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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

The effect of within-year variation in acorn crop size on seed harvesting by avian hoarders

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Abstract Spatial and temporal variation in resource distribution affect the movement and foraging behavior of many animals. In the case of animal-dispersed trees, numerous studies have addressed masting—the synchronizedvariation in seed production between years—but the fitness consequences of spatial variation in seedproduction within a year are unclear. We investigated the effects of variable acorn production in a population of valley oaks (*Quercus lobata*) on the composition and behavior of the avian-disperser community. We found that western scrub-jays (*Aphelocoma californica*), high-quality dispersers that store seeds in the ground, were attracted to, and exhibited increased per capita dispersal rates from, trees with large acorn crops. In contrast, acorn woodpeckers (*Melanerpes formicivorus*), low-quality dispersers that store acorns in trees where they are unlikely to germinate, increased per capita hoarding rates but did not attend trees with large seed crops in higher numbers, suggesting that the two species responded to resources on different spatial scales. Antagonistic interactions within and between species increased with the number of birds attending a tree, resulting in a potential cost for foraging birds, but did not reduce dispersal rates. Using a simulation model, we estimated that trees with large initial crops experienced a greater proportion (77 %) of high-quality seed dispersal events than trees with small crops (62 %). Our findings provide support for a mechanistic link between seed production and foraging behavior of seed dispersers as predicted by the predator dispersal hypothesis for the functional consequences of variable seed production in hoarder-dispersed trees.

Keywords Masting · Predator dispersal hypothesis · Scatter hoarding · Species interactions · Zoochory

Introduction

Food-hoarding seed predators are important dispersal vectors for many large-seeded trees. They regularly hoard more seeds than necessary, drop seeds during transport, or fail to recover all the seeds they cache (Vander Wall 1990; Pesendorfer et al. 2016). The fitness benefits dispersers provide to plants depend on their foraging behavior, movement, and preferred seed-storing locations (Schupp et al. 2010). Animal foraging and movement patterns in space, however, are often affected by variable resource distribution and the presence of intra- and interspecific competitors (Charnov 1976; Poulsen et al. 2002; Scofield et al. 2010). In plant populations with highly variable seed production between individuals, seed dispersal parameters may consequently vary by individual plant, depending on the size of its seed crop and the presence of multiple, competing seed dispersers. This relationship between resource distribution, disperser community composition, and seed dispersal patterns has recently received attention, but is still poorly understood (Schupp et al. 2010; Côrtes and Uriarte 2013). Here we investigate how the variation of seed crop size

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within a year among a population of oaks affects the composition of the trees' disperser community and the behavior of their avian seed dispersers.

Variable seed production of trees is hypothesized to affect the behavior of seed predators and dispersers in ways that ultimately benefit plant fitness (Vander Wall 2010; Zwolak et al. 2015). One hypothesis for how this may be accomplished is the predator satiation hypothesis, which states that large seed crops satiate predators and thus reduce relative predation of seeds (Kelly and Sork 2002). A nonexclusive alternative, the predator dispersal hypothesis, proposes that larger seed crops result in fitness benefits from increased seed dispersal by seed-hoarding animals. For plants with multiple seed dispersal vectors, this may mean that a larger number of dispersers attend a tree, or that more seeds are dispersed by higher-quality dispersers (Vander Wall 2002, 2010). Both hypotheses address interannual variation of seed crops, but if disperser behavior changes as a direct function of seed crop size in a particular tree, similar effects on seed dispersal may result from spatial seed crop variation within a season.

Seed dispersal by avian hoarders is often context dependent and changes with temporally variable seed availability and social dynamics. Optimal foraging theory predicts that animals should forage and hoard in ways that maximize acquired energy while minimizing potential costs, such as injury during antagonistic interactions or predation events (Charnov 1976; Gerber et al. 2004). In order to reduce search time and maximize hoarding rates, birds should thus attend trees with the largest seed crop and the smallest probability of antagonistic interactions. Clark's nutcrackers (*Nucifraga columbiana*), for example, preferentially forage on whitebark pine (*Pinus albicaulis*) stands with high-yielding cones, while avoiding stands with low-quality cones due to insect damage (Christensen et al. 1991). In a community of different dispersers, however, the spatial scale of perception, and thus the selection of foraging locations may vary among species (Morgan et al. 1997). The effects of such varying spatial scales on seed dispersal dynamics have not been previously explored.

Valley oaks (*Quercus lobata*) and their community of seed dispersers provide an excellent system to investigate the effect of seed availability and competition among dispersers on overall seed dispersal dynamics. *Q. lobata* is a masting species whose seed production varies strongly between years and exhibits geographic synchrony over hundreds of kilometers (Koenig and Knops 2000, 2013). Despite the high degree of synchrony between disparate populations, seed production also varies greatly among trees of a population within a given year (Koenig et al. 2003). From the perspective of the seed predators, this within-year variation provides the context for foraging decisions, and thus offers an opportunity to investigate the

functional connection between a tree's seed crop and the fate of its seeds.

The two main avian dispersers of *Q. lobata* acorns, western scrub-jays (*Aphelocoma californica*) and acorn woodpeckers (*Melanerpes formicivorus*), are both seed-hoarding species whose population size and stability are tightly connected to oak abundance, diversity, and acorn production (Koenig and Haydock 1999; Koenig et al. 2009). Western scrub-jays defend territories in pairs and scatter-hoard acorns by distributing single seeds in ground caches resulting in high-quality seed dispersal (Carmen 2004). Group-living acorn woodpeckers, in contrast, uniquely store acorns in "granaries" that they defend in cooperatively breeding groups (MacRoberts 1970). The two species therefore differ in their seed dispersal quality, as acorns stored in the ground are more likely to germinate successfully than the small number of acorns that woodpeckers inadvertently drop in the process of harvesting and storing them in granaries (Borchert et al. 1989; Scofield et al. 2010; Pesendorfer et al. 2016).

The two species of birds also vary in the estimated number of acorns they harvest each fruiting season: individual western scrub-jays cache upwards of 5000 acorns, while an individual acorn woodpecker stores on average less than 500 acorns (Koenig and Mumme 1987; Carmen 2004), although this number is probably considerably larger in good crop years. In years of large acorn crops, acorn woodpeckers harvest acorns at higher rates and transport them over shorter distances than in years of small crops (Koenig et al. 2008). Similarly, scatter-hoarding rates of island scrub-jays (*Aphelocoma insularis*), close relatives of western scrub-jays, are positively associated with annual acorn availability (Pesendorfer 2014). Moreover, island scrub-jays reduce seed dispersal rates when levels of territorial aggression are high, indicating that scatter-hoarding behavior can also change depending on the social context. Another bird species, Steller's jay (*Cyanocitta stelleri*), also regularly harvests *Q. lobata* acorns, but is less common and only removes a small proportion of acorns in our study area.

To determine how different crop sizes of individual *Q. lobata* trees affect the composition and behavior of the avian disperser community within a fruiting season, we quantified tree attendance and acorn harvesting behavior of its two main avian dispersers as well as their antagonistic interactions. Optimal foraging theory predicts that trees with large seed crops should attract more birds, but that antagonistic interactions should occur more frequently among birds at such trees due to competition for resources (Brown 2000). In contrast, visits to trees with smaller seed crops should entail a lower frequency of antagonistic interactions and associated costs, thus potentially attracting birds despite reduced foraging rates.

Table 1 Parameters included in analyses—names and descriptions

Parameter	Description
Acorn count	Number of acorns counted in 30 s; estimate of crop size
Acorns dropped	Number of unopened acorns dropped from crown (h^{-1})
Acorns eaten[a]	Number of acorns opened and (partially) consumed (h^{-1})
Acorns transported[a]	Number of acorns transported out of tree crown (h^{-1})
Acorns handled[a]	Combined number of eaten and transported acorns (h^{-1})
n (birds)	Maximum number of birds that attended tree (h^{-1})
Displacement rate	Number of aggressive displacements among birds; measure for antagonistic interactions, calculated among and between species

[a] Estimated for each bird species separately, for all species combined, and per capita

The two main avian dispersers might also show a different response to acorn crop size due to differences in their scale of perception (Morgan et al. 1997). Specifically, we predicted that western scrub-jays would respond more strongly to variation in acorn crops among individual trees because they are less spatially constrained in the non-breeding season than acorn woodpeckers that defend their granary trees year-round (Carmen 2004; Koenig et al. 2008). Since it is unclear whether overall dispersal rates by a species or per capita rates of individuals should be affected by acorn crop size, we analyzed the impact of individual crop size on behavioral rates measured both per capita and at the species level.

If large seed crops of individual trees result in predator satiation, we expected the proportion of acorns eaten to be negatively correlated with seed crop size. In contrast, if acorn crop size of *Q. lobata* affects disperser behavior as predicted by the predator dispersal hypothesis, the proportion of acorns harvested by high-quality dispersers (western scrub-jays) should be greater in trees with larger acorn crops (Vander Wall 2010).

Materials and methods

Study site and data collection

The study was conducted September–November 2014 at Hastings Natural History Reservation in central coastal California. The area has a Mediterranean climate and consists of oak savannah and woodlands dominated by *Quercus lobata*, *Quercus douglasii* and *Quercus agrifolia* (Koenig et al. 2008). In the year of the study, the *Q. lobata* population produced an intermediate acorn crop that varied considerably among individuals, while other oaks in the study area had generally poor crops (Koenig, Carmen and Knops, unpublished data). We selected 37 *Q. lobata* trees from which at least one acorn removal by a bird was observed; trees from which no acorns were removed invariably had imperceptibly small acorn crops.

To quantify acorn removal rates, we conducted 60-min focal tree observations during which we recorded the number of acorns eaten, transported, and dropped by animals (Table 1). We never observed the transport of more than a single acorn at a time, and thus, similar to previous studies, we assumed that a single acorn was transported during each flight (Gómez 2003; Pons and Pausas 2007). Before each focal tree watch, we estimated acorn crop size by conducting 30-s acorn counts, a reliable method quantifying relative acorn abundance (Koenig et al. 1994; Pesendorfer et al. 2014). During focal watches we recorded all intra- and interspecific displacements among birds to estimate antagonistic interactions among avian species and estimated the maximum number of individuals of each species that visited the tree (Table 1).

Individual trees were observed twice a week from the date that first seed removal was observed until the individual acorn crop was depleted. Occasionally, a large number (20 or more) of birds would frequent a specific tree during a focal watch requiring two observers to collect data; when this occurred one observer quantified the number of acorns leaving the tree with each bird species while a second observer quantified the number of acorns handled, eaten, and dropped. We excluded one extreme outlier from analysis: a watch during which we observed more than 30 western scrub-jays and several acorn woodpeckers transport more than 1000 acorns from a single tree in 1 h. The sheer number of acorns handled during this watch prevented the observer from recording reliable estimates of aggressive interactions and other focal-level parameters.

We calculated the hourly rate of acorn consumption and transportation for each focal watch and for each bird species separately (Table 1). Using the maximum estimated number of birds attending the tree during a focal watch, we calculated per capita rates for each species to analyze the effect on the behavior of individual birds. Finally, we calculated the number of acorns handled by each bird species as the sum of acorns eaten and transported, and the proportion of acorns handled, eaten, and dropped by each species for each focal watch.

Data analysis

To determine the effect of crop size and levels of inter- and intraspecific aggression on bird attendance and seed dispersal, we modeled the relationship between predictors and dependent variables on focal-level data using a set of generalized linear mixed models (GLMMs) that contained "tree" as a random effect to account for repeated sampling (Zuur 2009). First, we modeled the effect of acorn count on the number of birds by each species that attended a tree. Then, we investigated how within-tree acorn count and bird numbers affected the rate of observed aggression during a focal watch. Finally, we used a set of models to determine the effect of acorn crop, as well as intra- and interspecific rates of aggression, on the number and proportion of acorns consumed and transported by each species. We used binomial and Poisson error distributions in GLMMs for proportional data and behavioral rates (i.e., counts per hour), respectively. All models were fit by maximum likelihood (Zuur 2009).

Model fit was assessed by visual inspection of residual distributions across predictors. We used Wald type II tests to estimate χ^2-values and associated P-values for fixed effects. We only report df for fixed effects ($df = 1$ unless noted otherwise) because the residual df are estimated by methods that are subject to debate (Bolker et al. 2009). We also performed a multinomial analysis of acorn fate as a function of crop size and social dynamics; results confirmed those obtained from GLMMs. This analysis was, however, unable to account for repeated observations, and thus is not presented. All analyses were performed in R (R Core Team 2013) and we used the packages lme4 (Bates et al. 2012) for (G)LMMs and car (Fox and Weisberg 2011) for Wald Type II tests. Unless stated otherwise, values presented are means ± SEs.

Simulation model

To estimate the effect of a tree's initial acorn crop size on the total proportional removal of acorns by the two main dispersers, we simulated the relationship between initial acorn crop, its decline throughout the fruiting season, and the subsequent effect on harvesting rates by western

scrub-jays and acorn woodpeckers. First, we assigned trees to crop size categories (0–4) depending on the maximum acorn count of the season (Koenig et al. 1994). For each non-zero category, we modeled the linear rate of acorn decline as a function of relative (Julian) day after the first observed acorn removal. To account for potential non-linear relationships, we also constructed GLMs with 2nd order polynomials for each crop size category. The comparison of Akaike information criterion (AIC) values between the two types of models in each category, however, revealed that the fit of the polynomial GLMs was not better than that of linear models (i.e., ΔAIC < 2; Fig. A1; Table A2); thus linear models were used. Next, we used the intercepts and parameter coefficients of significant fixed effects from GLMMs of the focal-level data to simulate the relationship between acorn crop, bird attendance, and dispersal rates (Table A3). Finally, to compare the relative total contribution of western scrub-jays and acorn woodpeckers to the fate of acorns that are transported from trees, we calculated the area under the modeled curves for both dispersers in each crop size category.

Results

We recorded a total 196 h of focal observations on 37 trees (5.3 ± 0.4 h tree^{-1}, range 3–12 h). Annual acorn crop size, characterized by the maximum number of acorns counted in 30 s for each tree, ranged from three to 114 acorns, with an average of 42 ± 5 acorns. Of the 3707 acorns handled in *Q. lobata* trees during our observations, 772 (20.8 %) were dropped below the tree, 1200 (32.4 %) were consumed in the tree, and 1713 (46.2 %) were transported away by birds (Table 2). Altogether, western scrub-jays, acorn woodpeckers and Steller's jays handled 99.2 % of the 2935 acorns that were eaten or transported (Table 2); other species observed removing acorns included western gray tree squirrels (*Sciurus griseus*; 18 acorns), black-tailed deer (*Odocoileus hemionus*; four acorns), spotted towhees (*Pipilo maculatus*; one acorn), and oak titmice (*Baeolophus inornatus*; one acorn). No viable acorns remained on the ground by the end of the study period.

Table 2 Acorn fate by avian species

Acorns	Western scrub-jay (WESJ)			Acorn woodpecker (ACWO)			Steller's jay		
	Count	% All	% Species	Count	% All	% Species	Count	% All	% Species
Handled	2396	81.6		348	11.9		168	5.7	
Eaten	1083	90.3	45.2	36	3.0	10.3	87	7.3	51.8
Transported	1313	76.6	54.8	312	18.2	89.7	81	4.7	48.2

Total numbers and percentages of *Quercus lobata* acorns handled, eaten, and transported by different avian seed hoarders

Tree attendance, aggression and acorn removal

The number of western scrub-jays (2.7 ± 0.2) observed in a tree during a focal watch correlated positively with the acorn count on a tree ($\chi^2 = 22.0$, $P < 0.001$), while the number of acorn woodpeckers (1.8 ± 0.1) was not related to the acorn crop of the tree (Fig. 1a; $\chi^2 = 0.9$, $P = 0.34$). *Q. lobata* with large acorn crops thus attracted more western scrub-jays, but not more acorn woodpeckers.

We observed an hourly rate of 6.4 ± 1.1 displacements h^{-1} (range 0–95) that increased significantly with the number of western scrub-jays ($\chi^2 = 67.4$, $P < 0.001$) and acorn woodpeckers ($\chi^2 = 109.6$, $P < 0.001$) in a tree during a focal watch, as well as the acorn count of a tree ($\chi^2 = 25.8$, $P < 0.001$). Thus, the frequency of inter-specific aggressive interactions was associated with the number of birds in a tree and with acorn abundance. The majority of 1,258 observed displacements (75.9 %) was initiated by acorn woodpeckers and directed at western scrub-jays, whereas a lower proportion (20.3 %) of displacements was directed at other acorn woodpeckers, presumably from other groups (Table A1). In contrast, most aggression by the two jay species was directed intraspecifically.

Combined, all birds transported 9.2 ± 1.6 acorns h^{-1} (range 0–212). Acorn transportation rates by western scrub-jays (6.9 ± 1.5 h^{-1}) were higher than those of acorn woodpeckers (1.6 ± 0.3 h^{-1}) and Steller's jays (0.5 ± 0.1 h^{-1}), a pattern mirrored by per capita rates (western scrub-jay, 1.5 ± 0.1 h^{-1}; acorn woodpecker, 0.8 ± 0.1 h^{-1}; Steller's jay, 0.2 ± 0.1 h^{-1}). Western scrub-jays handled an average of 67.8 ± 3.1 % of acorns during focal watches, acorn woodpeckers 26.3 ± 2.9 %, and Steller's jays 4.2 ± 1.2 %. The two corvid species combined accounted for 97.6 % of acorns eaten in trees, and they consumed about half of the acorns they handled (Table 1).

Effects of acorn availability and aggression on seed fate

Birds consumed 25.9 ± 0.1 % of handled acorns during focal watches. This proportion increased with the number of scrub-jays present during a watch ($\chi^2 = 4.9$, $P = 0.03$), but did not correlate with the number of woodpeckers ($\chi^2 = 3.1$, $P = 0.08$) or the acorn count of the tree ($\chi^2 = 1.7$, $P = 0.20$). Similarly, the proportion of acorns dropped during a focal watch increased with the number of jays ($\chi^2 = 80.6$, $P > 0.001$), but not with the number of acorn woodpeckers ($\chi^2 = 0.2$, $P = 0.67$) or the acorn count ($\chi^2 = 0.6$, $P = 0.45$). Thus, the overall proportion of acorns eaten by birds, or relative pre-dispersal predation, was not affected by the availability of acorns in a tree.
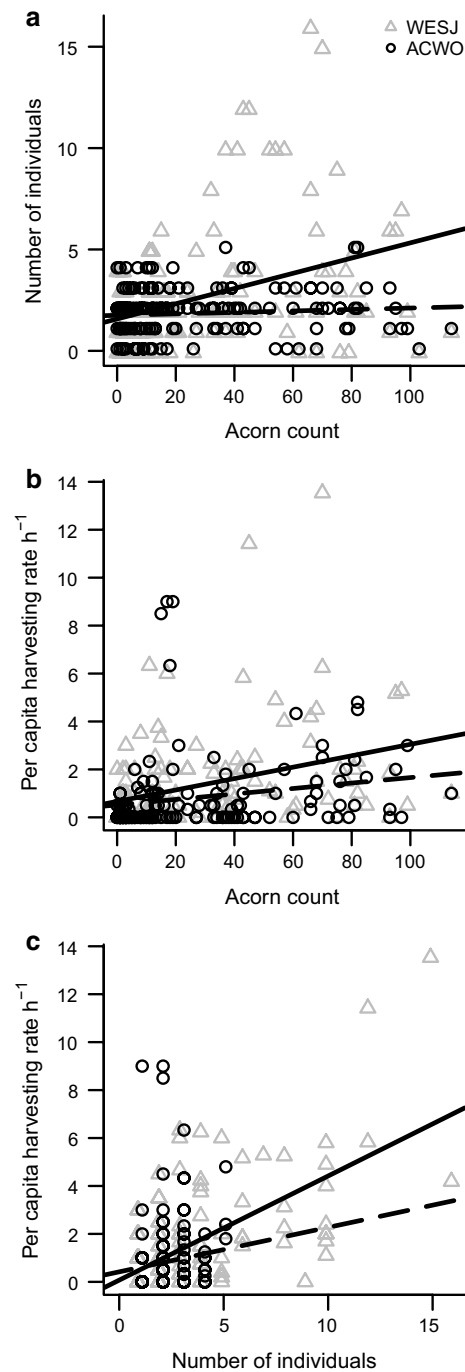

Fig. 1 The effect of acorn crop size on disperser attendance and harvesting behavior. **a** Acorn crop size affects attendance of western scrub-jays (*WESJ*; *gray triangles*, *solid line*), but not acorn woodpeckers (*ACWO*; *hollow circles*, *dashed line*). **b** Per capita acorn harvesting rates increase with acorn crop size. **c** Per capita acorn harvesting rates increase significantly with the attendance of conspecifics in western scrub-jays, but not acorn woodpeckers. *Lines* indicate linear fit to untransformed data. See Tables 2 and 3 for statistical models

Table 3 Predictors of acorn harvesting rates by the avian seed-hoarders WESJ and ACWO

Parameter	Overall removal rate			Per capita removal rate		
	B	χ^2	*P*	*B*	χ^2	*P*
WESJ						
n (WESJ)	*0.211*	*287.2*	*<0.001*	*0.354*	*28.3*	*<0.001*
n (ACWO)	0.044	0.9	0.347	−0.172	1.8	0.183
Acorn count	*0.021*	*115.4*	*<0.001*	0.010	3.7	0.053
Displacements	*0.021*	*54.4*	*<0.001*	*0.049*	*9.1*	*0.002*
ACWO						
n (ACWO)	*0.606*	*53.9*	*<0.001*	0.045	0.1	0.747
n (WESJ)	0.034	0.9	0.323	−0.015	<0.1	0.787
Acorn count	*0.016*	*25.9*	*<0.001*	*0.012*	*5.9*	*0.015*
Displacements	*0.172*	*56.6*	*<0.001*	*0.244*	*16.7*	*<0.001*

Model coefficients (*B*), χ^2-values, and associated *P*-values for (generalized) linear mixed models of overall and per capita removal rates in focal watches (*n* = 159). All models contained Individual tree as a random effect; all *df* = 1. Statistical significance indicated by *italic*. For abbreviations, see Table 2

The proportion of acorns taken by jays was higher in trees with more jays (χ^2 = 7.5, *P* = 0.006) and lower in trees with larger numbers of woodpeckers (χ^2 = 9.3, *P* = 0.002). The acorn count (χ^2 = 0.8, *P* = 0.28) and hourly displacement rate (χ^2 = 1.5, *P* = 0.23) did not affect the proportion of acorns transported by each bird species. The proportion of acorns taken by each species thus correlated with the number of individuals attending a tree, but not with aggression or the acorn crop.

Acorn transportation rates by western scrub-jays generally increased with the number of conspecifics attending a tree. Both per capita and overall transportation rates by scrub-jays were most strongly influenced by the number of individuals present. Moreover, the overall acorn removal rates by scrub-jays correlated strongly with a tree's day-specific acorn count (Fig. 1c; Table 2).

In contrast, acorn woodpecker transportation rates varied with acorn availability and intraspecific aggression during focal watches. Both the overall and per capita acorn removal rates by woodpeckers were positively correlated with the acorn counts on specific days, and also increased with the number of displacements against woodpeckers (Fig. 1b). The overall dispersal rate also correlated positively with the number of woodpeckers attending a tree (Table 3).

The effect of overall acorn crop on relative crop fate

The simulation model scaling the daily variation in dispersal dynamics to the entire fruiting season indicated that the overall proportion of acorns harvested by western scrub-jays was higher in trees with large relative seed crops, increasing from 62.4 % in trees with the smallest acorn crops (category 1) to 77.1 % in trees with the largest acorn crops (Fig. 2; Table 4). Thus, the initial acorn crop size of a

tree affected the proportion of the crop that was harvested by the different dispersers. Only 11 % of the trees observed in this study produced the largest category acorn crops, and the majority of trees produced small or very small acorn crops (Table 4).

Discussion

Our results demonstrate that, in the year of our study, *Q. lobata* trees with large acorn crops attracted more western scrub-jays and experienced higher seed removal rates, and suggest that these trees benefitted from increased high-quality dispersal as predicted by the predator dispersal hypothesis. The attendance and behavior of the disperser community at trees with different acorn crop sizes also indicate that western scrub-jays maximized foraging more efficiently than acorn woodpeckers, potentially due to their decreased territoriality during the non-breeding season. Intra- and interspecific aggression increased with the number of birds in a tree, implying that there are costs associated with attending trees with large seed crops. The functional response of high-quality seed dispersers to within-year variation of seed crops provides a mechanism potentially linking optimal foraging to the predator dispersal hypothesis of increased seed dispersal during high crop years.

Western scrub-jays handled, ate, and dispersed the majority of *Q. lobata* acorns in our study area. They also harvested seeds at higher per capita rates than the other avian species. Nonetheless, per capita harvesting rates by scrub-jays were low (1.5 acorns h^{-1}) compared to other studies of *Aphelocoma* jays. For example, congeneric island scrub-jays and Florida scrub-jays (*Aphelocoma coerulescens*) have been reported to hoard seeds at rates of
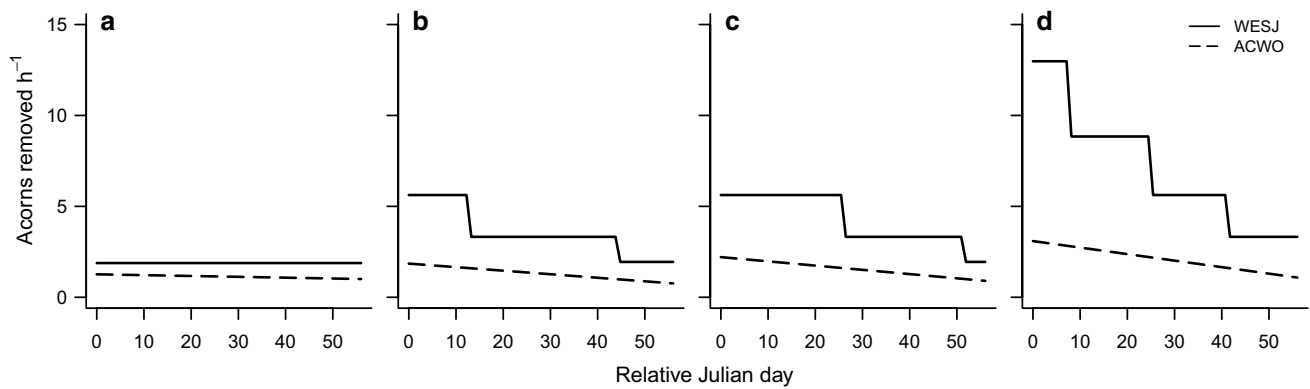
Fig. 2 Overall acorn crop size of individual trees affects the proportion of crops dispersed by WESJ (*solid line*) and ACWO (*dashed lines*). Using the findings from focal-level data, we simulated the effect of acorn crop size and its decline throughout the fall (by relative Julian day) on seed dispersal rates by the two disperser species. The proportional contribution to seed crop fate was estimated by comparing the areas underneath curves. See "Materials and methods" section and Table 4 for details. **a** Small acorn crop [initial 30-s acorn count (IAC) < 30], **b** small-medium crop (IAC < 60), **c** moderate crop (IAC < 90), and **d** large crop (IAC > 90). For other abbreviations, see Fig. 1

Table 4 Relative contribution of disperser species as a function of overall crop size

	Acorn crop size category			
	1	2	3	4
n (trees)	14	10	9	4
Initial acorn count (mean ± SE)	11.9 ± 1.6	36.5 ± 5.9	70.2 ± 4.5	101.3 ± 4.3
Total relative ACWO harvest	63.5	73.1	87.0	116.8
Total relative WESJ harvest	105.4	199.2	239.5	392.8
Proportion WESJ harvest (%)	62.4	73.2	73.3	77.1

Results of simulation model for acorn removal by ACWO and WESJ. See "Materials and methods" section for details of model construction. For abbreviations, see Table 2

5.1–17.2 acorns h^{-1}, but usually forage on multiple trees (DeGange et al. 1989; Pesendorfer et al. 2016). The low acorn availability on the two most common sympatric oak species during the study, *Q. douglasii* and *Q. agrifolia,* may have contributed to low dispersal rates, as scrub-jays were observed to transport acorns over distances as large as 2 km in order to hoard acorns on their territories (data not shown). In contrast, harvesting rates of acorn woodpeckers (0.8 acorns h^{-1}) were comparable to values reported for a low-productivity year in the same area [0.6 acorns h^{-1} (Koenig et al. 2008)].

The proportion of handled acorns that was consumed by birds in trees did not vary with crop size, and thus, at the level of individual trees within the year, large acorn crops did not result in satiation of avian predators. In the light of low acorn availability across the general landscape, we did not expect predator satiation to occur. Food-hoarding animals continue harvesting seeds even when immediate nutritional demands are met and predator satiation may thus only apply to non-hoarding seed predators (Vander Wall 1990).

Previous work also demonstrated that *Q. lobata* trees with large crops have a smaller proportion of insect-damaged acorns than trees with small crops (Koenig et al. 2002). This could have potentially increased the proportion of acorns consumed by seed-hoarding birds because they generally avoid insect-infested seeds with heavy damage (Dixon et al. 1997; Koenig and Benedict 2002; Jablonski et al. 2015). Insect infestation of acorns was not quantified for this study; in comparison to seed removal by birds, however, it appears to have little impact on the overall fate of the seed crop in California oaks (Koenig et al. 2002).

The size of acorn crops influenced seed dispersal rates of both of the primary avian dispersers of *Q. lobata*, as predicted by the predator dispersal hypothesis. Species-level harvesting rates strongly depended on the number of birds that visited a tree, both in western scrub-jays and acorn woodpeckers (Fig. 1a). In western scrub-jays, trees with larger acorn crops attracted a larger number of birds, while the number of acorn woodpeckers was probably determined by the size and presence of neighboring groups (Koenig et al. 2008).

The effect of acorn crop size on per capita removal rates, however, is surprising and hints at the proximate mechanism of predator dispersal effects. One of the functions of food hoarding is to remove clustered resources from competition (Andersson and Krebs 1978; Gerber et al. 2004). Larger accumulations of resources may thus elicit

increased foraging activity of birds attempting to maximize energy uptake, resulting in a functional response of foraging in avian hoarders to variation in seed crops, ultimately affecting seed dispersal rates (Brown 2000; Vander Wall 2002; Pesendorfer et al. 2016).

Displacement rates correlated positively with acorn harvesting rates of both bird species (Tables 2, 3), highlighting the potential costs of maximizing foraging rates. Apparently aggression failed to prevent competitors from harvesting acorns, as foraging rates did not decline as aggression increased, and may instead reflect competition for acorns within a tree. Intraspecific aggression in both species was positively associated with harvesting rates (data not shown), further suggesting that individuals from other territories were attracted to *Q. lobata* trees with large seed crops to obtain acorns. This high level of aggression, however, may also have prompted some birds to attend low-crop trees in order to avoid the costs of potential injury.

The number of individual competitors in a tree did affect dispersal dynamics. The proportion of acorns handled by the jays in a tree was reduced when large acorn woodpecker groups defended a tree, but increased with the number of scrub-jays present. The large number of scrub-jays observed in individual trees may in part have been driven by low acorn crops on other oaks in the area. Variable seed production among sympatric tree species dispersed by generalist hoarders can result in such community-level effects on seed dispersal (Lichti et al. 2014; Yi and Wang 2015). The number of acorn woodpeckers in a tree, however, was relatively stable. Larger woodpecker groups may therefore benefit by losing a smaller proportion of acorns to competitors. Conversely, western scrub-jays benefit from foraging in large groups, as this increases the proportion of acorns they remove from competition with the woodpeckers.

The difference in foraging behavior between the two dominant seed-harvesting species may be due to the spatial scale of perception of available resources when optimizing the balance between foraging benefits and costs (Brown 2000). Acorn woodpeckers cooperatively defend territories year-round that contain not only trees with cavities suitable for breeding but granaries in which the birds store acorns for the fall (Koenig and Mumme 1987). Granaries are filled with acorns that in general have been harvested no further than ~150 m from their granary trees (Koenig et al. 2008). Western scrub-jays, in contrast, are less territorial in the fall months than during the breeding season (Carmen 2004), and can thus take advantage of resources at larger distances from their breeding area by attending trees with large crops, even at long distances from their territory. Optimal foraging theory predicts that such differences in the scale of perception affects the functional response of foraging animals to

resource abundance (Morgan et al. 1997). The differential response by acorn woodpeckers and western scrub-jays thus suggests that their acorn-foraging behavior may be determined by resource dynamics on two different spatial scales. This may also explain the higher rates of aggression initiated by acorn woodpeckers, because on a small spatial scale a single tree with a large crop is potentially more valuable and thus worth the cost and risk of injury during confrontation.

The simulation model estimating the relationship between a tree's overall seed crop and the proportional dispersal by high- and low-quality dispersers further supports the role of these varying spatial scales. By scaling up from the behavior observed in focal watches to the population level, we found that large crop sizes result in a higher proportion of seeds removed by western scrub-jays, the high-quality seed dispersers for *Q. lobata* (Fig. 2). The increase in proportional removal by high-quality dispersers provides additional support for the predator dispersal hypothesis and underscores the impact of within-season variation of seed crop size on dispersal dynamics. The model also supports the hypothesis that an increase in per capita hoarding rates by scatter hoarders provides the mechanistic link between temporal and spatial variation in seed crops and the associated fitness benefits that plants obtain from their activity, within as well as between years.

The stark difference in dispersal quality between the two avian hoarders results in important fitness consequences of the spatial variation in seed crops. Acorn woodpeckers transport acorns to granary trees, where the seeds are stored until subsequent consumption (MacRoberts 1970). While the birds may occasionally drop a seed during transport, the likelihood of successful germination and seedling establishment is low for an acorn that leaves the tree with a woodpecker. In contrast, western scrub-jays hoard seeds in the ground, often at optimal depth for germination (Borchert et al. 1989), and corvids often hide substantially more seeds than they need to cover their energetic requirements in the subsequent winter (DeGange et al. 1989; Pesendorfer et al. in press). The 15 % increase in the proportion of acorns subject to such high-quality dispersal for trees with large acorn crops (Table 3) could thus provide an important fitness advantage to individual *Q. lobata* trees.

Masting is a population-level phenomenon and, in oaks, can range over hundreds of kilometers (Koenig and Knops 2013). The spatial scale of the trees' behavior thus reaches far beyond the home ranges of individual scrub-jays or woodpecker groups. In fact, much of the interannual variation in seed production seems to be associated with abiotic parameters, such as spring or summer temperatures (Kelly et al. 2013; Koenig et al. 2014). Nonetheless, predation and dispersal effects of variable seed production are likely to unfold on the spatial scale of the home ranges of the most

prevalent seed hoarders, which is determined by foraging decisions that maximize benefits and minimize potential costs (Morgan et al. 1997).

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