OAK MAST PRODUCTION AND ANIMAL IMPACTS ON ACORN SURVIVAL IN THE CENTRAL HARDWOODS

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Abstract.—As part of the Hardwood Ecosystem Experiment we measured mast production in white (*Quercus alba*) and black (*Q. velutina*) oak, and quantified the impacts of seed predators on acorn survival over a 3-year period. Specifically, we measured the proportion of acorns of each species infested with weevils (*Curculio* spp.), and the probability of acorn removal by seed predators from a system of semipermeable exclosures. The 3 years of the study included 2 years of high mast production in both species (2006-07) and 1 year of mast crop failure (2008). Across all 3 years, 19 percent of acorns were infested. The rate of weevil infestation was slightly higher for black oak than for white oak in each year, but infestation peaked for both species during the year of mast failure (2008). Overall, 39 percent of acorns in the exclosures were removed by seed predators. The probability of acorn removal was lower when squirrels were excluded, providing support for additive effects of different seed predators. The probability of removal was highest in 2008 during the year of mast failure. In the future, these pre-harvest data will be compared to data obtained following timber harvests conducted in winter 2009.

INTRODUCTION

Oak (*Quercus* L.) is a dominant overstory species group in the Central Hardwoods Region. Oaks have been labeled as both a keystone and "foundation" species in eastern deciduous forests (Ellison et al. 2005, Fralish 2004), performing a wide variety of functions in forest ecosystems. For example, oak-dominated forests promote biodiversity in the herbaceous understory because oak branch structure allows a large amount of sunlight to reach the forest floor (Fralish 2004, Horn 1971). Oaks also are known to provide habitat for many species of insects, fungi, and vertebrates and play an important role in hydrology and nutrient cycling (Brändle and Brandl 2001, Johnson et al. 2002). Among the most important functions of oak in the Central Hardwoods is the production of hard mast, an important food source for at least 44 species of birds, small mammals, and larger vertebrates such as white-tailed deer (*Odocoileus virginianus* Zimmerman) and black bear (*Ursus americanus* Pallus) (McShea et al. 2007). The importance of oak as a source of hard mast has greatly increased in the past century due to the decline of American chestnut (*Castanea dentata* [Marsh.] Borkh.) (Dalgleish and Swihart [in press], Diamond et al. 2000, McShea et al. 2007).

Oaks generally are shade-intolerant species, requiring disturbance to regenerate effectively (Larsen and Johnson 1998). An active cycle of natural and/or anthropogenic fire disturbance is thought to have promoted oak dominance in the Central Hardwoods before European settlement (Abrams 1992). Following settlement, cycles of land clearing for agriculture and subsequent abandonment maintained oak presence in

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the overstory (Fralish 1997). However, the advent of fire suppression and the creation of protected national and state parks in the 20th century have greatly reduced the frequency of disturbance in eastern forests (Abrams 1992, 2003). The result has been regeneration failure of oaks across the Central Hardwoods Region, as well as shifts in species assemblages within the oak genus (Abrams 2003, Aldrich et al. 2005). This altered disturbance regime favors the establishment of shade-tolerant climax species such as maple (*Acer* L.) and American beech (*Fagus grandifolia* Ehrh.) (Fralish 2003).

Loss of oak as a canopy dominant would have important ecological and economic impacts (Johnson et al. 2002, McShea et al. 2007). As a result, researchers have begun to develop forest management (i.e., timber harvest) strategies to promote oak regeneration (Dey and Parker 1996, Dey et al. 2008, Loftis 1990). Examples of management include even-aged methods (clearcuts and shelterwood harvests) and uneven-aged methods (group-selection or single-tree selection harvests). Management efforts have met with mixed success; ecological variables such as soil quality and moisture likely play a role in the outcome (Dey et al. 2009). Oak regeneration success is also heavily influenced by animals, including acorn weevils, small mammal seed predators, and deer (Marquis et al. 1976).

Weevils (*Curculio* L.) infest the acorns of all oak species in the Central Hardwoods. In a given year, as many as 50-90 percent of all acorns produced may be infested (Gribko 1995, Lombardo and McCarthy 2008, Marquis et al. 1976, Riccardi et al. 2004). Infested acorns are both less likely to be dispersed (Steele et al. 1996) and less likely to germinate successfully (Andersson 1992, Lombardo and McCarthy 2009). The interaction of oaks with small mammal seed predators is more complex. A large percentage of fallen acorns are eventually removed by seed predators such as white-tailed deer, gray squirrels (*Sciurus carolinensis* Gmelin), eastern chipmunks (*Tamius striatus* L.) and mice (*Peromyscus* Gloger) (McShea 2000, McShea et al. 2007). However, some seed predators (e.g., *S. carolinensis*) make many small caches of acorns, which may promote germination success (Barnett 1977, Smallwood et al. 2001, Steele et al. 2006).

Regardless of animals' influence on oak regeneration success, little is known about the impact of timber harvest strategies on oak mast production and subsequent predation by insects and small mammals. The Hardwood Ecosystem Experiment (HEE), a long-term replicated study in Indiana of forest ecosystem responses to timber harvest, provides an excellent experimental framework to address this knowledge gap. Our objectives in this study were to compare mast production by black (*Q. velutina* Lamb.) and white (*Q. alba* L.) oaks at several sites in southern Indiana over a 3-year period, and subsequently to assess the impacts of acorn weevils and seed predators on the acorn crop. Following the final year of this preliminary study, the experimental sites were harvested under several different management strategies with the goal of improving oak regeneration. Ultimately, our results will serve as a baseline for identifying changes in mast production and seed predation by weevils and small mammals following the silvicultural treatments.

Prior to the application of silvicultural treatments, we tested several hypotheses. We expected that acorn production would vary among the 3 years of the study, and that production would be different between the two oak species. Oaks are a masting species group, synchronizing with other trees in a region to produce very large or very small mast crops (Janzen 1971), but often lacking interspecific synchrony (Abrahamson and Layne 2003, Lombardo and McCarthy 2008, Lusk et al. 2007). We also expected that black and white oaks may be affected differently by acorn weevils; Lombardo and McCarthy (2008) found that a higher proportion of acorns in the red oak section (Lobatae) were infested than those in the white oak section (Quercus), but few studies have compared infestation levels between oak species.

To address the impacts of predators on the fate of fallen seeds, we sought to isolate the individual contributions of several acorn predators on the total amount of removals observed, in order to assess if those contributions were additive or compensatory. We expected that gray squirrels would be most prolific at removing fallen acorns (Bellocq et al. 2005). In addition, we expected that less desirable acorns (i.e., acorns that were broken, germinated, or infested with weevils) would be less likely to be taken by small mammals (Smallwood et al. 2001, Steele et al. 1996).

STUDY AREA AND DESIGN

A summary of site characteristics and the selection of research areas can be found in a previous chapter of this report (Kalb and Mycroft, this publication). Following the delineation of the research core areas, we selected mature black and white oak trees to be included in the study. We chose this pair of oak species because they are among the most dominant tree species in the region (Jenkins and Parker 1998), and to ensure that both oak sections were represented. Individual trees of reproductive age were chosen based on their location relative to future harvests.

The number and location of selected trees depended on the assigned management treatment of the unit. In each of the three control units, six trees of each species were selected, with two near the center of the research core and four >100 m away near the core edge. In the three units assigned uneven-aged management, six trees of each species were selected, with all trees adjacent to (but outside) the proposed 0.40-, 1.21-, and 2.02-ha patch cuts. In the even-aged units, the arrangement of trees differed between harvest types. Each even-aged unit contained four trees of each species associated with shelterwood harvests; half were adjacent to the future shelterwoods and half were selected as overstory trees within the shelterwoods to be retained during the harvest. Each even-aged unit also contained two trees of each species located adjacent to clearcut areas.

Across all experimental units, 108 trees were sampled in 2006, divided evenly among the three harvest treatments. In 2007, an additional experimental unit was added in Brown County State Park; four additional control trees were selected in this unit for a total of 112 trees sampled. Due to active timber harvesting in uneven- and even-aged units in the fall of 2008, 20 trees could not be sampled, yielding a sample size of 96 in the third year of the experiment. Overall, black and white oaks had diameters at breast height (d.b.h.) of 20.0±4.4 cm (mean ± standard deviation) and 19.5±4.5 cm, respectively.

MATERIALS AND METHODS

Mast Production

At each tree, two mast collection traps were established. Traps consisted of a 52cm × 33cm × 32cm plastic bin mounted atop a 2-m high polyvinyl chloride pipe driven into the ground. Bins were covered with chicken wire to prevent pilferage of seeds by animals while still allowing mast to fall into the trap. Traps were placed midway between the trunk and canopy edge underneath a limb. For trees adjacent to proposed harvest areas, one mast trap was placed on the side of the tree facing the harvest and one on the opposite side. For all other trees, one mast trap was oriented to the north of the trunk and the other to the south.

In the first year of the study (2006), traps were set up in October and checked five times at weekly intervals until the beginning of December. In 2007 and 2008, traps were set up in late August and checked eight times at 1- to 2-week intervals until December. Some traps were not sampled in uneven-aged units in 2008 due to ongoing timber harvests in the area. At each trap check, all acorns in the collection buckets were counted, identified to species, and removed.

Weevil Infestation

The majority of acorns removed from mast collection bins were examined for weevil infestation. In 2007 and 2008, a small number of additional acorns

were removed from the forest floor underneath the mast trees to increase the sample size. Acorns were X-rayed to identify damage caused by weevils (Dixon et al. 1997, Lombardo and McCarthy 2009). Acorns were marked according to source tree and collection date and X-rayed in groups of 50 using a Specimen Radiography X-ray System (Faxitron X-ray Corporation, Lincolnshire, IL). Weevil damage is indicated on the X-ray film by characteristic dark patterns within the acorn (Fig. 1; see Lombardo and McCarthy 2009: Fig. 1). We classified an acorn as infested if any portion of the acorn interior exhibited weevil damage.

Acorn Removal

A set of four semipermeable exclosures was established underneath each mast tree to assess the impacts of several groups of acorn predators. In the study forests, acorn predators include white-tailed deer, gray squirrels (and a few fox squirrels, *S. niger* L.), eastern chipmunks, and white-footed mice (*P. leucopus*). Each exclosure was a 0.75m × 0.75m square. The first exclosure allowed access to all wildlife species (deer, squirrels, chipmunks, and mice or D+S+C+M) and simply consisted of four wooden stakes designating a 0.75m × 0.75m area on the ground. The second excluded deer only (allowing access to S+C+M) and consisted of four wooden stakes covered on the sides and top by 3.8-cm wide hexagonally meshed chicken wire. The wire began 15 cm above the ground to allow access to squirrels and smaller wildlife. The third exclosure excluded squirrels and larger wildlife but allowed access to mice and chipmunks (C+M) and was a 0.75m × 0.75m × 0.2m wooden frame covered in 3.8-cm chicken wire. The final control exclosure was designed to prevent access by all vertebrate wildlife (A) and was a wooden frame of the same size but covered instead with 0.6-cm mesh hardware cloth.

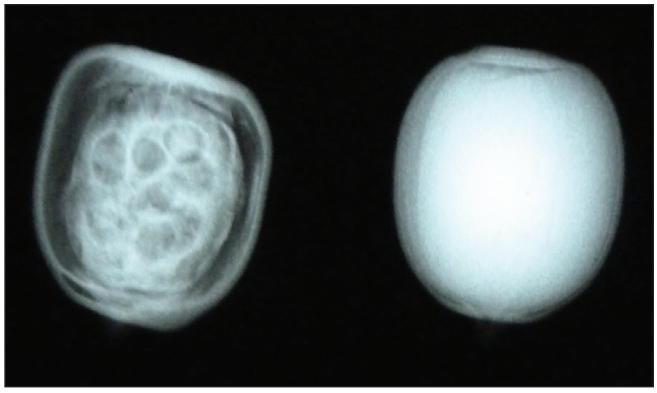

Figure 1.—X-ray of two black oak acorns; the acorn on the left is infested with weevil larvae and the acorn on the right is sound.

The four exclosures were arranged randomly on a north-to-south transect bisecting the trunk of the mast study tree. Two exclosures were placed to the north of the tree and two to the south. On each sampling occasion, acorns that had fallen into each exclosure were located and numbered with a black marker. It was impossible for acorns to fall naturally into the control exclosures, so the A exclosures were provisioned with a number of acorns equal to the average number inside the other three. On subsequent visits, the presence or absence of the marked acorns was determined. If an acorn was present, information about the acorn including the presence of weevil exit holes, germination status, and integrity of the acorn (broken or intact) was recorded.

ANALYSIS

Mast Production

The total number (count) of acorns collected at a given tree during a given sampling occasion was the response variable in this analysis. Overdispersion of these count data, with a variance ~5 times greater than the mean value, prevented analysis with simple Poisson regression. Instead, we fit a Poisson-lognormal model (Kéry 2010) which introduced an additional free parameter to allow the variance of the distribution to differ from the mean. Briefly, we modeled $C_{i,j,k}$, the observed acorn count at tree i during sampling period j of year k as $C_{i,j,k} \sim \text{Poisson}(\lambda_{i,j,k})$. The linear predictor for the Poisson intensity parameter λ was $\lambda_{i,j,k} = exp(\beta_q X_{q,ijk} + \varepsilon_{i,j,k})$ where β is a vector of slope parameters, X is a matrix of q covariate values,

and ε is distributed N(0, σ^2), to allow the variance to vary independently from λ. We included covariates for tree species, d.b.h., the length and date of sampling periods (in Julian day format), and proposed treatment in the linear predictor. In addition to the random error ε, we considered tree and year to be random effects.

Weevil Infestation

We estimated the effects of acorn-specific covariates on the infestation status z_i of individual collected acorns. Infestation z_i was modeled as $z_i \mid p_i \sim$ Bernoulli(p_i), where logit(p_i) is a linear function of covariates. The linear predictor included year, Julian day of sampling, Julian day of sampling centered squared, proposed management technique for the source site of acorn *i*, species of acorn *i* as fixed effects, and source tree as a random effect.

Acorn Removal

We related site- and acorn-specific covariates to the probability $\Phi_{i,j,k}$ that acorn *i* would be removed between sampling occasions *j-1* and *j* in year *k*. The presence $z_{i,j,k}$ of a given acorn *i* in an exclosure at sampling occasion *j* in year *k* took on a value of 0 or 1 and was modeled conditional on the acorn's state at the previous sampling occasion $z_{i,j-1,k}$ and probability of removal $\Phi_{i,j,k}$; that is, $z_{i,j,k} \mid z_{i,j-1,k}, \Phi_{i,j,k} \sim$ Bernoulli($\Phi_{i,j,k}$). Logit($_{\Phi i,j,k}$) was set equal to a linear predictor containing acorn- and site-specific covariates. Explanatory variables considered in this analysis were the fixed effects of Julian day of sampling for occasion *j*, Julian day of sampling centered squared, exclosure type for acorn *i*, proposed management treatment for acorn *i*, and the germination, weevil infestation, and shell status (i.e., broken or intact) of acorn *i* at time *j-1*. Length of time between sampling periods *j-1* and *j* was considered as a nuisance variable, and source tree and year were included as random effects.

Model Fitting

All regression models were fit in a Bayesian framework with non-informative priors. Slope parameters were assigned a normal prior distribution with mean 0 and variance 1,000, and variance parameters were assigned a lognormal distribution with mean 0 and variance 1 following Kéry (2010). All covariates were standardized by subtracting the mean and dividing by the standard deviation. Bayesian analyses were conducted using the software package WinBUGS (version 1.4.3; Cambridge, UK) (Spiegelhalter et al. 1996), which uses the Markov Chain Monte Carlo (MCMC) method to generate posterior distributions for the model parameters. WinBUGS was called from within R 2.10.0 (R Foundation for Statistical Computing, Vienna, Austria) using the R2WinBUGS library (Sturtz et al. 2005).

MCMC simulations were conducted with a minimum of 3 chains, 30,000 iterations, and a burn-in of 10,000 iterations. Convergence was assessed by calculating the Gelman-Rubin diagnostic Rhat (Brooks and Gelman 1998) for each estimate parameter. If we did not observe convergence in the distributions of all posterior parameters (Rhat > 1.1), MCMC chain length and burn-in were increased until convergence was achieved. Posterior predictive checks were performed on each regression model to assess goodness of fit; for the mast production model Pearson's chi-square residuals were compared between the actual data and data simulated based on the model, and for the other two analyses the sums of absolute residuals were compared. Bayesian p-values were calculated for each posterior predictive check. An individual covariate was considered to have an important effect if the 95-percent credible interval of its slope parameter did not contain zero.

RESULTS

Mast Production

We collected 1,140 acorns over the 3 years of the experiment (Table 1). The Poisson-lognormal model had acceptable fit; a posterior predictive check yielded a Bayesian p-value of 0.41 (0.5 is ideal).

Table 1.—Number of trees sampled and acorn sample sizes for the mast production, weevil infestation, and mast removal experiments in 2006-08.

Parameter	2006	2007	2008	Total
Trees sampled	108	112	96	
Total acorns collected in traps	355	670	115	1,140
Black oak (*Q. velutina*)	235	414	9	658
White oak (*Q. alba*)	120	256	106	482
Total acorns x-rayed for weevils	366	595	114	1,075
Black oak	265	423	8	696
White oak	101	172	106	379
Total acorns monitored for removal	1,041	1,827	240	3,108
Black oak	468	1,013	30	1,511
White oak	573	814	210	1,597

In general, white oaks produced fewer acorns than black oaks in our study area (Fig. 2), except in 2008, when there was a mast failure in black oak. The 95-percent credible interval for the species coefficient in the Poisson regression included zero (Table 2). However, 74 percent of the posterior distribution of the species coefficient was below zero, providing marginal support for lower production by white oak. Production by individual trees was positively correlated with d.b.h.; larger trees produced more acorns. Counts were negatively correlated with both Julian day of sampling and Julian day squared, indicating that production was highest early in the sampling period (September-October), declining later in the season. Proposed harvest treatment had no effect on acorn production among the trees we sampled.

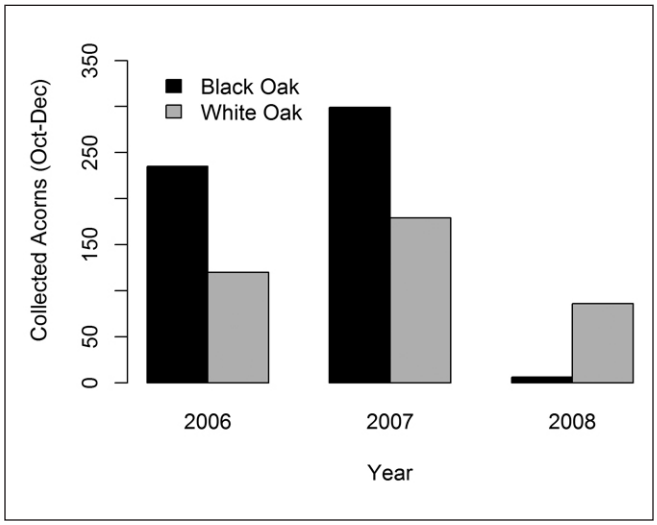

Figure 2.—Total acorns collected by species and year. Since sampling began in October 2006, only acorns collected in the months of October through December are included to allow direct comparisons between years.

Table 2.—Estimated parameter values for the Poisson-lognormal model of oak mast production. The value *f* represents the proportion of the posterior distribution for the parameter which has the same sign (positive or negative) as the mean. Parameters with 95-percent credible intervals which do not include zero are marked with an asterisk (*).

Parameter	Covariate type	Mean	SE	*f*
Intercept		-3.21	0.98	1.00
Tree species (WO=1)	indicator	-0.17	0.26	0.74
d.b.h.	continuous	0.33*	0.13	0.99
Sample day (Julian)	continuous	-1.06*	0.12	1.00
Julian day squared	continuous	-1.75*	0.13	1.00
Even-aged treatment effect	indicator	-0.46	0.31	0.93
Uneven-aged treatment effect	indicator	0.12	0.32	0.64

Weevil Infestation

A total of 1,075 acorns were X-rayed to identify weevil infestation (Table 1). The number of X-rayed acorns does not correspond exactly to the number removed from buckets because small numbers of acorns were lost following collection and/or added from the ground beneath the bucket. A posterior predictive check of the logistic regression model fit to the data yielded an acceptable Bayesian p-value of 0.39. Black oak acorns had a higher probability of infestation in all three sample years compared to white oak (Fig. 3, Table 3).

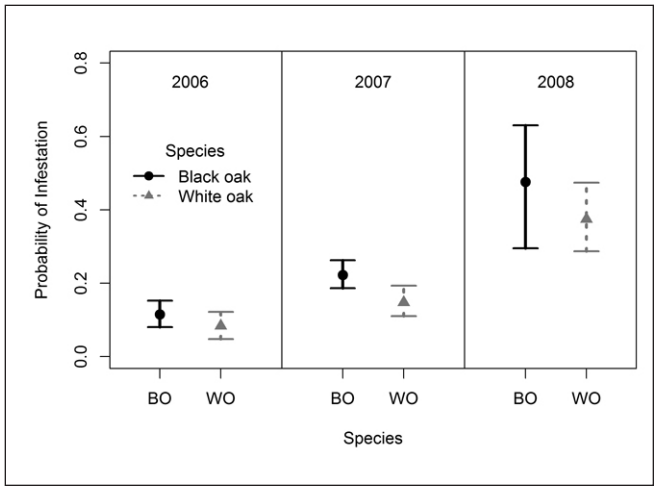

Figure 3.—Posterior distributions for the mean probabilities of acorn infestation, by acorn species and year. Error bars represent 95-percent credible intervals.

Infestation probability increased from 2006 to 2008 (Table 3). The high probabilities of infestation in both species in 2008 (Fig. 3) coincided with low mast production in white oak and a mast failure in black oak in 2008 (Fig. 2). In addition to the year effects, there was a negative correlation between Julian day of sampling and probability of infestation (Table 3); acorns collected later in the fall were less likely to have weevil damage. There were no differences in weevil infestation between areas selected to receive different silvicultural treatments.

Acorn Removal

Over the 3-year study period, 3,108 acorns were marked and monitored for removal (Table 1). Of these, 1,200 (39 percent) were removed from the exclosures at some point: 595 of 1,511 black oak acorns (39 percent) and 605 of 1,597 white oak acorns (38 percent). We used logistic regression to model the probability that an individual acorn was removed during a given time period [*j-1*, *j*]. Our model fit the data adequately, with a posterior predictive check of absolute residuals yielding a Bayesian p-value of 0.38.

There were no differences in the probability of removal between acorn species. However, acorn damage, weevil infestation, and germination were all negatively correlated with the probability of acorn removal (95-percent credible intervals excluding zero; Table 4). There were no differences in probability of removal between proposed treatment areas.

Table 3.—Estimated parameter values for the model of probability of acorn infestation. The value *f* represents the proportion of the posterior distribution for the parameter which has the same sign (positive or negative) as the mean. Parameters with 95-percent credible intervals which do not include zero are marked with an asterisk (*).

Parameter	Covariate type	Mean	SE	*f*
Intercept		-2.02	0.26	1.00
2007 year effect	indicator	0.72*	0.22	1.00
2008 year effect	indicator	1.96*	0.34	1.00
Acorn species (WO=1)	indicator	-0.52*	0.25	0.98
Sample day (Julian)	continuous	-0.18*	0.094	0.98
Julian day squared	continuous	0.015	0.084	0.58
Even-aged treatment effect	indicator	-0.084	0.27	0.62
Uneven-aged treatment effect	indicator	-0.071	0.26	0.62

Table 4.—Estimated parameter values for the model of probability of acorn removal by predators. The value f represents the proportion of the posterior distribution for the parameter which has the same sign (positive or negative) as the mean. Parameters with 95-percent credible intervals which do not include zero are marked with an asterisk (*).

Parameter	Covariate type	Mean	SE	*f*
Intercept		-4.34	0.60	0.99
Date and harvest treatment parameters				
Sample day (Julian)	continuous	0.049	0.055	0.82
Julian day squared	continuous	0.24*	0.065	1.00
Time between samples	continuous	-0.055	0.038	0.92
Even-aged treatment effect	indicator	0.12	0.26	0.67
Uneven-aged treatment effect	indicator	-0.011	0.27	0.52
Acorn characteristics				
Acorn species (WO=1)	indicator	-0.082	0.22	0.66
Acorn integrity (interact=1)	indicator	-0.48*	0.15	1.00
Germination status (germ=1)	indicator	-0.49*	0.15	1.00
Weevil status (infested=1)	indicator	-0.78*	0.21	1.00
Exclosure-type parameters (baseline = completely inaccessible exclosure)				
Squirrel and larger exclosure	indicator	3.39*	0.24	1.00
Deer and larger exclosure	indicator	4.09*	0.24	1.00
Open exclosure	indicator	3.91*	0.24	1.00

Acorns in all three exclosures accessible to at least some vertebrates (open, deer, and squirrel exclosures) had a higher probability of removal than acorns in the control, inaccessible exclosure (Table 4, Fig. 4). Differences between the three accessible exclosure types were more difficult to ascertain. The posterior distributions for the exclosure regression coefficients overlapped (Fig. 5), with the coefficient corresponding to squirrel exclosures having a smaller mean value, corresponding to a lower probability of removal.

In 2007 and 2008, the 95-percent credible interval for removal probability from squirrel exclosures did not overlap with the open or deer exclosures credible intervals, providing further evidence that excluding access to squirrels reduced the probability of acorn removal (Fig. 4). In the same years, probability of removal was higher from the exclosures that excluded only deer. In general, probabilities of removal were higher in 2008, corresponding to reduced mast production (Figs. 2 and 4).

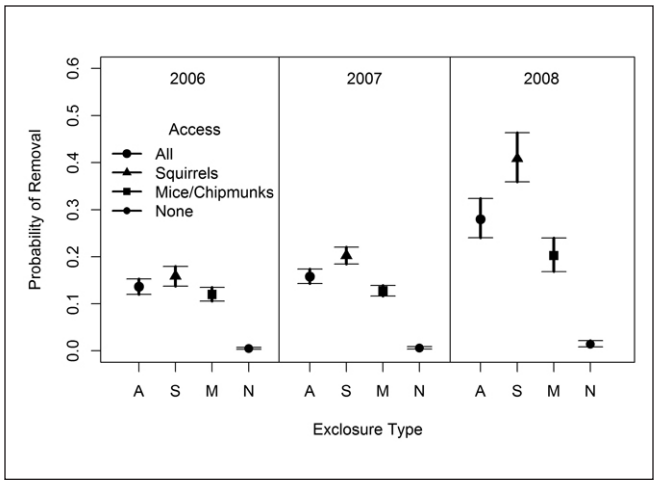

Figure 4.—Mean probabilities of removal from each exclosure type (for an individual sampling period) during the 3 years of the study. Exclosure O was open to all animals, D excluded deer, S excluded everything squirrel-sized and larger, and A (the control) excluded all vertebrates. Error bars represent 95-percent credible intervals.

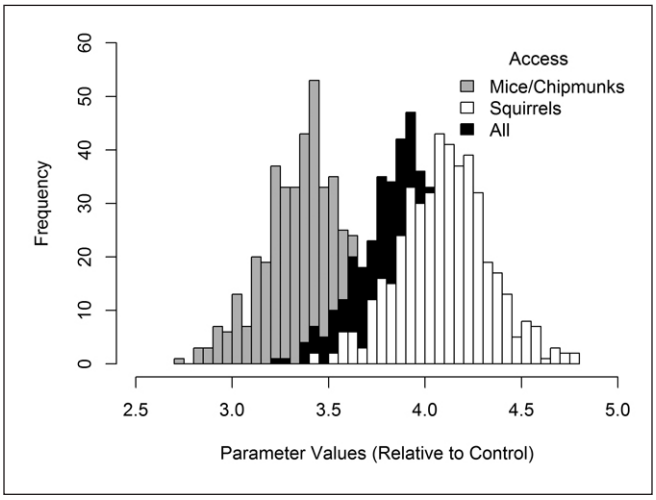

Figure 5.—Comparison of posterior distributions for the three exclosure-type parameters. The three parameter values are relative to removal from a control, i.e., a completely inaccessible exclosure.

DISCUSSION

Mast Production

This 3-year study included 2 years of abundant mast (2006-07) and 1 year of mast failure in black oak and partial mast failure in white oak (2008; Fig. 2). More black oak acorns were collected per sampling occasion (traps × sample periods) in the non-failure years, indicating that individual black oaks in our study region may be more valuable than white oaks for wildlife food production. This result is consistent with other studies that found black oak to generally be a larger producer of acorns than chestnut oak (*Q. prinus*) and white oak (Lombardo and McCarthy 2008, Sork and Bramble 1993, Sork et al. 1993).

Overall, however, our model did not identify a species effect that was statistically different from zero (Table 2). In the short duration of our study, production by black oak appeared to be more variable than white oak (Fig. 2), though the literature suggests it should be a consistent producer (Lombardo and McCarthy 2008, Sork and Bramble 1993, Sork et al. 1993). A longer record of production is necessary to accurately compare variability in production of acorns between these species. In addition, our study did not incorporate population-level information on oaks in the study area; consequently, we cannot make conclusions about the overall importance of the two oak species at our sites.

Though white and black oaks are common at our study sites, it is important to note that the total amount of mast available also depends on other hardwood species (especially chestnut oak, but also Northern red oak, *Q. rubra*, and the hickories, *Carya*). We did not monitor mast production by these species but because there is often a lack of interspecific synchrony in masting (Abrahamson and Layne 2003, Lombardo and McCarthy 2008, Lusk et al. 2007), they may buffer the total mast crop available for wildlife in the study area.

Weevil Infestation

We found higher rates of weevil infestation in black oak than in white oak in each year of the study (Fig. 3), and overall there was a significant species effect for white oak (Table 3)). Our results are consistent with the findings of Lombardo and McCarthy (2008), who found higher rates of infestation in black oak than in chestnut oak (which belongs to the white oak section) in southeastern Ohio. Black oak may be a more consistent mast producer than chestnut oak (Lombardo and McCarthy 2008) and white oak (Sork and Bramble 1993, Sork et al. 1993), which may allow the black oak population to support a larger number of weevils. A limitation of this study is that weevils were not identified to the species level, and different members of the genus *Curculio* appear to specialize on certain oak species (Gibson 1972, 1982). It is possible that the particular assemblage of individual *Curculio* species at our study sites is responsible for higher infestation in black oak. Nearly all acorns were collected from raised buckets, so we do not believe many of the acorns were infested with weevils in the genus *Conotrachelus* (Schonherr), which generally lays eggs in previously infested or broken acorns that have already fallen to the ground (Gibson 1964).

While there were year effects for both 2007 and 2008 (Table 3), infestation rates were highest for both species in 2008 (Fig. 3), corresponding to a mast failure in black oak and a reduced mast year in white oak (Fig. 2) across the study sites. The previous 2 years were good mast years for both white and black oak (Fig. 2), likely resulting in a large population of Curculio larvae undergoing diapause in the soil. When this population emerged from the soil in fall 2008, only a few acorns were available, resulting in very high rates of infestation. Lombardo and McCarthy (2008) identified a similar pattern in chestnut oak in southeastern Ohio. They found 86 percent of chestnut oak acorns were predated by weevils in a non-mast year, but only 26 percent were infested in a mast year. Unlike our study, however, they found black oak to have relatively consistent weevil predation regardless of the quantity of mast produced.

The mean probabilities of black oak acorn infestation that we observed across the 3 years of the study (0.12-0.48 for black oak, and 0.08-0.38 for white oak) were generally lower than in similar studies. For example, Lombardo and McCarthy (2008) reported that on average 79 percent of black oaks were infested over a 4-year period. Riccardi et al. (2004) found that 55 and 34 percent of black oaks were infested, respectively, in the 2 years of their study. The lower numbers we report may be due to differences in the assemblage of acorn weevil species between sites. Differences in host tree and weevil predator densities may also have an impact on weevil populations. For example, Anderson and Folk (1993) found that small mammal predators, especially white-footed mice and short-tailed shrews (*Blarina brevicauda* Say) reduced overwinter survival of acorn weevils in Indiana.

Acorn Removal by Predators

Overall, 39 percent of acorns were eventually removed from the exclosures across the 3 years of the study. Seed predators did not seem to preferentially remove either acorn species, but avoided acorns that were damaged, weevil-infested, or germinated (Table 4). Previous studies have demonstrated that gray squirrels, the primary dispersal agent in our system, are sensitive to acorn condition and are less likely to cache infested acorns (Steele et al. 1996). In addition, because white oak begins to germinate in the fall, squirrels are less likely to cache them for later use than acorns from the red oak section (Smallwood et al. 2001). The most likely explanation for this behavior is that broken, infested, and germinated acorns are more perishable and therefore less valuable to store for the winter months. Infested or broken acorns may still be removed and eaten immediately by the predator (Steele et al. 1996), but in years when mast is plentiful (2006-2007 in this study), predators may ignore less desirable acorns that are not intact. In the year of mast failure (2008), removal probability during a given sample period was very high (Fig. 4), and nearly all fallen acorns were removed by the end of the experiment regardless of their condition. The design of this experiment did not allow us to ascertain the fate of acorns post-removal, so we were unable to identify differences in the ultimate fate of acorns of varying species and conditions.

The system of semipermeable exclosures used in this study allowed us to identify the impacts of several groups of acorn predators on overall removal rates. When deer and turkeys (*Meleagris gallopavo*) were excluded, removal probabilities actually increased in each year (compare exclosures O and D in Figure 4), though differences between the two exclosures were not different from zero (Table 4). Posterior distributions for the slope parameters of the deer and open exclosure indicator variables overlapped almost completely (Fig. 5). Therefore, large animals like deer do not appear to be an important predator of acorns in this system as squirrels and smaller predators completely compensate for their effect when they are excluded. However, any predation by deer is a dead end for acorns, whereas removal by squirrels and other small mammals could result in either consumption or caching and later germination. Bellocq et al. (2005) also observed that removal rates were higher when deer were excluded than when they had access to the acorns, further evidence that deer are not an important

seed predator in our forest system. Increased rates of removal when deer are excluded appear to be counter-intuitive; fewer animals in total have access to the acorns. One possible explanation is that the deer exclosure itself provided shelter from airborne predators, increasing the probability that squirrels and mice would forage inside the exclosure.

We did not observe a statistically significant difference in removal probability when squirrels were excluded (Table 4), but the trend (Fig. 4) indicates that removal probability was reduced; the posterior distributions for the slope parameters corresponding to the deer and squirrel exclosures did not overlap greatly (Fig. 5). Differences in small mammal community composition and demographics (e.g., very high mouse and chipmunk populations) could be the reason we did not observe an additive effect of squirrel predation as strong as the one observed by Bellocq et al. (2005).

Treatment Effects and Predictions

One of the primary objectives of this study was to identify any differences in tree-level mast production and predation between HEE sites prior to applying the silvicultural treatments. In general, we did not observe many differences between trees in areas with different future management treatments. The parameters corresponding to proposed uneven- and even-aged treatment effects on probability of weevil infestation and probability of acorn removal were not statistically different from zero (Tables 3 and 4). Mast production was similar between trees in future control, uneven-, and even-aged management sites (Table 2). However, tree-level mast production was slightly lower at future even-aged sites (95 percent of the posterior distribution for the even-aged treatment parameter was less than zero).

Mast production in oaks can be highly variable from year to year (Sork et al. 1993), so it is possible that observed differences in production between trees are due to the short duration of the study. All sites at the HEE are relatively close together so it is unlikely that weather or site quality is responsible for lower production in trees at future even-aged treatment stands. Unfortunately, we are unable to scale our results up from tree-level to site-level comparisons because we did not account for population-level differences in oak between sites in this study. Still, these results provide a basis for attributing future observed differences in tree-level mast production and predation to silvicultural treatments, rather than to pre-existing site characteristics.

We anticipate that timber harvest with the goal of regenerating oak will increase acorn production. Harvesting at the clearcut and patch cut sites will increase light penetration to oaks on the edge of the cut, which will increase branch density and therefore acorn production (Johnson 1994, Verme 1953). However, these acorns play a minimal role in regeneration inside the clearcut (4.05 ha) and patch cut (0.40, 1.21, and 2.02 ha) harvest sites. In general, the primary dispersal agents in this system (small mammals and the blue jay, *Cyanocitta cristata* L.) do not move acorns deep into recently harvested areas (Nixon et al. 1980). More importantly, any seedlings that do develop from dispersed acorns following harvest will not be competitive without silvicultural intervention (Sander 1972). The primary source of regeneration in the harvested areas will be seedlings of sufficient size (>1.4 m tall) established prior to harvest and stump sprouts (Sander 1972, Sander et al. 1984).

Dominant and codominant oaks are retained in the overstory during the first phase of the shelterwood method for regeneration (Loftis 1990). Removal of the midstory and some competing trees should increase light availability for oaks in the overstory, increasing acorn production (Johnson 1994). Evidence in the literature is inconclusive. Thinning had a positive effect on red oak acorn production in New England (Healy 1997) but had minimal effects on chestnut and black oak production in Ohio (Lombardo and McCarthy 2008). Bellocq et al. (2005) found that production of red oak in Ontario appeared to increase when visual estimates were used, but no differences between treatments were observed in the number of

acorns collected in traps. Responses in production to shelterwood harvests may be species-specific (Lombardo and McCarthy 2008); in addition, any increases in production due to increased light may have begun after the time period following harvest covered by these studies.

Currently, little is known about the effects of harvest treatments on vertebrate and invertebrate acorn predators. Thinning and shelterwood harvests do not appear to change weevil infestation rates (Bellocq et al. 2005, Lombardo and McCarthy 2008). Weevil infestation of acorns produced by trees on the edge of clearcuts and patch cuts is also unlikely to be affected. Predation by small mammals following harvest likely depends on population levels relative to the amount of mast available. Bellocq et al. (2005) found no differences in rates of acorn removal by predators between shelterwoods and control stands, but there were also no treatment effects on the abundance of small mammals. A limitation of this and previous studies is that the ultimate fate of removed acorns was not determined. Future work should focus on identifying differences in seed fate between treatments, since removal could have either a positive (if the acorn is cached and forgotten) or negative (if the acorn is eaten) effect on seedling establishment.

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