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Context-dependent seed dispersal by a scatter-hoarding corvid

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Summary

1. Corvids (crows, jays, magpies and nutcrackers) are important dispersers of large-seeded plants. Studies on captive or supplemented birds suggest that they flexibly adjust their scatter-hoarding behavior to the context of social dynamics and relative seed availability. Because many corvid-dispersed trees show high annual variation in seed production, context-dependent foraging can have strong effects on natural corvid scatter-hoarding behavior.

2. We investigated how seed availability and social dynamics affected scatter-hoarding in the island scrub jays (*Aphelocoma insularis*). We quantified rates of scatter-hoarding behavior and territorial defense of 26 color-marked birds over a three-year period with variable acorn crops.

3. We tested whether caching parameters were correlated with variation in annual seed production of oaks as predicted by the predator dispersal hypothesis, which states that caching rates and distances should vary with seed abundance in ways that benefit tree fitness. We also tested whether antagonistic interactions with conspecifics would affect scatter-hoarding adversely, as found in experimental studies.

4. Caching behavior varied with acorn availability. Caching distances correlated positively with annual acorn crop size, increasing by as much as 40% between years. Caching rates declined over time in years with small acorn crops, but increased when crops were large. Acorn foraging and caching rates were also negatively correlated with rates of territorial aggression. Overall foraging rates, however, were not associated with aggression, suggesting that reduced dispersal rates were not simply due to time constraints.

5. Our field results support laboratory findings that caching rates and distances by scatter-hoarding corvids are context-dependent. Furthermore, our results are consistent with predictions of the predator dispersal hypothesis and suggest that large seed crops and social interactions among scatter-hoarders affect dispersal benefits for oaks and other masting tree species.

Keywords: *Aphelocoma*, context dependence, Corvidae, *Quercus*, scatter-hoarding, seed dispersal, species interactions

Introduction

Seed dispersal is central to plant life history because it lays the template for subsequent processes that determine the spatial distribution of offspring (Howe & Miriti 2004). For animal-dispersed plants, the frequency, distance and arrival habitat of dispersed seeds depend on animal foraging behavior and movement. Disperser behavior is often context-dependent because it varies with seed availability, habitat configuration, interactions among dispersers, predation pressure and the animal's satiation or motivational state (Pons & Pausas 2007; Levey, Tewksbury & Bolker 2008; Côrtes & Uriarte 2013). Identifying contextual drivers of disperser behavior is thus crucial to understanding

spatial seed dispersal patterns, especially under temporally variable conditions (Cousens *et al.* 2010). A majority of evidence for context-dependent seed dispersal in scatter-hoarding birds, however, comes from experimental studies or anecdotes because it is difficult to quantify in the field (Pesendorfer *et al.* 2016a). Here, we use behavioral field observations of a scatter-hoarding bird to investigate the context dependence of seed caching across two temporally variable factors: seed availability and social dynamics.

Scatter-hoarding members of the Corvidae (crows, jays, magpies and nutcrackers) are important seed dispersers for many large-seeded plants with strong annual variation in seed crop size (Vander Wall & Beck 2012; Pesendorfer *et al.* 2016a). Birds scatter-hoard seeds by transporting them, often over long distances, and storing them in small, spatially dispersed caches for later consumption (Tomback 1982; Gómez 2003). Hoarder-dispersed trees, such as oaks (*Quercus* spp.) and pines (*Pinus* spp.), typically produce highly variable numbers of seeds per year, with cyclical bumper crops that are spatially and temporally synchronized. This phenomenon is known as masting or mast-fruiting (Koenig & Knops 2000; Kelly & Sork 2002). Circumstantial evidence suggests that corvid caching behavior is sensitive to natural variation in seed availability. Johnson *et al.* (1997) report low rates of scatter-hoarding by blue jays (*Cyanocitta cristata*) in a year of low acorn productivity. Christensen, Whitham & Balda (1991) used observations and experiments to show that Clark's nutcrackers (*Nucifraga columbiana*) harvest a larger proportion of seeds from pinyon pine (*P. edulis*) trees with higher numbers of pine cones. The direct relationship between temporal variation in seed availability and seed dispersal parameters, such as caching rates and distances, has not been investigated in wild corvids.

Two hypotheses for the functional basis of masting make different predictions about the effect of variable seed crops on seed dispersal. The well-supported "predator satiation hypothesis" states that bumper crops overwhelm seed predators, thereby reducing the proportion of seeds consumed by predators while increasing the proportion of dispersed seeds (Silvertown 1980; Kelly & Sork 2002; Espelta *et al.* 2008). The "predator dispersal hypothesis" expands the predator satiation hypothesis and proposes that bumper years not only affect the proportion of seeds consumed, but also improve seed dispersal benefits for the plants (Vander Wall 2010). Increased dispersal benefits may result from various processes, including preferential hoarding of larger seeds, or more frequent dispersal over longer distances, but the underlying mechanisms are generally still poorly understood (Vander Wall 2002; Jansen, Bongers & Hemerik 2004; Vander Wall & Beck 2012). Because scatter-hoarders continue dispersing seeds even when satiated, large crops both meet dispersers' immediate food requirements and lead scatter-hoarders to cache more seeds than necessary to cover energetic costs

(Pesendorfer *et al.* 2016a). This would result in a larger number of unrecovered seed caches at greater distances from the source plant following high-productivity years (Vander Wall & Beck 2012).

Quantitative studies of the effect of temporally variable seed availability on scatter-hoarding behavior have been restricted to rodents and provide a mixed picture about the relationship between seed abundance and seed dispersal. Some species increase dispersal rates in years of high seed production (Vander Wall 2002), while others show reduced dispersal rates (Jansen, Bongers & Hemerik 2004; Li & Zhang 2007; Xiao, Zhang & Krebs 2013). Seed dispersal distances also vary with seed crop size. Some studies report increased distances in years of large crops (Vander Wall 2002; Jansen, Bongers & Hemerik 2004; Li & Zhang 2007), but dispersal distances can also decline (Xiao, Zhang & Krebs 2013). Seed dispersal by scatter-hoarding rodents thus appears to be generally sensitive to seed abundance, but the affected parameters and the direction of the response varies among the rodent systems studied.

Social interactions have also been hypothesized to affect scatter-hoarding behavior. Studies of captive or food-supplemented birds show that scatter-hoarders perform cache protection behavior when conspecifics are present, including hiding food out of sight (Heinrich & Pepper 1998; Bugnyar *et al.* 2007), creating false caches or reducing caching rates (Dally, Clayton & Emery 2006; Toomey, Bowman & Woolfenden 2007). Cache suppression by social context is hypothesized to be the most effective behavior to reduce cache pilfering, because corvids use observational spatial memory to retrieve caches they see others make (Bugnyar *et al.* 2007). These findings suggest the social environment shapes scatter-hoarding behavior, but we do not have data from unmanipulated, wild populations.

Here, we examine the ecological and social context of scatter-hoarding in the island scrub jay, *Aphelocoma insularis*, endemic to Santa Cruz Island, California. This island provides a simplified system to investigate dispersal dynamics because island scrub jays are the only scatter-hoarding species present, and the majority of woody vegetation is dominated by two oak species, *Q. pacifica* and *Q. agrifolia* (Junak *et al.* 1995). Our study has three objectives. First, we quantify scatter-hoarding of acorns by island scrub jays to describe natural caching rates and distances. Secondly, we test whether jay scatter-hoarding behavior followed predictions of the predator dispersal hypothesis. A significant correlation between acorn counts and dispersal parameters, such as caching rates and distances, would provide support for the hypothesis (Vander Wall 2010). Thirdly, we tested the hypothesis that social interactions influenced jay caching rates and distances. We expected a negative correlation between antagonistic interaction frequency and acorn caching behaviors, as previously found for captive *Aphelocoma* (Dally, Clayton & Emery 2006).

Materials and methods

data collection

Study site and acorn surveys

Fieldwork was conducted in fall (Sep – Dec) 2009–2011 on Santa Cruz Island (34° 0′ N, 119° 45′ W), part of Channel Islands National Park, California, USA. Located 40 km off the coast of southern California, the island has a mediterranean climate with cool wet winters and warm dry summers. All work was conducted on three previously established study plots that spanned a range of scrub-jay habitat quality (Figure S1): Coches Prietos Canyon (115 ha), Field Station (226 ha) and Portezuela (163 ha). Island scrub jays occur in chaparral habitat, where they occupy home ranges of 3.5 ha ± 0.2 ha (mean ± SE) with 63% ± 2% cover of oak chaparral vegetation interspersed with open grassland and scrub vegetation (Sillett *et al.* 2012; Caldwell *et al.* 2013).

To monitor acorn availability, we conducted annual acorn counts on 150 *Q. pacifica* and *Q. agrifolia* trees that were randomly chosen across the three study plots in 2009 (see Pesendorfer *et al.* 2014 for details). These two species represent > 95% of individual oaks on Santa Cruz Island (Junak *et al.* 1995). Two observers counted all acorns detected in 15 s on each tree's crown, and their counts were summed. These "30-second acorn counts" are commonly used to measure the relative annual acorn production of individual oaks (e.g. Koenig *et al.* 1994; Pesendorfer *et al.* 2014; Pesendorfer & Koenig 2016), and are thus a good proxy for annual acorn production (Pons & Pausas 2012). Counts were performed at the beginning of oak fruiting season when jays were first observed transporting acorns from oaks. Because island scrub jays are the only animals that remove acorns from oaks on Santa Cruz Island, we assumed that relative acorn availability declined linearly with calendar week within each field season (Garcia & Ortiz-Pulido 2004; Espelta, Bonal & Sanchez-Humanes 2009; Pesendorfer & Koenig 2016).

Behavioral observations

We observed foraging and scatter-hoarding behavior of color-marked, territorial jays to quantify seed acquisition and transportation. Birds were captured and fitted with a unique combination of four colored leg bands and a unique USGS numbered leg band (see Caldwell *et al.* 2013 and Langin *et al.* 2015 for details), following protocols approved by the National Zoological Park's Institutional Animal Care and Use Committee, the U.S. Geological Survey Bird Banding Lab, and the California Department of Fish and Game. Like many island-endemics, island scrub jays are relatively tame, and the low stature of oak chaparral allows for reliable behavioral observation from vantage points. In 2009, 26 focal individuals in 13 territories (Figure S1) were visited twice weekly to record opportunistic observations of one foraging and one caching event per individual following 5 min of acclimation. We expanded our effort to include the study of behavioral rates in 2010 and 2011. This entailed 30-min observations on the same focal individuals studied in 2009 (henceforth referred to as "focal follows"). We recorded all foraging and caching behavior, as well as social interactions (Altmann 1974) observed between 07:00 and 15:00 h; start times for each individual varied throughout field seasons. Observations began after 5 min of acclimation time once a bird was located, and terminated

whenever a bird was out of sight for more than 10 min. Only follows longer than 5 min were used for analysis.

The behavioral data collected during focal follows included foraging and caching events, as well as territorial aggression. Data for foraging observations included the behavior used to acquire food (e.g. glean, or sally), food type, plant species and whether the acquired item was consumed or cached (i.e. dispersed). Observations were considered a single foraging event if the bird manipulated the same location repeatedly in sequence (e.g. four pecks to remove a piece of bark), but separate events if the same action was applied to areas more than 10 cm apart. If a bird cached a food item, we recorded, if possible, the type of item, the species of the cached seed, transportation distance, seed arrival habitat type, as well as the presence of another jay that could potentially observe the caching. Caching distances <100 m were estimated by eye. Longer distances were measured with laser range finders. Distances above 100 m were recorded to the closest 10 m, and all observations were recorded on digital voice recorders. Whenever the view of a bird was obstructed so that observation of a foraging action was impossible, the bird was considered out of sight. Rates of foraging and dispersal were calculated as the number of events observed during the time a bird was in sight, scaled to hourly rates. Displacements of conspecifics, the most common antagonistic interactions, were obvious to observers and often followed by conspicuous chases over long distances. Displacement rates h^{-1} were therefore calculated for the whole duration of a follow.

The significant variation in acorn counts between plots and years (Figure S2; Pesendorfer *et al.* 2014), as well as the daily variation in displacement rates, allowed us to test whether jay foraging and caching behavior varied with acorn availability and conspecific aggression. We included *Calendar Week* as proxy for within-season decline in acorn availability, because the decline in acorn availability tends to be linear within the fall season (Pesendorfer & Koenig 2016).

statistical analysis

We used an information theoretic approach to determine the relationship between context variables and caching behavior (Burnham & Anderson 2002). First, we constructed a global LMM for each dependent variable, with context parameters and their first-order interactions as fixed effects (see below). All models included *Individual* nested in *Plot* as a random effect to control for both repeated sampling and non-independence in the use of the same habitat. All regressors were standardized by rescaling to a mean of 0 and standard deviation of 0.5 to facilitate the biological interpretation of interactions of fixed effects (Schielzeth 2010; Gelman & Su 2015). We used model selection to determine whether a single model best fits the data. Because none of the models achieved model weight > 0.9, we calculated model-averaged parameter estimates, their 95% confidence intervals and relative importance for all fixed effects across models with ΔAIC < 4. This provides a conservative estimate of standardized parameters and their significance as determined by the overlap of the 95% CI with 0 (Grueber *et al.* 2011). All statistical analyses were performed in *R* version 3.2.2 (R Development Core Team 2015). Linear mixed models were constructed in *lme4* (Bates *et al.* 2014), standardized with *arm* (Gelman & Su 2015), followed by model selection and averaging in *MuMIn* (Barton 2015).

To determine whether foraging and caching rates varied with acorn availability and territorial aggression, we modelled the relationship between behavioral rates (overall foraging rate h^{-1}, acorn foraging rate h^{-1}, acorn caching rate h^{-1}) during focal follows ($n = 262$) and context parameters (acorn count, calendar week and displacement rate). We present standardized parameter estimates, their 95% confidence intervals and relative variable importance. The predicted, model-averaged relationship between acorn caching rates and within-season acorn availability are plotted for each study plot/year combination.

We also modelled the relationship between caching distances and context parameters. First, we determined whether caching distances varied with acorn availability within and between field seasons. Here, we used the data set of all valid caching observations, collected *ad libitum* and during focals ($n = 791$). The data are comparable for several reasons; they were collected on the same individuals over the whole time period, only that fewer caching observations were recorded in 2009, and we avoided a bias for highly visible dispersal events (i.e. over long distances) by spending a 5-min waiting period after finding the animal. Caching distances followed a Gamma distribution and were thus log-transformed ($\log(x + 1)$) to approach normality in errors and modelled as a function of acorn count and calendar week. Secondly, we investigated whether caching distances were associated with behavioral rates during focal follows. To do so, we constructed a model of caching distances of caches observed during focal follows ($n = 339$), with acorn foraging, acorn caching and displacement rates, as well as acorn count and calendar week as fixed effects. Here, we did not include interactions between parameters, as none of the additional fixed effects were significant predictors on their own.

Results

behavioral observations

We collected 888 caching and 3403 foraging observations over the three field seasons. The jays cached acorns almost exclusively (879 observations; 99%), but we also observed the caching of two arthropods, four manzanita berries (*Arctostaphylos* spp.), one wild cucumber seed (*Marah macrocarpus*), one island cherry (*Prunus ilicifolia*) and one lemonade berry fruit (*Rhus integrifolia*). In 2009, we recorded opportunistic observations of 395 foraging and 245 caching events. During the 2010 and 2011 field seasons, we recorded 389 focal follows for 26 individual birds, 262 of which also included data on aggressive interactions. We recorded an average ($\pm$ SE) of 5.5 ± 0.2 follows per individual in 2010 and 9.7 ± 0.2 follows per individual in 2011. Mean follow length was 22 min 36 s ($\pm$ 23 s), and the birds were in sight for an average of 12 min 5 s ($\pm$ 15 s). Birds were in sight for $54.7 \pm 1.4\%$ of the duration of focal follows in 2010, and for $60.0 \pm 1.2\%$ in 2011 and performed 2.5 ± 0.3 displacements, 38.5 ± 2.8 foraging maneuvers and 7.2 ± 0.5 caches per hour.

context dependence of behavioral rates

Overall foraging rates did not vary significantly with acorn availability or displacement rates. No context parameters were significant predictors of hourly foraging rates (Table 1a). Furthermore, model selection indicated that no model fit the data better than the null model, that is overall foraging rates did not vary with the context we measured (Table S1).

In contrast, acorn foraging and caching rates declined with calendar week (our proxy for within-season variation in seed availability), but only when initial acorn availability on the plots was low (LMM interaction acorn count 9 cal. week; foraging: $B = 0.145 \pm 0.056$; caching $B = 5.958 \pm 2.120$). The interaction between acorn count and calendar week showed high relative variable importance and was a significant predictor of both acorn foraging rates and acorn caching rates (Table 1b and 1c). Model-predicted acorn caching rates increased with calendar week in the two study plots with large acorn crops (FS and PZ) in 2010, while they declined over the same period when annual acorn crops were low: CPC plot in 2010, and all plots in 2011 (Figure 1a). The slope of the relationship between calendar week and caching rates changed from –0.998 under the lowest acorn availability (acorn count = 0.9) to 0.941 when acorns were abundant (acorn count = 19.9; Figure 1a). The birds' scatter-hoarding behavior therefore varied systematically with acorn availability, as predicted by the predator dispersal hypothesis.

Territorial aggression also affected acorn foraging and caching rates. Both rates correlated negatively with displacement rates during focals (acorn foraging $B = -0.480 \pm 1.118$; acorn caching: $B = -2.319 \pm 0.983$), and displacement rate was a significant predictor with high relative variable importance (Table 1b–c). Jays effectively stopped caching acorns when rates of territorial aggression were high (Figure 2).

context dependence of caching distance

Dispersal distances of acorns varied significantly with acorn availability, but not with acorn foraging or displacement rates. Overall, jays transported acorns 38.5 ± 1.6 m, with a maximum distance of 400 m (Figure 1b). The analysis of all observed caching distances indicated that dispersal distances correlated positively with acorn counts (LMM for log-transformed caching distances: $B = 0.017 \pm 0.040$) and declined strongly with calendar week as the season progressed ($B = -0.101 \pm 0.018$); their interaction, however, was not significant (Table 2a). The model for the subset of caches observed during focal follows ($n = 339$ caches with observed dispersal distance) provided similar estimates for the role of acorn availability (LMM for log-transformed caching distances: $B = 0.031 \pm 0.013$) and its decline over

Table 1. The effect of acorn availability and displacement rate on foraging and caching behavior of island scrub jays: (a) overall foraging rate, (b) acorn foraging rate, (c) acorn caching rate

Parameter	β	95% CI		B	SE	RI
(a) Overall foraging rate						
Intercept	37.567	32.631	42.503	50.921	28.413	
Acorn count	−6.591	−14.938	1.756	−0.724	1.598	0.70
Displ. rate	2.196	−6.171	10.564	1.649	4.888	0.38
Week	−3.288	−11.107	4.532	−0.508	0.861	0.39
Acorn count × week	0.791	−16.593	18.176	0.011	0.147	0.04
Acorn count × displ. rate	18.498	−8.216	3.929	0.185	0.131	0.16
Week × displ. rate	−9.188	−22.363	3.988	−0.209	0.149	0.07
(b) Acorn foraging rate						
Intercept	13.483	11.506	15.460	87.447	19.378	
Acorn count	1.972	−1.293	5.237	−6.207	2.436	0.89
Displ. rate	**−3.486**	**−6.513**	**−0.460**	**−0.480**	**1.118**	**0.90**
Week	**−4.999**	**−8.031**	**−1.966**	**−1.679**	**0.441**	**1.00**
Acorn count × week	**8.791**	**2.163**	**15.418**	**0.145**	**0.056**	**0.89**
Acorn count × displ. rate	−2.184	−11.855	7.486	−0.022	0.050	0.17
Week × displ. rate	0.567	−4.455	5.588	0.013	0.057	0.16
(c) Acorn caching rate						
Intercept	7.453	6.233	8.672	7.453	0.622	
Acorn count	−0.113	−2.163	1.937	−0.113	1.046	0.94
Displ. rate	**−2.319**	**−4.246**	**−0.392**	**−2.319**	**0.983**	**0.92**
Week	**−2.828**	**−4.718**	**−0.938**	**−2.828**	**0.964**	**1.00**
Acorn count × week	**5.958**	**1.803**	**10.113**	**5.958**	**2.120**	**0.94**
Acorn count × displ. rate	−2.137	−8.240	3.967	−2.137	3.114	0.26
Week × displ. rate	0.536	−2.631	3.703	0.536	1.616	0.23

Model-averaged standardized (models with scaled and centered predictor variables) parameter estimates (*β*), their 95% confidence intervals, metric estimates (*B*), their standard error (SE) and relative variable importance (*RI*) for fixed effects of LMMs of behavioral rates, containing *Individual* nested in *Plot* as random effect. Parameters averaged over subset of models with ΔAIC < 4. Bold indicates *β* estimates with 95% CI that do not overlap with 0. See Tables S1–S3 for model selection parameters. (*n* = 262 focal watches).

calendar weeks ($B = -0.071 \pm 0.030$), but indicated no correlation between dispersal distance and the rates of acorn foraging and caching, or displacement rates (Table 2b).

Discussion

Our findings demonstrate that scatter-hoarding behavior by island scrub jays is highly context-dependent. Acorn caching varied systematically with the highly variable acorn crops; caching rates increased, and distances were higher in years with greater acorn availability, while in years of low acorn crops, caching rates declines rapidly, and caching distances declined as much as 40%. These results are consistent with predictions of the predator dispersal hypothesis, which posits that, in addition to satiating seed predators, large seed crops of masting tree species may enhance long-distance dispersal by scatter-hoarding corvids (Vander Wall 2002, 2010). Furthermore, acorn foraging and caching rates declined with increased territorial aggression, while overall foraging activity remained stable (Table 1, Figure 2). This result suggests a connection between social dynamics and scatter-hoarding behavior that has not been previously demonstrated under natural conditions. Combined, our findings underscore the context dependence of seed dispersal by scatter-hoarding corvids, and

provide clues about the complex interactions between plant and animal behavior that determine the outcome of seed dispersal interactions.

ISLAND SCRUB JAYS AS SEED DISPERSERS FOR OAKS

Our results emphasize the central ecological role of island scrub jays on Santa Cruz Island, which has a reduced number of oak seed predators and dispersers when compared to mainland California (Morrison *et al.* 2011). Extrapolating the observed caching rate of 7.2 acorns hour^{-1} to a whole fruiting season of oaks (~110 d), individual island scrub jays cache 3500 (range: 2750–5000) acorns per year, assuming the birds forage for five hours a day. The population of island scrub jays, recently estimated at 2270 individuals (Sillett *et al.* 2012), could thus cache more than 7 million acorns year^{-1} on Santa Cruz Island.

The jays' hoarding behavior affected the spatial distribution of dispersed acorns. The birds transported acorns for an average of 38.5 m and up to 400 m before they were cached in the ground. Such dispersal is likely a key symbiotic benefit that oaks receive from scatter-hoarding birds, and the spatial signature of such seed dispersal was also reflected in the reconstruction of oak habitat expansion on Santa Cruz Island (Dahlin, Asner & Field 2014).
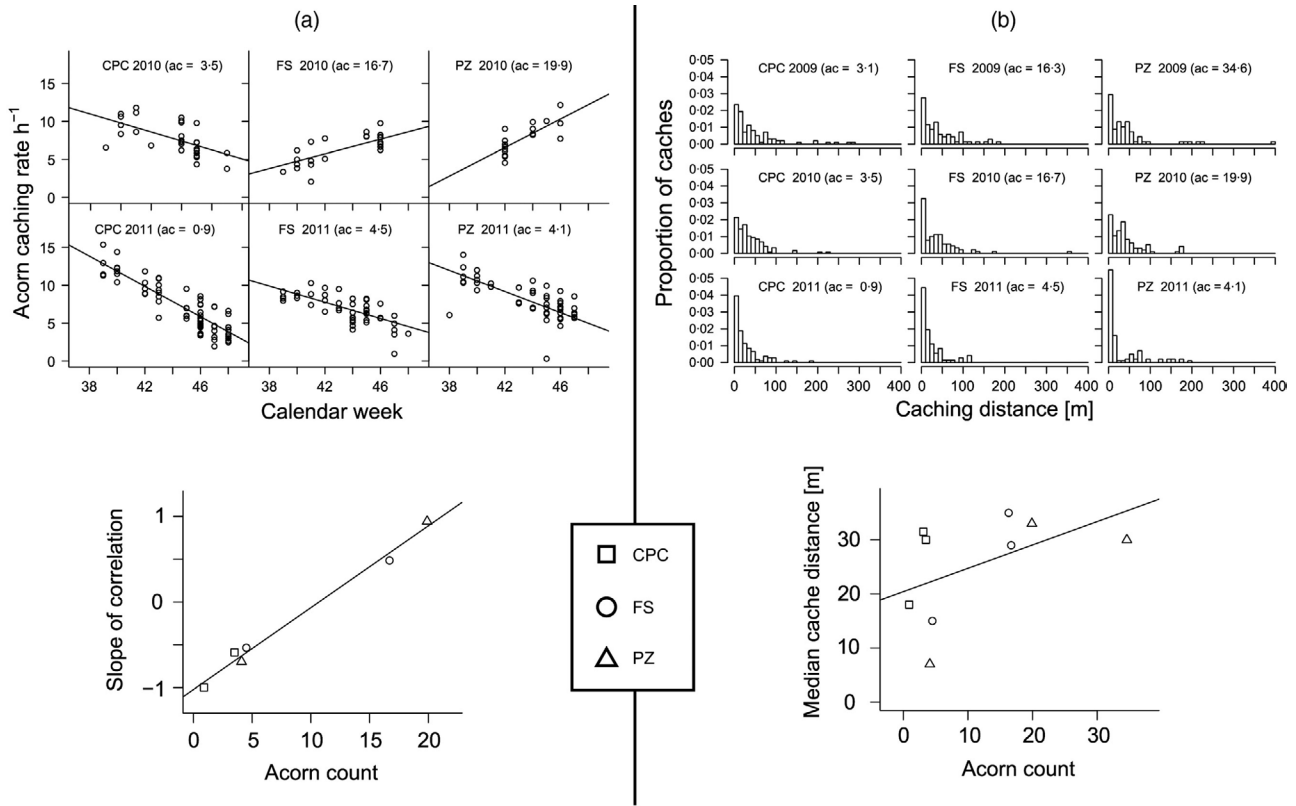
Figure 1. The context dependence of acorn caching by island scrub jays on acorn availability; (a) acorn caching rates and (b) acorn caching distances. Plot-wide acorn crop (mean acorn count/tree) indicated in each panel. (a) Model-predicted relationship between calendar week and caching rates for the three study plots (CPC – Coches Prietos, FS – Field Station, PZ – Portezuela) in 2010 and 2011. Solid line indicates linear fit for each subset of data. Sample sizes (CPC 2010: $n = 29$, 2011: $n = 71$; FS 2010: $n = 27$, 2011: $n = 57$; PZ 2010: $n = 17$, 2011: $n = 61$). Lower plot shows relationship between acorn count and the slope between week and hourly caching rate (b) Histograms of proportional distribution of dispersal distances for each plot/year combination. (Samples sizes CPC, 2009: $n = 98$; 2010: $n = 117$; 2011: $n = 106$; FS, 2009: $n = 69$; 2010: $n = 89$; 2011: $n = 72$; PZ, 2009: 68; 2010: $n = 96$; 2011: $n = 100$). Lower plot shows relationship between acorn count and median dispersal distance for plot/year combinations. See Tables 1c and 2a for model results.
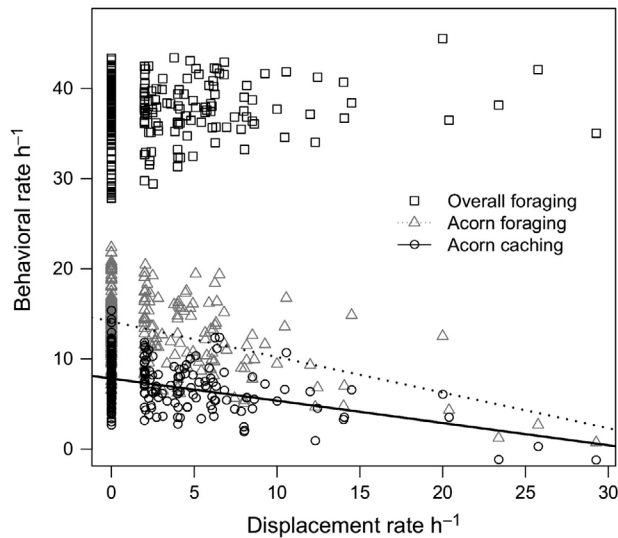

Figure 2. The context dependence of acorn caching by island scrub jays on territorial aggression. Model-predicted relationship between displacement rates, overall foraging, acorn foraging and acorn caching rates by island scrub jays during focal follows ($n = 262$). See Table 1 for statistical analysis.

CONTEXT-DEPENDENT SCATTER-HOARDING

Oaks on Santa Cruz Island received increased seed dispersal benefits from scatter-hoarding jays when acorn crops were large. Our finding that caching rates and distances varied systematically with acorn availability support predictions of the predator dispersal hypothesis, which states that variable production of large seed crops by oaks has a function beyond satiation of seed predators. We found that mean caching distances in study plots increased by as much as 40% when acorns were abundant (Figure 1b), based on annual October acorn surveys, and that caching rates by the jays changed with variation in acorn crops. Our findings therefore suggest that the context dependence of seed dispersal on seed abundance can significantly affect seed dispersal benefits trees receive from scatter-hoarding corvids.

The variation in dispersal rates with the social context of territorial aggression could point to a more complex, indirect effect of acorn crop variation on scatter-hoarding. As hypothesized, acorn foraging and caching rates correlated negatively with territorial aggression while caching

Table 2. The context dependence of acorn caching distances by island scrub jays. (a) Effect of acorn availability and calendar week on log distance of all observed caches. (b) The relationship between acorn availability, calendar week, relevant behavioral rates and log caching distances observed during focal follows .

Parameter	β	95% CI		B	SE	RI
(a) All observed caches (*n* = 791)						
Intercept	3.036	2.792	3.280	7.130	0.803	
Acorn count	**0.313**	**0.057**	**0.569**	0.017	0.040	0.72
Week	**−0.277**	**−0.398**	**−0.033**	−0.101	0.018	1.00
Acorn count × week	−0.033	−0.453	0.386	−0.001	0.002	0.19
(b) Caches observed during focals (*n* = 339)						
Intercept	2.668	2.374	2.962	5.570	1.509	
Acorn count	**0.379**	**0.061**	**0.696**	0.031	0.013	0.86
Week	**−0.372**	**−0.677**	**−0.066**	−0.071	0.030	0.95
Acorn foraging rate	−0.297	−0.623	0.029	−0.011	0.006	0.63
Acorn caching rate	0.064	−0.313	0.441	0.004	0.012	0.22
Displacement rate	−0.013	−0.296	0.270	−0.003	0.027	0.20

Model-averaged standardized (models with scaled and centered predictor variables) parameter estimates (*β*), their 95% confidence intervals, metric estimates (*B*), their standard error (SE) and relative variable importance (*RI*) for fixed effects of LMMs of log-transformed caching distance that contained *Individual* nested in *Plot* as random effect. Parameters averaged over subset of models with ΔAIC < 4. Bold indicates *β* estimates with 95% CI that do not overlap with 0. See Tables S3 and S4 for model selection parameters.

distance remained unchanged. This result echoes findings from studies with captive or provisioned western scrub jays in which rates of scatter-hoarding behavior were negatively affected by the presence of conspecific competitors (Dally, Clayton & Emery 2006; Toomey, Bowman & Woolfenden 2007). This effect of social context is hypothesized to reduce cache pilferage by competing conspecifics (Bugnyar *et al.* 2007). Interestingly, displacement rates in our study were not correlated with acorn availability (results not shown), suggesting that other factors, such as the number of non-breeders in the population, may drive territorial aggression (Carmen 2004). Moreover, recent work has shown that the mean winter abundance of scrub jays across California is correlated with the state-wide acorn crop preceding the previous winter (Koenig *et al.* 2009). Therefore, the variation in acorn production of oaks could affect the rate of seed dispersal indirectly by affecting local population density of jays and thus territorial aggression. Combined, the predator dispersal effects and social interactions among conspecifics may further increase the year-to-year variation in seed dispersal rates by jays.

This study was based on observational data collected over three years and thus has caveats that limit inference and highlight directions for future work. First, we tested masting-related hypotheses with acorn survey data, but we did not actually observe a mast year. Longer term studies are needed to confirm the patterns we describe here. We also assumed that acorn crops decline linearly with calendar, but our study was not designed to quantify changes in acorn crop sizes within seasons. Recent work on different California oak species, however, suggests that acorn crops decline linearly on trees when jays are the main dispersers, and that the slope of decline depends on initial crop size (Pesendorfer & Koenig 2016). We attempted to account for a linear decline in acorn availability by including an interaction between annual acorn count and calendar week in our models. However, studies explicitly designed to measure seasonal acorn availability would be useful. Finally, this study cannot identify the mechanisms underlying correlations between acorn crop size, jay social dynamics and seed dispersal parameters. Future experiments should examine the mechanisms underlying context dependence of corvid seed dispersal by manipulating acorn crops. Because many aspects of seed dispersal by scatter-hoarding birds are still poorly understood, such experiments would provide important contributions to the exciting field of dispersal ecology.

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Supporting Information follows the **References**.

Appendix S1. Supporting figures.

Appendix S2. Supporting information for statistical analyses.

Appendix S1: Supporting Figures

Figure S1: Location of study plots (yellow polygons) and focal territories on Santa Cruz Island, CA
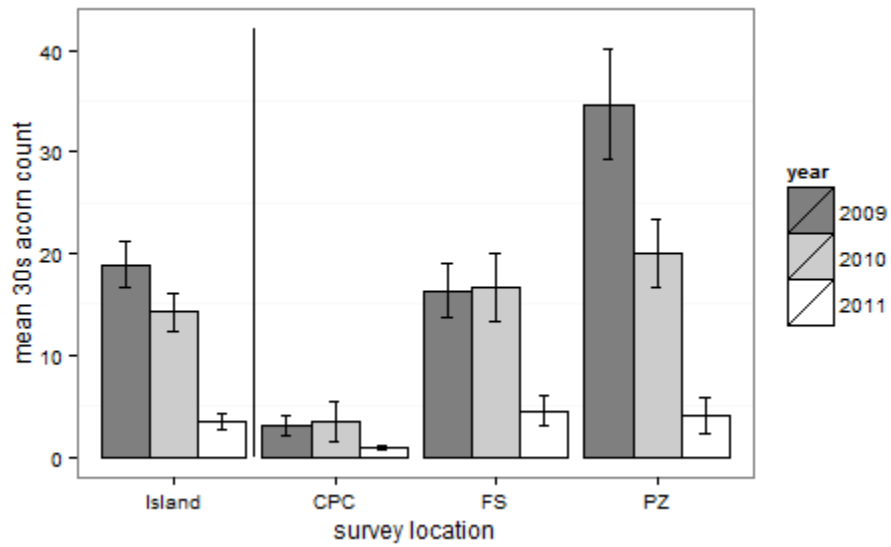
Figure S2: Island-wide (left) and plot-wide (right) acorn availability over the three-year study period.

Bars indicate mean 30s acorn count per tree, whiskers denote standard error. Island-wide survey n = 200 trees, plot-wide surveys: CPC n =40 trees, FS n = 58 trees, PZ n = 52 trees).

Appendix S2: Supporting Information for Statistical Analyses

Linear Mixed Model of Overall Foraging Rate

fixed effects: acorn count, calendar week, displacement rate, 1st order interactions

random effects: individual nested in plot

global model: Overall foraging rates ~ (acorn count + calendar week + displacement rate) ^2 + (1|plot/individual)

Table S1: Model selection for global linear mixed model of overall foraging rates during focal follows (n = 262). Degrees of freedom, AICc, ΔAIC and model weight. Only models with dAIC < 4 shown.

model parameters	df	AICc	ΔAIC	weight
acorn count	5	2566.1	0.00	0.198
null	4	2566.7	0.57	0.149
acorn count + week	6	2567.4	1.25	0.106
acorn count + displ. rate + acorn count x displ. rate	7	2568.0	1.91	0.076
acorn count + displ. rate	6	2568.2	2.05	0.071
week	5	2568.3	2.14	0.068
displacement rate	5	2568.7	2.54	0.055
acorn count + week + displ. rate	7	2569.4	3.30	0.038
acorn count + week + displ. rate + disp. rate x week	8	2569.5	3.33	0.037
acorn count + week + disp. rate + disp. rate x a. count	8	2569.5	3.34	0.037
acorn count + week + acorn count x week	7	2569.5	3.35	0.037
acorn count + week + displ. rate + a. count x week + a.count x displ. rate	9	2570.2	3.86	0.029

Linear Mixed Model of Acorn Foraging Rate

fixed effects: acorn count, calendar week, displacement rate, 1st order interactions

random effects: individual nested in plot

global model: acorn foraging rates ~ (acorn count + calendar week + displacement rate) ^2 + (1|plot/individual)

Table S2: Model selection for global linear mixed model of acorn foraging rates during focal follows (n = 262). Degrees of freedom, AICc, ΔAIC and model weight. Only models with dAIC < 4 shown.

model	df	AICc	ΔAIC	weight
acorn count + week + displ. rate + acorn count x week	8	2066.3	0.00	0.377
a. count + week + displ. rt + a. count x disp. rate + a.count x week	9	2068.2	1.95	0.142
a. count + week + displ. rt + a. count x week + displ. rt x week	9	2068.2	2.10	0.132
displacement rate + week	6	2069.2	2.93	0.087
a. count + week + a. count x week	7	2069.2	2.95	0.086
null	4	2084.3	18.05	0.000

Linear Mixed Model of Acorn Caching Rate

fixed effects: acorn count, calendar week, displacement rate, 1st order interactions

random effects: individual nested in plot

global model: acorn caching rates ~ (acorn count + calendar week + displacement rate) ^2 + (1|plot/individual)

Table S3: Model selection for global linear mixed model of acorn caching rates during focal follows (n = 262). Degrees of freedom, AICc, ΔAIC and model weight. Only models with dAIC < 4 shown.

model	df	AICc	ΔAIC	weight
acorn count + week + displ. rate + a. count x week	8	1825.3	0.00	0.402
a. count + week + displ. rate + a. count x displ. rate + a. count x week	9	1827.0	1.66	0.176
a. count + week + displ. rate + a. count x week + displ. rate x week	9	1827.3	2.01	0.147
a. count + week + a. count x week	7	1828.7	3.36	0.075
a. ct + week + displ. rt + a. ct x week + a. ct x displ. rt + displ. rt x wk	10	1829.1	3.75	0.062
displ. rate + week	6	1829.2	3.89	0.057
null	4	1841.4	16.10	0.000

Linear Mixed Model of Acorn Caching Distance

fixed effects: acorn count, calendar week, 1ˢᵗ order interactions

random effects: individual nested in plot

global model: acorn caching distance ~ (acorn count + calendar week) ^2 + (1|plot/individual)

Table S4: Model selection for global linear mixed model of acorn acorn caching distance (n = 791). Degrees of freedom, AICc, ΔAIC and model weight. Only models with dAIC < 4 shown.

Model Selection

model	df	AICc	ΔAIC	weight
acorn count + week	6	2573.0	0.00	0.529
week	5	2574.3	1.29	0.278
acorn count + week + a. count x week	7	2575.0	2.01	0.193
null	4	2620	47.24	0.000

Linear Mixed Model of Acorn Caching Distance During Focal Follows

fixed effects: acorn count, calendar week, acorn foraging rate, acorn caching rate, displacement rate

random effects: individual nested in plot

global model: acorn caching distance ~ acorn count + calendar week + acorn foraging rate + acorn cac. rate + displ. rate + (1|plot/individual)

Table S5: Model selection for global linear mixed model of acorn acorn caching distance (n = 336). Degrees of freedom, AICc, ΔAIC and model weight. Only models with dAIC < 4 shown.

model	df	AICc	ΔAIC	weight
acorn count + acorn foraging rate + week	7	1148.3	0.00	0.224
acorn count + week	6	1149.4	1.17	0.125
acorn count + acorn foraging rate + acorn caching rate + week	8	1150.0	1.71	0.095
acorn count + acorn foraging rate + displacement rate + week	8	1150.3	2.08	0.079
acorn foraging rate + week	6	1150.6	2.38	0.068
acorn count + acorn caching rate + displacement rate	7	1151.3	3.06	0.049
acorn count + displacement rate + week	7	1151.5	3.25	0.044
week	5	1151.8	3.50	0.039
acorn count	5	1152.9	3.61	0.037
acorn count + ac. foraging rate + ac. caching rate + displ. rate + week	9	1152.1	3.81	0.033
null	4	1155.0	6.71	0.008