1/ Is pollination the key to understanding oak masting?

Acorns, Acorns Everywhere, But Not in Every Year

Ian Pearse and Walt Koenig
Cornell University Lab of Ornithology
159 Sapsucker Woods
Ithaca, NY 14850, USA
ianspearse@gmail.com

ABSTRACT

Populations of oaks have mast seed production, where the entire population of trees produces either a large or small acorn crop in a given year. The ecological consequences of mast or non-mast years are profound and affect the abundance of everything from deer to insects to Lyme disease pathogens, but the causes of oak masting are poorly understood. We analyzed 30-year dataset of acorn production in *Quercus lobata* Née throughout California. We found a high degree of synchrony of acorn crop among *Q. lobata* trees. Acorn production in a given year showed a strong negative correlation with acorn production in a previous year and a strong positive correlation with weather patterns. Populations with highly synchronized flowering produce more acorns. These factors combined predicted over 60% of the variation in the size of acorn crops in a given year suggesting that acorn crops may be forecast with knowledge of flowering, spring weather, and the production of acorns in the previous year.

Keywords: oak masting, acorn, seed set, Moran effect, pollination

Introduction

It was fall 2006 in Northern California. I had just moved across the country and reentered the university with a budding interest in oaks. On the hunt for valley oak acorns *(Quercus lobata* Née*)*, I purchased an orchard ladder and searched several trees around my girlfriend's cabin near Lodi. None of them had any acorns. I drove 50 mi/80 km to Davis to find a few squirrel-damaged acorns, I continued to Oakland where I found only a handful of acorns within the reach of my ladder, and I decided that I would have to plant something else, as it was just too difficult to find these seemingly rare Californian acorns.

The mysteries of masting

People refer to the "boom or bust" patterns of seed set in populations of plants as "masting" or "masting behavior". How and why plants mast remains an unsolved mystery for ecologists, but there is little doubt of the enormous ecological consequences of masting that reach far beyond the hapless acorn collector. A bad year for acorns results in high death rates and low birthrates of animals that eat acorns such as deer, mice, and many birds (McShea, 2000). In fact, the idea that granivores will not be able to eat all the acorns in a masting year is the main theory for why masting behavior is so important for oak reproduction, on an evolutionary time scale. In low-production years, the decrease in population of these consumers cascades throughout the entire ecosystem often with unexpected consequences for organisms that have little to do with acorns directly. For example, in the oak forests of eastern North America, the prevalence of Lyme disease is linked to oak masting. The ticks that carry Lyme disease feed on deer and mice that feed on acorns (Jones et al., 1998). Equally unexpected, low acorn crops seem to be related to outbreaks of gypsy moths, a common forest pest. In low-acorns years, mouse populations decrease, and fewer gypsy moth pupae get eaten by mice (Elkinton et al., 1996). The relationship between pulsed acorn production and granivory is a bit of a cat and mouse game but it is still unclear how oaks manage to pull it off.

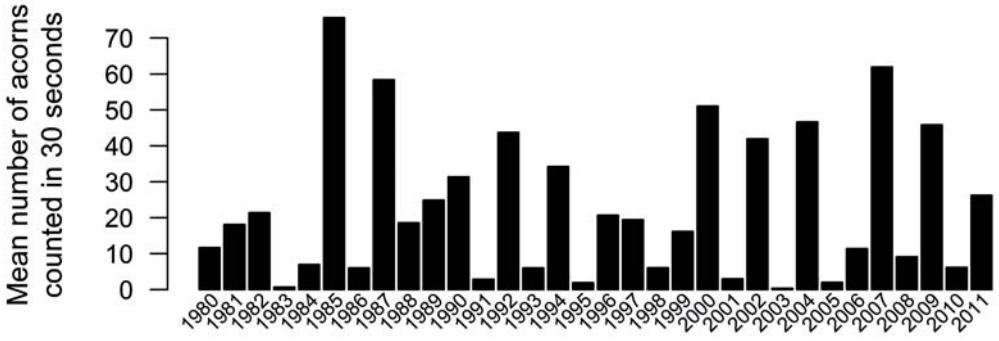

Figure 1/ Valley oak acorns counted at Hastings Reserve over the last 32 years. The crop of acorns varied dramatically between years, and this is indicative of masting.

What is known

From decade-long surveys of acorns (Figure 1), we know three main things about masting in oaks. First, individual trees have extremely variable acorn crops from year to year. This is the boom or bust that characterizes masting. Second, most of the trees within a population or even over a very broad geographic range tend to be synchronized in the size of their acorn crops. So, in 2006, even if I had driven 600 km/372 mi south to Los Angeles to find acorns, I would have likely been equally disappointed. Third, the pattern of acorn production in oaks is not cyclical or periodical. This is to say that oaks do not have a good acorn year every other year or every third year or at any other predictable time interval. So, knowing that 2006 was a bad acorn year and 2007 was a good acorn year, there would have been no way to predict that 2008 was going to be an intermediate acorn year for valley oaks.

The Moran Effect

And herein lies the mystery: there are relatively few ways to imagine entire populations of oaks across thousands of kilometers synchronizing their acorn crop. Research has focused on two main explanations for the synchrony of oak masting. First, it is possible that the synchrony in events is simply driven by some external factor like weather. For example, on February 1, 2011 an above-average number of airline passengers slept in airports from Oklahoma City to Toronto. These individuals did not all independently choose uncomfortable sleeping arrangements at the same time, nor did they decide to do this as a group. They were all simply ticket holders on flights that happened to be delayed because of a large winter storm. This idea, known to ecologists as the Moran Effect, is an appealing explanation for large-scale population trends, as weather patterns tend to be similar over large distances. Because of this, the Moran Effect is the most common hypothesis for explaining oak masting (Koenig et al., 1999). Curiously, though, the years with weather patterns that seem good for acorn production (like years with adequate rain or temperatures) are not necessarily years with high acorn production (Koenig et al., 1996). This suggests that if weather is the driving factor that synchronizes the production of acorns across regions, it is some more subtle side-effect of weather, not simply those years with weather that allows the trees to generally do better. In fact, the one component of weather that correlates very well with the size of the acorn crop in several species is early springtime temperature (Koenig et al., 1999; Perez-Ramos et al., 2010). Early springtime weather may then affect how many female flowers get pollinated.

Synchronization

The second hypothesis is that synchronized events may occur if there is coordination between individuals. For example, at one minute and sixteen seconds into the Russian 2012 Olympic synchronized swimming routine, all of the swimmers emerged feet-first from the swimming pool. Their perfect synchrony was not because each swimmer independently thought that would be a great time to surface, nor was it because of some external event affecting London. It was because those swimmers had coordinated between themselves beforehand. Here, the analogy to oaks is more difficult, as it is hard to imagine oak trees conferring among each other to decide when to set seed. However,

there is at least one major social event in the life of an oak where an individual interacts with others in a population: during sex. Specifically, the receipt of pollen on a female oak flower is dependent upon both the quantity and the timing of pollen production by its neighbors. The possibility that acorn masting may be caused by pollen interactions between trees is so intriguing that it has attracted several mathematicians, who have shown that the local effects of pollen interactions can synchronize acorn production over very broad geographic scales (Satake and Iwasa, 2000; 2002). This is also consistent with patterns of acorn production that we observe in forests.

2/ The phenology (timing) of oak flowering affects the acorn set of oak trees.

Is pollination the key to understanding masting?

Interestingly, both the Moran Effect (weather) hypothesis and the coordination hypothesis suggest that pollination might be the key to understanding oak masting. Historically, researchers have thought that pollination was simply never a problem for oaks, as they are wind pollinated and they tend to produce a lot of pollen. I mean, each spring millions of those little oak pollen grains even try to pollinate my nose!

Researchers have thus assumed that it is the sheer energy that it takes to mature a full crop of acorns that limits their production, not pollination. Recently, however, some workers have found substantial indirect evidence that pollen limitation, a reduction in acorn set based on a lack of pollen receipt by flowers, may actually be important for oaks. First, estimates of the distance that pollen travels vary substantially, and some suggest that most of the pollen from an individual tree may only travel a matter of meters (Sork

et al., 2002), though this is a matter of considerable current debate (Abraham et al.,). Moreover, isolated trees in at least some cases produce correspondingly fewer acorns than trees with many pollen-bearing neighbors (Knapp et al., 2001; Abraham et al., 2011).

Looking at isolation in a different way, it has been found that oak trees that flower at the extremes of the season (either very early or very late) are isolated in time from their neighbor, and they also produce fewer acorns than trees that flower in the middle of spring (Koenig et al., 2012). If trees that are isolated in either space or time depend on very specific conditions to get enough pollen to produce a full acorn crop, this may determine which years are good or bad for acorn crops.

Conclusion

Acorn masting is a conspicuous and important feature of oak forests. The study of masting in oaks is quite a commitment in that it requires counting acorns over many years at many places. Many people are making that commitment, and our understanding of masting behavior is increasing dramatically. It appears that, in particular, large-scale weather events as well as population-level events like pollination are important in determining whether it is a mast year or not. Simultaneously, research is showing that individual trees might suffer from a lack of pollination in some years, further pointing to pollination as an important factor in acorn set. Putting all of this information together allows us to predict acorn production before it happens. So, next year we hope to be able to guess how many acorns will be on your oak trees before they are actually matured!

Photographers. Title page: Ian Pearse (a masting year for *Quercus lobata).* Photos 1-2: Ian Pearse.

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