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Spatially biased dispersal of acorns by a scatter-hoarding corvid may accelerate passive restoration of oak habitat on California's largest island

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Abstract

Scatter hoarding by corvids (crows, jays, magpies, and nutcrackers) provides seed dispersal for many large-seeded plants, including oaks and pines. When hoarding seeds, corvids often choose nonrandom locations throughout the landscape, resulting in differential survival of seeds. In the context of habitat restoration, such disproportional storing of seeds in areas suitable for germination and establishment can accelerate expansion and recovery of large-seeded tree populations and their associated ecosystems. Here, we investigate the spatial preferences of island scrub jays *Aphelocoma insularis* during scatter hoarding of acorns (*Quercus* spp.) on Santa Cruz Island. We use a large behavioral data set on the birds' behavior in combination with seedling surveys and spatial analysis to determine whether 1) island scrub jays disproportionally cache seeds in specific habitat types, and 2) whether the preferred habitat type is suitable for oak regeneration. Our results show that the jays nonrandomly cache acorns across the landscape; they use chaparral and coastal sage scrub disproportionally while avoiding open and grassy areas. The areas used most often for caching were also the areas with the highest oak seedling densities. We discuss the potential role of these findings for the recovery of Santa Cruz Island's oak habitat since the 1980s.

Seed dispersal by animals facilitates habitat recovery following disturbance (McConkey et al. 2012; Pesendorfer et al. 2016a). As anthropogenic habitat fragmentation and its negative consequences are becoming more pronounced on a global scale (Haddad et al. 2015), tree species dispersed by animals often prove more resilient than trees reliant on abiotic dispersal (Montoya et al. 2008; McConkey et al. 2012). Such resilience to fragmentation likely arises from the fact that animals often perform spatially nonrandom dispersal of seeds to areas suitable for germination and establishment (Wenny 2001; Purves et al. 2007). In the context of habitat maintenance and restoration, nonrandom dispersal can therefore serve as an important ecosystem service by reducing the costs of management actions (Pesendorfer et al. 2016a). However, despite a recent upsurge in research on seed dispersal by animals (Côrtes and Uriarte 2013) and the recognition of its important contribution to conservation goals (Wenny et al. 2011; McConkey et al. 2012), the behavioral mechanisms underlying the formation of spatial seed dispersal patterns in zoochory are still poorly understood (Cousens et al. 2010). Here, we investigate how spatial preferences by a seed-hoarding bird can result in spatially biased dispersal of acorns, and discuss how this ecosystem service may have accelerated the restoration of oak chaparral on a Southern California island.

Scatter-hoarding corvids—crows, jays, magpies, and nut-crackers—that store seeds in small caches across the landscape provide important ecosystem services as dispersers for large-seeded plants (Hougner et al. 2006; Whelan et al. 2008), and have been used to restore oak and pine habitat (Pesendorfer et al. 2016a). These valuable seed dispersal interactions become imperiled when corvid numbers become too low to maintain ecologically relevant levels of seed dispersal (Culliney et al. 2012), or when herbivores, particularly livestock, reduce seed availability or survival to levels that prevent sustainable recruitment (McConkey et al. 2012). Targeted management actions, however, can reverse such collapses and restore ecosystem services that accelerate the recovery of habitat.

A striking example of successful restoration of corvid seed dispersal is the recovery of oak vegetation dynamics on Santa Cruz Island in Southern California's Channel Island National Park. Over 150 years of intense cattle *Bos taurus* and sheep *Ovis aries* ranching activity on the island resulted in large-scale habitat degradation and fragmentation, and the establishment of large feral populations of sheep, pigs *Sus scrofa* and turkeys *Meleagris gallopavo* (Morrison 2011). All 4 species negatively affected the island's vegetation community. Total and native plant cover and diversity were reduced, nonnative plants spread quickly, and the diversity, composition and abundance of native fauna changed (Van Vuren and Coblentz 1987; Beltran et al. 2014). Managers removed cattle, sheep, pigs, and turkeys from the island between the 1980s and 2007 (Morrison et al. 2011). Santa Cruz Island is now free of nonnative herbivores and the vegetation has responded rapidly: 28 years after the initial intervention, passive vegetation recovery resulted in a 52% increase of woody cover including oak chaparral, and a drastic reduction of areas that are bare or covered in grass (Beltran et al. 2014). Autoregressive models of the vegetation changes on Santa Cruz Island (Dahlin et al. 2014) suggest that the scale and spatial autocorrelation of the recovery in medium-height chaparral vegetation coincides with the home range size and dispersal distances observed for island scrub jays *Aphelocoma insularis*, the primary disperser of the island scrub oak *Quercus pacifica*, the dominant plant of oak chaparral on the island (Junak et al. 1995).

While changes in the vegetation of Santa Cruz Island can be attributed to a number of factors, seed dispersal by island scrub jays likely plays a pivotal role in the ongoing recovery of oak chaparral. Endemic to the $250 \, km^2$ island, the jay is one of the most range-restricted passerines in the United States and itself the focus of large-scale conservation efforts (Morrison et al. 2011; Sillett et al. 2012; Morrison 2014). Like many corvids, the jays almost exclusively place acorns in the ground, and transport a majority to areas unreachable by gravity. Individual jays cache 3,500–5000 acorns per year, and frequently transport them farther than 100 m and up to 400 m from the parent plant (Pesendorfer et al. 2016b). Home ranges of territorial pairs span 3.5 ± 0.2 ha (mean ± standard error (SE)), that contain $63 \pm 2\%$ of oak chaparral cover but also a variety of other vegetation types such as grass-covered and barren areas, coastal sage scrub, and large riparian trees (Caldwell et al. 2013). These vegetation types vary strongly in their suitability for oak recruitment (Stratton 2010; Pesendorfer 2014); habitat preferences by caching jays could thus increase survival of seeds and seedlings—the hallmark of directed dispersal (Wenny 2001).

Here, we use a combination of spatial analysis, behavioral observations, and vegetation surveys to investigate whether island scrub jays displayed habitat preferences when caching acorns, and whether such preferences resulted in the disproportional arrival of island scrub oak acorns to areas in which their seedlings thrive. To quantify the birds' scatter-hoarding and space-use behavior, we collected behavioral observations over 3 oak fruiting seasons. We then used Compositional Habitat Analysis (Aebischer et al. 1993) on home range-level data ($n = 13$ home ranges, 26 jays) to determine whether the birds showed significant habitat selectivity when caching acorns. Finally, we compared these data with the proportional distribution of oak seedlings among vegetation types, informing us about the potential role of the birds in driving oak dispersal dynamics.

Materials and Methods

Fieldwork was conducted between September to December 2009 and 2011 on Santa Cruz Island in Channel Islands National Park, California. With a mediterranean climate of cold, wet winters and hot dry summers, the island is composed of habitat typical of coastal Southern California, including coastal sage scrub, oak woodlands, and oak chaparral dominated by island scrub oak (Junak et al. 1995; Fischer et al. 2009). We conducted our work on 3 large study plots established to study island scrub jay demography: Coches Prietos Canyon (115 ha), Field Station (226 ha), and Portezuela (163 ha). Island scrub jays occupy home ranges of 3.5 ± 0.2 ha (mean ± SE) with $63 \pm 2\%$ cover of chaparral vegetation interspersed with open grassland and scrub vegetation (Caldwell et al. 2013).

Behavioral observations and home range data

We quantified the scatter-hoarding behavior of 26 color-banded, territorial island scrub jays. All birds were fitted with a unique combination of color bands and an individually numbered USGS metal band; see Caldwell et al. (2013) and Langin et al. (2015) for details on jay capture methods. Like many island residents, island scrub jays are less shy than their mainland sister taxa (Haemig 1988) and the vegetation structure allowed for continuous observation from vantage points throughout the birds' home ranges (Pesendorfer et al. 2016b). Using *ad libitum* (2009) and focal follow (2010–2011) strategies, we recorded scrub jay foraging, scatter-hoarding, and territorial behavior. Each home range was visited twice a week and, to avoid bias for obvious foraging such as fly catching, the recording of observations started 5 min after the bird was located. In 2009, we collected 1 foraging and 1 caching observation for each visit. In 2010–2011, we conducted 30-min focal follows, during which all foraging, caching, and social behavior were recorded (see Pesendorfer et al. 2016b for details).

We collected GPS point locations of individuals to estimate the home range of territorial pairs. In 2009, we collected 3 GPS points, spaced 5 min apart, for each visit to a home range (Caldwell et al. 2013). Similarly, for focal follows in 2010–2011, we noted birds' location at the start, as well as every 10 min and recorded the GPS points after the follow, thus resulting in 4 points per follow. If the bird was lost before the intended follow period ended, we recorded the final location at which it was observed.

We quantified jays' habitat use while caching acorns by recording the substrate (e.g. soil, leaf litter) or, if the acorn was cached below vegetation, the plant species for each observed caching location. Using this information, each cache was then categorized into 1 of the 7 vegetation categories (Supplementary Table 1). Data on rates of foraging and scatter-hoarding as well as dispersal distances are reported elsewhere (Pesendorfer et al. 2016b). We observed the placement of 536 caches in the ground in 13 jay home ranges (Supplementary Table 2).

To determine the proportion of available vegetation types in the home range of each territorial pair, we combined our data on the jays point locations with publicly available vegetation data for the area. We pooled the GPS points collected during jay focal follows in September to November, 2009–2011, and constructed minimum convex polygons in ArcMap 10.0 (ESRI 2011) for each jay home range. We then used a multistep process to estimate the proportion of the home ranges covered by 7 vegetation categories: baccharis (BAC), chaparral (CHA), coastal sage scrub (CSS), grass or unvegetated (GRO), oak woodland (LGO), riparian (RIT), and other large trees (TRE). We first combined a published vegetation map for 2007 with LiDAR data collected in 2010 (Cohen et al. 2009; USGS 2010). The 2007 vegetation map describes plant alliances over broader areas and has minimum mapping units (MMUs) of 0.5 ha, and was thus of much coarser resolution than the LiDAR data with MMU = 1 m^2. Therefore, we used the Cohen et al. (2009) map to determine the area of the vegetation categories in each home range. Next, we subtracted the digital elevation model layer of the LiDAR data from the digital surface model to obtain the height of the vegetation for each square meter. Finally, we subtracted the area covered by vegetation lower than 25 cm from the area of each vegetation type and added it to the category GRO, as these areas were bare or covered in short vegetation, such as grass. This process generated an estimate of relative availability of each habitat type in jay home ranges (Supplementary Figure 1).

We conducted thorough surveys of 3 representative jay home ranges to estimate the relative distribution of oak seedlings. Following the assembly of the home range maps, we used the "trail" function in the GPS units to track our progress as we meticulously examined the complete surface area of each home range. For each detected seedling (<50 cm height), we recorded a GPS waypoint with a Trimble ® Geo 4 precision GPS unit, as well as the vegetation below which it was found.

Habitat selectivity for caching

We used Compositional Habitat Analysis (Aebischer et al. 1993) to compare jay use of caching vegetation categories to the estimated proportion of those vegetation types in each home range (Supplementary Table 2). Compositional data analysis compares the pairwise, log-ratio differences of the used and available proportions to a multivariate normal distribution with a mean of zero. If significantly nonrandom habitat use is found, the vegetation types can be ranked using the differences in log-ratios (Aebischer et al. 1993). The procedure is sensitive to small values, so we limited the analysis to the 4 dominant vegetation categories that collectively accounted for 93% of caches (BAC, baccharis; CHA, chapparal; CSS, coastal sage scrub; and GRO, grassy or open areas).

Finally, we tested if the spatial distribution of oak seedlings reflected the jays' caching preferences. We used Fisher's exact tests for each home range to compare the number of seedlings counted in each vegetation category to expected counts if the seedlings were distributed according to habitat availability. We also compared the seedling counts with the number of caches that we observed focal jays place in each vegetation category.

Results

Island scrub jays showed clear habitat selectivity when caching acorns ($n = 13$ home ranges, $\Lambda = 0.064$, $P = 0.002$). Coastal sage scrub (CSS) received an average ($\pm$ SE) $17.6 \pm 3.2\%$ of caches in a home range, but covered only of $5.7 \pm 1.6\%$ of the jays' home range

area. Similarly, $53.1 \pm 3.5\%$ of caches were placed under chaparral plants (CHA) that accounted for $30.1 \pm 3.8\%$ of ground cover. In contrast, the jays cached $14.7 \pm 2.5\%$ of acorns in bare or grassy areas (GRO), even though this vegetation category covered $52.7 \pm 2.5\%$ of home ranges (Figure 1). The analysis ranked the 4 categories from highly selected to avoided as: CSS > CHA > BAC > GRO.

Oak seedlings were nonrandomly distributed among the vegetation categories (Fisher's exact tests: Coches Prietos: $n = 141$, df = 3, $P < 0.0001$; Field Station: $n = 41$, df = 3, $P < 0.0001$; Portezuela: $n = 158$, df = 3, $P < 0.0001$). The general patterns of seedling distribution were similar across home ranges (Figure 2). The majority (52–78%) were growing below chaparral plants, including the island scrub oak, which comprised just 30% of home range vegetation. Coastal sage scrub held 19% of seedlings, more than expected by habitat availability (5%). Open, grassy areas that cover 53% of home ranges, however, held only 14% of seedlings (Figure 2). The distribution of seedling counts for each vegetation category did not differ significantly from the distribution of jay caches among these categories in 2 of the 3 home ranges surveyed (Fisher's exact tests:
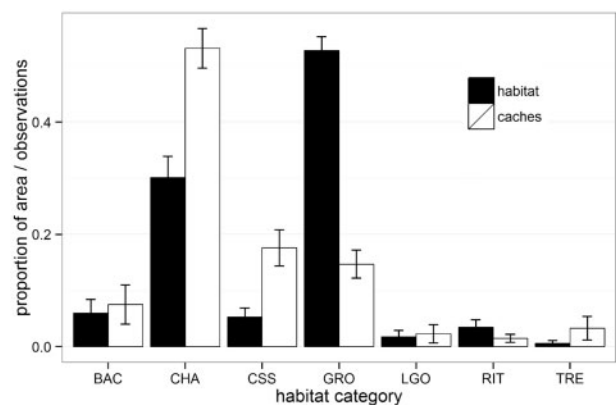

Figure 1. Habitat preference of caching island scrub jays. Bars indicate mean proportion of available habitat (black bars) and proportion of caches (white bars) of 13 territorial pairs in vegetation categories. Whiskers denote SEs. BAC, baccharis; CHA, chaparral; CSS, coastal sage scrub; GRO, grass/open; LGO, large oaks; RIT, riparian trees; TRE, other trees.
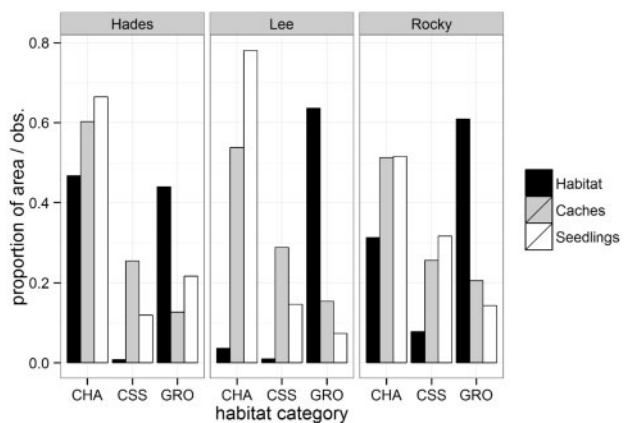

Figure 2. Proportional distribution of available habitat (black bars), caches (gray bars), and oak (*Quercus* spp.) seedlings (white bars) across habitat types in 3 representative home ranges of island scrub jays. BAC, baccharis; CHA, chaparral; CSS, coastal sage scrub; GRO, grass/open; LGO, large oaks; RIT, riparian trees; TRE, other trees.

Coches Prietos: $n = 141$, df $= 3$, $P = 0.0053$; Field Station: $n = 41$, df $= 3$, $P = 0.091$; Portezuela: $n = 158$, df $= 3$, $P = 0.26$).

Discussion

Island scrub jays cached acorns nonrandomly with respect to vegetation type. Birds avoided open areas and grasslands, and placed most acorns below vegetation of chaparral and coastal sage scrub, the vegetation types with the highest density of oak seedlings. The birds' habitat selectivity may thus be one of the important drivers of the spatial distribution of *Q. pacifica* seedlings. This ecosystem service would enhance the passive recovery of oak chaparral on Santa Cruz Island.

Scatter hoarding of seeds only provides the first step in a sequence of biological processes that determine the eventual reproductive success of oaks. Following caching, an unknown proportion of cached seeds is recovered by jays, whereas some acorns that remain in the ground fail to germinate. Without data on acorn survival and germination rates for different vegetation types, however, untangling seed dispersal from these other processes that may have led to high seedling numbers in those areas is difficult (Levine and Murrell 2003). For example, in absence of habitat differences in seed germination and seedling growth, the jays' habitat selectivity for cache sites could be the only drivers of recruitment variation. Considering the important role of nurse plants in the recruitment of oaks in mediterranean environments, however, post-dispersal survival of *Q. pacifica* is likely higher in the caching locations selected by island scrub jays (Callaway and D'Antonio 1991; Callaway 1992). Our findings therefore echo results from studies on a wide array of corvids that perform some degree of directed dispersal—the disproportionate dispersal of seeds into areas of high recruitment (Johnson et al. 1997; Wenny 2001; Wenny et al. 2011; Pesendorfer et al. 2016a).

More research is needed to understand the habitat preferences of island scrub jays during scatter hoarding. Their goal should be to recover as many cached seeds as possible, and not to lose them to germination. Some work with captive corvids suggests, however, that the birds rely heavily on landmarks when recovering caches, which may explain their preference for the edge of existing vegetation (Pesendorfer et al. 2016a). Similarly, in the dry landscape of the fall season on Santa Cruz Island, jays may select cache sites in soft substrates, such as the leaf litter that accumulates below chaparral and coastal sage scrub vegetation. We occasionally observed jays attempting to cache in sparse grass or open dirt; after several attempts of pushing an acorn into the ground, they would retract and place it below a nearby shrub. The birds may also cache near vegetation to avoid being seen by other jays. Corvids generally possess excellent spatial memory that they use to pilfer each other's caches (Dally et al. 2006). Future experimental work designed to investigate jay preferences for acorn cache sites under field conditions would be especially informative.

We hypothesize that dispersal of acorns provides 2 major benefits to island scrub oaks. First, seed dispersal to nearby oak chaparral patches likely enhances gene flow, contributing to the maintenance of existing oak populations. Second, seed dispersal into coastal sage scrub vegetation facilitates succession toward oak chaparral (Knapp 2010). The birds' selectivity for chaparral and coastal sage scrub as acorn caching sites should favor germination, seedling establishment, and recovery of oak-dominated vegetation on Santa Cruz Island.

Other recent studies allude to the important role of island scrub jays in the recovery dynamics of Santa Cruz Island's oak habitat. First, island scrub oak populations on islands that lack avian seed dispersers are declining despite intensive conservation efforts (Knapp 2010). Second, the rapid recovery of woody vegetation, and oak chaparral in particular, on Santa Cruz Island suggests that this dispersal-limited group of plants is outpacing other growth types, such as native grasses and wind-dispersed trees (Beltran et al. 2014). Third, autoregressive modeling of Santa Cruz Island's vegetation dynamics since livestock removal suggest that the scale and pace of habitat recovery carry the signature of jay seed dispersal (Dahlin et al. 2014). Combined, these studies suggest that the removal of feral herbivores and the presence of an avian seed disperser have been central to the observed recovery of oak habitats on Santa Cruz Island.

Our results also add to the growing evidence that proactive re-establishment or reintroduction of seed dispersal vectors can be combined with other management actions, such as herbivore control and seed addition in the context of disease mitigation, to accelerate the restoration of oak ecosystems (Hougner et al. 2006; Wenny et al. 2011; McConkey et al. 2012). Channel Islands National Park provides a particular suitable opportunity for such action. Santa Rosa Island, located 12 km from the western shore of Santa Cruz Island, was once home to island scrub jays, but the local population has since gone extinct (Morrison et al. 2011). Chaparral and woodland habitats on Santa Rosa are highly degraded, and the island has only been free of nonnative herbivores since 2012. The reintroduction of the island scrub jay, a highly range-restricted species of management concern, would provide a cost-effective way to accelerate the restoration and expansion of oak chaparral on Santa Rosa Island (Morrison et al. 2011). While such an intervention would be controversial, we believe that a well-prepared reintroduction, using state-of-the-art decision-making tools and safeguards, provides a promising path forward (Morrison 2014). The success story of Santa Cruz Island may, therefore, serve as a beacon in a world of increasing habitat destruction and ecosystem degradation.

Supplementary Material

Supplementary material can be found at http://www.cz.oxfordjournals.org/.

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