ARTICLE

A test of the predator satiation hypothesis, acorn predator size, and acorn preference

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Abstract: Mast seeding is hypothesized to satiate seed predators with heavy production and reduce populations with crop failure, thereby increasing seed survival. Preference for red or white oak acorns could influence recruitment among oak species. We tested the predator satiation hypothesis, acorn preference, and predator size by concurrently measuring acorn production, mouse abundance, and white versus red oak acorn removal rates in exclosures allowing access by mice (HW), squirrels and smaller-sized vertebrates (WW), or all-sized vertebrates (C) for 12 years. Annual removal rate varied, but virtually all acorns were eventually removed from all exclosure types all years except one. Acorns were removed more slowly from HW than from WW or C exclosures, indicating that large vertebrates were not major acorn consumers, locally. Red and white oak acorn removal rates were similar except in two years, when red oak acorns were removed more rapidly. Removal slowed with increasing acorn crops, suggesting that heavy crops can "swamp" predators. Removal rate was negatively correlated with crop size the previous fall. A positive trend between mouse abundance and crop size the previous fall was evident; abundance decreased sharply the year following crop failures but not after moderate or heavy crops, suggesting that poor crops can dampen acorn predation the following year.

Key words: acorn, acorn predator, acorn preference, mast seeding, masting, oak, predator satiation, rodent populations.

Résumé : On croit que la production massive de semences rassasie les prédateurs de graines mais qu'une faible production réduit leurs populations et augmente ainsi la survie des graines. La préférence pour les glands de chêne rouge ou de chêne blanc pourrait influencer le recrutement parmi les espèces de chênes. Nous avons testé l'hypothèse du rassasiement des prédateurs, la préférence des glands et la taille des prédateurs en mesurant en même temps la production de glands, l'abondance des souris et le taux de disparition des glands de chêne rouge et de chêne blanc à l'intérieur d'exclos accessibles aux souris (HW), aux écureuils et aux plus petits animaux (WW) ou aux vertébrés de toute taille (C) pendant 12 ans. Le taux annuel de disparition variait mais pratiquement tous les glands ont éventuellement disparu dans tous les types d'exclos et à tous les ans à l'exception d'une année. Les glands disparaissaient plus lentement dans les exclos HW que WW ou C, indiquant que les grands vertébrés n'étaient pas localement de gros consommateurs de glands. Les taux de disparition des glands de chêne rouge et de chêne blanc étaient semblables à l'exception de deux années, alors que les glands de chêne rouge ont disparu plus rapidement. La disparition ralentissait avec l'augmentation de la production de glands, ce qui indique que les récoltes abondantes peuvent submerger les prédateurs. Le taux de disparition était négativement corrélé au volume de la récolte de l'automne précédent. Il y avait une tendance positive évidente entre l'abondance des souris et le volume de la récolte de l'automne précédent; l'abondance diminuait brusquement l'année qui suivait une faible récolte mais pas à la suite d'une récolte modérée ou abondante, ce qui indique que les faibles récoltes peuvent diminuer la prédation des glands l'année suivante. [Traduit par la Rédaction]

Mots-clés : gland, prédateur de glands, préférence pour une espèce de glands, production massive de graines, paisson, chêne, rassasiement des prédateurs, populations de rongeurs.

Introduction

Acorns function as a keystone resource in mixed oak *Quercus* spp. forests by influencing rodent populations (Wolff 1996) that, in turn, serve as prey for carnivorous raptors, mammals, and snakes. Increased rodent and raptor densities may drive songbird populations through increased nest predation (Ostfeld and Keesing 2000; Clotfelter et al. 2007). Rodents may also influence the prevalence of Lyme disease in their role as a vector (Jones et al. 1998) and influence the intensity of gypsy moth *Lymantria dispar* (Linnaeus, 1758) outbreaks by consuming their pupae (Elkinton et al. 1996). Acorn production also affects deer *Odocoileus virginianus* (Zimmermann, 1780) populations that, in turn, have major impacts on forest structure and regeneration through browsing (Tilghman 1989).

Successful oak reproduction requires adequate seed production and subsequent survival of seeds and seedlings (Loftis and McGee 1993). Oaks exhibit wide fluctuations in acorn production among years, locations, species, and individuals (Downs and McQuilkin 1944; Christisen and Korschgen 1955; Sharp and Sprague 1967; Goodrum et al. 1971; Beck 1977; Feret et al. 1982; Sork et al. 1993; Koenig et al. 1994). Episodic, synchronous production or failure to produce acorns (masting) by intraspecific sympatric oaks occurs at irregular intervals, although asynchronous production with moderate crop yields is also common (Rose et al. 2012). Acorn predation by vertebrates or insects frequently destroys up to 90% of acorns, often resulting in substantially reduced oak regeneration (Marquis et al. 1976;

Galford et al. 1991; Crawley and Long 1995; Espelta et al. 2009) and potentially altering the composition of forests over time.

The "predator satiation hypothesis" states that masting by oaks (or other species) allows a higher proportion of acorns to escape predation by satiating acorn predators with an over-abundance during mast years and by reducing predator populations during non-mast years so that more acorns escape predation the following year (Janzen 1971; Silvertown 1980; Kelly and Sork 2002). Several studies have found relatively lower rates of acorn disappearance where mast production was high and higher rates where mast production was low (Burns et al. 1954; Christisen and Korschgen 1955; Dunkeson 1955; Goodrum et al. 1971; Marquis et al. 1976). Wolff (1996) reported that white-footed mouse *Peromyscus leucopus* (Rafinesque, 1818) or deer mouse *Peromyscus maniculatus* (Wagner, 1845) acorn stores were depleted by January in most years but lasted throughout winter during years of high acorn production. The proportion of acorns infested by insect larvae also decreases in high-yield mast years (Downs and McQuilkin 1944; Beck 1977; Crawley and Long 1995). Others report rapid removal rates of acorns by acorn predators, regardless of crop yield (French 1985; McShea and Schwede 1993). Downs and McQuilkin (1944) found that many acorns survive in good crop years if deer populations are low, but most acorns are eaten when deer populations are high, regardless of crop size. Acorn survival and the likelihood of successful oak recruitment appear to be an interplay between acorn production, site conditions, and scarcity of both acorn predators and vertebrate herbivores (Crawley and Long 1995).

Several studies show a "lagged" relationship between acorn crop size and populations of acorn predators the subsequent year, likely due to their greater over-winter survival and reproductive rates when food supply is high or vice versa. Wolff (1996) found a strong, positive relationship between acorn production and densities of *Peromyscus* spp. and chipmunks *Tamias striatus* (Linnaeus, 1758) the following year. The red-headed woodpecker *Melanerpes erythrocephalus* (Linnaeus, 1758) (Smith and Scarlett 1987), acorn woodpecker *Melanerpes formicivorus* (Swainson, 1827) (Hannon et al. 1987; Koenig and Mumme 1987), gray squirrel *Sciurus carolinensis* Gmelin, 1788 (Burns et al. 1954; Nixon et al. 1975; Kurzejeski 1989), black bear *Ursus americanus* Pallas, 1780 (Pelton 1989), and European wild hog *Sus scrofa* Linnaeus, 1758 (Matschke 1964) populations are also positively correlated with the previous year's hard mast production.

Predator preference for acorns in the white *Quercus* or red *Lobatae* oak taxonomic sections (henceforth termed white oak and red oak groups, respectively) could differentially influence acorn survival rates and, potentially, recruitment success among oak species (Crawley and Long 1995). Acorns within the two groups differ in lipid content, tannin concentration, and germination characteristics, all cited as possible reasons for preference. Acorns in the red oak group, including black oak *Quercus velutina* Lam., northern red oak *Quercus rubra* L., and scarlet oak *Quercus coccinea* Münchh., among other species, contain high lipid (18%–25%) and tannin (6%–10%) concentrations relative to acorns in the white oak group, including white oak *Quercus alba* L. and chestnut oak *Quercus montana* Willd. (5%–10% and 0.5%–2.5%, respectively) (Smallwood and Peters 1986). Acorns in the red oak group overwinter before germinating the following spring, whereas those in the white oak group germinate immediately after they drop in autumn (Fox 1982). Nutrient stores are rapidly transferred from the acorn to the developing taproot (Fox 1982), and lower tannin levels are associated with higher perishability of red oak acorns. Differences in tannin concentration, lipid content, and perishability have all been suggested to influence acorn preference and whether they are consumed immediately or cached (Smith and Follmer 1972; Short 1976; Lewis 1980, 1982; Smallwood and Peters 1986).

We experimentally tested the predator satiation hypothesis, relative predation pressure by different-sized acorn predators (e.g., mouse, squirrel, or deer sized), and preference for red or white oak acorns by concurrently measuring acorn production, relative abundance of mice, and rates of white and red (scarlet, in this case) oak acorn removal in exclosures with different-sized openings, over a 12-year period. Our experiment was designed to test whether (*i*) vertebrate acorn predators are primarily mice-sized, squirrel-sized, or smaller or deer and other large vertebrates; (*ii*) white or red oak acorns are "preferred" (removed faster) by vertebrate predators; (*iii*) inter-annual variation in acorn removal rate is correlated to prior- or current-year acorn production; (*iv*) relative abundance of mice is correlated with prior-year acorn production.

Methods

Study area

The Bent Creek Experimental Forest (BCEF) encompasses a 2400 ha watershed within the Pisgah National Forest in western North Carolina. Annual precipitation averages 140 cm (Owenby and Ezell 1992), and elevation ranges from 700 m to 1070 m. Winters are short and mild, and summers are long and warm. Oak, including primarily scarlet oak, chestnut oak, black oak, northern red oak, and white oak, compose approximately 47% of mature (≥30.5 cm diameter at breast height (dbh, 1.3 m) trees and 21% of pole-sized (12.7–<30.5 cm dbh) trees within BCEF (Greenberg et al. 2014). Other common tree species include blackgum *Nyssa sylvatica* Marshall, sourwood *Oxydendrum arboreum* (L.) DC., occasional shortleaf pines *Pinus echinata* Mill. on drier sites, and tulip poplar *Liriodendron tulipifera* L. on moist slopes and coves. Red maple *Acer rubrum* L., hickory *Carya* spp., and flowering dogwood *Cornus florida* L. are common throughout.

Vertebrate exclosures and acorn removal

We used a randomized block split-plot design with nine, randomly selected study sites (blocks) located 0.4–4 km apart and three acorn predator exclosure treatments, as follows: (*i*) excluded vertebrates larger than mice, constructed with 0.5 cm × 0.5 cm mesh hardware cloth with ten 2.54 cm² access holes cut at ground level (HW); (*ii*) excluded vertebrates larger than squirrels or jays, constructed with 5 cm × 10 cm mesh hardware cloth (WW); (*iii*) open controls (C) that allowing access by all-sized acorn predators. Three of each exclosure type (HW, WW, and C) were constructed in each study site, for a total of nine exclosures per site, with the following exceptions: one WW in one study site was destroyed during the first study year (1998) and never used; one HW in the same study site was destroyed in 2006 and never repaired; one HW in a different site was destroyed in year 2006 but was repaired for use in 2007. HW, WW, and C were circular, with an area of approximately 0.46 m²; both HW and WW were 0.46 m in height.

Experimental white and scarlet ("red" for the purpose of this article) oak acorns were purchased annually from F.W. Schumacher Co., Inc., to increase likelihood of a consistent acorn supply. Acorns were float-tested by field collectors prior to purchase by the seed company; a subsample was cut to test for soundness and float-tested again by the seed company as needed to assure soundness at time of sale (Don Allen, Schumacher Co., Inc. personal communication). We kept acorns refrigerated after receipt until field deployment (<1 week). Each fall (November – early December) in 1998–2009, an equal number of white and red oak acorns (16 per species most years; rarely 8, 10, or 14 per species, contingent on availability) were marked with a small dot of white or red paint, respectively, and placed on the leaf litter surface within all exclosures and controls. Remaining acorns were counted approximately 2, 6, 14, 30, 62, 126, and 365 days after placement all years, except in the last year (2009), when the last count was 126 days after deployment. "Natural" (nonexperimental) acorns falling into exclosures or controls were removed at each visit. After approxi-

mately 1 year, remaining acorns were discarded and replaced with new, marked experimental acorns for the next annual cycle.

Acorn crop measurement

We measured acorn production in several areas within the BCEF watershed. Trees included in our acorn sampling were from a long-term study of acorn production on 290 individual oak trees of five common species within the BCEF. We randomly selected trees to represent a wide range of size classes (12.7–108.0 cm dbh), elevations (646–1067 m), and topographic features (i.e., aspect, slope position, and percent slope). We measured dbh of all sample trees during winter 2006–2007. Most trees were 80–120 years old and in dominant or codominant (a few were intermediate) crown positions. Species in the red oak group included black oak ($n = 22$), northern red oak ($n = 55$), and scarlet oak ($n = 50$) for a total 127 individual trees; in the white oak group, species included chestnut oak ($n = 84$) and white oak ($n = 79$) for a total 163 individual trees.

During 1997–2010, we collected acorns in circular, 0.46 m² traps placed randomly beneath the tree crowns. The number of traps per tree was approximately proportional to the basal area (2–14 per tree) until 2004, when we standardized to three traps per tree for consistency. The number of acorns produced per tree each year was calculated by multiplying the mean number of acorns per m² of trap area by the estimated crown area for that tree (Rose et al. 2012). Crown area per tree was estimated using existing crown diameter equations for each species based on dbh (Bechtold 2003) and, then, the crown area was calculated using the formula for a circle. Acorns were collected at approximately 2-week intervals from mid-August through the completion of acorn drop in late fall. For the purpose of this study, we counted all well-developed acorns and did not distinguish between insect-damaged and sound acorns or between different acorn sizes. Crop size estimates probably were conservative because trap tallies did not account for acorns removed by squirrels or other arboreal consumers. We used the mean number of acorns per oak tree (all species combined) as our metric of crop size.

We also sampled natural acorn density on the ground within each of the nine exclosure sites, during the same week that marked, experimental acorns were deployed. Acorns were counted in twenty 0.46 m² circular plots that were randomly selected each year, but they were always spaced at least 20 m apart plus a randomly chosen distance. We used the mean number of total acorns (all species combined) per year as our estimate of total ground acorn availability. The mean number of acorns per oak tree (described above) measured at the watershed scale was significantly correlated with acorn density on the ground (study site scale) during the week of experimental acorn deployment (Pearson correlation; $p < 0.001$; $r = 0.94$), indicating that both estimates were analogous metrics of acorn crop size. Thus, we used the mean number of acorns per oak tree (all species combined) per year as our estimate of acorn crop size in all statistical analyses.

Small mammal trapping

We trapped small mammals at four mature forest, closed-canopy sites within BCEF in 1997–2010 (originally selected as part of a different study; Greenberg 2002). Trapping arrays consisted of 30–40 (30–38 in 1998–1999 and 40 each year thereafter) Sherman live traps (7.7 cm × 9.0 cm × 23.3 cm) baited with rolled oats and spaced approximately 10 m apart in a grid. Traps were open for four consecutive nights during summer or early fall (June–October). Traps were checked each morning, and captured rodents were identified, marked using size 1 Monel ear tags (National Band and Tag Co., Newport, KY), and released. Recapture rates were high (mean 97.9%, not including years when no mice were captured) and often included multiple recaptures of the same individuals. Therefore, we used the mean number of first-

Table 1. Results of repeated measures mixed model ANOVA comparing days to 95% acorn removal by exclosure type, acorn species, and year (1998–2009) with replication over nine sites at Bent Creek Experimental Forest, Asheville, North Carolina.

Variable	Degrees of freedom (numerator, denominator)	F	p value
ET	2, 16	16.0	<0.001
Acorn species	1, 538	2.9	0.09
ET × acorn species	2, 538	0.6	0.53
Year	11, 539	25.5	<0.001
ET × year	22, 538	1.1	0.30
Acorn species × year	11, 538	2.8	0.001
ET × acorn species × year	22, 538	0.3	1.00

Note: Days to removal were interpolated based on the time interval between acorn counts. Exclosure types (ET) were as follows: controls, permitting access by all-sized animals; hardware cloth with 2.54 cm holes for access by mouse-sized animals and smaller vertebrates; and welded wire, permitting access by squirrel-sized animals and smaller vertebrates.

captured mice per 100 trapnights (TNs) as an approximation of mouse density within BCEF for use in statistical analyses.

Statistical analyses

We explored using exponential decay models (survival curves), but acorn removal rates were often extremely rapid (complete removal by first or second check, within 2–6 days after experimental acorn placement in exclosures) and thus did not fit an exponential relationship. In other situations, acorns remained throughout the year. Thus, to avoid relying on one or more models that may or may not represent the data accurately, we decided to base the analysis on the empirical data. We used a randomized block split–split plot model with repeated measures (PROC MIXED; SAS 9.4) to test fixed effects including exclosure type, acorn species, year, and their interactions on days to 95% of acorns removed. We could not determine the exact number of days to 95% removal because acorn monitoring was not daily. Therefore, we linearly interpolated the number of days to 95% removal using days since deployment when <5% remaining was first observed and days since deployment on the preceding count date. Because there were three (seldom two) exclosures that served as subsampling per experimental unit, removal days were simply averaged for that observation. If acorn removal never reached 95% within a given year, that observation (days to 95% removal) could not be computed and was thus treated as missing in the ANOVA. Such occasions were rare except in 1998, when >5% of total acorns remained in nearly half of exclosures and controls by year-end. Thus, estimates of removal rates for 1998 are conservative and do not account for observations where >5% of acorns were never taken. Replication was by means of the random factor, nine sites (blocks). Exclosure type was the main plot factor, acorn species was the split-plot factor, and annual cycle was the split–split plot factor. The repeated measures subject factor was the site × exclosure type × acorn species interaction term with a covariance matrix used to account for any possible correlation between the years.

Plotting of the residuals over predicted and inspection of histograms for normality revealed highly kurtotic and skewed distributions. Therefore, we applied a logarithmic transformation to the response variable (days to 95% removal) to satisfy the normality and homogeneity of variance assumptions. Main effects (exclosure, acorn species, and annual cycle) and interactions were considered significant with an overall experimental α of ≤0.05. Least square means were computed for the fixed effects and comparisons performed with Tukey's test.

Differences in removal rates among years were not of particular interest except in how they correlated with current or prior-year crop size or with relative abundance of mice (described below). However, when interactions were present, we performed parti-

Fig. 1. Least square means (back transformed from log scale) (+SE) days to 95% acorn removal by (*a*) exclosure type and (*b*) acorn species each year at Bent Creek Experimental Forest, Asheville, North Carolina, 1998–2009. Exclosure types allowed access by (*i*) mice only (hardware cloth with 2.54 cm access holes), (*ii*) squirrel-sized vertebrates and smaller vertebrates (welded wire), or (*ii*) all-sized vertebrates (control).
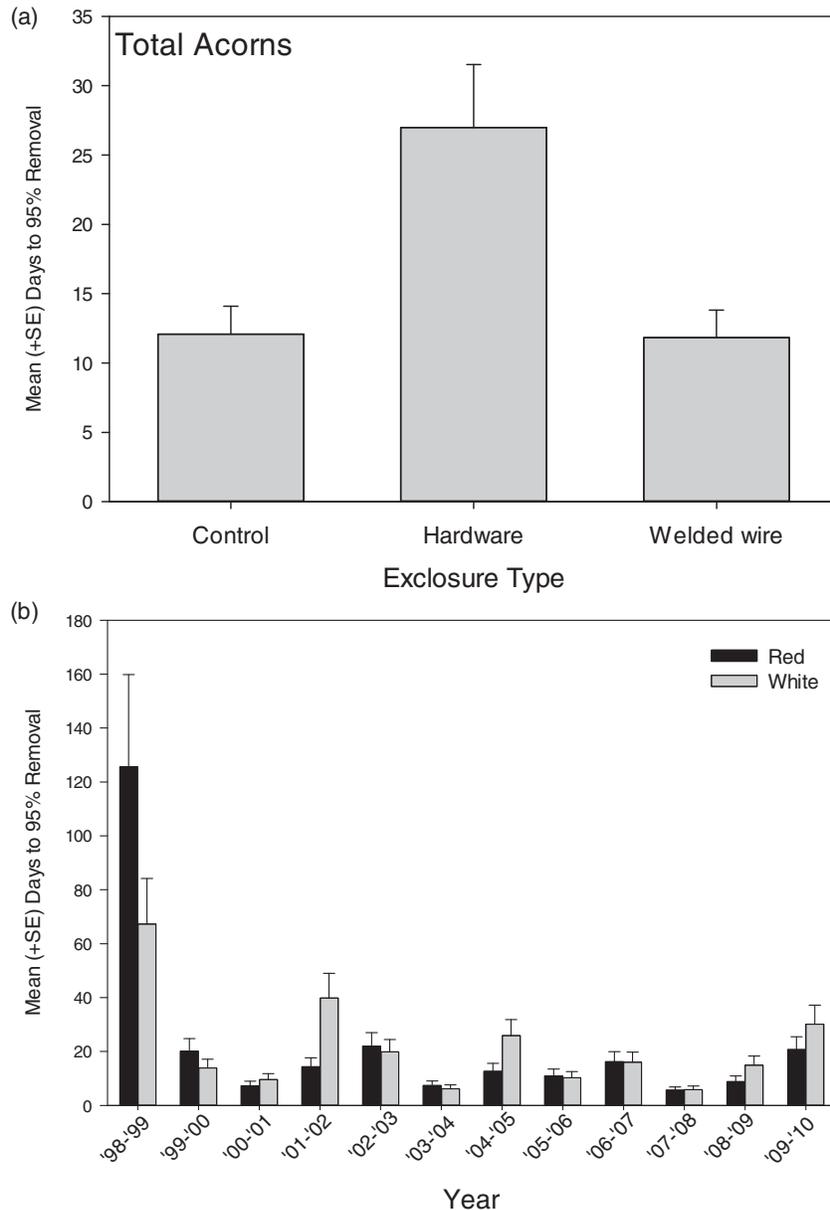
tioned *F* tests (SLICE option in PROC MIXED; SAS 9.4) to examine the significance of treatments within identified years and years within identified treatments. We compared treatment least square means using an adjusted Tukey's test.

We used Kendall's tau rank correlations to test whether annual (*n* = 12 years) days to 95% acorn removal for each of the three exclosure treatments was influenced by (*i*) current- or prior-year (lagged) total acorn crop or (*ii*) relative abundance of mice (first captures per 100 TNs). We also correlated prior-year (lagged) total acorn crop with relative abundance of mice to examine whether mouse populations were influenced by the previous year's acorn crop. Because we were looking for generalized trends, and due to our limited sample size, we used a Type I error rate of 0.10 instead of 0.05, which increased the statistical power and reduced the Type II error rate for significance testing in correlations. Kendall's test was selected over Pearson tests because the response variable (days to 95% removal) did not meet assumptions of normality.

Results

The analysis showed that total acorns were removed more slowly from HW than from C or WW (Table 1; Fig. 1*a*). As there was a significant acorn species × year interaction (Table 1; Fig. 1*b*), their cell means were further analyzed instead of their main effects, using tests of effect slices. Removal rates differed ($p < 0.05$) between acorn species in 2001 and 2004. Partitioned *F* tests indicated that in 2001 and 2004, red oak acorn removal was more rapid than white oak removal. There were also significant slice effects between years within both red and white oak acorn species, but no formal tests were performed because our interest was not in all 66 specific pairwise differences between years. However, the annual trend in removal rates shows that acorn removal rates of both species were substantially slower in 1998, after which annual red oak acorn removal rates were more consistent than white oak acorn removal rates (Fig. 1*b*).

Table 2. Results of Kendall's tau rank correlations of mean acorn crop size (acorns per oak tree) (1998–2009) on mean days to 95% removed, crop size the previous autumn (1997–2008) on mean days to 95% removed, and relative abundance of mice on mean days to 95% removed, by exclosure type, at Bent Creek Experimental Forest, Asheville, North Carolina.

Exclosure type	*p* value	Tau
Mean crop size: mean days to 95% removed		
C	0.07	+0.394
HW	0.10	+0.364
WW	0.10	+0.364
Mean crop size previous autumn: mean days to 95% removed		
C	0.07	−0.394
HW	0.10	−0.364
WW	0.27	−0.242
Mean mice/100TNs: mean days to 95% removed		
C	0.21	−0.277
HW	0.58	−0.123
WW	0.58	−0.123
Mean crop size previous autumn: mean mice/100TNs		
—	0.11	+0.338

Note: Exclosure types were as follows: controls, permitting access by all-sized animals (C); hardware cloth with 2.54 cm holes for access by mouse-sized animals and smaller vertebrates (HW); and welded wire, permitting access by squirrel-sized animals and smaller vertebrates (WW). TNs, trapnights.

Mean (standard error, SE) annual mouse (all *Peromyscus* spp.) abundance ranged from 0.0 (0.0) to 2.5 (1.1) per 100 trapnights; annual acorn crop size (mean number of acorns per oak tree) ranged from 21.7 (6) to 3968 (852) within the study period. Kendall's tau rank correlations indicated a significant ($p < 0.10$) positive relationship between the current-year acorn crop and number of days to 95% removed for all exclosure treatments (Table 2; Fig. 2*a*). Correlations indicated a significant negative relationship between acorn removal rate and acorn crop the previous year for C and HW but not for WW (Table 2; Fig. 2*b*). Relative abundance of mice was not correlated with days to 95% removal for any exclosure type ($p \geq 0.21$; Table 2; Fig. 3). Relative abundance of mice was only marginally ($p = 0.11$; Table 2) correlated with acorn crop size the previous year, although mouse abundance decreased sharply following years of crop failure (Fig. 4).

Discussion

Our results generally supported the predator satiation hypothesis (Janzen 1971; Silvertown 1980; Kelly and Sork 2002); acorn removal was faster during years with low acorn production and decreased with increasing acorn production, suggesting that acorn predators were satiated or "swamped" with an over-abundance of acorns during years of higher acorn abundance. Despite this, we found no relationship between relative abundance of mice and acorn removal rate. Other studies have shown longer persistence of acorns following heavy acorn crops (Christisen and Korschgen 1955; Goodrum et al. 1971; Wolff 1996), suggesting that predator satiation can occur. Crawley and Long (1995) reported that satiation occurred after some, but not all, peak years of acorn production and for some, but not all, acorn predators. We also found a negative relationship between acorn crop size and acorn removal rate the following year, suggesting predation pressure on acorns was reduced the year after poor acorn production.

Despite modest differences in removal rate among most years, removal was virtually complete during all study years except 1998. During our 12-year study, >5% of acorns remained after a year in only 45 of 952 (4.7%) total "patches" (all exclosures and controls). Acorn removal was notably slower in 1998 than all other years, with >5% of acorns remaining in 46.3% of exclosures or controls by the end of the year, compared with 0.0%–2.5% in all other years.

This suggests that acorn escape from predation in abundance may be episodic and infrequent.

We did not record acorn position within exclosures but observed that the occasional acorn escaping predation between counts was often found below the ground surface, having fallen into cracks or crevices in the soil over time. Other studies have found that acorn survival time and the likelihood of seedling recruitment from acorns was higher for buried than surface-placed acorns (Crawley and Long 1995; Pérez-Ramos and Marañón 2008). Acorn predation can also vary among habitats, likely due to differences in cover and acorn concealment, and acorn predator populations (Marquis et al. 1976; Kikuzawa 1988; Crawley and Long 1995; Wei et al. 2000; Kennedy 2005; Pérez-Ramos and Marañón 2008). Both temporal and spatial variations in acorn predation are likely important determinants of acorn survival and spatial patterns of oak reproduction.

We found only a marginally significant ($p = 0.11$) relationship between acorn crop size and the relative abundance of mice the following year, suggesting that acorn crop size is not the sole factor driving mouse populations. Notably, mouse abundance sharply decreased the year following each of the three acorn crop failures in 1997, 2003, and 2007. However, moderate to high crop sizes did not appear to strongly affect mouse abundance the following year. Several other studies corroborate our results, finding little additional impact of heavy mast crops relative to moderate crops on mouse density the following summer (McShea and Rappole 1992; Kellner et al. 2016). Others report a positive, seemingly linear relationship between acorn production and rodent density the following summer (McShea and Rappole 1992; Ostfeld et al. 1996; Wolff 1996). Wolff (1996) reported that surplus acorns resulted in winter breeding of mice (but none in other years) and higher winter survivorship, leading to higher mouse abundance the year following high acorn production. Clotfelter et al. (2007) suggest that acorns, as well as other biotic and abiotic factors, likely influence rodent population dynamics. Our results suggest that acorns are an important food resource for mice, but moderate-sized crops are adequate to maintain relatively stable populations, with no additional effect of heavy crop-sizes.

Effectiveness of predator satiation as an evolutionary strategy by oaks to enhance seed survival by reducing acorn predation (Janzen 1971; Silvertown 1980; Kelly and Sork 2002) would require synchronous acorn production, or nonproduction, by all sympatric oak species. In our study and others (Sork et al. 1993; Liebhold et al. 2004), moderate or heavy acorn production by some oak species often augmented poor production by another species such that acorns were available to acorn predators most years; complete crop failure (all oak species) occurred during three of the 14 years sampled (Rose et al. 2012). Studies reporting similar temporal patterns of seeding fluctuation among sympatric oak species show mediation in part by weather conditions (Sork et al. 1993; Kelly and Sork 2002; Espelta et al. 2008), and drought-induced crop failure may contribute to reduced acorn predation (Espelta et al. 2008). Regardless of whether synchronous, interspecific temporal patterns of acorn production is weather mediated or "strategic", our study provides some evidence that infrequent, complete crop failure may reduce predator populations and slow acorn removal rates the following year, potentially allowing more acorns to survive.

We did not track the fate of acorns after removal and, therefore, cannot address whether they were consumed (destroyed), cached, or scatterhoarded or whether the fate of red and white oak acorns differed. Our results indicate that mice are major consumers or hoarders of acorns; squirrels and squirrel-sized predators such as blue jays (*Cyanocitta cristata* (Linnaeus, 1758)) are also important, whereas large predators such as deer, black bear, and turkey do not substantially contribute to acorn predation within our study area. Acorn removal from HW, accessible only to mice, was much slower (least square means (SE); 27.0 (4.5) days to 95% removal)

Fig. 2. Correlations between (*a*) mean number of acorns per oak tree (crop size) or (*b*) prior-year mean crop size and mean days to 95% acorn removal (based on the interpolated days to 95% removal averaged over the two acorn species and nine sites (*n* = 18 for each mean)) from each of three exclosure types at Bent Creek Experimental Forest, Asheville, North Carolina, 1998–2009. Exclosure types allowed access by (*i*) mice only (hardware cloth with 2.54 cm access holes); (*ii*) squirrel-sized vertebrates, and smaller (welded wire), or (*iii*) all-sized vertebrates (control).
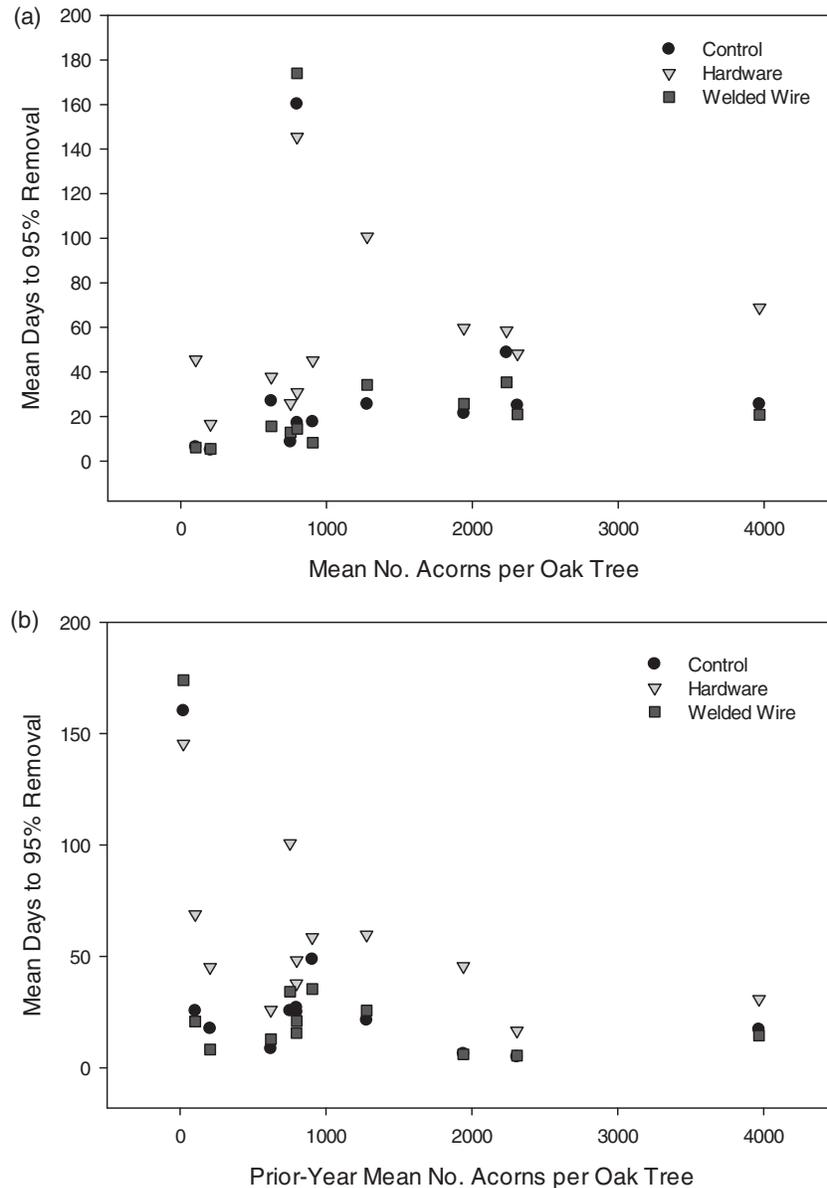
than from WW (11.8 (2.0) days) or C (12.1 (2.0) days); nonetheless, virtually all acorns were eventually removed from all exclosure types nearly every year. We found no difference in acorn removal rate between WW, accessible to squirrel- and jay-sized predators plus mice, and C, accessible to all acorn predators. In contrast, Bellocq et al. (2005) estimated that mice took 33% of northern red oak acorns, whereas squirrels and chipmunks removed 50% of acorns from fall through spring. Crawley and Long (1995) also reported that rabbit exclusion fencing reduced complete acorn removal from 1 to 3–7 days, but all acorns were eventually removed, presumably by birds or rodents. Wei et al. (2000) reported that all acorns deployed on the ground disappeared within 2 days. Kikuzawa (1988) reported that temporal patterns of acorn disappearance differed among years within a mature forest and that the rate of acorn disappearance was related to rodent populations. Avian species such as Corvids are also known to play a major role in acorn predation and dispersal (Pesendorfer et al. 2016). Popula-

tion densities of different acorn predator species and their impact on acorn survival and oak regeneration likely vary among years and locations.

We found little indication of acorn species preference in our study. Overall, both red and white acorns were removed at similar rates (least square means (SE) 14.7 (2.1) and 16.8 (2.4) days to 95% removal, respectively) except in 2001 and 2004, when red oak acorns were removed faster than white oak acorns. Red and white oak acorns were removed at similar rates from HW, albeit more slowly, than from WW or C, indicating that mice, as well as larger vertebrates, utilize both acorn species.

Some studies suggest that rates of consumption versus caching, presumably for later consumption, may differ between red and white oak acorns. Fox (1982) reported that squirrels more frequently selected red oak acorns over ungerminated white oak acorns in trials, and tended to eat white oak acorns but cache red oak acorns. Other studies report that squirrels are more likely to

Fig. 3. Correlations between mean number of mice per 100 trapnights and mean days to 95% acorn removal from each of three exclosure types at Bent Creek Experimental Forest, Asheville, North Carolina, 1998–2009. Exclosure types allowed access by (*i*) mice only (hardware cloth with 2.54 cm access holes); (*ii*) squirrel-sized vertebrates and smaller vertebrates (welded wire), or (*iii*) all-sized vertebrates (control).
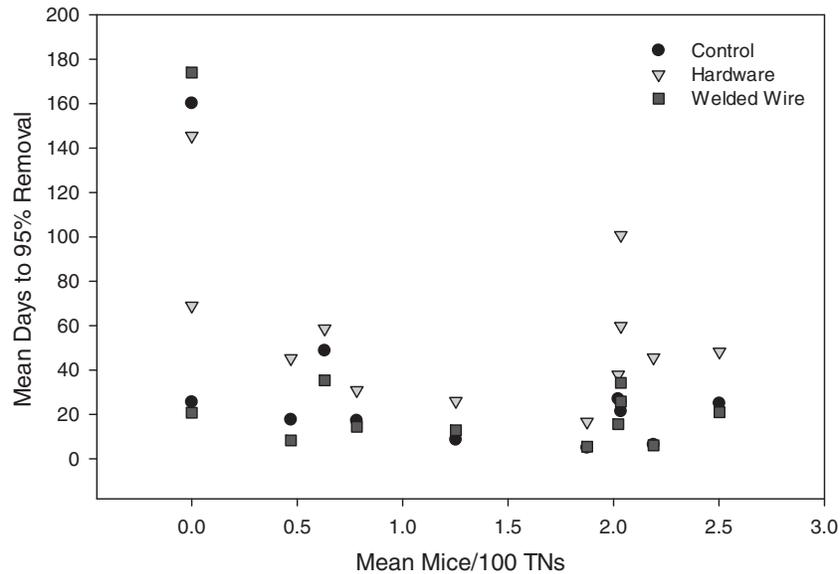
Fig. 4. Mean number of acorns per oak tree (crop size) and mean number of individual mice captured per 100 trapnights (from pre-study 1997 to post-study 2010) at Bent Creek Experimental Forest, Asheville, North Carolina.
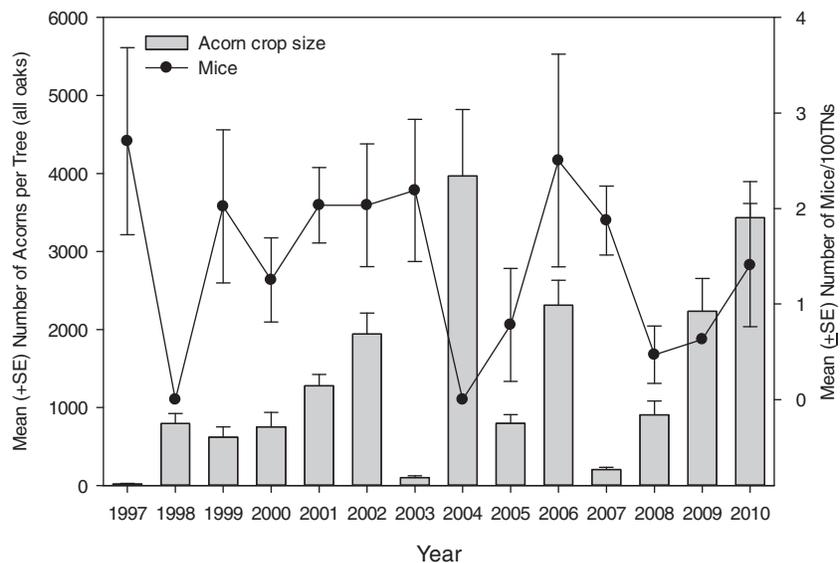
consume the highly perishable white oak acorns but cache less perishable red oak acorns (Hadj-Chikh et al. 1996; Steele et al. 1996). Tannin content is generally higher in red oak than white oak acorns and is associated with perishability, but acorn preference by squirrels appeared to be only indirectly related to tannin content (Hadj-Chikh et al. 1996). Smallwood et al. (2001) found that squirrels consumed high-tannin red oak acorns that were close to germination (red oak acorns germinate in spring, long after dropping from trees in autumn) and lower-tannin white oak acorns (white oak acorns germinate before or immediately after dropping from trees in fall), showing that germination schedule, rather than tannin level influenced their decision to consume or cache acorns, regardless of the species.

Other studies indicate that seed caching, or scatter hoarding by vertebrates such as blue jays, is greater during mast years, increasing the likelihood of seed dispersal and escape from predation (Vander Wall 2002; Pesendorfer et al. 2016). Wolff (1996) reported that sound acorns were found in mouse nest boxes throughout winters of high acorn production, but none were present in nest boxes or on the ground after January in years of low production, indicating that surplus acorns are often cached. In contrast, Sork (1984) found that vertebrate predators consumed >99% of metal-tagged northern red oak acorns during a year when northern red oak acorn production was high, illustrating that acorn predation can be intense. Similarly, Li and Zhang (2003) reported that 51%–74% of tagged acorns were eaten by rodents in situ; most of the other acorns were dispersed and eventually eaten, with only a small proportion of acorns surviving.

We conclude that in situ acorn escape from predators in substantial numbers is rare, despite variable rates of acorn removal among years. Substantial numbers of acorns remained in exclosures after only 1 of 12 years tested. Removal rates were slower

from exclosures allowing access by mice only but did not differ between exclosures allowing access by squirrel-sized predators or smaller-sized predators and open access controls, suggesting that large vertebrates such as deer are not important acorn predators in our study area. We found little evidence of acorn preference, as red and white oak acorns were removed at similar rates all years except two. However, we could not determine if red and white oak acorns were differentially consumed and destroyed or cached with the possibility of survival. Acorn removal rate slowed with increasing acorn crop size, suggestive of predator satiation. We also found a negative relationship between acorn crop size and removal rate the following year and a marginally positive relationship between acorn crop size and relative abundance of mice the following year; however, no relationship was found between mouse abundance and acorn removal rates. Reduced mouse populations were evident after complete acorn crop failures. Moderate acorn crops were produced most years in our study due to acorn production by at least one of five major oak species. We suggest that predator satiation in relation to oak masting may be more evident where fewer oak species occur and crop failure (by all oak species) is more frequent.

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