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Context-dependent post-dispersal predation of acorns in a California oak community

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ABSTRACT

Seed dispersal and predation play important roles in plant life history by contributing to recruitment patterns in the landscape. Mast-seeding – extensive synchronized inter-annual variability in seed production – is known to influence the activity of acorn consumers at source trees, but little is known about its effect on post-dispersal predation. We conducted a planting experiment over three years to investigate the relationship between habitat-level post-dispersal predation and landscape-wide acorn production of three sympatric oak species (*Quercus* spp.). We measured post-dispersal predation in three oak-dominated habitats – savanna (under *Q. lobata*), forest edge (under *Q. agrifolia*), and woodland (under *Q. douglasii*) – as well as in chaparral and open fields. Overall, landscape-level predation was similarly high among study years, averaging 61.4%. Neither species nor mass of planted acorns affected predation. Habitat had a significant effect on post-dispersal predation risk with acorns disappearing most rapidly in chaparral and least rapidly in woodlands. However, a significant interaction between year and habitat ($Z = -4.5$, $P < 0.001$) showed that the hierarchy of predation risk among habitats was inconsistent among years. Using annual acorn census data from local populations of each oak species, we found that predation risk in oak-dominated habitats was significantly and positively related to acorn production of the overstory species ($Z = -9.53$, $P = 0.009$). Our findings add to growing evidence that seed dispersal, predation, and regeneration are context-dependent on annual variation in community-level seed production, and we discuss the potential consequences of these dynamics on oak recruitment and animal behavior.

1. Introduction

Seed dispersal plays an important role in the life history of plants, as it drives geographic distributions of species as well as local recruitment patterns (Levine and Murrell, 2003). Successful dispersal does not guarantee survival, however, since recruitment outcomes depend on the habitat to which seeds are dispersed (Schupp and Fuentes, 1995). Abiotic factors including light, moisture, and soil type and biotic conditions such as facilitation and/or competition from established vegetation at the arrival location dictate the probability of germination, seedling establishment, and subsequent survival to reproductive maturity (Schupp, 1993). Consequently, post-dispersal seed predation poses a considerable barrier to recruitment for many taxa, yet its relationship to arrival habitat can be difficult to predict (Christianini and Galetti, 2007; Hulme, 1994; Vaz Ferreira et al., 2011).

In heterogenous landscapes, the unequal distribution of food resources among habitats influences the habitat associations of potential predators and their propensity to track seed resources (García et al., 2011). Spatial and temporal variation in seed production are known to drive both short-term effects on feeding behavior as well as delayed effects on consumer populations (Bogdziewicz et al., 2016; Curran and Leighton, 2000). Generalist feeding tendencies of many seed consumers predict that these consumer-resource dynamics are subject to the context of resource production at the community level, rather than being influenced solely by the production and dispersal patterns of a single species (Kuang and Chesson, 2009; Lichti et al., 2014; Xiao and Zhang, 2016). Nevertheless, most studies involving seed predation have adopted a narrow perspective of resource-consumer dynamics in considering seed resources from the scope of a single population. In this three-year study, we investigate how arrival habitat affects post-dispersal predation of acorns in a Mediterranean landscape dominated by multiple sympatric oak species with high annual variation in acorn

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production.

For many plant populations, both pre- and post-dispersal seed predation tend to be density-dependent such that areas with clustered seeds attract more predators and increase the probability that a seed is consumed (Beckman et al., 2012; Janzen, 1970). However, for mast-seeding plants that show high interannual variability and synchrony in reproduction, the intensity and frequency of reproduction may have adaptive value for reducing seed predation (Kelly and Sork, 2002; Koenig and Knops, 2000). According to the *predator satiation hypothesis*, predators are overwhelmed by bumper crops in mast years, thus increasing the proportion of seeds that survive (Silvertown, 1980). The extent to which predators are satiated, however, depends on seed availability at a larger scale than a single tree. A nonexclusive alternative, the *predator dispersal hypothesis,* proposes that some predators that hoard seeds in the ground may respond to high seed production by dispersing larger quantities of seeds to more distant caching sites (Pesendorfer et al., 2016b; Zwolak et al., 2016). In communities of multiple mast-seeding plants, however, the activity of seed predators and dispersers is not only affected by seed production of individual plants or populations, but also by the seed production of other sympatric taxa (Lichti et al., 2014; Pesendorfer and Koenig, 2017; Xiao and Zhang, 2016). Despite this reality, few studies have investigated how community-level seed production affects the spatial patterns of post-dispersal predation.

At our study site in central coastal California, woodlands and savannas are dominated by three oak species – valley oak (*Quercus lobata*), coast live oak (*Q. agrifolia*), and blue oak (*Q. douglasii*) – whose acorns are consumed by corvids (California Scrub-Jay *Aphelocoma californica*, Steller's Jay *Cyancitta stelleri*, American Crow *Corvus brachyrhynchos*, Yellow-billed Magpie *Pica nuttalli*), woodpeckers (Acorn Woodpecker *Melanerpes formicivorus*), rodents (ground squirrels *Otospermophilus beecheyi*, deer mice *Peromyscous* spp., wood rats *Neotoma* spp., pocket gophers *Thomomys bottae*), and large mammals such as black-tailed deer (*Odocoileus hemionus columbianus*) and introduced pigs (*Sus scrofa*). California Scrub-Jays are the most important seed hoarders in the system, and they frequently transport acorns up to several kilometers away from source trees and cache them in variety of habitats in the landscape (Pesendorfer and Koenig, 2016).

Previous studies in this system have revealed that the rate and distance of acorn scatter-hoarding varies with species- and community-level seed production of the three oak species (Pesendorfer and Koenig, 2017, 2016). To determine whether post-dispersal predation is similarly context-dependent on seed production in cache arrival locations, we conducted a planting experiment for which we distributed acorns to five habitat types most commonly used by scatter-hoarding jays. Our goal was to test the hypothesis that the relative risk of post-dispersal predation among arrival habitats varies with the population-level seed production of the species below which the acorns are cached. We predicted that there should be high inter-annual variability in acorn predation risk in habitats with oak trees and that there should be higher predation in habitats where the dominant oak species produces abundant acorns in any given season.

As an alternative to landscape- and habitat-level factors, we tested the effects of acorn characteristics on predation risk. We predicted that if acorn characteristics determine predation, large seeds should be more prone to removal by predators, since such seeds provide a higher reward relative to handling time, and that *Q. lobata* acorns should be preferred over *Q. agrifolia* acorns given their lower tannin concentration (Koenig and Faeth, 1998).

2. Methods

2.1. Study area

The study was conducted from October through December 2014–2016 at the Hastings Natural History Reservation in central coastal California. The landscape is characterized by a Mediterranean vegetation community with a heterogeneous mosaic of grassland, oak savanna, mixed hardwood woodland, and chaparral scrub (McMahon et al., 2015). We identified five distinguishable habitats in the study area in which California Scrub-Jays are known to cache seeds most frequently (Pesendorfer and Koenig, 2016). Cache sites were characterized primarily by overstory vegetation and ground substrate (Table 1, Schubert et al. unpubl.). Grassland habitats (OPEN) are dominated by non-native Mediterranean grasses, with savannas distinguished by patches of scattered remnant *Q. lobata* (QULO). Mature woodlands in the study region include all three oaks and a number of other hardwood species. Most woodland habitat on site, however, is composed of secondary stands dominated by a canopy of *Q. douglasii* (QUDO). Forest edge and riparian fragments are dominated by large *Q. agrifolia* trees (QUAG). Finally, chaparral habitat (CHAP), found on south-facing slopes, is predominantly composed of chamise (*Adenostoma fasciculatum*) and California lilacs (*Ceanothus* spp.).

Table 1
Summary of California Scrub-Jay caching observations by habitat, August–November 2014.

Habitat Type	Dominant Vegetation Cover	Ground Substrate	Other Features
QUDO	*Quercus douglasii*	leaf litter, soil	woodland
QUAG	*Quercus agrifolia*	leaf litter	forest edge
QULO	*Quercus lobata*	grass, soil	isolated tree (savanna)
OPEN	non-native perennial grasses	grass, soil	no trees within 25 m
CHAP	*Adenostoma fasciculatum, Ceanothus* sp.	sclerophyllous leaf litter	chaparral edge

2.2. Experimental design

Each year, 200 *Q. lobata* acorns and 200 *Q. agrifolia* acorns were collected from a minimum of 10 individuals per species and stored in a refrigerator for 7–14 days at 2 °C until planting experiments were initiated. Acorns were inspected visually for exit holes produced by weevils (*Curculio* spp.) and mass was determined using a digital balance. Since scatter-hoarding jays are known to avoid parasitized acorns infested with weevils, acorns containing signs of parasitism were excluded from the study (Dixon et al., 1997; Rockwell et al., 2013). Sixteen acorns (8 *Q. lobata* and 8 *Q. agrifolia*) were planted 15 cm apart in five replicate plots of the five habitat types located at least 40 m apart. Acorns were planted to simulate caching by scrub-jays, inserted vertically into a narrow impression in the substrate with the pointed end oriented downward, and the "cache" was covered lightly with the surrounding substrate. In all 3 years of the study, all acorns were planted over a period of 1–2 days in late October.

Survival of individual acorns was determined during weekly plot visits over the subsequent 5 weeks in 2014, 7 weeks in 2015, and 8 weeks in 2016, depending on the onset of winter season rains. Heavy rain obscured acorn planting position for many plots and, thus, was the main factor in deciding when monitoring was discontinued. Both acorn species that we tested for our experiments are known to germinate within the time frame of our monitoring period (Griffin, 1971). However, we did not measure germination, since unnecessary disturbance to the ground near to where other acorns were buried may have influenced predator activity. During each plot visit, we carefully inspected the surface of the ground for tracks, fecal samples, and any removed or damaged acorns. During the first two study years, we rotated a single motion-sensor trail camera among plots to obtain visual confirmation of predators. By combining these two approaches we were able to infer the identity of the predators in many cases; however, data were not consistent enough to permit quantitative analysis of different predator