Behavioral Ecology and Sociobiology (2018) 72: 85
https://doi.org/10.1007/s00265-018-2498-2

ORIGINAL ARTICLE

# Does aggression avoidance drive oak tree attendance by corvid scatter-hoarders?

Mario B. Pesendorfer[1,2,3] · Walter D. Koenig[1,3,4]

Received: 10 November 2017 / Revised: 23 April 2018 / Accepted: 27 April 2018 / Published online: 7 May 2018


## Abstract

We investigated the role of species- and community-wide seed production by a community of oaks (*Quercus* spp.) in influencing tree attendance and aggression among California scrub-jays (*Aphelocoma californica*), corvids that are seed dispersal mutualists, and acorn woodpeckers (*Melanerpes formicivorus*), near-exclusive seed predators. We tested the hypothesis that scrub-jays reduce their attendance in response to seed crop size on *Quercus lobata*, the species preferentially attended by acorn woodpeckers, and therefore reduce the risk of potential injury from aggression when community-level seed production enables them to forage on other trees (the "aggression-avoidance" hypothesis). Results indicated that scrub-jay attendance correlated positively with *Q. lobata* crops during the year when community-level seed production was low, resulting in high levels of aggression. In contrast, during the 2 years when acorns of other species were abundant in the landscape, scrub-jays reduced attendance at *Q. lobata* and experienced less aggression. Similarly, we found that the scrub-jays experienced equally low rates of aggression at *Q. douglasii* trees that were attended by fewer acorn woodpeckers. These results support the aggression-avoidance hypothesis and illustrate how resource and social dynamics may interact to determine the attendance of mutualistic seed dispersers at oak species competing for seed dispersal. Furthermore, they show that intra- and interspecific social interactions at the seed source, as well as at caching locations, affect the scatter-hoarding behavior of wild corvids.

## Significance statement

Food-hoarding animals play a central role in determining the seed fate of large-seeded trees, both in the role of predators and dispersers. Tree attendance and seed hoarding, however, are often context-dependent, varying with population- and community-level seed production, and with intra- and interspecific social dynamics. In California oak communities, acorn woodpeckers—seed predators—compete with California scrub-jays—high-quality seed dispersers—for acorns on preferred trees, resulting in considerable levels of aggression. Using behavioral observations at two species of oaks, one of which is preferred by the woodpeckers, we determined that aggression avoidance explained tree attendance behavior of the scrub-jays, but only when landscape-wide seed production allowed them to forage elsewhere. Our results show for the first time that seed dispersal by hoarding animals can be affected by intra- and interspecific aggression at the seed source.

**Keywords** Aggression · *Aphelocoma californica* · Context-dependence · *Melanerpes formicivorus* · *Quercus lobata* · *Quercus douglasii* · Scatter-hoarding · Seed dispersal

Communicated by P. A. Bednekoff

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s00265-018-2498-2) contains supplementary material, which is available to authorized users.

✉ Mario B. Pesendorfer
mbp67@cornell.edu

1 Lab of Ornithology, Cornell University, Ithaca, NY, USA

2 Migratory Bird Center, Smithsonian Conservation Biology Institute, Washington, DC, USA

3 Hastings Natural History Reservation, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924, USA

4 Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, USA

## Introduction

Avian hoarders play a central role in seed predation and dispersal dynamics of many large-seeded trees (Vander Wall 2001; Pesendorfer et al. 2016a). Because food-hoarding behavior is often context-dependent, however, the impact of birds on seed fate can vary strongly with local and landscape-wide seed production (Vander Wall 2002; Pesendorfer and Koenig 2016; Pesendorfer et al. 2016b). For mast-seeding trees—species with synchronous intermittent bumper crops of seeds or fruit—such context-dependence has important fitness consequences, as species interactions with hoarders can change from seed predation to seed dispersal mutualism depending on the size of the seed crop (Jansen et al. 2004; Siepielski and Benkman 2007; Bogdziewicz et al. 2016). Furthermore, seed hoarders can drive indirect competition among multiple mast-seeding species because relative seed production levels and antagonistic interactions among hoarders can affect tree attendance and seed hoarding rates, ultimately driving seed fate (Lichti et al. 2014; Yi and Wang 2015; Pesendorfer and Koenig 2017). The behavioral mechanisms underlying such context-dependence, however, are still poorly understood (Cousens et al. 2010). We investigated tree attendance and antagonistic interactions by two avian seed hoarders to test the hypothesis that inter- and intraspecific aggression, or the avoidance thereof, mediates the birds' variation in tree attendance in response to acorn abundance, thus contributing to indirect competition for seed dispersal among the trees.

Indirect ecological effects arise when two species interact via a third, such as shared prey or predators (Chase et al. 2002). One such effect, termed "apparent predation," occurs when Species A increases the mortality of Species B by diverting the mutualistic effects of Species C (Lichti et al. 2014; Pesendorfer and Koenig 2017). In a California oak community, for example, we found that California scrub-jays (*Aphelocoma californica*), high-quality seed dispersers that cache seeds into the ground throughout the landscape, were the dominant hoarders of *Q. lobata* (valley oak) acorns, accounting for 77% of all acorns hoarded, when competing that *Quercus douglasii* (blue oak) had very low acorn crops (2014; Fig. 1). In the following year, when competing *Q. douglasii* produced a large acorn crop, the jays only accounted for 36% of hoarded *Q. lobata* acorns, which were produced at similar levels (2015; Fig. 1). In contrast, the proportion of acorns removed by acorn woodpeckers (*Melanerpes formicivorus*), near-exclusive seed predators, increased from 18 to 59%, therefore strongly affecting seed mortality. Importantly, our analysis showed that the rate of intra- and interspecific aggression experienced by the jays declined precipitously in response to their reduced attendance at valley oaks (Pesendorfer and Koenig 2017). Therefore, we hypothesized that jays avoid *Q. lobata* trees when acorns of other species are available to reduce the risk of injury from aggression by competing conspecifics and woodpeckers.

The scatter-hoarding behavior of corvids is sensitive to social context and resource abundance. To avoid cache pilferage, for example, the birds will use a variety of cache protection strategies such as mock caching and re-caching if observed (Dally et al. 2006), or position themselves in a way to avoid observation of the cache location by others (Bugnyar and Kotrschal 2002). Similarly, if experiencing high levels of pilfering, black-billed magpies (*Pica pica*) reduce the spatial density of caches (Clarkson et al. 1986). The rate of hoarding may also vary with social context: When territorial aggression is frequent, island scrub-jays (*Aphelocoma insularis*) reduce the rate at which they handle and cache acorns, but not other food items (Pesendorfer et al. 2016b). When attending trees with large seed crops, however, California scrub-jays displayed increased per capita hoarding rates with the number of individuals present, despite high levels of interspecific aggression from woodpeckers (Pesendorfer and Koenig 2016). This suggests that the interaction between resource abundance and social effects determines where and when California scrub-jays attend oaks to hoard acorns. We further found that the jays responded flexibly to landscape-wide variation in acorn crops while acorn woodpeckers did not, suggesting that these corvids optimize foraging over larger spatial scales (Pesendorfer and Koenig 2016).

In contrast to scrub-jays, acorn woodpeckers are more oak-dependent and spatially restricted in their foraging. These cooperative breeders live in groups of 2–15 individuals that defend year-round territories around "granary trees" with specialized storing structures, consisting of several thousand holes into which acorns are placed individually (MacRoberts and MacRoberts 1976). At our study site, the woodpeckers strongly prefer *Q. lobata* for nest and granary trees among available oaks (Hooge et al. 1999) and most frequently hoard their acorns (Koenig et al. 2008). California scrub-jay acorn preferences are unclear, but *Q. lobata* acorns are generally significantly larger and contain lower concentrations of defense compounds (tannins) than *Q. douglasii* acorns (Koenig and Faeth 1998). It is therefore likely that jays preferentially feed on *Q. lobata* acorns.

Acorn woodpecker groups vigorously defend their granary and preferred acorn source trees from avian and mammal intruders and usually displace California scrub-jays with ease by conducting aerial passes (MacRoberts 1970). When intruders are reluctant to leave, however, we have observed physical contact between woodpeckers and California scrub-jays, and in least two occasions, woodpeckers were observed using their feet to actively pull jays from their perching locations, only releasing them mid-air after falling together for several meters (MBP, personal observations). Acts of intraspecific aggression with similar intensity are often observed during so-called "power struggles," during which multiple coalitions of siblings are competing for a breeding vacancy in an acorn

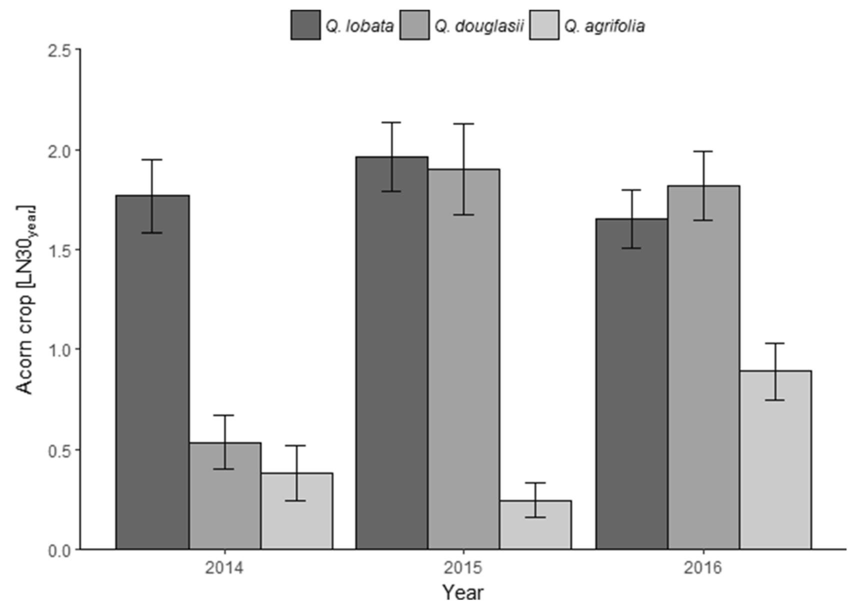


**Fig. 1** Landscape-wide acorn production 2014–2016 in the three dominant oak species at Hastings Natural History Reservation. Mean (± SE) $LN30_{year}$ for 84 *Q. lobata*, 60 *Q. douglasii*, and 52 *Q. agrifolia* trees

woodpecker group. Such confrontations frequently feature pecking, hitting with wings or feet, and grappling in mid-flight and on the ground (Koenig 1981; Hannon et al. 1985). For California scrub-jays, aggressive encounters with acorn woodpecker groups therefore pose a serious risk of injury.

Here, we test the hypothesis that California scrub-jays experience reduced intra- and interspecific aggression when community-wide seed production allows them to shift foraging to trees with fewer competitors (the "aggression-avoidance" hypothesis). The focus of this study is on the decision of the birds to attend trees, one facet of the multiple factors shaping their foraging decisions. We explored the relationship between tree attendance, per capita and species-level hoarding rates elsewhere (Pesendorfer and Koenig 2016, 2017), and discuss the results of the current study in light of our previous findings. We compared tree attendance, and inter- and intraspecific aggression directed at jays (i) within *Q. lobata* across years with variable community-wide seed production and (ii) between *Q. lobata* and *Q. douglasii* in 2016. We predicted that community-wide seed production would determine whether jays attend oaks that are attended by fewer conspecifics and woodpeckers, thereby experiencing fewer aggressive displacements per hour.

## Methods

### Study site and data collection

The study was conducted at the Hastings Natural History Reservation (HNHR) in central coastal California during acorn fruiting season (September–December) from 2014 to 2016. The study area consists of oak habitat dominated by three oak species, valley oak *Q. lobata*, blue oak *Q. douglasii*, and coast live oak *Q. agrifolia* (Koenig et al. 2008). Arboreal removal of acorns is predominantly performed (> 94%) by California scrub-jays and acorn woodpeckers. Steller's jays (*Cyanocitta stelleri*) remove < 5% of acorns and were not considered for this study.

Landscape-wide seed production at HNHR was estimated using annual acorn counts on 84 *Q. lobata*, 52 *Q. douglasii*, and 60 *Q. agrifolia* trees (Koenig et al. 1994). Using binoculars, two observers counted as many acorns as possible in 15 s; counts were then added for each tree (N30). Each year, a set of trees ("focal trees") was selected that spanned the range of acorn production values and was observed weekly throughout the fruiting season until their crops were depleted (Table 1). Acorn production of focal trees was recorded on two temporal

**Table 1** Summary statistics for focal trees

| | *Q. lobata* | | | *Q. douglasii* |
|---|---|---|---|---|
| Year | 2014 | 2015 | 2016 | 2016 |
| *N* trees | 37 | 44 | 38 | 12 |
| Acorn production ($LN30_{year}$) | 3.4 ± 0.2 | 3.3 ± 0.1 | 3.4 ± 0.1 | 3.9 ± 0.2 |
| Observation effort per tree (h) | 5.3 ± 0.4 | 6.9 ± 0.4 | 4.7 ± 0.3 | 4.8 ± 0.4 |
| Californian scrub-jay attendance ($N_{CASJ}$) | 2.7 ± 0.2 | 1.0 ± 0.1 | 2.1 ± 0.2 | 1.7 ± 0.2 |
| Acorn woodpecker attendance ($N_{ACWO}$) | 1.9 ± 0.1 | 1.7 ± 0.1 | 2.0 ± 0.2 | 1.1 ± 0.2 |

scales. First, annual seed production ($N30_{year}$) was determined at the beginning of the fruiting season. Second, because acorn availability declines throughout the fruiting season, a single observer also conducted 30-s counts before recording behavioral data ($N30_{day}$; Pesendorfer and Koenig 2016). For analysis, the count from each tree was *ln*-transformed ($LN30 = ln(N30 + 1)$) to reduce skew in the data.

To determine rates of tree attendance, intraspecific aggression, and interspecific aggression of California scrub-jays and acorn woodpeckers, we conducted 60-min watches of individually marked focal trees ("focal watches"). After a 5-min habituation period, the observer recorded the arrival and departure of all birds, their acorn foraging and hoarding, and physical displacements. A displacement was defined as the change of location by an individual that was aggressively approached by another, independent of the final outcome—that is, whether the displaced individual left the tree or relocated within the tree. Finally, the observer estimated the number of unique individuals of each bird species that attended the tree ($n_{CASJ}$, $n_{ACWO}$). While there were color-banded individuals of both species in the study area, the nature of the observations, focused on tree attendance and foraging, made it impossible to record band combinations. Therefore, the number of attending birds was estimated based on behavioral and spatial cues such as the direction from which they arrived, the number of birds simultaneously observed in the focal tree during the watch, in the context of the general knowledge of surrounding woodpecker territories and scrub-jay caching areas (Pesendorfer and Koenig 2016, 2017). The voice recording lasted the length of the focal watch and allowed us to record the timing of behavioral events during subsequent transcription into data files. The data were then used to calculate hourly behavioral rates per species and per capita for each focal watch (Pesendorfer and Koenig 2016). It was not possible to record data blind because our study involved behavioral observations of animals in the field.

## Statistical analyses

To estimate the change in annual landscape-wide seed production, we constructed linear mixed models of *ln*-transformed annual acorn counts ($LN30_{max}$) for the complete sample of each of the three dominant oak species at HNHR (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*), and for the more restricted sample of *Q. lobata* focal trees. The models contained "year" as a categorical fixed effect and "tree identity" as a random effect to account for repeated sampling (Zuur et al. 2009). To compare the annual seed production of *Q. lobata* and *Q. douglasii* focal trees in 2016, we used a one-way ANOVA.

To investigate the interrelationships between seed crop size ($LN30_{day}$), bird attendance, and aggression in trees of the two oak species, we constructed linear mixed models of focal watch data. First, we used data from the three field seasons to investigate how annual variation in relative seed production affected the behavioral dynamics in *Q. lobata*. We constructed models with species attendance, intraspecific, and interspecific aggression as dependent variables, along with seed crop size ($LN30_{day}$) and number of competitors as fixed effects. To determine the effect of community-wide variation in annual seed production, we also included year and its interaction with the other fixed effects. In a second set of analyses, we used the data from the 2016 field season to compare the behavioral dynamics between *Q. lobata* and *Q. douglasii*. At our study site, *Q. douglasii* trees occur at much higher densities than *Q. lobata*, but comparatively few larger individuals carry most acorns, making acorn harvesting harder to predict and observe. By collecting pilot data in the 2015 field season, we developed a method to reliably identify *Q. douglasii* trees visited by jays, allowing us to collect comparable data to that of *Q. lobata* trees. These models also contained seed crop size and number of competitors as fixed effect but featured "species" rather than year as an additional fixed effect. Similar to the previous analyses, we also included the interaction terms between species and the other fixed effects. All models contain tree identity as a random effect to account for repeated sampling (Zuur et al. 2009).

To analyze the causal relationship between the observed variables each year, we conducted separate confirmatory path analyses for each year/tree species combination while accounting for repeated sampling of focal trees (Shipley 2009; Lefcheck 2016). Model structure was based on the linear mixed models above, and support for the graphical hypotheses was assessed using Fisher's *C* test, for which $P > 0.05$

**Table 2** Drivers of attendance in *Q. lobata* focal trees 2014–2016. (a) California scrub-jay (CASJ) attendance per hour and (b) acorn woodpecker (ACWO) attendance per hour as a function of daily acorn crop estimate ($LN30_{day}$) and study year

| | $\chi^2$ | *df* | *P* |
|---|---|---|---|
| (a) $N_{CASJ}$ | | | |
| $LN30_{day}$ | 18.1 | 1 | *< 0.001* |
| $N_{ACWO}$ | 30.5 | 1 | *< 0.001* |
| Year | 79.2 | 2 | *< 0.001* |
| $LN30_{day}$ × year | 24.8 | 2 | *< 0.001* |
| $N_{ACWO}$ × year | 23.3 | 2 | *< 0.001* |
| (b) $N_{ACWO}$ | | | |
| $LN30_{day}$ | 4.4 | 1 | *0.035* |
| $N_{CASJ}$ | 33.1 | 1 | *< 0.001* |
| Year | 9.0 | 2 | *0.011* |
| $LN30_{day}$ × year | 6.4 | 2 | *0.042* |
| $N_{CASJ}$ × year | 0.6 | 2 | 0.734 |

$\chi^2$, degrees of freedom and *P* values of Wald Type II tests for fixed effects in linear models with "tree identity" as random effect. Full modeling results are presented in Tables S1 and S2

Italicized values indicate $P < 0.05$

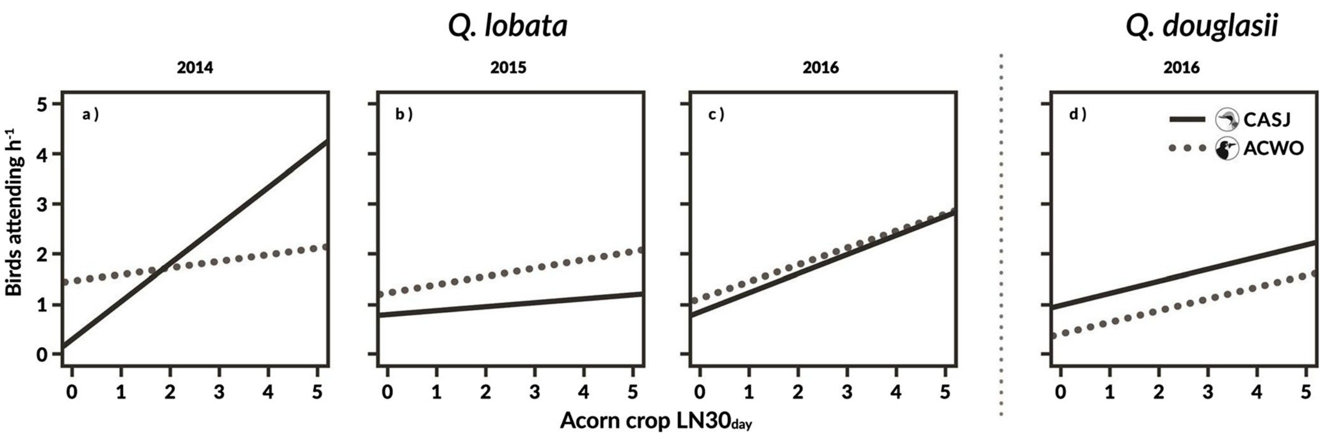


**Fig. 2** Context-dependent attendance of avian hoarders at *Q. lobata* (2014–2016; **a**–**c**) and *Q. douglasii* (2016; **d**) focal trees. Number of unique individuals attending during hourly watches as a function of acorn crop; solid line: California scrub-jays (CASJ); dotted line: acorn woodpeckers (ACWO). Lines indicate linear relationship from Linear Mixed Models presented in Tables 2, 3, and S1–S4

confirms the directionality of effects (Shipley 2009). We provide individual analyses for each year in Appendix S2.

All analyses were conducted in R 3.1 (R Development Core Team 2016). Linear mixed models (LMMs) and general linear mixed models (GLMMs) were constructed with "lme4" (Bates et al. 2015), and we report degrees of freedom, $\chi^2$, and $P$ values of fixed effects from Wald Type II tests in the package "car" (Fox and Weisberg 2011). Full LMM results are presented in Appendix S1. Confirmatory path analyses were conducted in the package "piecewiseSEM" (Lefcheck 2016). Unless noted otherwise, we report mean ± standard error (SE) throughout.

## Results

Landscape-wide seed production ($LN30_{year}$) at HNHR differed significantly in the 3 years of the study in *Q. douglasii* ($\chi^2 = 32.4$, $df = 2$, $P < 0.001$; Fig. 1) and *Q. agrifolia* ($\chi^2 = 23.5$, $df = 2$, $P < 0.001$), but not in *Q. lobata* ($\chi^2 = 4.8$, $df = 2$, $P = 0.09$). Annual seed production by the smaller sample of focal trees did not differ significantly between study years in *Q. lobata* (Table 1; $\chi^2 = 0.3$, $df = 2$, $P = 0.85$), or among *Q. lobata* and *Q. douglasii* in 2016 ($F_{1,48} = 3.0$, $P = 0.09$).

We conducted a total of 680 h of *Q. lobata* focal watches with an average of 5.7 ± 0.2 h per focal tree per year. In 2016, we also recorded 58 h of focal watches on *Q. douglasii* with an average of 4.8 ± 0.4 h per tree.

Overall, tree attendance at *Q. lobata* focal trees was similar for California scrub-jays ($N_{CASJ}$ 1.75 ± 0.09) and acorn woodpeckers ($N_{ACWO}$ 1.83 ± 0.07) but varied as a function of the available acorn crop, both on individual trees ($LN30_{day}$) as well as between years with different landscape-wide acorn crops, as identified by their interaction term (Table 2 (a); Fig. 2a–d). Specifically, California scrub-jays' tree attendance was strongly affected by acorn crops in 2014, when acorns of other species were scarce (Fig. 2a), but not in subsequent years when acorns of other species were relatively abundant (Fig. 2b–d). In contrast, acorn woodpeckers showed a weak attendance response to acorn crops that differed significantly as a function of year but strongly correlated with scrub-jay attendance (Fig. 2a–d; Table 2 (b)).

Attendance of the two bird species at *Q. lobata* focal trees was positively correlated (Table 2 (a, b); $\chi^2 > 30$, $P < 0.001$). In 2016, California scrub-jays attended *Q. douglasii* focal trees more frequently than acorn woodpeckers ($N_{CASJ}$ 1.7 ± 0.2; $N_{ACWO}$ 1.1 ± 0.2; paired $t$ test $t = -3.0$, $df = 57$, $P = 0.004$). However, attendance of California scrub-jays still correlated with that of acorn woodpeckers and did so more

**Table 3** Drivers hourly attendance at *Q. lobata* and *Q. douglasii* in 2016 for (a) California scrub-jays (CASJ) and (b) acorn woodpeckers (ACWO) as a function of daily acorn crop estimate ($LN30_{day}$) and oak species

| | $\chi^2$ | *df* | *P* |
|---|---|---|---|
| (a) $N_{CASJ}$ | | | |
| $LN30_{day}$ | 3.3 | 1 | 0.069 |
| $N_{ACWO}$ | 19.7 | 1 | *< 0.001* |
| Oak species | < 0.01 | 1 | 0.991 |
| $LN30_{day}$ × oak sp. | 0.7 | 1 | 0.389 |
| $N_{ACWO}$ × oak sp. | 6.8 | 1 | *0.009* |
| (b) $N_{ACWO}$ | | | |
| $LN30_{day}$ | 3.7 | 1 | 0.053 |
| $N_{CASJ}$ | 21.0 | 1 | *< 0.001* |
| Oak species | 2.8 | 1 | 0.093 |
| $LN30_{day}$ × oak sp. | 0.2 | 1 | 0.643 |
| $N_{CASJ}$ × oak sp. | 2.7 | 1 | 0.100 |

$\chi^2$, degrees of freedom, and $P$ values of Wald Type II tests for fixed effects in linear models with "tree identity" as random effect. Full modeling results are presented in Tables S3 and S4

Italicized values indicate $P < 0.05$

strongly in *Q. douglasii* (LMM $B = 0.73$, $t = 5.0$) than in *Q. lobata* (LMM $B = 0.25$, $t = 3.0$) as indicated by the significant interaction of woodpecker attendance and tree species in the GLMM (Table 3).

Intraspecific aggression among California scrub-jays in *Q. lobata* varied significantly among years. It was highest when landscape-wide seed production was low in 2014 but remained low in the two subsequent years when acorns were available in the other species (Figs. 3 and 4). The number of scrub-jays attending a tree during a focal watch was the best predictor of overall intraspecific displacement rates in both oak species (Tables 4 (a) and 5), and the relationship was weaker in *Q. lobata* when landscape-wide acorn crops were large (Fig. 3a–d). In 2016, the slope of the relationship with overall displacement rates was not significantly different between the two oak species, as identified by the non-significant interaction between scrub-jay attendance and tree species (Table 5; Fig. 2c, d). Per capita displacement rates among scrub-jays in 2016 were very low and did not correlate with attendance or acorn crop.

Interspecific aggression by acorn woodpeckers toward California scrub-jays exhibited the similar pattern as

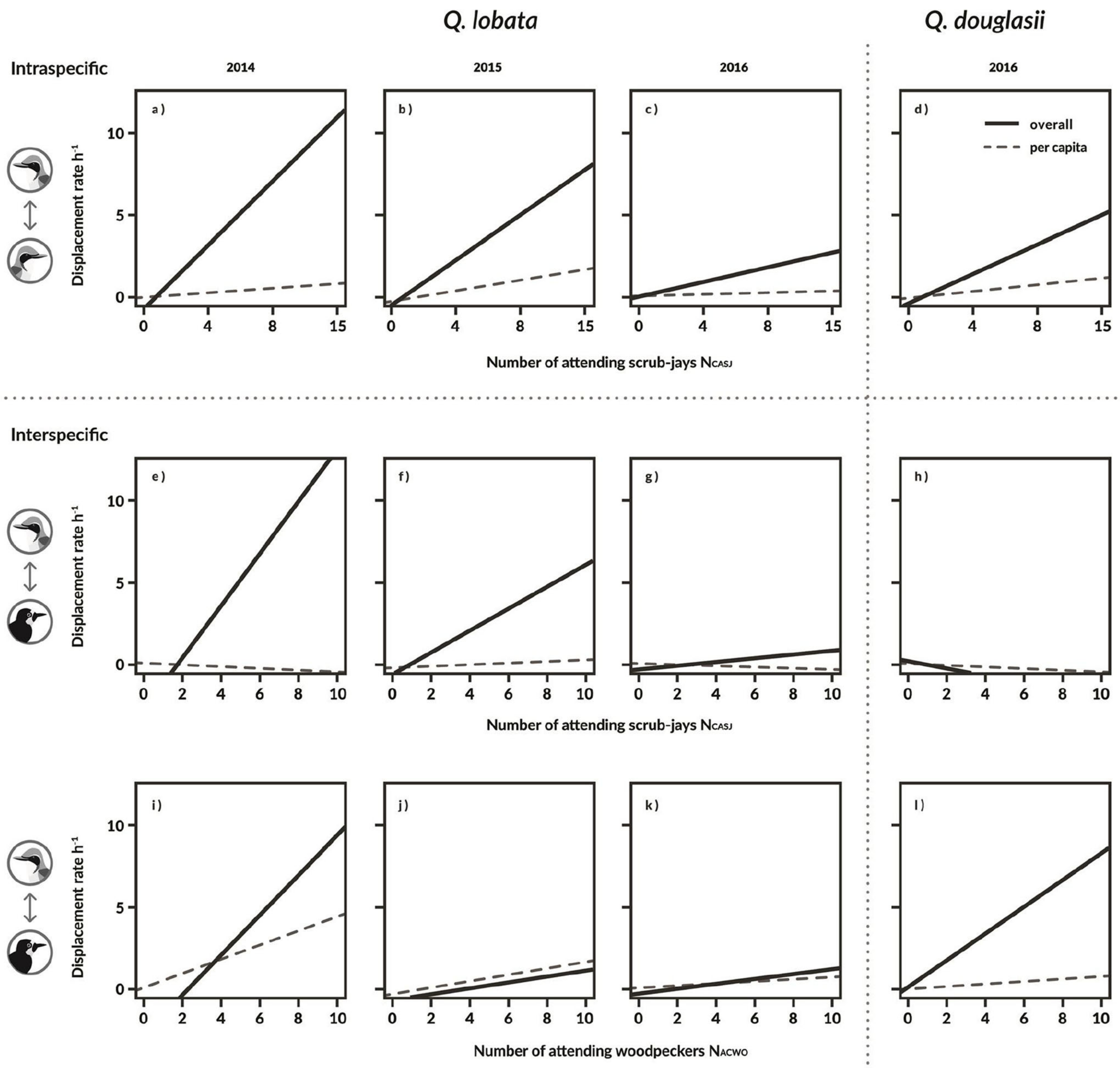


**Fig. 3** Context-dependent aggression at *Q. lobata* and *Q. douglasii* focal trees. Hourly rates of intraspecific displacements among California scrub-jays (CASJ) as a function of the number of attending scrub-jays (CASJ → CASJ; **a**–**d**) and interspecific displacements (ACWO ←→ CASJ) as a function of the number of scrub-jays (**e**–**h**) and acorn woodpeckers (ACWO; **i**–**l**) attending. Solid lines indicate overall rates, dashed lines per capita rates. Lines indicate linear relationship from linear mixed models in Tables 4, 5, and S5–S12

intraspecific aggression. Of the 968 observed aggressive interactions among the two species, all but 4 consisted of acorn woodpeckers displacing California scrub-jays. Overall, the woodpeckers attacked the jays significantly more frequently in *Q. lobata* trees when landscape-wide acorn abundance was low in 2014 compared to the following years (Figs. 3 and 4). The observed displacement rates correlated strongly with attendance by both species, but, in *Q. lobata*, the strength of that relationship was weaker when acorns were abundant (Tables 4 and 5; Fig. 3e–l). In *Q. douglasii*, overall interspecific aggression was more strongly correlated with attendance by either species than in *Q. lobata* (Table 5), while there was no difference in the slope of the significant relationship of their attendance with per capita displacement rates (Fig. 3k, l).

Path analyses confirmed that tree attendance by California scrub-jays was the strongest driver of per capita intraspecific displacement rates in 2014 and 2015, when landscape-level seed production was poor to intermediate (Figs. S1 and S2). In 2016, interspecific per capita displacement rates were negatively correlated with scrub-jay attendance, while the attendance of acorn woodpeckers remained the main driver of aggression throughout (Figs. S3 and S4).

**Data availability** The data associated with this manuscript is publicly available at figshare (https://figshare.com/s/59cc7879c0283b43e255).

**Table 4** Drivers of overall and per capita displacement rates directed at California scrub-jays (CASJ) in *Q. lobata* trees. (a) Intraspecific displacements (CASJ > CASJ) and (b) interspecific displacements by acorn woodpeckers (ACWO > CASJ) as a function of daily acorn crop estimate ($LN30_{day}$), bird attendance ($N_{CASJ}$, $N_{ACWO}$), and study year

| | Overall | | | Per capita | | |
|---|---|---|---|---|---|---|
| | $\chi^2$ | *df* | *P* | $\chi^2$ | *df* | *P* |
| (a) CASJ > CASJ | | | | | | |
| $LN30_{day}$ | 0.2 | 1 | 0.676 | 1.4 | 1 | 0.234 |
| $N_{CASJ}$ | 158.5 | 1 | *< 0.001* | 27.7 | 1 | *< 0.001* |
| Year | 12.8 | 2 | *0.002* | 10.3 | 2 | *0.006* |
| $LN30_{day}$ × year | 0.2 | 2 | 0.927 | 0.9 | 2 | 0.633 |
| $N_{CASJ}$ × year | 57.5 | 2 | *< 0.001* | 10.9 | 2 | *0.004* |
| (b) ACWO > CASJ | | | | | | |
| $LN30_{day}$ | 0.4 | 1 | 0.549 | 5.8 | 1 | *0.016* |
| $N_{ACWO}$ | 11.4 | 1 | *< 0.001* | 25.2 | 1 | *< 0.001* |
| $N_{CASJ}$ | 63.4 | 1 | *< 0.001* | 2.6 | 1 | 0.110 |
| Year | 29.5 | 2 | *< 0.001* | 42.3 | 2 | *< 0.001* |
| $LN30_{day}$ × year | 0.5 | 2 | 0.785 | 2.9 | 2 | 0.232 |
| $N_{ACWO}$ × year | 15.4 | 2 | *< 0.001* | 19.9 | 2 | *< 0.001* |
| $N_{CASJ}$ × year | 32.5 | 2 | *< 0.001* | 6.7 | 2 | *< 0.001* |

Full modeling results are presented in Tables S5–S8

Italicized values indicate $P < 0.05$

## Discussion

Our results illustrate that tree attendance by California scrub-jays in response to seed crop size in *Q. lobata* varied strongly across years with different levels of community-wide seed production. Specifically, when landscape-wide seed production was poor, scrub-jays attended *Q. lobata* in high numbers and experienced high levels of intra- and interspecific aggression. Conversely, when acorn production by other oak species increased landscape-wide availability, scrub-jays reduced their attendance at *Q. lobata* trees in which many woodpeckers were present and consequently experienced lower levels of interspecific aggression. Similarly, scrub-jays experienced reduced intraspecific aggression as fewer individuals attended *Q. lobata*. The comparison with behavioral dynamics of the birds in *Q. douglasii* trees in 2016 revealed that the scrub-jays attending trees other than *Q. lobata* also experienced comparatively low levels of aggression when there were low levels of attendance by both avian hoarders. Interestingly, we also found that when acorn crops were high in 2016, per capita rates of intraspecific displacement by woodpeckers decreased as the number of attending scrub-jays increased. These findings support the hypothesis that the avoidance of aggression mediates the attendance of seed dispersers to *Q. lobata* acorn crops.

The results broadly reflect differences in the foraging strategies and life histories of the two avian hoarders. California scrub-jays are opportunistic generalists that only defend breeding territories in the spring, allowing them to optimize their foraging behavior over large spatial scales and were observed flying up to 1.5 km to obtain acorns (Carmen 2004; Pesendorfer and Koenig 2016). In contrast, acorn woodpecker groups defend smaller, year-round territories, and obtain a majority of their annual acorn hoard within 200 m of the granary tree, except in years of extremely low acorn production, when they travel up to 800 m for acorns (MacRoberts and MacRoberts 1976; Koenig et al. 2008).

The two species also differ in their sensitivity to spatial variation in oak abundance and diversity, as well as the temporal variation in acorn crops. Across California, their populations show stronger fluctuations in areas with low oak diversity than in areas with multiple oak species, but this relationship is more pronounced in acorn woodpeckers. Similarly, acorn woodpecker population sizes increase with overall oak abundance in the landscape—a relationship not detected in California scrub-jays (Koenig and Haydock 1999; Koenig et al. 2009). Finally, population sizes of both species show lagged responses to annual variation in acorn production, but again, the woodpecker populations fluctuate more in response to acorn crops than scrub-jay populations (Koenig et al. 2009, 2011). Combined, these findings suggest that acorn woodpeckers should invest strongly in defending their key winter resource, while scrub-jays appear to be more flexible in adjusting their foraging behavior, both in space and time.

**Table 5** Drivers of overall and per capita displacement rates directed at California scrub-jays (CASJ) in *Q. lobata* and *Q. douglasii* trees in 2016 as a function of daily acorn crop estimate ($LN30_{day}$), bird attendance ($N_{CASJ}$, $N_{ACWO}$), and study year

| | Overall | | | Per capita | | |
|---|---|---|---|---|---|---|
| | $\chi^2$ | *df* | *P* | $\chi^2$ | *df* | *P* |
| CASJ > CASJ[a] | | | | | | |
| $LN30_{day}$ | < 0.1 | 1 | 0.876 | < 0.1 | 1 | 0.991 |
| $N_{CASJ}$ | 32.2 | 1 | *< 0.001* | 2.6 | 1 | 0.104 |
| Oak species | 1.7 | 1 | 0.260 | 1.1 | 1 | 0.301 |
| $LN30_{day}$ × oak sp. | 0.4 | 1 | 0.591 | 0.3 | 1 | 0.613 |
| $N_{CASJ}$ × oak sp. | 3.69 | 1 | 0.054 | 1.9 | 1 | 0.256 |
| ACWO > CASJ[b] | | | | | | |
| $LN30_{day}$ | 0.1 | 1 | 0.549 | 2.6 | 1 | 0.106 |
| $N_{ACWO}$ | 20.8 | 1 | *< 0.001* | 20.2 | 1 | *< 0.001* |
| $N_{CASJ}$ | 3.4 | 1 | 0.065 | 8.8 | 1 | *0.003* |
| Oak species | 1.3 | 1 | 0.255 | 2.7 | 1 | 0.103 |
| $LN30_{day}$ × oak sp. | 0.9 | 1 | 0.344 | < 0.1 | 1 | 0.858 |
| $N_{ACWO}$ × oak sp. | 17.8 | 1 | *< 0.001* | 0.1 | 1 | 0.714 |
| $N_{CASJ}$ × oak sp. | 6.4 | 1 | *0.011* | 0.6 | 1 | 0.440 |

Full modeling results are presented in Tables S9–S12

Italicized values indicate $P < 0.05$

[a] Intraspecific displacements (CASJ > CASJ)

[b] Interspecific displacements by acorn woodpeckers (ACWO > CASJ)

## Seed fate consequences

The context-dependence of the key mutualists' tree attendance strongly affects annual seed fate in this system. We previously found that the per capita acorn hoarding rates by California scrub-jays at HNHR not only exhibited a functional response to acorn abundance in trees but also increased with the number of conspecifics attending a tree. Consequently, species-level removal rates by the corvids, the fitness-relevant metric from the tree perspective, exhibit a curvilinear relationship to seed abundance on individual trees within years of low community-wide seed production (Pesendorfer and Koenig 2016, 2017). When considering the annual variation in seed production of the dominant competing species over the long-term (Koenig et al. 1994; WDK and J. M. H. Knops, unpublished data), our finding of aggression-mediated tree attendance suggests that *Q. lobata* may only experience proportionally high levels of seed dispersal approximately once a decade, which may contribute to the low levels of recruitment and regeneration of this oak species (Tyler et al. 2006).

Our study demonstrates that not only intraspecific competition and aggression but also interactions with other seed-hoarding species affect the scatter-hoarding behavior of wild corvids at the seed source. Several studies have shown that cache pilferage and observation by competitors during cache deposition induce cache protection strategies in corvids (Clarkson et al. 1986; Dally et al. 2006; Clary and Kelly 2011) and in rodents (Steele et al. 2008; Muñoz and Bonal 2011). Surprisingly, however, little is known about the role of predation pressure on scatter-hoarders and its effect on seed fate (Steele et al. 2011; Gallego et al. 2017), despite the fact that most theoretical treatments posit that the risk of predation, combined with extended handling times for food items, is an important driver of the evolution of food hoarding (Andersson and Krebs 1978; Stapanian and Smith 1978, 1984; Gerber et al. 2004). Similarly, theoretical and quantitative studies have considered the importance of (reciprocal) intra- and

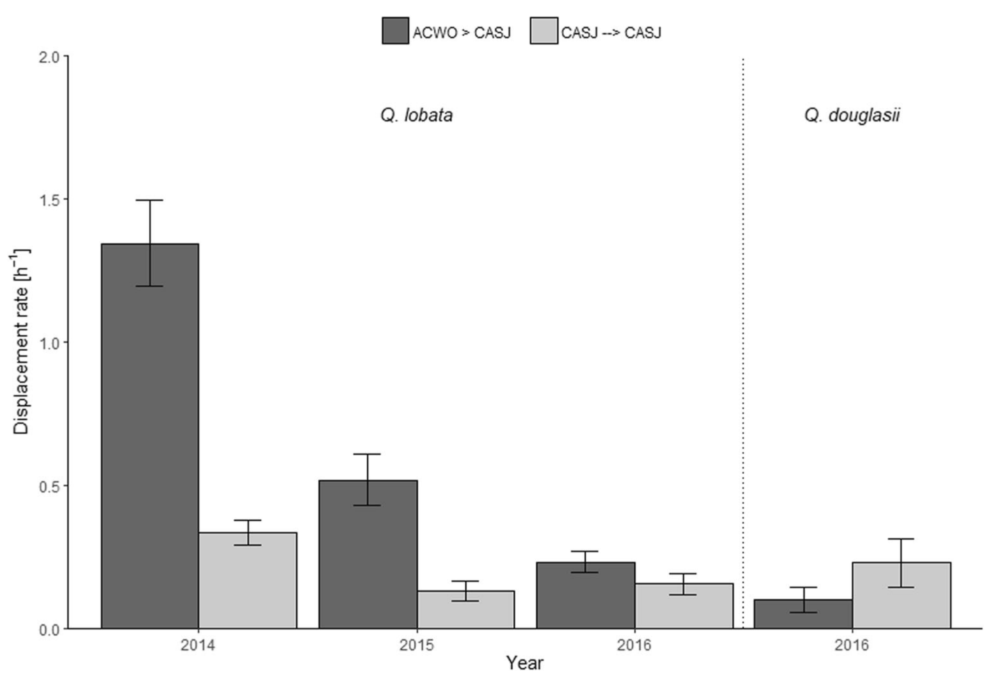


**Fig. 4** Inter- and intraspecific aggression aimed at California scrub-jays (CASJ) in *Q. lobata* (2014–2016) and *Q. douglasii* (2016). Per capita rates of aggressive displacements per hour (± SE) by acorn woodpeckers (ACWO, dark gray bars) and conspecifics (CASJ, light gray bars)

interspecific cache pilferage (Vander Wall and Jenkins 2003; Vander Wall et al. 2009), yet, to our knowledge, none has previously addressed interspecific interactions at the seed source. This highlights the fact that experimental and captive studies of scatter-hoarding in corvids far outnumber field studies (Brodin 2010; Pesendorfer et al. 2016a), potentially ignoring real-world challenges faced by the birds.

From the perspective of plant-animal interactions and community ecology, our findings further emphasize that in addition to variable resource dynamics and intraspecific social interactions, the effectiveness of seed dispersal by scatter-hoarders varies with community context, both in terms of seed production by multiple plant species (Lichti et al. 2014; Yi and Wang 2015; Pesendorfer and Koenig 2017) and as a function of seed hoarder and predator population dynamics and the resulting interspecific interactions (Xiao et al. 2013; Pesendorfer and Koenig 2016). Integrating context-dependence into mutualism and competition networks could therefore provide a first step in capturing the complex dynamics among species that ultimately drive reproductive success and community assembly in masting plants (Levine and Murrell 2003; Chamberlain et al. 2014; Bogdziewicz et al. 2016).

**Acknowledgments** We would like to thank the director of the Hastings Natural History Reservation, V. Voegeli, for logistical support, Kachina Rowland, Spencer Schubert, John Zeiger, Jenna Kohles, Natasha Stepanova, and Jason Lacson for assistance with data collection, Dana Pesendorfer for help with the figures, and two anonymous reviewers and the subject editor for constructive comments on the manuscript.

**Funding** This research was funded by National Science Foundation grant DEB-1256394 to WDK.

## Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study did not require the capture, handling, or marking of animals and only relied on non-intrusive observation of animals from a distance.

## References

Andersson M, Krebs J (1978) On the evolution of hoarding behavior. Anim Behav 26:707–711

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bogdziewicz M, Zwolak R, Crone EE (2016) How do vertebrates respond to mast seeding? Oikos 125:300–307

Brodin A (2010) The history of scatter hoarding studies. Phil Trans R Soc B 365:869–881

Bugnyar T, Kotrschal K (2002) Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? Anim Behav 64:185–195

Carmen WJ (2004) Noncooperative breeding in the California scrub-jay. Stud Avian Biol 28:1–100

Chamberlain SA, Bronstein JL, Rudgers JA (2014) How context dependent are species interactions? Ecol Lett 17:881–890

Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002) The interaction between predation and competition: a review and synthesis. Ecol Lett 5:302–315

Clarkson K, Eden SF, Sutherland WJ, Houston AI (1986) Density dependence and magpie food hoarding. J Anim Ecol 55:111–121

Clary D, Kelly DM (2011) Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). Anim Cogn 14:735–744

Cousens RD, Hill J, French K, Bishop ID (2010) Towards better prediction of seed dispersal by animals. Funct Ecol 24:1163–1170

Dally JM, Clayton NS, Emery NJ (2006) The behavior and evolution of cache protection and pilferage. Anim Behav 72:13–23

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage Publishers, Thousand Oaks

Gallego D, Morán-López T, Torre I, Navarro-Castilla A, Barja I, Díaz M (2017) Context dependence of acorn handling by the Algerian mouse (*Mus spretus*). Acta Oecol 84:1–7

Gerber LR, Reichman OJ, Roughgarden J (2004) Food hoarding: future value in optimal foraging decisions. Ecol Model 175:77–85

Hannon SJ, Mumme RL, Koenig WD, Pitelka FA (1985) Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. Behav Ecol Sociobiol 17:303–312

Hooge PN, Stanback MT, Koenig WD (1999) Nest-site selection in the acorn woodpecker. Auk 116:45–54

Jansen PA, Bongers F, Hemerik L (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecol Monogr 74:569–589

Koenig WD (1981) Space competition in the acorn woodpecker: power struggles in a cooperative breeder. Anim Behav 29:396–409

Koenig WD, Faeth SH (1998) Effects of storage on tannin and protein content of cached acorns. Southwest Nat 43:170–175

Koenig WD, Haydock J (1999) Oaks, acorns, and the geographical ecology of acorn woodpeckers. J Biogeogr 26:159–165

Koenig WD, Mumme RL, Carmen WJ, Stanback MT (1994) Acorn production by oaks in central coastal California: variation within and among years. Ecology 75:99–109

Koenig WD, McEntee JP, Walters EL (2008) Acorn harvesting by acorn woodpeckers: annual variation and comparison with genetic estimates. Evol Ecol Res 10:811–822

Koenig WD, Krakauer AH, Monahan WB, Haydock J, Knops JMH, Carmen WJ (2009) Mast-producing trees and the geographical ecology of western scrub-jays. Ecography 32:561–570

Koenig WD, Walters EL, Haydock J (2011) Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. Am Nat 178:145–158

Lefcheck JS (2016) piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7:573–579

Levine JM, Murrell DJ (2003) The community-level consequences of seed dispersal patterns. Annu Rev Ecol Evol Syst 34:549–574

Lichti NI, Steele MA, Zhang H, Swihart RK (2014) Mast species composition alters seed fate in North American rodent-dispersed hardwoods. Ecology 95:1746–1758

MacRoberts MH (1970) Notes on the food habits and food defense of the acorn woodpecker. Condor 72:196–204

MacRoberts MH, MacRoberts BR (1976) Social organization and behavior of the acorn woodpecker in central coastal California. Ornithol Monogr 21:1–115

Muñoz A, Bonal R (2011) Linking seed dispersal to cache protection strategies. J Ecol 99:1016–1025

Pesendorfer MB, Koenig WD (2016) The effect of within-year variation in acorn crop size on seed harvesting by avian hoarders. Oecologia 181:97–106

Pesendorfer MB, Koenig WD (2017) Competing for seed dispersal: evidence for the role of avian seed hoarders in mediating apparent predation among oaks. Funct Ecol 31:622–631

Pesendorfer MB, Sillett TS, Koenig WD, Morrison SA (2016a) Scatter-hoarding corvids as seed dispersers for oaks and pines: a review of a widely distributed mutualism and its utility to habitat restoration. Condor 118:215–237

Pesendorfer MB, Sillett TS, Morrison SA, Kamil AC (2016b) Context-dependent seed dispersal by a scatter-hoarding corvid. J Anim Ecol 85:798–805

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna http://www.R-project.org

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368

Siepielski AM, Benkman CW (2007) Extreme environmental variation sharpens selection that drives the evolution of a mutualism. Proc R Soc Lond B 274:1799–1805

Stapanian MA, Smith CC (1978) A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884–896

Stapanian MA, Smith CC (1984) Density-dependent survival of scatterhoarded nuts: an experimental approach. Ecology 65:1387–1396

Steele MA, Halkin SL, Smallwood PD, McKenna TJ, Mitsopoulos K, Beam M (2008) Cache protection strategies of a scatter-hoarding rodent: do tree squirrels engage in behavioral deception? Anim Behav 75:705–714

Steele MA, Bugdal M, Yuan A, Bartlow A, Buzalewski J, Lichti NI, Swihart R (2011) Cache placement, pilfering, and a recovery advantage in a seed-dispersing rodent: could predation of scatter hoarders contribute to seedling establishment? Acta Oecol 37:554–560

Tyler CM, Kuhn B, Davis FW (2006) Demography and recruitment limitations of three oak species in California. Q Rev Biol 81:127–152

Vander Wall SB (2001) The evolutionary ecology of nut dispersal. Bot Rev 67:74–117

Vander Wall SB (2002) Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83:3508–3516

Vander Wall SB, Jenkins SH (2003) Reciprocal pilferage and the evolution of food-hoarding behavior. Behav Ecol 14:656–667

Vander Wall SB, Enders MS, Waitman BA (2009) Asymmetrical cache pilfering between yellow pine chipmunks and golden-mantled ground squirrels. Anim Behav 78:555–561

Xiao Z, Zhang Z, Krebs CJ (2013) Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. J Ecol 101:1256–1264

Yi X, Wang Z (2015) Context-dependent seed dispersal determines acorn survival of sympatric oak species. Plant Ecol 216:123–132

Zuur AF, Smith GM, Savaeliev AA, Ieno EN, Walker N (2009) Mixed effects models and extensions in ecology with R. Springer, New York