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Source: *Florida Scientist*, Vol. 63, No. 1 (Winter, 2000), pp. 1-7

Published by: Florida Academy of Sciences, Inc.

Stable URL: <https://www.jstor.org/stable/24321049>

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Florida Scientist

QUARTERLY JOURNAL OF THE FLORIDA ACADEMY OF SCIENCES

DEAN F. MARTIN, *Editor*

BARBARA B. MARTIN, *Co-Editor*

Volume 63

Winter, 2000

Number 1

Biological Sciences

AN EXPERIMENTAL TEST OF THE PREDATOR SATIATION HYPOTHESIS: AT WHAT LEVEL MIGHT IT APPLY?

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ABSTRACT: *The Predator Satiation Hypothesis posits that synchronous masting of fruits or nuts will maximize the probability of satiating local seed predators, allowing some seeds to escape predation and germinate. Although the hypothesis is usually applied at the population level to explain synchronous reproduction of many individuals, it also might apply at the individual level. In fact, if individual trees were able to satiate local predators, it would reduce selection for synchronous reproduction at the population level. We tested whether individual laurel oaks, *Quercus hemisphaerica*, could satiate their acorn predators. We simulated mast conditions by adding many acorns under the canopies of some trees, while adding few to other, non-mast trees. We then monitored the rate of acorn removal from both mast and non-mast trees. We predicted that non-mast trees would have a higher rate of acorn removal because they would not be able to satiate the major seed predator at our study site, the gray squirrel, *Sciurus carolinensis*. The results did not support our prediction; we found no difference in the removal rate of acorns from mast and non-mast trees. This may be attributable to two characteristics of our study site: the unusually high density of gray squirrels during the year of our study, and the size of *Q. hemisphaerica* trees at the site, which may have been too small to produce enough acorns to satiate such a large number of seed predators. We conclude that the Predator Satiation Hypothesis is most likely to find support at the level of a population, not at the level of individual trees. Predator satiation appears to be a population level phenomenon, with benefits to individual trees.*

ACORNS are a key food source for many animals (Martin et al., 1951; Van Dersal, 1940; Sork et al., 1983; Smith and Scarlett, 1987). Their importance is demonstrated by the management efforts given to acorn crops.

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One such management technique is to eliminate factors that delay germination, thereby ensuring that a seedling will establish before a seed predator consumes the acorn. However, all management techniques are complicated by large variation in acorn crop sizes from one year to the next—a pattern called masting.

Masting occurs in cycles that are species specific (Koenig and Knops, 1995). One reason is that different oak species require different numbers of years for their acorns to mature. This is an important factor in determining the number of years between large and small crops (Koenig and Knops, 1995). During a mast year, all oaks in a population of a particular species produce enormous crops in synchrony. Such populations can consist of individuals as far apart as 2,500 km (Koenig and Knops, 1997). Masting cycles not only have dramatic effects on populations of acorn consumers (Ostfeld et al., 1996; McShea and Schwede, 1993), but also on economically and ecologically important organisms such as gypsy moths, *Lymantria dispar*, and deer mice, *Peromyscus leucopus*, which harbor the tick vector for the bacteria (*Borrelia burgdorferi*) that causes Lyme disease in humans (Jones et al., 1998). When mice are abundant, they suppress outbreaks of gypsy moths. However, abundant mice also increase the risk of Lyme disease (Jones et al., 1998). Understanding such mast-dependent ecological chain reactions is important for predicting and managing forests and for human health. Yet, we do not even understand the evolutionary basis for why some tree species mast in the first place (e.g., Koenig et al., 1994).

Four main hypotheses explain why masting occurs. First, the Resource Matching Hypothesis states that seed crops are determined by resource levels that fluctuate annually, giving rise to the masting patterns observed (Norton and Kelly, 1988). Second, the Seed Dispersal Hypothesis posits that masting patterns are due to competition among trees for a limited number of animals that disperse their seeds (Ims, 1990). Third, the Wind Pollination Hypothesis proposes that wind pollinated trees produce flowers and fruit in synchrony to assure adequate concentration of pollen during a mast year (Nilsson and Wästljung, 1987; Norton and Kelly, 1988). Finally, the Predator Satiation Hypothesis predicts that during mast years, oaks will produce more seeds than can be eaten by local seed predators, so that some escape predation and germinate (Silvertown, 1980). Implied in the Predator Satiation Hypothesis is that seed predators will starve or move elsewhere during non-mast years, when few or no seeds are produced.

This study addresses the Predator Satiation Hypothesis. At issue is the scale at which predator satiation occurs. In particular, to what extent can a single tree satiate its local seed predators? During a non-mast year, we simulated mast conditions for some trees and monitored acorn removal by seed predators beneath these and control (non-mast) trees. If the Predator Satiation Hypothesis holds on the level of an individual, more acorns should be removed from non-mast trees because their predators would not be satiated. This result would demonstrate a selective advantage to masting for individ-

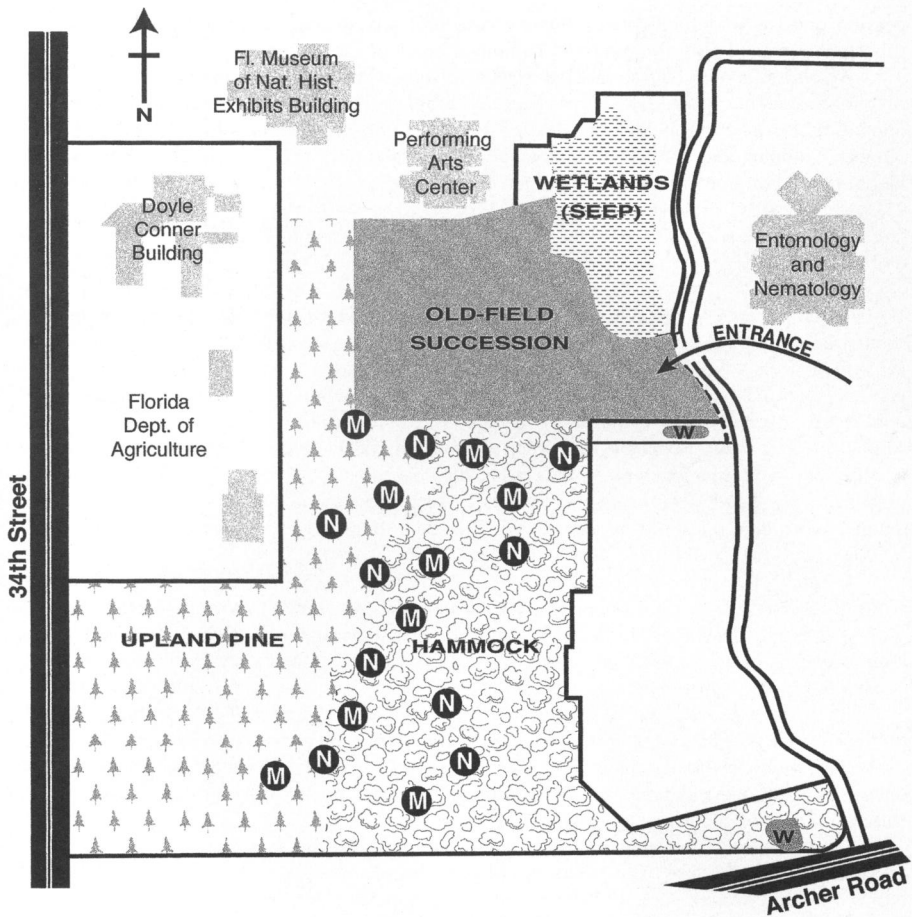


FIG. 1. Map of the Natural Area Teaching Laboratory showing the distribution of mast (M) and non-mast (N) trees within the upland pine and hammock habitats. (Figure adapted from <http://csssivr.entnem.ufl.edu/~walker/natl.htm>.) “W” denotes wetlands.

ual trees and would call into question the Predator Satiation Hypothesis for synchronous mastings at the population level. If, on the other hand, non-mast trees do not have a larger proportion of acorns removed, this would suggest a selective advantage of synchronous mastings at the population level.

METHODS—Study site and species—This experiment was conducted at the Natural Area Teaching Laboratory (NATL) at the University of Florida, Gainesville, Florida. NATL is a 40-acre forest composed of three approximately equal sized habitats: upland pine, hammock, and old-field succession (Figure 1). The upland pine habitat is a well-drained, predominantly sandy-soiled, longleaf pine (*Pinus palustris*) area and is burned every 3 to 5 years. The hardwood hammock is a mesic habitat composed of trees such as oaks and hickories (e.g., *Quercus* spp., *Carya glabra*), along with understory shrubs (e.g., *Vaccinium arboreum*). The old-field suc-

cession consists of loblolly pine (*Pinus taeda*) and mixed hardwoods. The oak trees used in this study spanned only the pine and hammock areas of the forest.

We chose to study laurel oak, *Quercus hemisphaerica*, because it was not masting the year of our study. Thus, we could experimentally simulate mast conditions for some trees, while leaving others as controls. When selecting trees, we chose individuals that did not have overlapping canopies and did not hang over a firebreak or trail. All trees had a diameter breast height (DBH) of greater than 14 cm, which eliminated trees that were not reproductively mature. The average DBH of selected trees was 23.6 cm (SD = 8.0, range = 14.6 to 36.0 cm). Few laurel oaks at the study site were larger than those used, although elsewhere they grow considerably larger.

Experimental design—We randomly assigned 9 of the 18 trees into the mast group, then randomly assigned the remaining 9 trees to the non-mast group (Fig. 1). Mast trees were those for which mast conditions were simulated by placing many acorns under their canopies. In contrast, non-mast trees had few acorns put under their canopies to compare rates of removal between the two treatment groups. All trees of the same group were greater than 50 m apart. This distance was used because our experimental unit was each tree, and manipulation of each tree needed to be independent. In particular, we spaced trees far enough apart that individual gray squirrels, *Sciurus carolinensis*, the major seed predator at NATL, would likely not encounter more than one masting tree. Gray squirrels at our study site have home range sizes of 2,500–10,000 m² (M. Spritzer, 1997).

At other sites, we collected acorns from November 1997 to January 1998. Acorns were still falling from the trees in January, although peak fall was earlier. Acorns were handled with gloves to avoid transfer of human scent, which affects detection of objects by terrestrial mammals (Whelan et al., 1994). All acorns were placed in water and only those that sunk were considered viable. Only viable acorns, approximately 5,850, were used in the experiment.

For mast trees, we placed 600 acorns under the tree's crown. This number reasonably mimics a mast year for the size of laurel oaks we studied (Downs, 1944; Downs and McQuillen, 1944). We monitored daily removal of 50 of these 600 acorns beginning in the early afternoon on the day following completion of experimental set-up. For non-mast trees, only 50 acorns were placed under the tree canopies and all were monitored.

Acorns of mast and non-mast trees were monitored in the same way. To distinguish the 50 acorns under each tree from others and to keep them in place, we drove 3 wooden toothpicks into the ground around each of these acorns. To reduce conspicuousness of the toothpicks, we dyed them dark brown, which generally matched the color of the sticks and leaf litter on the ground. The toothpicks did not protrude above the top of the acorns; they did not appear conspicuous. To easily relocate the acorns, we placed them approximately 31 cm away from the tree trunks in a circular pattern. So that attention would not be drawn to a potential food source whenever a toothpick was spotted, we scattered other dyed toothpicks under the canopy of all trees used in the study.

Trees were paired for data analysis; each mast tree was paired with a non-mast tree, giving a total of nine pairs. Trees were first grouped according to habitat to control for heterogeneity of the forest (i.e. oaks in hammock area were not grouped with oaks in the pine area). After this grouping, trees with similar DBH were paired to control for differences in crop sizes. Acorns were placed under both trees of each pair on the same day.

The experiment was set up on 19 and 20 January, 1998. We monitored acorn removal from 21 to 23 January, 1998. The experiment was terminated on 23 January because all marked acorns had been removed from all trees.

Statistical methods—Data were analyzed non-parametrically with a Wilcoxon matched-pairs signed-rank test because the data (i.e., trees) were paired. Also, the acorns were removed rapidly and completely, yielding a small sample of days and resulting in non-normal distributions of percentages of acorns removed across populations of mast and non-mast trees. Thus, the statistical test we had planned to use, a repeated measures ANOVA, was inappropriate.

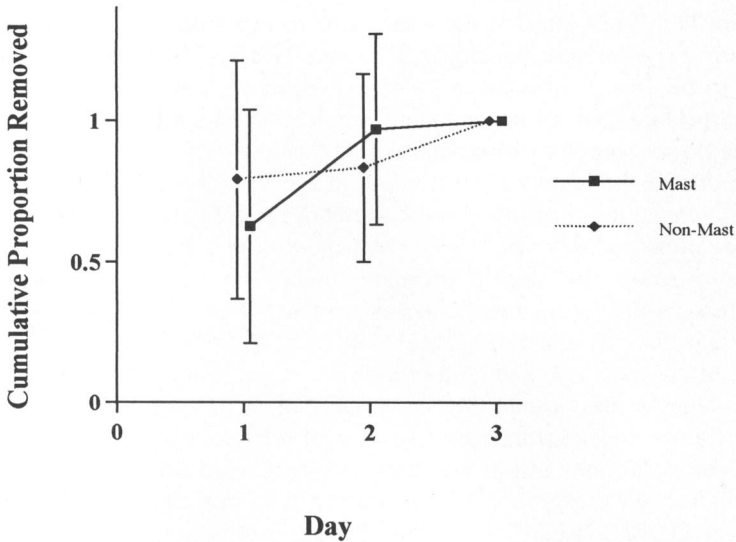


FIG. 2. Cumulative proportions of acorns removed from mast and non-mast trees for the three days data were collected. The vertical bars represent standard deviations. The data points have been off-set for clarity.

RESULTS AND DISCUSSION—On 21 January (day 1) more acorns had been removed from the non-mast trees than from the mast trees (Figure 2). By day 2, the pattern had reversed and more acorns had been removed from mast trees. Most or all acorns likely were eaten by squirrels, as we noticed many broken shells and a colleague (M. Spritzer) saw squirrels foraging near our experimental plots. We could statistically analyze data only for day 1, because by day 2 too many pairs of trees had complete removal and therefore could not be included in the analysis. We found no significant difference in the number of marked acorns removed from mast and non-mast trees ($T = 9$, $N = 7$, $p > 0.05$; test based on seven pairs because two pairs had differences of zero and therefore had to be excluded).

We found no effect of masting on acorn removal at the level of individual trees. Equal removal from mast and non-mast trees on the first day of monitoring, plus complete removal of all acorns by day 3 clearly indicates that single laurel oaks of the size we studied cannot satiate local predator populations when squirrel density is high. Consequently, selection is likely to favor masting at the population level, assuming satiation is feasible at that scale.

A key factor determining whether acorn predators can be satiated was not addressed in our study. In particular, predator satiation depends not only on acorn abundance, but also predator abundance. Generally, in the year following a mast year, acorn predators experience an increase in their population sizes (McShea and Schwede, 1993; Wolff, 1996). Indeed, at our

study site laurel oak mast the year prior to our study and, as a result, the gray squirrel population density was unusually high. Trapping data show the density to be 14 squirrels/ha in 1997 (M. Spritzer, 1997). In this context, it is not surprising that all acorns were quickly consumed.

Rapid and complete removal of 6,000 acorns in 3 days is noteworthy because one of the primary predictions of the Predator Satiation Hypothesis is that synchronous masting should occur in an area that experiences heavy seed predation (Silvertown, 1980). During the next couple of years, laurel oak at our study site should produce few or no acorns and the squirrel population should begin to decline as a result (Kurzejeski, 1989). If acorn predation is low by the next laurel oak mast year (i.e., low seed predator population sizes), some seeds may survive to germinate, thereby providing an advantage to individuals that irregularly mast in synchrony.

Finally, our results raise the question of why relatively small trees mast at all. Even if all oaks at our site had each produced 600 acorns, it is likely that predation on those acorns would have been complete. If, however, our site had been dominated by huge laurel oaks, each producing 10,000 acorns, some acorns would likely have escaped consumption. We suggest that the reason small individuals mast is because the size of an individual oak's neighbors is essentially impossible to predict. By producing even small mast crops, small oaks can take advantage of predator satiation by nearby and much larger individuals, as well as taking advantage of years in which acorn predator populations are low. Indeed, the key to understanding predator satiation in oaks that mast seems to lie in the unpredictability of masting cycles, the crop size of neighboring trees, and the population density of predators.

ACKNOWLEDGMENTS—Financial support for this project was provided by the Ronald E. McNair Postbaccalaureate Program at the University of Florida. Many thanks to Mark Spritzer for his helpful comments and suggestions. Thanks also to Barbara Pepper, Cliff Pepper, and Gayanga Weerasekera for their help in the field, and to Laurie Walz for help with the illustrations.

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Florida Scient. 63(1): 1–7. 2000

Accepted: April 27, 1999.