

# Ontogeny of food-caching site preferences in young Florida Scrub-Jays: evidence of learning or changing social status?

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**ABSTRACT.** Florida Scrub-Jays (*Aphelocoma coerulescens*) are cooperative breeders endemic to Florida's oak scrub. In autumn, Florida Scrub-Jays cache thousands of acorns and exhibit behaviors that appear to balance cache site selection against food degradation or cache robbery. However, both experience and position within a social dominance hierarchy could affect individual cache preferences. We examined the cache site preferences of birds with differing levels of caching experience and at different strata within a complex social dominance hierarchy. Our objective was to determine how experience, social position, and social context when caching influenced microhabitat preferences, and if these change as jays age, gain experience, and their social position changes. Naïve first-year birds preferred to cache in well-hidden, densely vegetated sites with relatively high soil moisture content. Naïve birds also cached farther from provisioning points if observed by a socially dominant bird than when they were alone or in the presence of birds of equal social status. Experienced adults preferred to cache in open, dry sandy sites and social context at the time of caching did not influence their preferences. As naïve birds aged, they gained experience and their social position changed. Experienced second-year birds shifted their preference to more open, drier sites, and did so more often when they remained subordinate within their group rather than becoming dominant breeders. Second-year birds that remained subordinate did not alter their caching behavior if observed by dominant birds. These patterns suggest that after gaining experience, jays learned which sites were more appropriate for caching and shifted their preference, regardless of their changing social status. We suggest that the risk of cache loss to food degradation might be greater than the risk of pilfering for Florida Scrub-Jays, especially for birds in any social strata except the most subordinate, but this requires additional study.

**RESUMEN.** **Ontogenia de preferencia para obtener alimento de parte de individuos jóvenes de *Aphelocoma coerulescens*: evidencia de aprendizaje o cambio de estatus social?**

Al arrendajo (*Aphelocoma coerulescens*) es un criador cooperativo endémico del matorral de roble de Florida. En el otoño, estas aves almacenan miles de bellotas y exhiben una conducta que parece balancear la selección del lugar de almacenaje con la posibilidad de que esta pueda ser robada o que las bellotas no se degraden. Sin embargo, tanto la experiencia como la posición en la jerarquía social de estas aves puede afectar las preferencias individuales en donde se almacenen las bellotas. Examinamos la preferencia en los lugares de almacenaje con diferentes niveles de experiencia y la posición que ocupa un individuo dentro de un complejo sistema jerárquico de dominancia. Nuestro objetivo fue determinar como la experiencia, la posición social, y el contexto social, contribuyen en las preferencias de selección de microhábitat, y si estos cambios influyen, con cambios en la posición social, al ganar experiencia y edad de las aves. Las aves ingenuas de primer año prefirieron almacenar las bellotas en lugares bien escondidos, con densa vegetación, y con suelos relativamente altos en humedad. Este grupo también escondió la comida en lugares más lejos, de los puntos de aprovisionamiento, si eran observadas por individuos dominantes en comparación que cuando estaban solas o eran observadas por individuos de igual rango social. Los adultos experimentados, prefirieron almacenar en lugares abiertos, arenosos y secos, y el contexto social no influyó en la preferencia del lugar de almacenaje. Según la edad de los jóvenes incrementó, estos ganaron experiencia y de igual manera cambio su posición social. Las aves de segundo año cambiaron sus lugares de almacenaje a lugares más abiertos y secos y lo hicieron con mayor frecuencia aun cuando se mantuvieron como subordinados, dentro del grupo, en vez de ser individuos dominantes y reproductivos. Este patrón sugiere que, al ganar experiencia, los arrendajos aprenden que lugares son más apropiados para almacenar y cambias sus preferencias, sin importar su estatus social. Sugerimos que el riesgo de perder las bellotas, al estas degradarse, pudiera ser mayor que el riesgo de robo, particularmente para aves de cualquier nivel social, excepto para los más subordinados, aunque esta apreciación necesita mayor estudio.

*Key words:* food hoarding, foraging, habitat selection, microsite, social dominance

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Food-caching has evolved across many different taxa to allow organisms to survive periods of low food abundance (Koenig and Mumme 1987, Petit et al. 1989, Woodrey 1990, Jacobs and Liman 1991, Waite and Reeve 1993, Lahti et al. 1998, McKenzie et al. 2005, Xiao et al. 2013, Pravosudov et al. 2015, Croston et al. 2017). Caching is adaptive in concert with behavioral strategies that ensure cached items are successfully retrieved (Andersson and Krebs 1978, Grodzinski and Clayton 2010, van der Veen et al. 2020). However, even though many caching species exhibit spatial memory, cached items may be lost to degradation, predation by heterospecifics, or pilfering by conspecifics, reducing recovery success. Buried foods may decay by rotting or fungal infection associated with variations in microhabitat and soil moisture (Neuschulz et al. 2015) and degradation rates may vary among different food types and different cache locations. Some hoarding species have well-developed episodic memory (de Kort et al. 2005) of what they cached, where, and when. Caching choices are refined based on observational learning of positive and negative cache recovery (van der Vaart et al. 2011). This enables caching species to learn through trial and error how decay rates vary depending on the environment and food item to maximize cache recovery success (Clayton et al. 2005, de Kort et al. 2007). Such plastic learning also allows caching species to adjust to changes in environmental and social context (Pravosudov and Lucas 2000, Montoya and Gutierrez 2016).

Most caching species of birds are scatter rather than larder hoarders (Vander Wall 1990), which refers to the spatial dispersion of cached food items. Scatter hoarding, at its most extreme, is one item stored at each cache site. Scatter hoarding may have evolved to reduce cache loss due to predation, but among territorial scatter hoarders that live in social groups, an additional source of cache loss is pilfering (Vander Wall and Jenkins 2003). Many species have strategies to reduce pilferage by conspecifics (Bugnyar and Kotrschal 2002, Dally et al. 2006a, Clayton et al. 2007), but behavioral responses may vary with the social context of observers at the time of caching (Pravosudov and Lucas 2000). Some species modify their caching

behavior depending on the social or dominance status of nearby observers (Lahti et al. 1998, Dally et al. 2006b, Kalinowski et al. 2015). When observed during caching, some may prefer to cache in private by flying farther (Dally et al. 2005), caching behind screening vegetation (Legg and Clayton 2014), or re-caching an item when no longer being observed (van der Vaart et al. 2012). However, strategies to minimize pilfering may counteract strategies to minimize degradation, requiring trade-offs in cache site selection or flexible site selection based on the relative risks of pilfering and degradation (Toomey et al. 2007, Kulahci and Bowman 2011).

Scatter hoarding of oak acorns and pine seeds is a widely distributed mutualism for species in the family Corvidae (Pesendorfer et al. 2016a). Corvids are highly intelligent (Wright et al. 2017), and many studies have focused on the cognitive solutions to caching problems in a variety of species in the family, for example, Pinyon Jays (*Gymnorhinus cyanocephalus*, Balda et al. 1997), California Scrub-Jays (*Aphelocoma californica*, de Kort et al. 2005), Clark's Nutcrackers (*Nucifraga columbiana*, Balda and Kamil 1992), Common Ravens (*Corvus corax*, Bugnyar et al. 2007), and Eurasian Jays (*Garrulus glandarius*, Shaw and Clayton 2012) among others. Corvids are widely distributed around the world in a variety of ecosystems, each of which might exert different selection pressures on cognitive solutions to caching. In addition, the social structure of corvids varies from extremely social, communally nesting permanent flocks to cooperative breeders to monogamous pairs, with different social structures influencing the risks of conspecific pilfering (Clayton and Emery 2007).

Florida Scrub-Jays (*Aphelocoma coerulescens*) are cooperative breeders endemic to xeric oak scrub habitats of Florida, a fire-mediated ecosystem (Woolfenden and Fitzpatrick 1984, 1996). They live in social groups with a socially dominant breeding male and female, and subordinate offspring from previous years that have not yet dispersed and act as helpers during subsequent breeding seasons (Woolfenden and Fitzpatrick 1977). Throughout the year, but most often during the fall, all members of a group harvest and scatter hoard as many as 6000 to 7000 acorns of several species (*Quercus geminata*, *Q. inopina*,

*Q. chapmanii*, and *Q. myrtifolia*) per individual (DeGange et al. 1989). Most caches are placed in patches of bare sand, within leaf litter or grass along the perimeter of oak patches (edge habitat), or in vegetated patches under oaks and palmettos. Jays often use palmettos or the cones and branches of *Pinus elliotii* and *P. clausa* for temporary storage. Florida Scrub-Jays defend territories year-round, and caches are usually placed within an individual's breeding territory or along adjacent territory boundaries (Woolfenden and Fitzpatrick 1977). Jays demonstrate caching preferences for high tannin oaks (Fleck and Woolfenden 1997), which presumably reduces rates of post-cache degradation (Dearing 1997). Jays also regularly re-cache recovered acorns, but prefer re-caching in drier sites, typically open bare sand patches, than the original caching site (Kulahci and Bowman 2011), which suggests awareness of environmental conditions that may influence degradation rates (Grodzinski and Clayton 2010).

Jays also appear sensitive to the dominance status of jays present when caching. Cache pilferage frequently occurs either when breeders pilfer from subordinates or older helpers pilfer from yearlings (DeGange et al. 1989, Toomey et al. 2007). Dominant birds regularly pilfer the caches of subordinates (DeGange et al. 1989), but subordinates counter this by flying farther and caching in denser vegetation when observed by a dominant bird (Toomey et al. 2007). Observable differences in caching skills exist between young and experienced animals in selecting high quality sites (Smith 1972, MacDonald 1976, Smith and Reichman 1984, Jacobs et al. 2014) and juvenile jays are no different. They regularly cache non-food objects (DeGange et al. 1989) and cache at the immediate site where they harvest foods. Young birds are also at the bottom of the social hierarchy and, thus, their caches are most likely to be pilfered by adults and they are more likely to change their caching decisions based on social context than higher-ranking individuals (Toomey et al. 2007).

We followed the ontogeny of caching behavior in young Florida Scrub-Jays over a period of two years to better understand how caching decisions change over time as birds gain experience, but also as they ascend the

social hierarchy in their social groups. We compared caching behavior of naïve and subordinate birds with older, more experienced and socially dominant breeders relative to social context at the time of caching and microhabitat caching preferences. In the subsequent year, we re-measured the changing preferences and social sensitivity of the naïve first-year birds (now experienced second-year birds), after they had the opportunity to refine their preferences through learning or because of their changed social status. We predicted that, after gaining experience, birds would shift their caching preference toward more open sites, but those that remained as subordinates within their group dominance hierarchy would shift less than those that ascended to the top of the dominance hierarchy by obtaining breeding positions.

## METHODS

Our study was conducted at Archbold Biological Station (ABS) in Highlands County, Florida (27.10°N, 81.21°W), located near the south end of the Lake Wales Ridge. Our observations were of uniquely color-banded birds, part of the long-term study population at ABS (Woolfenden and Fitzpatrick 1984, Mumme et al. 2015, Fitzpatrick and Bowman 2016). The age, sex, and social status of all members of every family group were known. Data were collected from February to May 2016 and 2017, and all caching observations and microhabitat data were collected from 08:00 to 13:00. Jays cache acorns primarily in the fall, but are extremely focused on this task and less tolerant of human presence, thus we conducted our observations in the spring by providing jays with peanuts and observing their caching behavior. Jays readily cache peanuts year-round, and this experimental method has been used during spring in two previous studies examining caching behavior in Florida Scrub-Jays at ABS (Toomey et al. 2007, Kulahci and Bowman 2011). The observations also generally conform to behavioral patterns observed in this and other corvid-oak mutualisms (Bossemma 1979, DeGange et al. 1989, Garcia et al. 2002, Clayton et al. 2005, Pesendorfer et al. 2016a,b).

**Field methods.** We recorded observations of caching behavior and microhabitat associations in 2016 and 2017. In 2016, we

recorded the caching behavior of 39 naïve first-year birds (hatched in 2015; hereafter, naïve first-year [FY]) and 48 older (2 yr +), experienced (hereafter, experienced adults) birds in 39 territories. All but one of the experienced adults observed in 2016 were breeders. In 2017, we repeated observations on 20 of the surviving birds from the 2015 FY cohort (hereafter, experienced second-year [SY]) using the same protocol to collect caching observations and characterize caching sites and the associated random sites. Of these, 14 individuals had transitioned to breeders and six remained as helpers in their natal territory. In 2016, each individual (experienced adults and FY) was observed at least twice and the number of observations per individual ranged from 2–4. In 2017, all SY birds were observed caching twice. The 20 SY birds were observed in both years so their caching behavior during the two years could be compared. During each observation session, we located the family group of a focal individual without drawing the group away from their territory. We attempted to feed all focal birds when alone, but most observations were of focal birds in the company of other jays of the same or neighboring families. Once a focal individual was located and we recorded the band combinations of other birds present, we provided the focal bird with a single half peanut (still in the shell), consistent with previous caching experiments with the jays (Toomey et al. 2007, Kulahci and Bowman 2011). We started our observations when the focal individual picked up the offered peanut. We followed the individual if it moved to a different spot to cache the peanut. We terminated the observation if the bird ate the peanut, if another bird kleptoparasitized the peanut, or we were unable to follow the focal bird. When we were able to follow a bird, we flagged the cache location and returned within 24 h to record the microhabitat association, soil moisture content, percent canopy cover, percent leaf litter, distance from feeding location, and whether the cache site was shaded by overhead vegetation. All caching events occurred either in the interior or on the boundaries of the focal bird's territory.

We defined microhabitat associations as either bare open sand, vegetated, or edge. Bare open sand was any cache location in bare sand  $\geq 1$  m from the nearest vegetated

patch. Edge sites were cache locations in bare sand  $< 1$  m from a vegetated patch (but not just a solitary plant). Edge sites were often near leaf litter along the perimeter of oak stands, thus able to hold more moisture, but represent a different vegetation structure than the interior of large oak stands. Vegetated sites were considered any cache site with living vegetation, such as under oaks and pines, or in grassy patches. These microhabitats are representative of the composition of Florida scrub habitat and similar classifications have been used in this system (Kulahci and Bowman 2011). We recorded the straight-line distance (m) from the area where we gave the bird the peanut to the cache site. Locations of both provisioning and cache sites were recorded using the smart-phone app Collector (ESRI 2015a) and subsequently downloaded to ArcMap (ESRI 2015b), allowing us to accurately determine distances. At each cache site, we selected a random point, determined from a random distance and direction, and measured the same habitat metrics. These points served as a random sample of available caching habitat to which sites selected by jays could be compared.

We determined the social rank of all observing birds based on both social status and age. We identified all birds based on their unique band combinations. Breeders were dominant to non-breeders regardless of sex. Males were dominant to females, but only within social classes. For non-breeders, older birds were dominant to younger birds (Woolfenden and Fitzpatrick 1977). From these hierarchies, we determined if any of the observing birds were socially dominant to the focal individual.

**Data analysis.** We analyzed the caching observations of 87 individuals (48 experienced adult, 39 FY/SY birds) across 2016 and 2017 (Table S3). Date, location, and social context differed during each observation. Jays occupy scrub that has a great deal of habitat heterogeneity both within and among territories (Mumme et al. 2015) such that every individual had access to all microhabitat types and high and low soil moisture levels, thus we assumed that each caching observation was not landscape-biased. In addition, social contexts at the time of caching varied greatly, from alone to surrounded by all family members.

We used an ANOVA to determine if soil moisture at selected cache sites varied significantly among the three microhabitat types for both 2016 and 2017. If significant differences were detected, a Tukey's post hoc test was run. We used a linear mixed effects model (LME) to determine factors affecting differences in the soil moisture at observed cache sites using the difference between the mean of each individual's random point soil moisture values and each observed soil moisture value as a response variable. LME fixed effects included jay age, year, percent leaf litter, number of cover species, percent canopy cover, microhabitat type, presence of an observing dominant jay, and number of jays observing; we used individual jay ID as a random effect. All potential significant interactions were tested. To determine if social pressure influenced caching distances, we used linear models with social status and whether a dominant was observing as an interaction term and the number of jays observing as a predictor as well. We also used a *t*-test to determine if distance-to-cache differed between SY helpers and breeders in 2017.

We tested for significant selection of microhabitat associations using compositional analysis at the third-order scale according to Johnson's (1980) hierarchy to determine if jays selected particular microhabitats for caching disproportionately compared to available caching sites (Aebischer et al. 1993). Third-order habitat selection was measured by comparing the proportion of times an individual cached in each microhabitat type relative to the number of times each microhabitat type occurred across all the random points for that given territory (Manly et al. 2007). If jays cached in any microhabitat association at a higher proportion than was available, this indicated a preference; lower proportions indicated avoidance. These were run using all birds, and then individually for each of our three categories, including naïve FY birds and experienced adults in 2016, and experienced SY birds in 2017. The compositional analysis was run using the *compans* function in the *adehabitats* package in R (Calenge 2006), and all zero values that occurred in the used habitat proportions were replaced with 0.01 (Aebischer et al. 1993). Additionally, using the same proportion data from caching observations as previously mentioned, we

calculated Manly resource selection ratios using the 'widesIII' function in the *adehabitats* package to quantify preference across each of the three microhabitats, and for each individual jay (Calenge 2006, Manly et al. 2007). We then used individual Manly selection ratios for each microhabitat as a response variable in separate LME models constructed to test the effects of age, sex, year, and social status on caching site preferences. For each model, we included the Manly ratios for a given microhabitat type as the response variable and age class, sex, year, social status as predictors, with territory included as a random effect.

Model selections for all LMEs were evaluated using second-order Akaike information criterion adjusted for small sample sizes to rank competing models (AICc; Hurvich and Tsai 1989, Burnham et al. 2011). We generated AICc tables and compared competing models based on  $\Delta$ AICc and model weight ( $W_i$ ). All statistical analyses were carried out in R statistical software (R Core Team 2017 v. 3.3.3) using the R packages *lme4* (v. 1.1–19), *lmerTest* (v. 3.0–1), *adehabitats* (v. 3.1), *MASS* (v. 7.3), and *AICcmodavg* (2.2–2) (Venables and Ripley 2002, Calenge 2006, Bates et al. 2015, Kuznetsova et al. 2017, Mazorelle 2017). Values are provided as means  $\pm$  1 SD, and all statistical tests were considered significant at  $P < 0.05$ .

## RESULTS

**Soil moisture differences.** Soil moisture varied significantly among the three microhabitat associations (ANOVA  $F_{2,5} = 2.5$ ,  $P = 0.004$ , Fig. 1), and open sand patches were significantly drier (Tukey post hoc tests,  $\bar{x} = 0.93 \pm 2.72\%$  moisture,  $N = 89$ ) than vegetated patches ( $\bar{x} = 3.25 \pm 4.99\%$  moisture,  $N = 115$ ), but not edge patches ( $\bar{x} = 2.27 \pm 3.67\%$  moisture,  $N = 37$ ). Soil moisture of edge and vegetated sites did not differ significantly.

**Changes in cache distances.** Naïve FY birds cached farther from provisioning locations when being observed by a socially dominant jay ( $F_{2,15} = 7.5$ ,  $P = 0.005$ ), but were not more likely to cache in a vegetated site or travel farther relative to the number of observing individuals (mean =  $1.2 \pm 1.5$ ). The caching behavior of experienced adults

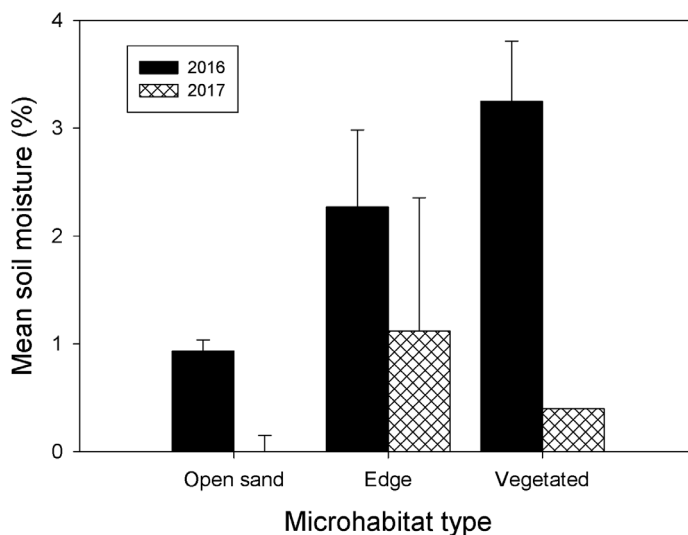


Fig. 1. Soil moisture differed significantly ( $P = 0.023$ ) among three different microhabitat types in 2016 ( $P = 0.023$ ), but not in 2017, a much drier year overall. Error bars represent standard deviation.

was not sensitive to social context, but most were breeding birds and thus the socially dominant bird of their sex in their family group.

In 2017, social context had no influence on the caching decisions of SY birds, including either distance or the choice of more vegetated sites. As naïve FYs, these same birds cached 24.3 additional meters from their provisioning point if observed by a dominant bird than they did in 2016. In addition, the number of birds observing a caching event and the presence of new yearlings in the territory of the second-year jays did not significantly influence caching distance.

**Factors influencing cache conditions.** We examined various factors associated with the soil moisture of cache sites. After evaluating models using AICc selection, there was only one top model to predict soil moisture at cache sites. The top model included jay age, year, canopy cover, and microhabitat type as predictor variables (Table 1), indicating that all four predictors influence the soil moisture of chosen cache sites. Evidence of a negative correlation existed between jay age and soil moisture at cache sites (estimate and 95% confidence interval;  $-4.60$  ( $-10.5$  to  $-13.0$ )), with older and experienced birds caching in much drier sites (Tables 1 and S1). Among these sites,

soil moisture was drier when percent canopy cover was low ( $0.02$  ( $-0.005$  to  $0.04$ ; Tables 1 and S1). There was a strong association between open sand sites and drier soil moisture sites ( $1.34$  ( $-4.7$  to  $0.07$ )) compared to cache sites in vegetated microhabitats, which predicted higher moisture values ( $9.53$  ( $-18.7$  to  $-21.0$ ); Tables 1 and S1). As expected, year was a strong predictor of soil moisture ( $-7.37$  ( $-10.5$  to  $-6.0$ )), with 2017 being a much drier year than 2016 (Fig. 1, Tables 1 and S1).

**Naïve versus experienced 2016.** From 203 observations of naïve FY birds ( $N = 39$ ) and experienced adults ( $N = 48$ ) combined in 2016, we detected no significant preferences for caching in particular microhabitats ( $\Lambda = 0.97$ ,  $P = 0.22$ ). However, the distribution of microhabitat types where naïve and experienced jays cached differed (Fig. 2); thus, we compared caching preferences of naïve and experienced birds separately. Naïve FY birds ( $N = 39$ ) exhibited a significant preference to cache in vegetated sites and avoided caching in open bare sand patches ( $\Lambda = 0.54$ ,  $P = 0.002$ , Fig. 3). Experienced adults ( $N = 48$ ) strongly preferred to cache in bare sand and avoided caching in vegetated locations ( $\Lambda = 0.73$ ,  $P = 0.002$ , Fig. 3).

**Changing preferences from naïve FY to experienced SY.** In 2017, we repeated

Table 1. Model selection results for factors that influence the soil moisture of observed cache sites of Florida Scrub-Jays. Best model is in bold font.

Model <sup>a</sup>	K	AIC	$\Delta$ AIC	$W_i$
<b>Age + Year + Cancov + Microtype</b>	<b>6</b>	<b>366.25</b>	<b>0.00</b>	<b>0.29</b>
Age + Year + No_Watching + Cancov + Microtype	5	366.36	0.10	0.27
Age + Year + No_Watching + Cancov + Covsp + Microtype	5	366.36	0.10	0.27
Age + Year + Leaf + No_Watching + Cancov + Covsp + Microtype	7	368.73	2.48	0.08
Age + Year + Leaf + No_Watching + Cancov + Covsp + Microtype + Domobs	6	368.76	2.50	0.08
Null	3	386.23	19.98	0.00

<sup>a</sup>Age = age class of focal individual, Year = year of caching observation. Leaf = percent leaf litter cover at cache site, cancov = percent canopy cover at cache site, domobs = whether or not a dominant individual was observing the focal individual cache, No\_Watching = number of individuals watching focal individual, microtype = microhabitat type of cache site, and covsp = number of cover species at cache site.

observations on the 20 surviving birds from the 39 naïve FY birds (54%) sampled in 2016. Of these 20, 14 had attained breeding status and were the socially dominant birds in their groups and six remained as socially subordinate helpers. Having gained caching experience, these jays showed a marked preference for open sand sites and avoided vegetated patches ( $\Lambda = 0.41$ ,  $P = 0.004$ , Fig. 3), which was a dramatic shift toward more open sand habitats than their preferences as yearlings (Fig. 3).

When evaluating the factors that influence changes in caching preference (i.e., Manly ratios), we found that models that included age and social status as predictors for each microhabitat category consistently had the lowest  $\Delta$ AICc and highest weights (Table 2). The best models for open sand and edge ratios had both age and status as predictors, whereas only age was present in the top model for predicted Manly ratios of vegetated sites (Table 2). Results from the top models were consistent with the compositional analysis, confirming that experienced adults and SY birds preferred caching in open sand and edge habitats whereas FY birds preferred vegetated sites (Fig. 3, Tables 2 and S2). This pattern indicates a strong shift by SYs away from vegetated cache sites compared to the more open sand and edge sites used when they were naïve FYs (Fig. 3, Tables 2 and S2). Interestingly, the top models for open sand and edge microhabitats indicated that experienced SY non-breeders were positively correlated with high Manly ratios compared to SY breeders

(Table 2). This result was contrary to what would be expected if social status was influencing cache site decisions; socially subordinate birds that were experienced non-breeders tended to cache in more open sites than SY breeders (Fig. 4). Among individual birds, all but one either maintained the same type of cache sites or shifted to more open sites as they changed from naïve to experienced cachers (Fig. 4).

## DISCUSSION

We found that young Florida Scrub-Jays shifted their cache site preferences from vegetated to open sites, regardless of their social status as older birds. Significantly, these birds were no longer sensitive to social context in their caching behavior, with both dominant and subordinate second-year birds caching in more open, drier sites. These patterns suggest that jays shifted their preference based on learning rather than change in the potential for pilfering because of their position in the social hierarchy of the family group.

We found that naïve first-year jays were sensitive to social context and flew farther to cache when observed by a socially dominant bird, consistent with previous work (Toomey et al. 2007). In addition, they preferred to cache in vegetated sites, even though those sites had a higher soil moisture content that has been associated with an increased risk of degradation of the cached food stores (Vander Wall 1990). DeGange et al. (1989) found that juvenile and adult Florida Scrub-Jays

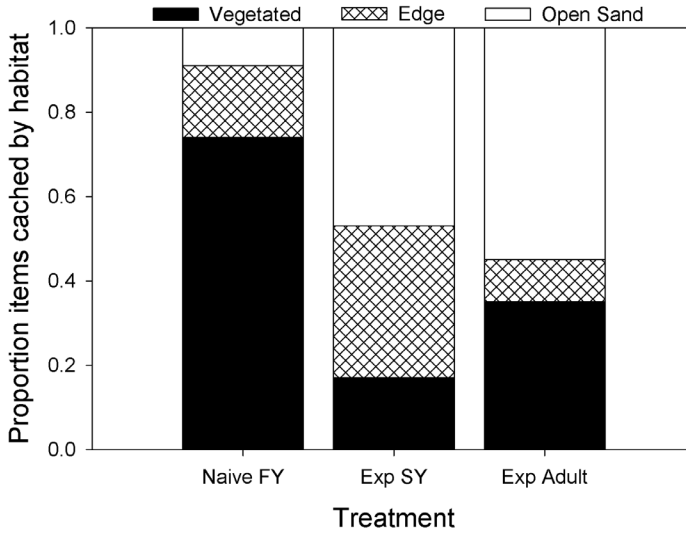


Fig. 2. Differences in frequency distribution of cached items relative to microhabitat association across all three categories of Florida Scrub-Jays, including naïve FY birds, experienced SY birds, and experienced adults. The naïve FY and experienced adult comparisons are for different birds observed in 2016. The naïve FY and experienced SY birds are the same birds observed in 2016 and again in 2017.

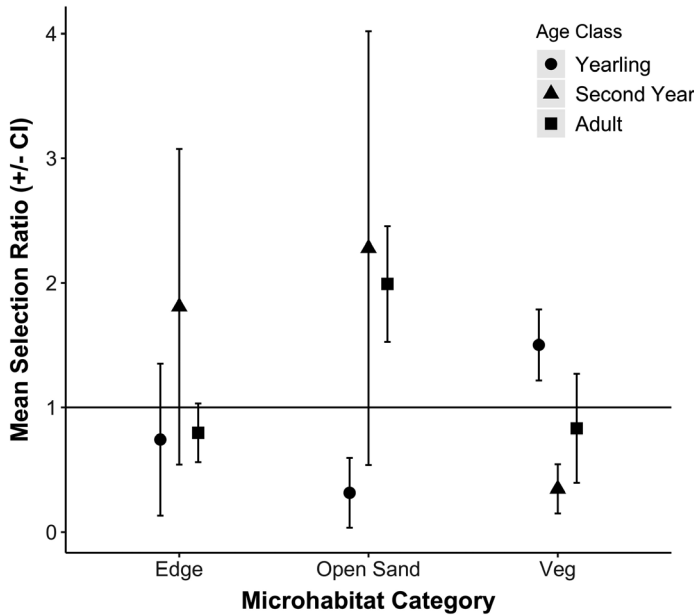


Fig. 3. Mean Manly selection ratios for each age class of Florida Scrub-Jays relative to microhabitat type. A ratio of 1.0 (horizontal line) indicates cache site use is consistent with availability (i.e., no preference/avoidance). Circles represent yearlings (FY), triangles represent experienced second-year birds (SY), and squares represent experienced adults. Error bars represent confidence intervals.

cached at the same rate, but that juveniles recovered caches at lower rates and spent more time foraging, indicating that juveniles

might be naively caching in vegetated spots where caches have rotted. Naïve first-year birds are at the bottom of the social



Table 2. Model selection results for the predictors of caching site preference by Florida Scrub-Jays for each microhabitat type. Best models are in bold font.

Model <sup>a</sup>	K	AIC	ΔAIC	W <sub>i</sub>
<i>Open sand</i>				
<b>Age + Status</b>	<b>6</b>	<b>366.25</b>	<b>0.00</b>	<b>0.29</b>
Age	5	366.36	0.10	0.27
Age + Year	5	366.36	0.10	0.27
Age + Status + Sex	7	368.73	2.48	0.08
Age + Sex	6	368.76	2.50	0.08
Null	3	386.23	19.98	0.00
<i>Edge</i>				
<b>Age + Status</b>	<b>7</b>	<b>846.01</b>	<b>0.00</b>	<b>0.70</b>
Age + Status + Sex	6	849.76	3.75	0.11
Age + Status + Year	6	849.76	3.75	0.11
Age + Sex	6	850.67	4.65	0.07
Age	5	854.44	8.43	0.01
Age + Year	5	854.44	8.43	0.01
Null	3	862.27	16.26	0.00
<i>Vegetated</i>				
<b>Age</b>	<b>5</b>	<b>334.05</b>	<b>0.00</b>	<b>0.38</b>
Age + Year	6	335.07	1.02	0.23
Age + Status	6	335.07	1.02	0.23
Age + Sex	6	336.81	2.76	0.10
Age + Status + Year	7	337.77	3.72	0.06
Null	3	342.15	8.10	0.01

<sup>a</sup>Age = age class of focal individual, Year = year of caching observation, status = social status of the focal individual, and sex = sex of the individual.

dominance hierarchy and their choice of vegetated sites is likely an effort to cache in private and reduce pilfering by more dominant individuals. However, it could also reflect a lack of experience with how various sites affect food longevity. Over time, young jays receive positive and negative reinforcement about the quality of food recovered from different sites and their caching preferences may shift to more open, potentially drier microhabitat associations.

Cache protection strategies to reduce pilfering are common and diverse among corvids (Dally et al. 2006a, Clayton et al. 2007). Juvenile Common Ravens as young as six months will cache behind screening vegetation if being observed by another bird (Bugnyar et al. 2007). Juveniles might learn these tactics early in development, well before they have experiential learning with the fate of foods placed in different microhabitat associations. Dominant Florida Scrub-Jays often

pilfer the caches of subordinates soon after the initial caching (DeGange et al. 1989). However, observational learning of cache fates in different caching sites might take months, occurring only after birds have retrieved those caches and assessed their condition. Thus, it might not be surprising that young jays choose caching sites by prioritizing pilfering reduction strategies over those that might minimize cache degradation.

By their second year, cache preferences of Florida Scrub-Jays in our study shifted to more open and edge habitats and were not sensitive to social context when caching, even if they remained as non-breeders and thus subordinate to the breeding pair. We provide evidence that naïve birds may prefer to cache in vegetated sites because they are subordinate, but that they learn to cache more in open sand or edge sites as they age. This suggests that shifts in microhabitat cache site selection are not just due to a release from subordinate status because SY non-breeders preferred to cache in open sand more than SY breeders. In apparent contrast, Toomey et al. (2007) found that awareness of social context was not limited to juvenile Florida Scrub-Jays and that older helpers adjusted their caching behavior when a breeder was present. We recognize that this result is based on a limited sample size of 20 individuals observed in subsequent seasons and that further research is required to tease apart the role of social context on caching preference relative to learning optimal microhabitats and reducing risk of pilfering.

Despite their shift in preference to open sites, experienced SY birds in 2017, regardless of social dominance status, still made some caches in vegetated sites. We did find that the experienced SY birds cached in vegetated sites more frequently than experienced and socially dominant birds did in 2016. This may have been a response to different environmental conditions in 2017. In 2016, cumulative rainfall for the five months prior to our observations totaled 57.65 cm, whereas the total was only 16.51 cm in 2017. If selection of appropriate caching sites constitutes a trade-off between reducing cache exposure to factors that might increase the risk of degradation, then we might expect that, under drier conditions, birds might use more vegetated sites that might be more private than open sites,

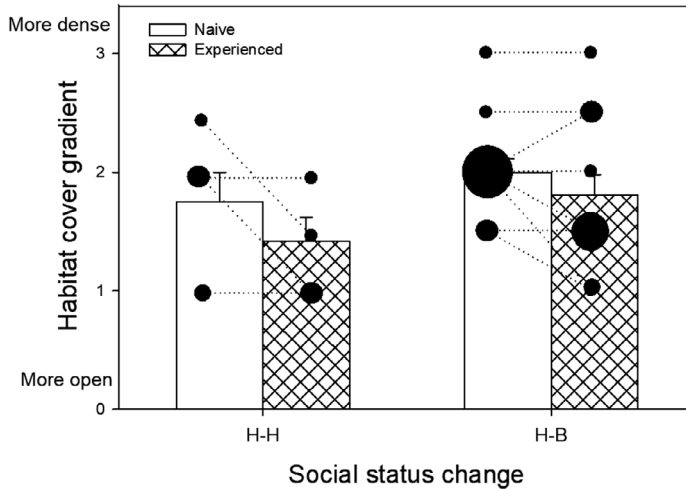


Fig. 4. Shifts in the relative openness of sites (bare sand, very open; vegetated, very dense) chosen as cache sites by naïve FY birds from 2016 to 2017 when all were experienced SY birds, but the dominance status of birds may have changed. Some remained as helpers (H-H, dominance status unchanged,  $N = 6$ ) and others transitioned to breeders (H-B, dominance status increased,  $N = 14$ ). Each dot represents the mean habitat choice for birds in that category, when scored as 1 for open sand, 2 for edge, and 3 for vegetated. Because points overlap, dot sizes are based on the number of individuals with that value. Lines connect values of the same individual between years.

without incurring the cost of increased risk of degradation. Soil moisture in the Florida scrub is highly variable between seasons and among microhabitat types and is already known to influence re-caching decisions (Weekley et al. 2007, Kulahci and Bowman 2011), thus potentially selecting for rapid learning and plastic responses to environmental conditions by cachers that seek to minimize cache degradation. Such fast, flexible learning may be essential to survival in environments where conditions that might affect food decay vary greatly over short temporal spans (de Kort et al. 2005). Spatial memory of corvids allows them to track the decay of each food item in different habitats over time (Grodzinski and Clayton 2010).

Florida Scrub-Jays regularly recover, assess, and then either eat, discard, or re-cache acorns (DeGange et al. 1989, Kulahci and Bowman 2011). They discard acorns too degraded to eat, eat those in the early stages of decay or germination and re-cache the intact and most viable. When re-caching, they move acorns to different sites that tend to have lower soil moisture (Kulahci and Bowman 2011), thus potentially lengthening the viability of the cache as food. Because soil

moisture varies across microhabitat types, additional research is needed to evaluate the role of habitat structure and fire history on caching decisions. We also acknowledge that peanuts used in this study may differ in their storage viability compared to acorns and this should be quantified in future studies.

Few investigators have examined the development of caching behavior in wild birds (Smith 1972, Bugnyar et al. 2007), and, to our knowledge, none have tracked individuals between years to observe how behavior changes from experience. Jays depend on acorn caches in the winter and early spring when other food sources are scarce. Acorn production and winter rainfall are highly variable from year to year (Abrahamson and Layne 2003), which could affect the amount or longevity of jay caches. Group size varies depending on past reproduction thus influencing intra-group dominance hierarchies and pilfering pressures. Significant reductions in the cached food supply of jays could have important fitness consequences and thus exert strong selection on flexible and rapid learning and cache protection strategies. Accordingly, we found that juvenile jays change their preference in cache site selection as they age,

regardless of concomitant changes in their position in the within-group social hierarchy, suggesting that they learn what constitutes a good cache site. However, additional study to determine the relative roles of degradation, predation, and pilfering in the proportional loss of cached acorns is needed to better place these behavioral strategies into perspective.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

**Table S1.** Results and summary statistics of final linear mixed effect model (in bold in Table 1) predicting significant factors influencing the soil moisture of observed cache sites by different-aged Florida Scrub-Jays.

**Table S2.** Results and summary statistics of linear mixed effect models (in bold in Table 2) predicting caching preferences of Florida Scrub-Jays in three microhabitats.

**Table S3.** Full dataset of caching sites of Florida Scrub-Jays and randomly selected sites.