Evolutionary Drivers, Proximate Mechanisms, and Spatial Synchrony of Acorn Production in Oaks

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ABSTRACT

Masting behavior – the highly variable and synchronized production of seeds by a population of plants – is common among oaks and has dramatic effects on resource dynamics and community structure. Based on the California Acorn Survey, our long-term study of acorn production by California oaks, we summarize the major hypotheses driving this phenomenon along with some of the questions remaining to be answered about masting at both the functional (ultimate) and mechanistic (proximate) levels of analysis. We also discuss one of the key issues regarding the definition of masting, namely what constitutes a population. This latter issue has recently been addressed by quantifying spatial synchrony, the spatial and temporal scale at which acorn production is synchronous. The drivers of spatial synchrony differ dramatically depending on the spatial scale of interest; at the relatively small spatial scale of individual trees a few km apart, the primary drivers for one species we have studied in detail, *Quercus lobata* Née (valley oak) are local environmental factors such as soil nutrients and water availability, whereas at the large spatial scale of several hundred km the drivers of both differences in overall productivity and spatial synchrony are primarily more general environmental factors, specifically weather.

Keywords: California Acorn Survey, economy of scale, masting, Moran effect, pollination efficiency, predator satiation, resource matching

Introduction

Masting or mast-fruiting, the highly variable and synchronized production of seeds by a population of plants, has been recognized for over 250 years (Ellis 1743: "Under these trees, the hogs generally get pork in a maste-year"; cited in the Oxford English Dictionary). It is only much more recently, however, that workers have investigated this enigmatic phenomenon critically and begun to understand both its ecological drivers and evolutionary implications.

One of the earlier evolutionary considerations of mast-fruiting can be found in Stearns (1976), who briefly outlined several hypotheses for mast-fruiting as part of his discussion of life-history adaptations to different kinds of environments. The start of the modern scientific investigation of masting behavior, however, can reasonably be attributed to Silvertown (1980), who was the first to conduct a meta-analysis with the goal of testing the most long-standing and durable evolutionary hypothesis for this phenomenon, the idea that masting behavior increases the survival of seeds by reducing the probability of seed predation (the "predator satiation" hypothesis). Following Silvertown's review, subsequent papers generally focused on the implications of masting behavior for seed dispersal and seedling survival. This changed with the landmark paper by Norton and Kelly (1988), which analyzed variable seed production by the rimu (*Dacrydium cupressinum* Sol. ex G. Forst.), a New Zealand coniferous tree. Norton and Kelly's key contribution was to identify alternative hypotheses for masting behavior and to point out that most involved an "economy of scale" such that occasional larger episodes of reproduction are more efficient than more regular, smaller ones.

Hypotheses involving some economy of scale include not only predator satiation but the possibility that a higher proportion of flowers may be successfully fertilized in mast years (the "pollination efficiency" hypothesis) and the hypothesis that masting occurs following events that portend environmental conditions favorable to seedling establishment (the "environmental prediction" hypothesis). The key feature of all economy of scale hypotheses is that they require more from the plants than simply responding to current conditions; in other words, they are an adaptive response to some ecological factor and thus a product of selection. As such, they require an evolved mechanism on the part of the plant to produce the highly variable patterns of reproduction characteristic of this phenomenon.

The senior author's interest in masting behavior stems from a long-term study, still ongoing, of the acorn woodpecker (*Melanerpes formicivorus* Swainson), a species common in California whose extraordinary social behavior is matched only by its unique habit of individually storing acorns, often by the thousands, in special trees modified by the birds called storage trees or granaries (Photo 1). As part of this study, we noted that almost everything about these birds, from their family-living behavior to their reproductive success, seemed to be dependent on the size of the acorn crop, which varied dramatically from year to year. Oddly, however, there was relatively little information on the factors that drove such variability, and thus we initiated what we now call the California Acorn Survey in autumn of 1980.

The original goal of the California Acorn Survey was to use brief (15 s by each of two observers for a total of 30 s) visual counts of acorns (Koenig et al. 1994a) on marked trees to quantify annual variation in seed production by the various species of oaks at our study site and use the data to gain a greater understanding of the ecological variables