitta cristata*) prior to mast-fall. Deer cannot consume an entire mast crop, but their foraging will shorten the length of the mast season for mast-dependent species. Sciurids focus on hickory nuts during early mast-fall and acorns later in the mast season (Smith and Follmer, 1972). The ability of squirrels to locate and exploit high-density pockets of seeds (Stapanian and Smith, 1984) would explain their increased consumption of marked acorns after mast-fall. This strategy, however, is dependent on acorns persisting after mast-fall. A shortened mast season could increase competition for acorns and limit those species that do not process these seeds quickly.

Preference of deer for early successional habitat (Harlow, 1984) does not appear to ameliorate the effect of high densities of deer on acorn availability within forest interiors. High densities of deer have the primary effect of changing vegetation structure (Alverson et al., 1988; Hough, 1965; Kroll et al., 1986). A secondary effect from consumption by deer of limited mast-crops may explain the negative correlation between densities of white-tailed deer and small mammals in some eastern forests (Brooks and Healy, 1988). Keystone species have a dominant effect on community diversity because of their behavior or numbers (Paine, 1980; Terborgh, 1988). If deer serve as a keystone species within forested ecosystems of eastern North America, then densities of deer will be negatively correlated with densities of mast-dependent species. This relationship should be more apparent following low acorn-crop years, when a larger portion of the acorn crop will be consumed by deer before leaf-fall, and the shift to high-

er foraging efficiencies by smaller mammals. The relationship also should be more evident in areas where densities of deer are high due to loss of predators, favorable habitat, or absence of hunting.

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