

Competing for seed dispersal: evidence for the role of avian seed hoarders in mediating apparent predation among oaks

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Summary

1. In communities of large-seeded tree species, generalist seed hoarders often link the temporally variable dynamics of various species in ways that can result in indirect ecological interactions. A special case of such interactions is ‘apparent predation’ – when variation in seed production of one tree species changes the outcome of the interaction between seed hoarders and another tree species from seed dispersal mutualism to predation.

2. We investigated how two species of avian hoarders responded to differences in acorn availability among individual valley oaks (*Quercus lobata*) and across a landscape dominated by blue oaks (*Q. douglasii*) to determine whether seed dispersal and predation dynamics result in apparent predation between these oak species.

3. California scrub-jays (*Aphelocoma californica*), high-quality seed dispersers with large spatial scales of resource perception, showed strong numerical and functional responses to individually large *Q. lobata* acorn crops when landscape-level acorn crops were low, but the numerical response was not observed when *Q. douglasii* produced a good acorn crop the subsequent year. In contrast, acorn woodpeckers (*Melanerpes formicivorus*), which are significant acorn predators, exhibited a consistent functional response to individual *Q. lobata* acorn crops independent of landscape-wide availability. Consequently, *Q. lobata* experienced increased predation and a near absence of high-quality seed dispersal when *Q. douglasii* acorns were abundant.

4. Our results suggest that apparent predation among oak species can arise from contrasting responses of generalist seed predators and dispersers to acorn availability on different spatial scales. Thus, the spatial scale of resource perception, which can differ greatly among generalist seed hoarders, may provide a proximate mechanism underlying indirect, temporally variable ecological effects such as apparent predation among sympatric species of large-seeded trees.

Key-words: *Aphelocoma californica*, apparent predation, competition, masting, *Melanerpes formicivorus*, *Quercus*, scatter-hoarding, seed dispersal mutualism

Introduction

Interspecific competition among sympatric species often occurs through indirect effects that are modulated by a common predator (Chase *et al.* 2002). In such interactions, population cycles play an important role, as they change the numerical and functional responses of the shared predator, potentially to the point where an interaction changes from predation to mutualism (Abrams, Holt & Roth 1998). A special case of such indirect effects occurs

when the shared predator is also a mutualistic seed disperser, as is often the case with scatter-hoarding animals that both consume and cache seeds within the landscape.

Recently, such interactions have been termed *apparent predation* (Lichti *et al.* 2014), as the functional shift is not of predation pressure, but rather of mutualism strength, yet still results in increased predation of one species' seeds. Because seed dispersal mutualisms involving generalist scatter-hoarders tend to be context-dependent (Yi & Wang 2015; Pesendorfer *et al.* 2016a), apparent predation is potentially common in forest communities with shared seed dispersers. In addition, seed production of different

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masting species in plant communities can affect the outcome of conditional mutualisms with scatter-hoarding generalists, resulting in reduced seed dispersal rates and increased predation of one masting species' seeds over another (Lichti *et al.* 2014). Generalist predators and dispersers thus provide a dynamic link for temporally variable ecological interactions among tree species (Abrams, Holt & Roth 1998), driving complex interactions that can reverberate through multiple trophic levels (Schmidt & Ostfeld 2008).

In this context, preferences for acorn attributes such as size, tannin content or relative energetic value affect the hoarders' decisions to consume, store or ignore the acorns of competing species (Johnson, Thomas & Adkisson 1993; Steele *et al.* 1993; Fleck & Woolfenden 1997). A number of rodent species, for example, tend to cache high-tannin seeds that store for longer without rotting and immediately consume low-tannin seeds that would otherwise germinate quickly (Vander Wall 1990; Xiao, Chang & Zhang 2008). For seeds that are preferentially eaten rather than stored, the presence of seeds preferred for caching may thus change the plant–animal interaction from a seed dispersal mutualism to one of predation, resulting in apparent predation between the two seed-bearing tree species (Xiao & Zhang 2016). Such indirect effects among members of the same plant community highlight the role of mast species composition in determining seed dispersal and predation outcomes.

In addition to preferences for seed characteristics, the spatial distribution of available seeds and the scale of perception of different hoarding species can affect their foraging and seed dispersal behaviour (Morgan, Brown & Thorson 1997). Hoarding species with different home range sizes may consequently show dissimilar responses to spatial variation in seed crop sizes (Pesendorfer & Koenig 2016a). When multiple tree species compete for generalist seed dispersers, apparent predation may thus not only arise due to seed traits but also due to the interaction between the spatial ecology of low- and high-quality seed dispersers and the patterns of seed production by competing masting species.

Here we report on how the harvesting of valley oak (*Quercus lobata*) acorns by two avian hoarders with different spatial scales of perception, the California scrub-jay (*Aphelocoma californica*) and the acorn woodpecker (*Melanerpes formicivorus*), varies with seed crop sizes of individual trees as well as acorn availability on the landscape scale. At our study site in central coastal California, valley oaks are part of a mosaic of oak savanna and oak woodland dominated by coast live oaks (*Q. agrifolia*) and blue oaks (*Q. douglasii*). Annual seed production of *Q. lobata* and *Q. douglasii* populations is generally synchronous (often over large geographical scales; Koenig & Knops 2013), while *Q. agrifolia* acorn crops are less synchronous with the prior two species (Koenig *et al.* 1994). In a given year, landscape-level acorn availability thus typically differs from species-level seed production.

California scrub-jays and acorn woodpeckers are the dominant hoarders of acorns at our study site but differ in their seasonal space use and seed dispersal quality. While population size and stability of both species are tightly connected to oak diversity, abundance and acorn production (Koenig & Haydock 1999; Koenig *et al.* 2009), seed dispersal quality by California scrub-jays is greater because they scatter-hoard seeds in the ground (Pesendorfer *et al.* 2016b). In contrast, acorn woodpeckers are cooperative breeders that store acorns in specialized 'granary' trees (MacRoberts 1970) and only disperse acorns when inadvertently dropping them during transport, thus providing comparatively low-quality seed dispersal. Unlike scrub-jays that move long distances to forage during non-breeding season (Carmen 2004), acorn woodpecker groups defend year-round territories and mostly hoard acorns from oaks within 150 m of their nest trees (Koenig, McEntee & Walters 2008). This difference in spatial scales of resource perception determines the numeric and functional response to within-year variation of seed crop sizes in *Q. lobata* (Pesendorfer & Koenig 2016a).

Previously, we found that when landscape-level acorn availability was low, *Q. lobata* with large acorn crops attracted more California scrub-jays, which in turn increased their per capita acorn foraging rates. Acorn woodpeckers, in contrast, displayed increased rates of aggression against scrub-jays in trees with large crops, but did not attend trees in higher numbers or increase their foraging rates (Pesendorfer & Koenig 2016a). Scrub-jays therefore faced significant costs, including potential injury from woodpecker attacks as well as attacks from conspecifics, when attending trees with large crops. In the light of the low overall acorn availability, however, these costs were likely offset by the high relative value of acorns. Here we compare these findings with data from the subsequent year in which landscape-level acorn availability was significantly higher because of increased acorn production by *Q. douglasii*.

California scrub-jays generally forage over wider areas than do acorn woodpeckers in search of acorns; that is, they have a greater scale of resource perception. Consequently, we predicted that scrub-jays would take advantage of the alternative acorn sources made available by increased landscape-level acorn production by reducing their attendance at *Q. lobata* trees – favoured by acorn woodpeckers (Koenig & Benedict 2002) – thereby reducing the risk of injury from aggression. We therefore expected a reduction in the numerical (attendance) and functional (per capita hoarding rates) response compared to the year with low landscape-level acorn availability, resulting in overall reduced high-quality seed dispersal (species-level hoarding rates). Conversely, we predicted that acorn woodpeckers would reduce rates of aggression and increase their foraging rates on favoured *Q. lobata* acorns in the year when *Q. douglasii* was more productive. In combination, we predicted that the increase in landscape-level acorn availability would reverse the patterns we

observed in the previous year and result in reduced high-quality dispersal for all *Q. lobata* trees, even those with large acorn crops. *Q. douglasii*, the competing oak species, would thus increase predation and reduce high-quality dispersal of *Q. lobata* seeds, resulting in apparent predation.

Materials and methods

STUDY SITE AND DATA COLLECTION

The study was conducted during the autumn fruiting season (September–December) of 2014 and 2015 at the Hastings Natural History Reservation (HNHR) in central coastal California (36°38'27" N, 121°55'88" W). The 2500-acre reserve is composed of mixed hardwood forests dominated by *Quercus agrifolia*, oak woodlands and savanna dominated by *Q. douglasii* and, to a lesser degree, *Q. lobata* interspersed by perennial grasslands and old fields. At higher elevations, *Q. kelloggii* and *Q. chrysolepis* are also present at low densities, but make up a small percentage of basal cover and are thus not considered further. At HNHR, *Q. agrifolia* is the most common oak, followed by *Q. douglasii*, which occurs in significantly higher numbers than *Q. lobata*, but only covers slightly more basal area due to smaller size (McMahon *et al.* 2015).

Each year, we selected a set of *Q. lobata* trees ('focal trees') spanning the range of acorn crop sizes to determine the relationship between acorn crop and rates of acorn removal, consumption and transportation by birds. To estimate landscape-wide acorn availability, we quantified the annual acorn crop of the dominant oak species by conducting acorn counts on 84 *Q. lobata*, 60 *Q. agrifolia* and 52 *Q. douglasii* trees that are part of a long-term study. Two observers used binoculars to count as many acorns as possible in 15s, and the counts were added into the 30-s count (N30; Koenig *et al.* 1994). For statistical analysis, we log-transformed acorn counts ($\text{LN30} = \ln(\text{N30} + 1)$) because the variance of untransformed acorn counts generally increases with the mean. We quantified acorn availability on two temporal scales. To determine the overall annual seed production of an individual, we used the transformed maximum acorn count for the field season (LN30_{max}). Because acorn availability declines as animals forage throughout the fruiting season, we also estimated the acorn availability on a given date by conducting 30-s acorn counts before starting behavioural observations (LN30_{day} ; Pesendorfer & Koenig 2016a).

To quantify rates of acorn foraging and hoarding, as well as antagonistic behaviour within and among avian hoarding species at focal trees, we conducted 60-min observations ('focal watches') twice a week throughout the fruiting season until the tree's acorn crop was depleted. Focal watches were initiated following a five-min habituation period after arrival in the observation location, usually 20–30 m from the focal tree. For the following 60 min, we used binoculars to quantify the arrival and departure of all acorn-handling species, their acorn foraging behaviour as well as inter- and intraspecific antagonistic interactions, as identified by physical displacements (Table 1). All observations were recorded on a continuous voice recording, which allowed us to determine timing of events during subsequent transcription to data sheets. In addition, we estimated the maximum number of individuals of each bird species that attended tree crowns throughout the focal watch, which allowed us to estimate species-level and per capita harvesting rates by birds (Table 1). Lastly, we calculated the proportional removal of acorns by each bird species for each focal watch.

DATA ANALYSIS

To compare annual seed production between focal trees in 2014 ($n = 37$) and 2015 ($n = 44$), we conducted *t*-tests of LN30_{max} for

Table 1. Names and descriptions of parameters included in analyses

Parameter	Description
Year	Study year (2014 or 2015), used as proxy for landscape-wide acorn availability
Acorn count	Number of acorns counted in 30 s; <i>ln</i> -transformed estimate of annual crop size (LN30_{max}), as well as for the day of each focal watch (LN30_{day})
Acorns dropped	Number of unopened acorns dropped from crown h^{-1}
Acorns eaten*	Number of acorns opened and (partially) consumed in crown h^{-1}
Acorns transported*	Number of acorns transported out of tree crown h^{-1}
Acorns handled*	Combined number of eaten and transported acorns h^{-1}
Displacements	Number of antagonistic displacements among birds h^{-1}
<i>n</i> (birds)	Maximum number of individuals that attended tree h^{-1}

*Estimated for each bird species separately, for all species combined, and per capita (= species total/number of individuals present).

the trees that were observed in both years (paired; $n = 17$), or in one year (unpaired; $n = 47$), and obtained an overall *P*-value using the weighted *Z*-test (Dewey 2014). To estimate the change in landscape-wide acorn availability between years, we constructed a linear mixed model (LMM) of *ln*-transformed annual acorn counts (LN30_{max}) for the three dominant oak species (*Q. lobata*, *Q. douglasii* and *Q. agrifolia*). Each model contained the fixed effect *Year* and the random effect *TreeID* to account for repeated sampling.

To investigate how overall species-level and per capita harvesting rates and aggression varied with acorn availability across the landscape and on the focal *Q. lobata* trees, we constructed a series of generalized linear mixed models (GLMM) of focal-level data with daily acorn count (LN30_{day}) and year. All models contained *Tree ID* as random effect to account for repeated sampling. *Year* was entered as categorical variable and considered a proxy for landscape acorn availability. We also included the interaction between LN30_{day} and *Year* as a fixed effect to account for the effects of landscape-wide acorn availability on the perception of individual acorn crops of *Q. lobata* trees. To avoid problems with collinearity among fixed effects, we standardized LN30_{day} by scaling and centring the variables (Bolker *et al.* 2009). For proportional and count data (e.g. displacements h^{-1}), we conducted GLMMs with binomial and Poisson error distributions, respectively. However, GLMM residuals for attendance and species-level behavioural rates were generally overdispersed and fitted values provided a poor fit to observed values. Therefore, we conducted LMMs of *ln*-transformed dependent variables instead (Zuur *et al.* 2009). Inference for all models was based on χ^2 with d.f. = 1, unless noted otherwise, and associated *P*-values from Wald type-II tests (Fox & Weisberg 2013).

We first determined whether attendance by California scrub-jays and acorn woodpeckers, quantified by the estimated maximum number of individuals (n_{acwo} , n_{wesj}), varied with the year, acorn crop, their interaction or the attendance of competing species. Next we investigated whether displacement rates varied with year, acorn crop, their interaction or the attendance by each species. We then modelled the effects of year, acorn count, their interaction, aggression rate and bird attendance on per capita and species-level rates of acorn consumption and harvesting. Finally,

we determined the relationship of the same fixed effects with the proportion of acorns transported by each species. We did not include statistical interactions of *Year* with bird attendance or rates of aggression because these varied so strongly between years that doing so prevented models from converging. Our analysis therefore assumes that aggressive interactions among birds (when present) are similar between years. We report parameter estimates B , χ^2 values and associated P -values for significant effects in the text and present full model results in Table 3. Unless stated otherwise, values reported and means \pm SE.

To investigate the causal relationship between the observed variables, we conducted a confirmatory path analysis that accounted for repeated sampling at focal trees (Shipley 2009; Lefcheck 2016). Model structure was based on the findings of the statistical analyses above and confirmed using Fisher's C test, for which $P > 0.05$ confirms directionality of assessed effects (Shipley 2009). After the inclusion of all models that contained significant effects in our initial analysis, we added the relationships between the numerical (attendance) and functional (per capita hoarding rates) response and the species-level hoarding rate. These models included the same parameter transformations as above in order to adhere to model assumptions. Finally, we included the correlated errors between the functional responses of acorn woodpeckers and California scrub-jays to account for additional external drivers of foraging behaviour. Path analysis details are presented in Appendix S1 (Supporting Information).

All analyses were conducted in R 3.2.2 (R Core Team 2015) and associated packages; GLMMs were constructed in LME4 version 1.1-7 (Bates *et al.* 2014), χ^2 and associated P -values obtained in *car* (Fox & Weisberg 2013), and the weighted Z -test conducted in *METAP* version 0.6 (Dewey 2014). Confirmatory path analysis was conducted in the package *PIECEWISESEM* (Lefcheck 2016), and associated LMMs were constructed with the package *NLME* (Pinheiro *et al.* 2015).

Results

We recorded 196 h of focal observations on 37 *Q. lobata* trees in 2014 (5.3 ± 0.4 h tree⁻¹) and 301 h on 44 trees in 2015 (6.9 ± 0.4 h tree⁻¹); 17 of the trees were observed in both years. Annual acorn crops on focal trees ($N_{30_{\max}}$) in 2014 ranged from 3 to 114, with a mean of 42.4 ± 5.4 , while in 2015, they ranged from 1 to 82, with a mean of 35.5 ± 3.7 . The annual acorn crops for focal trees ($LN_{30_{\max}}$) were not significantly different between the 2014 and 2015 data sets for *Q. lobata* (t -test for paired trees: $t = 0.4$, d.f. = 16, $P = 0.66$; t -test for unpaired trees: $t = 0.1$, d.f. = 42.1, $P = 0.91$; weighted $Z = 0.1$, overall $P = 0.90$).

Landscape-wide acorn availability was significantly higher in 2015 than in 2014 because the acorn crop of *Q. douglasii* was nearly tenfold greater (Fig. 1; 2014: $N_{30_{\max}} = 2.3 \pm 0.7$; 2015: $N_{30_{\max}} = 21.1 \pm 4.6$; LMM for $LN_{30_{\max}}$ between the two years: $\chi^2 = 42.9$, $P < 0.001$). *Quercus agrifolia* crops were low in both years and did not differ significantly (2014: $N_{30_{\max}} = 4.7 \pm 2.4$; 2015: $N_{30_{\max}} = 1.8 \pm 0.9$; $\chi^2 = 0.9$, $P = 0.35$). Similarly, landscape-wide *Q. lobata* acorn crops did not differ significantly between years (2014: $N_{30_{\max}} = 19.1 \pm 3.4$; 2015: $N_{30_{\max}} = 18.6 \pm 2.9$; $\chi^2 = 1.8$, $P = 0.18$). (Note that landscape-wide *Q. lobata* acorn crop estimates are lower than those of focal trees because of the inclusion of trees that did not produce acorns.)

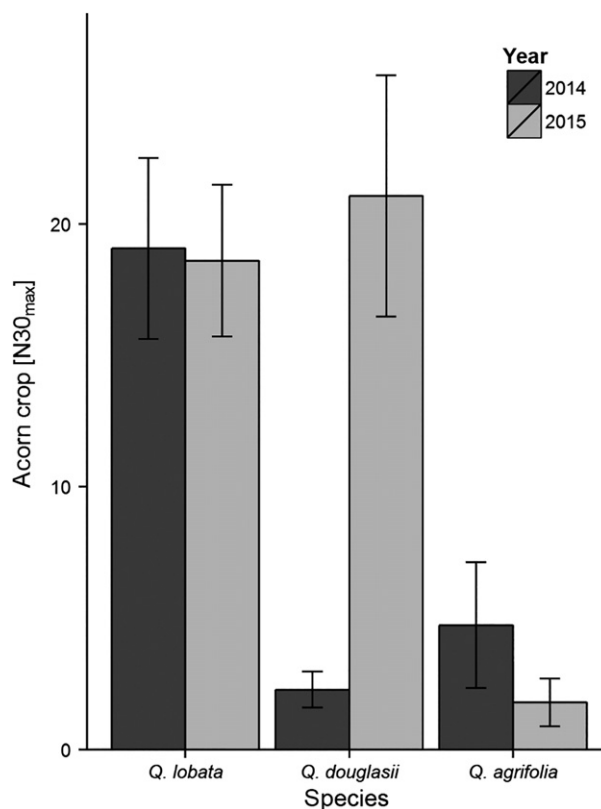


Fig. 1. Landscape-wide acorn availability at Hastings Reservation in the two study years: Mean (\pm SE) $N_{30_{\max}}$ values for *Quercus lobata* ($n = 84$ trees), *Q. douglasii* ($n = 60$) and *Q. agrifolia* ($n = 52$). See Results for statistical comparisons.

AGGRESSION

Overall aggression, quantified by displacement rates during focal watches, was more frequent in 2014 when acorns were scarce in the landscape (Table 2; 2014: 6.4 ± 0.8 h⁻¹; 2015: 1.2 ± 0.2 h⁻¹, $\chi^2 = 132.6$, $P < 0.001$), and increased with an individual tree's acorn count ($LN_{30_{\max}}$: $B = 0.19$, $\chi^2 = 38.3$, $P < 0.001$), but not their interaction ($Year \times LN_{30_{\max}}$: $B = 0.006$, $\chi^2 = 0.3$, $P = 0.56$). Displacement rates also correlated strongly with attendance by each species (n_{acwo} : $B = 0.40$, $\chi^2 = 222.7$, $P < 0.001$; n_{wesj} : $B = 0.15$, $\chi^2 = 190.9$, $P < 0.001$). In 2015, intra- and interspecific rates of aggression were significantly lower for acorn woodpeckers ($Year$: $ACWO > ACWO$: $B = -1.7$, $\chi^2 = 64.4$, $P < 0.001$; $ACWO > WESJ$: $B = -1.0$, $\chi^2 = 63.3$, $P < 0.001$) and California scrub-jays showed less intraspecific aggression at *Q. lobata* trees ($B = -0.93$, $\chi^2 = 25.1$, $P < 0.001$). In summary, we observed fewer aggressive interactions, particularly those aimed at California scrub-jays, when acorns were abundant in 2015.

NUMERICAL, FUNCTIONAL AND OVERALL RESPONSE BY HOARDERS

The numerical response of the number of birds attending *Q. lobata* trees correlated positively with the acorn crop of

Table 2. Mean (\pm SE) rates of intra- and interspecific aggression h^{-1} among dominant avian hoarders at *Quercus lobata* trees in years of low (2014; $n = 196$ h of observation) and high (2015; $n = 301$ h) landscape acorn availability. Bold values indicate significant differences between years, see Results for statistical models

↓ Aggressor/Recipient →	2014		2015	
	California scrub-jay	Acorn woodpecker	California scrub-jay	Acorn woodpecker
California scrub-jay	1.4 \pm 0.3	0.01 \pm 0.01	0.2 \pm 0.1	0.01 \pm 0.01
Acorn woodpecker	3.7 \pm 0.7	1.0 \pm 0.1	0.5 \pm 0.1	0.3 \pm 0.1

individual *Q. lobata* trees, but this relationship varied with year and bird species (Table 3a). The number of California scrub-jays attending *Q. lobata* trees was higher in 2014 ($2.7 \pm 0.2 \text{ h}^{-1}$; 2015: $1.0 \pm 0.1 \text{ h}^{-1}$) and increased strongly with individual acorn count in 2014 ($B = 0.36$) when landscape acorn availability was low, while the response was significantly weaker in 2015 when acorn availability was relatively high (Fig. 2a; $B = 0.12$; $Year \times \text{LN30}_{\text{day}}$: $\chi^2 = 15.5$, $P < 0.001$). Scrub-jay attendance correlated positively with acorn woodpecker attendance (n_{acwo} : $\chi^2 = 23.3$, $P < 0.001$).

In contrast, tree attendance by acorn woodpeckers was similar between years (Fig. 2b; 2014: $1.9 \pm 0.1 \text{ h}^{-1}$; 2015: $1.7 \pm 0.1 \text{ h}^{-1}$) and best predicted by the presence of California scrub-jays (Table 3a; n_{wesj} : $\chi^2 = 27.8$, $P < 0.001$). The significant interaction between *Year* and LN30_{day} indicated that woodpecker attendance correlated more strongly with the acorn crop in 2015 than in 2014 (Fig. 2b; $Year \times \text{LN30}_{\text{day}}$: $\chi^2 = 6.4$, $P = 0.011$), but the relationship was weak in both years (LMM for 2014: $B = 0.09$; 2015: $B = 0.12$).

The functional response of individual birds, quantified by the per capita rate of acorn hoarding, varied with immediate acorn availability on the focal tree and the presence of conspecifics, but not between years or its interaction with acorn count (Table 3b). Hoarding rates of individual California scrub-jays increased most strongly with acorn availability on focal trees (Fig. 2c; LN30_{day} : $\chi^2 = 8.7$, $P = 0.003$) and the number of jays foraging in that tree (n_{wesj} : $\chi^2 = 19.5$, $P < 0.001$). This pattern was mirrored for acorn woodpeckers in the presence of their conspecifics (Table 3b; LN30_{day} : $\chi^2 = 8.7$, $P = 0.003$; n_{acwo} : $\chi^2 = 9.6$, $P = 0.002$).

Combined, the functional and numerical response to *Q. lobata* and landscape-wide acorn availability resulted in strong differences in the rates at which each species removed acorns, which was also reflected in the total numbers of acorns removed (Tables 3c and 4). In the year of low landscape-wide acorn availability, California scrub-jays showed high removal rates from trees with large acorn crops, while removal rates were low across all trees when acorn were abundant (Fig. 2e; $Year \times \text{LN30}_{\text{day}}$: $\chi^2 = 8.7$, $P = 0.04$). This difference was largely driven by the numerical response by the jays, which also further increased the functional response (Table 3b and c). In contrast, acorn woodpecker removed acorns at higher rates from trees

with larger acorn crops, but this response was driven by per capita removal rates and did not change between years of different landscape-wide acorn availability (Fig. 2f).

A path analysis based on a piecewise structural equation model confirmed the directionality of these relationships (Fig. 3). *Year* was the strongest driver of the scrub-jays' numerical response, which then increased the species-level hoarding rate directly, as well as indirectly by affecting the birds' functional response. Furthermore, the analysis showed that aggression increased in response to bird attendance and that it had only a small effect on overall acorn hoarding rates. The rate at which acorn woodpeckers removed acorns from *Q. lobata* trees was mainly driven by their functional response, the increase of per capita foraging rate on trees with large acorn crops.

Discussion

Our results suggest that seed predation and dispersal of *Q. lobata* acorns by avian hoarders vary both with the acorn crop of individual trees and with community-wide acorn availability, largely driven by *Q. douglasii*. Acorn woodpeckers, which are low-quality seed dispersers with a relatively small spatial scale of resource perception, exhibited a functional response to acorn abundance – increased per capita acorn hoarding rates at trees with large acorn crops – and their behaviour was not significantly altered by differing landscape-wide acorn availability between years (Fig. 3). In contrast, California scrub-jays, high-quality dispersers with a relatively large spatial scale of perception, showed both the numerical and functional responses to *Q. lobata* acorn crops when landscape-wide acorn availability was low, but this response was absent in the subsequent year when *Q. douglasii*, the dominant oak species in the area, had larger acorn crops. In combination, the different responses of these avian hoarders to variation of individual- and landscape-level acorn availabilities resulted in strongly reduced high-quality dispersal for *Q. lobata* trees when competing oak species in the community produced more acorns (Fig. 4). While previous work has shown that mast species composition can affect the general effectiveness of seed dispersal by rodents because of their preferences for certain seed traits (Lichti *et al.* 2014; Xiao & Zhang 2016), our study suggests that such community effects could also arise from the spatial scale over which acorn-hoarders forage. In 2014, when

Table 3. Context dependence of (a) numerical, (b) functional response and (c) species-level acorn hoarding rates h^{-1} by California scrub-jays and acorn woodpeckers on acorn count of individual *Quercus lobata* and across the landscape (*Year*), as well as on aggression and species attendance (b and c only)

Parameter*	<i>B</i>	SE	χ^2	<i>P</i>
(a) Numerical response (attendance)				
<i>California scrub-jays</i>				
Year (2015)	-0.567	0.059	13.2	< 0.001
Acorn count (LN30 _{day})	0.216	0.040	105.5	< 0.001
<i>n</i> _{acwo}	0.090	0.019	23.3	< 0.001
Year × acorn count	-0.199	0.050	15.5	< 0.001
<i>Acorn woodpeckers</i>				
Year (2015)	0.067	0.062	1.5	0.225
Acorn count (LN30 _{day})	-0.047	0.040	4.2	0.040
<i>n</i> _{wesj}	0.070	0.013	27.8	< 0.001
Year × acorn count	0.150	0.049	9.3	0.002
(b) Functional response (per capita harvesting rates)				
<i>California scrub-jays</i>				
Year (2015)	0.048	0.139	0.3	0.557
Acorn count (LN30 _{day})	0.240	0.104	8.7	0.002
<i>n</i> _{wesj}	0.278	0.041	46.8	< 0.001
<i>n</i> _{acwo}	0.014	0.043	0.1	0.752
Displacement rate	0.051	0.011	20.9	< 0.001
Year × acorn count	-0.079	0.128	0.4	0.535
<i>Acorn woodpeckers</i>				
Year (2015)	-0.067	0.142	0.2	0.653
Acorn count (LN30 _{day})	0.274	0.106	9.9	0.002
<i>n</i> _{wesj}	0.014	0.041	0.1	0.735
<i>n</i> _{acwo}	0.237	0.044	28.4	< 0.001
Displacement rate	0.013	0.011	1.3	0.260
Year × acorn count	-0.115	0.130	0.8	0.376
(c) Overall response (species-level harvesting rates)				
<i>California scrub-jays</i>				
Year (2015)	-0.070	0.063	1.1	0.289
Acorn count (LN30 _{day})	0.205	0.047	19.9	< 0.001
<i>n</i> _{wesj}	0.243	0.019	171.6	< 0.001
<i>n</i> _{acwo}	-0.004	0.020	<0.1	0.831
Displacement rate	0.026	0.005	23.3	< 0.001
Year × acorn count	-0.120	0.058	5.9	0.039
<i>Acorn woodpeckers</i>				
Year (2015)	-0.008	0.077	<0.1	0.937
Acorn count (LN30 _{day})	0.178	0.055	14.4	< 0.001
<i>n</i> _{wesj}	0.018	0.022	0.7	0.416
<i>n</i> _{acwo}	0.224	0.024	87.5	< 0.001
Displacement rate	0.004	0.006	0.6	0.455
Year × Acorn count	-0.080	0.067	1.4	0.232

*Parameter estimates (*B*), their standard error (SE) and associated χ^2 values and *P*-values for fixed effects of LMMs with *Individual Tree* as slope-only random effect. Note that for (a) and (c), dependent variables were *ln*-transformed for analysis. See Materials and methods for specifics on model construction. Bold values denote statistically significant effects.

Q. lobata acorns competed with few other acorns in the landscape for generalist seed dispersers, foraging behaviour in each tree reflected its acorn crop size, both by the large attendance and high per capita harvesting rates (Pesendorfer & Koenig 2016a).

Attendance at large-crop trees was also associated with the significant costs of aggressive intra- and interspecific encounters. The confirmatory path analysis indicated that the frequency of aggressive interactions was largely driven

by the numerical response of the competing bird species. In 2015, when tree attendance by California scrub-jays was strongly reduced, we barely recorded any aggressive displacement among and within the two species. This may have been the consequence of jays to maximizing their benefits over a much larger scale by foraging on *Q. douglasii* acorns. In turn, acorn woodpeckers were able to optimize foraging behaviour on their preferred acorns under reduced competition. Consequently, *Q. lobata* trees experienced a higher proportion of low-quality seed dispersal. The combination of different spatial scales of resource perception by the two species of hoarders and individual and community-wide acorn availabilities appeared to result in a strong effect on the proportional distribution of acorns harvested by high- and low-quality dispersers of *Q. lobata* acorns.

In addition to the relative availability of acorns, other mechanisms may have contributed to the shift in foraging behaviour between years. The variation in acorn foraging by the California scrub-jays could, in part, be due to a preference for *Q. douglasii* acorns. This is unlikely, however, because jays generally prefer low-tannin seeds with high nutritional value, and *Q. douglasii* acorns contain more than 30% hydrolysable tannins compared to less than 8% in *Q. lobata* acorns (Koenig & Faeth 1998). Similarly, Florida scrub-jays (*A. coerulescens*) prefer caching acorns that rapidly lose tannins after caching (Fleck & Woolfenden 1997), and both California scrub-jays and blue jays (*Cyanocitta cristata*) exhibit negative responses to diets with high-tannins, phenolic compounds that interfere with regular digestion of proteins (Koenig & Heck 1988; Fleck & Tomback 1996; Dixon, Johnson & Adkisson 1997). Furthermore, whereas *Q. douglasii* acorns contain slightly higher levels of proteins and lipids than *Q. lobata* (Koenig & Heck 1988), *Q. lobata* acorns are on average about 40% heavier than *Q. douglasii* acorns (Aizen & Patterson 1990), thus providing more energy per transported acorn.

Additional caveats in our study deserve consideration in future work. For example, additional study years would allow us to obtain quantitative estimates of the response of avian hoarders to the interaction of acorn preferences and their relative availability, as well as further details about the effect of variation in landscape-wide acorn production. Specifically, increased acorn production by *Q. agrifolia*, the dominant oak species at our study site, may result in more complex indirect interactions among the oak species, all mediated by seed predators and dispersers. Nonetheless, the strong differences we observed between the two years of our study provide qualitative support for the role of avian hoarders as mediators of indirect ecological effects among coexisting oak trees.

In addition, potential covariates of acorn production, including differences in predation pressure and insect abundance, may have differed between years but were not addressed in this study. When foraging on oaks, adult California scrub-jays and acorn woodpeckers mostly face

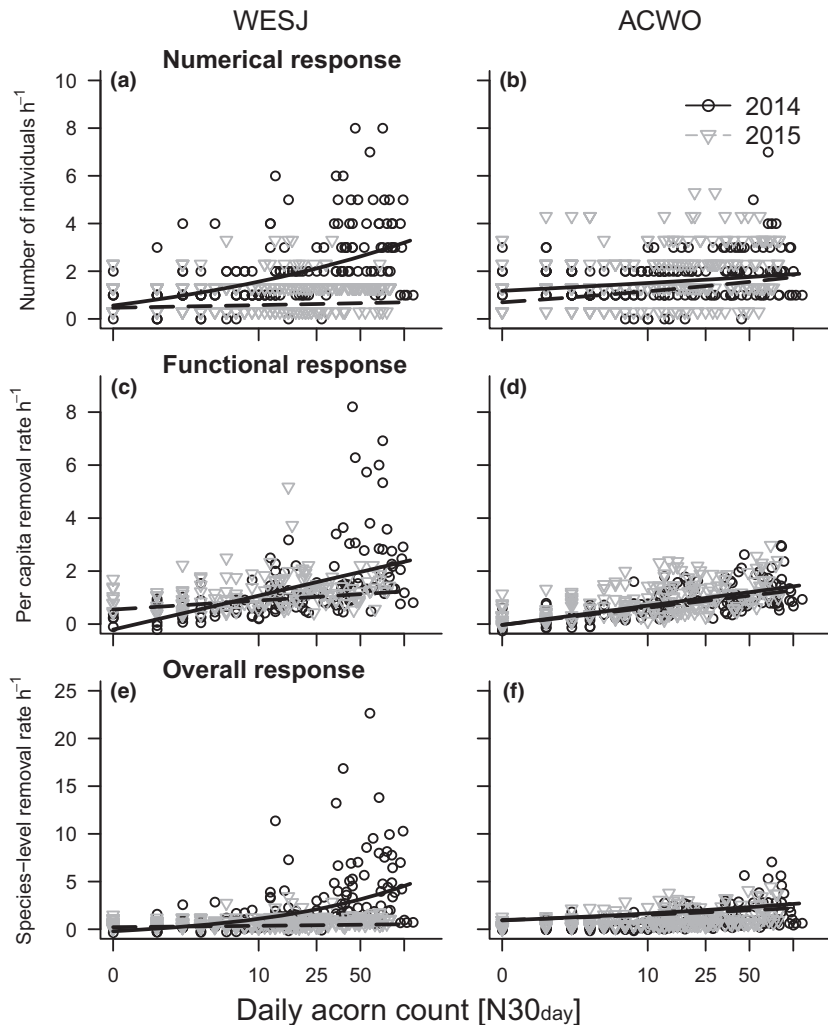


Fig. 2. Context dependence of *Q. lobata* acorn harvesting by California scrub-jays (WESJ) and acorn woodpeckers (ACWO) as a function of daily individual acorn count ($LN30_{day}$) in years of low (2014) and high (2015) landscape acorn availability; (a, b) numerical response, (c, d) functional response and (e, f) overall response. Model-predicted, back-transformed values from models presented in Table 2. Lines indicate modelled relationships between parameters (dashed lines: 2014, $n = 196$ h of focal observations; solid lines: 2015, $n = 301$ h). For illustrative purposes, three outliers were excluded from panel e, each with $LN30_{day} > 4$ and species-level hoarding rate > 25 .

Table 4. Fate of *Quercus lobata* acorns handled by dominant avian hoarders in years of low (2014) and high (2015) landscape acorn availability

Acorns*	California scrub-jay			Acorn woodpecker		
	Count	% _{all}	% _{spec}	Count	% _{all}	% _{spec}
2014						
Handled	2396	81.6		348	11.9	
Eaten	1083	90.3	45.2	36	3.0	10.3
Transported	1313	76.6	54.8	312	18.2	89.7
2015						
Handled	366	41.1		475	53.4	
Eaten	80	79.2	21.9	6	5.9	1.3
Transported	286	36.2	78.1	469	59.4	98.7

*Total count, percentage of all acorns and percentage within each species of acorns handled, eaten and transported during focal observations in 2014 ($n = 196$ h of observation) and 2015 (301 h); dropped acorns excluded.

predation pressure by aerial predators, predominantly by Cooper's hawks (*Accipiter cooperii*) and great horned owls (*Bubo virginianus*) (Koenig *et al.* 1995; Curry, Townsend Peterson & Langen 2002). Systematic surveys for avian

predators might potentially reveal interannual differences in predation pressure that could have unexpected effects on the foraging behaviour of the birds across years.

Acorn crop size variation also affects the proportion of acorns that is infested with weevil (*Curculio* spp.) and other insect larvae and could affect acorn choice preferences by California avian hoarders. Larger acorn crops generally result in lower proportional weevil infestation for *Q. lobata* (Koenig, Knops & Carmen 2002). If pre-dispersal predation by insects drives interspecific variation in acorn harvesting, these findings would thus suggest a pattern opposite to the one found: in years of low overall acorn crops, acorn harvesting rates by birds that avoid infested acorns should be lower, as the proportion of infested acorns is higher (Pesendorfer & Koenig 2016a; Pesendorfer *et al.* 2016b).

APPARENT PREDATION IN COMMUNITIES OF MASTING SPECIES

The interaction we observed among competing oak species can be considered a case of apparent predation because the changes in acorn harvesting were not mediated by a

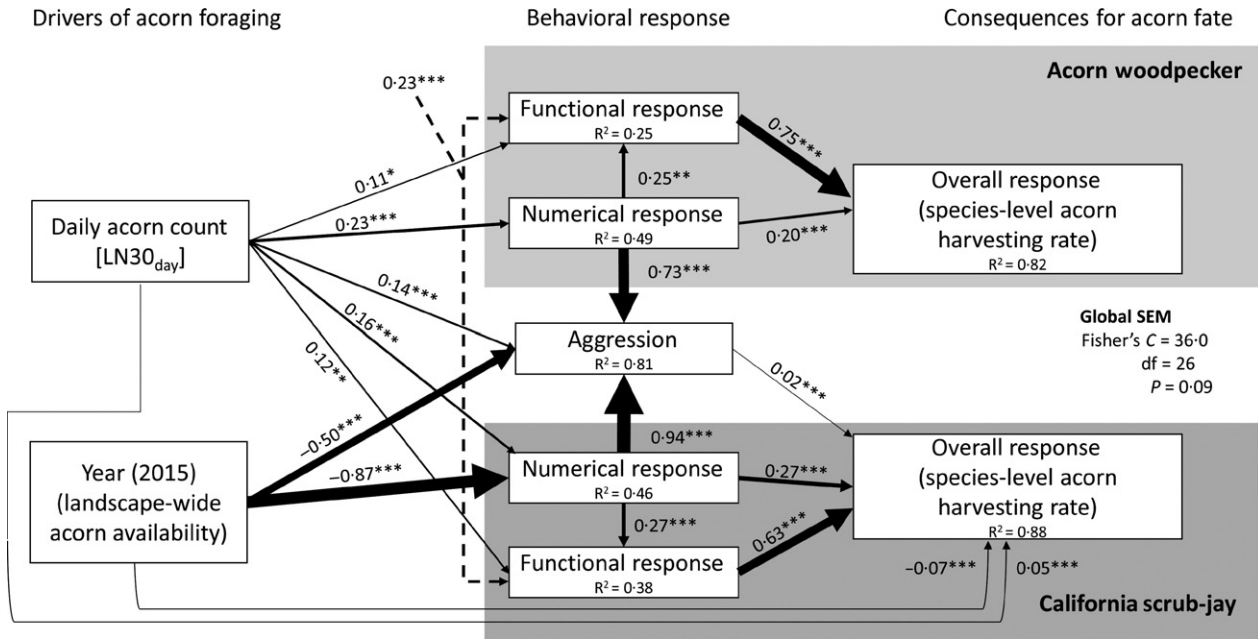


Fig. 3. Confirmatory path analysis of relationship among drivers, behavioural response and acorn hoarding rates of California scrub-jays and acorn woodpeckers on *Quercus lobata* trees. Boxes represent measured variables (*functional response*: per capita harvesting rate; *numerical response*: number of birds attending tree; *overall response*: species-level harvesting rate). Arrows represent unidirectional relationships among variables, and thickness is scaled based on the magnitude of the standardized regression coefficient, which is indicated above paths. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Component model R^2 is shown in boxes of response variables. All models contained random effect *Tree ID* to account for repeated sampling of focal trees. See Appendix S1 for details.

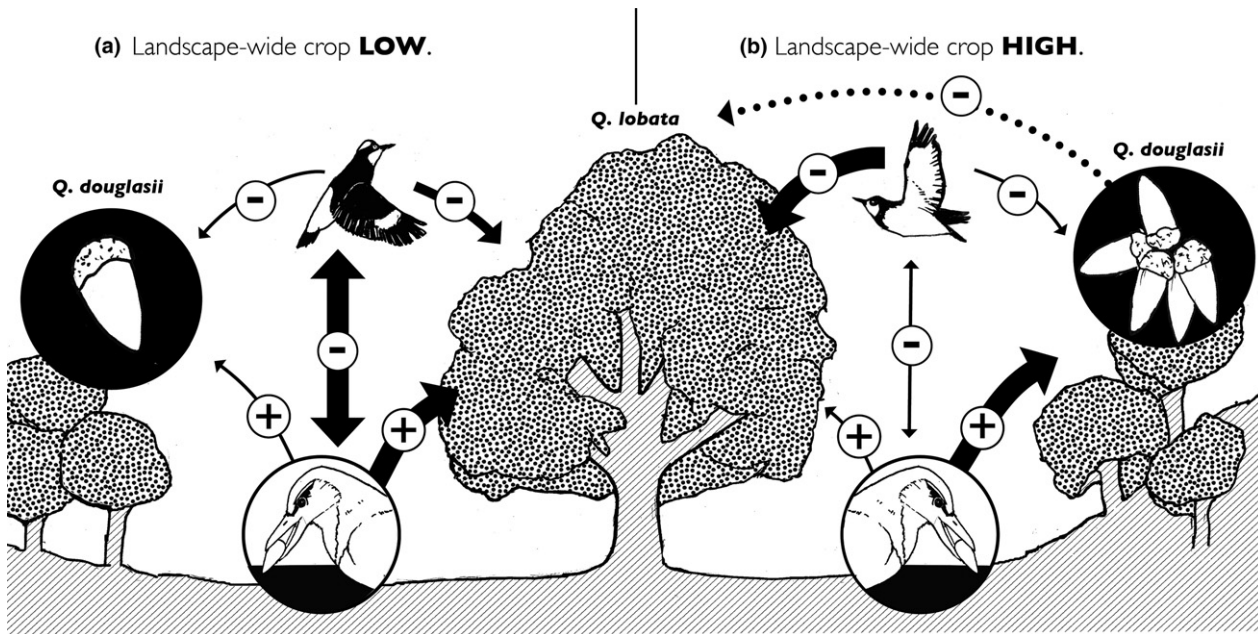


Fig. 4. Schematic representation of apparent predation among *Quercus lobata* and *Q. douglasii* at Hastings Reservation: (a) when landscape-wide acorn availability, driven by *Q. douglasii*, was low, California scrub-jays (*Aphelocoma californica*) showed a strong numerical and functional responses to *Q. lobata* acorn crops, providing high-quality seed dispersal; (b) when *Q. douglasii* acorn crops were large, *Q. lobata* acorns were predominantly harvested by acorn woodpeckers, low-quality dispersers that are mostly predators. Therefore, seed production in *Q. douglasii* indirectly affected the seed fate of *Q. lobata* acorns, as indicated by the dashed arrow.

‘pure’ predator, but rather by the allocation of the mutualistic interactions to a different plant partner. The only significant change in landscape-wide acorn availability was

driven by *Q. douglasii* acorns, which received increased high-quality dispersal from California scrub-jays when acorns were abundant, causing the previously mutualistic

interaction between *Q. lobata* and the jays to largely disappear. Interestingly, the change was mediated by a numerical response in tree attendance that differs from other indirect interactions in which the numerical response is driven by differing demographic responses of predators or prey (Abrams, Holt & Roth 1998). Scrub-jay and woodpecker demographic rates are indeed associated with crop sizes in oaks, but usually with a lag of 1 or 2 years (Koenig & Haydock 1999; Koenig *et al.* 2009). The change in numerical response to *Q. lobata* acorns we observed occurred within a much shorter time span and was therefore likely due to a spatial shift in foraging rather than demographic shifts in the bird populations. These changes in apparent predation effects mediated by seed dispersers would constitute a novel pathway for indirect interactions among sympatric competitors.

In communities with multiple masting species, indirect effects mediated by context-dependent seed dispersal by generalist hoarders may have wide-ranging effects on relative recruitment of plant species and thus on community composition. Recently, Yi & Wang (2015) showed that in a Chinese community of three competing oak species, acorn removal rates and seedling establishment were determined by the relative levels of seed production. Similarly, Lichti *et al.* (2014) reported that seed traits of American chestnut (*Castanea dentata*) and acorns drive context-dependent seed dispersal effects in hardwood forests of eastern North America.

As a consequence of apparent predation, masting species should experience selection for asynchronous masting patterns if they rely on the same generalist disperser. In our study system, two of the three species of common oaks are strongly synchronized in their acorn production (Koenig & Knops 2013). Other drivers of masting, such as economies of scale associated with increased pollination efficiency and similar abiotic drivers of population-level seed production, presumably counteract such selection for asynchrony. On a broader scale, temporally variable indirect effects mediated by shared predators and dispersers may provide a mechanism for coexistence among species, allowing species that are generally out-competed (in this case for seed dispersal) to be more successful in some years (Kneitel & Chesson 2004). Disentangling the long-term fitness consequences of such interactions among coexisting oaks will require additional years of research. This study provides a qualitative account of potential mechanisms underlying such indirect effects, thus laying the foundation for a quantitative understanding of the phenomenon of apparent predation.

In summary, our findings demonstrate the considerable differences that can exist in the interactions between seed predators and seed producers from one year to the next. In order to gain a more complete understanding of the selective drivers of synchronous seed production within and among species of large-seeded trees, it is thus paramount to explore the fitness consequences of temporally variable seed production in the light of context-dependent

seed dispersal and predation and the cumulative fitness effects over a plant's lifetime.

Authors' contributions

M.B.P. and W.D.K. conceived and designed the study; M.B.P. collected and analysed the data; M.B.P. and W.D.K. wrote the manuscript.

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Data accessibility

Data are deposited in Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.1sc1s> (Pesendorfer & Koenig 2016b).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Confirmatory path analysis details.

Table S1. Missing paths in D-Sep analysis.

Table S2. Confirmatory path analysis results.