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Preferences of avian seed-hoarders in advance of potential American chestnut reintroduction

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ABSTRACT

Nut-bearing trees such as oaks (*Quercus* genus) and American chestnut (*Castanea dentata*, hereafter: chestnut) rely on scatter-hoarding animals for seed dispersal. With the pursuit of blight-resistant chestnuts for eventual reintroduction into eastern hardwood forests of the United States, it becomes important to understand how foraging preferences of avian seed-hoarders will influence chestnut dispersal in oak-dominated forests. Using six seed selection trials over three years and two "seasons" (early fall and late fall), we assess the relative seed preferences – when gathering seeds for hoarding or consumption – of five species of avian seed dispersers in southeast Ohio. In each trial, we presented an equal number of chestnuts and two species of common acorns, black (*Q. velutina*) and white oak (*Q. alba*), to wild birds on feeding platforms monitored by cameras. We used Bayesian discrete choice models to determine preferences of each species, and estimate the influence of natural variation in background mast availability (i.e., different years and seasons). Blue Jays (*Cyanocitta cristata*) showed a consistent preference for the seeds of black oak over chestnut over white oak, and the strength of preference for black oak increased in late season when acorns were scarce. Other species showed variable preferences, with White-breasted Nuthatch (*Sitta carolinensis*) the only species to prefer chestnuts over both acorns, though sample size was small (n = 26 selections). Our results suggest chestnuts are used by a host of avian seed-hoarders that may facilitate dispersal of chestnut, particularly in years of black oak mast failure.

1. Introduction

The American chestnut (*Castanea dentata*; hereafter: chestnut) was once a canopy dominant species across much of the eastern hardwood region (Russell 1987) of the United States, and its seeds likely supported dozens of mammal and bird species. Though we have little data on wildlife foraging preferences before the decline of chestnut in the early 20th century, numerous anecdotal historical accounts (Thoreau 1906, Bolgiano and Novak 2007) and several recent studies suggest that chestnuts were a highly desirable resource that formed the foundation of a complex food web (Dalgleish and Swihart 2012, Blythe et al. 2015). Whether wildlife prefer chestnut has become an important question in recent years, as efforts to restore it to the eastern hardwood ecosystem intensify (Clark et al. 2014). This is especially relevant for species that will not only benefit from the use of chestnut seed, but will also potentially provide seed dispersal services, thus enhancing reintroduction efforts.

The decline of American chestnut occurred over several decades in the early 20th century, as a result of the introduced chestnut blight fungus (*Cryphonectria parasitica*) that infected and killed billions of mature trees (Anagnostakis 1987). Chestnuts remain today mainly as stump sprouts, and there have been efforts to produce blight-resistant trees through both hybrid-backcross breeding with Chinese chestnut (*Castanea mollissima*) and producing transgenic strains of pure American chestnut trees (Jacobs et al. 2013, Steiner et al. 2017, Newhouse and Powell 2021). Although hybrid breeding has been less successful than originally hoped in imparting blight-resistance (Steiner et al. 2017), there has nevertheless been great progress, and transgenic trees are currently under regulatory review in the United States (Newhouse et al. 2020, Westbrook et al. 2020). The eventual restoration of chestnut will be a long and slow process, but it is crucial to understand how the reintroduction of a once-dominant species will alter current plant-animal interactions and forest dynamics (Gustafson et al. 2017).

One plant-animal interaction critical to chestnut restoration and the persistence of other nut-bearing trees, is the seed dispersal mutualism with animals that cache nuts for winter consumption (Vander Wall

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2001). When an animal fails to retrieve a cached nut, it may germinate and grow into an offspring of the parent tree. Furthermore, animals transport nuts tens to thousands of meters from the parent tree, where competition and seed predation are often reduced, allowing the tree to colonize new habitat patches (Siepielski and Benkman 2008). Scatter-hoarding animals in particular, such as some squirrels (*Sciurus* genus) and corvids (crows, magpies, and jays), serve as the most efficient dispersal agents for these trees since most nuts are cached in different locations, amounting to thousands of cache sites per animal each year (Darley-Hill and Johnson 1981, Steele and Smallwood 2002). To understand how chestnuts will disperse across the landscape when (or if) restoration plantings begin, one must examine the suite of scatter-hoarding behaviors that animals employ. Furthermore, one must examine these behaviors under varying conditions to determine how chestnut dispersal may be context-dependent. In particular, the relative availability of different mast species can impact the dispersal effectiveness of scatter-hoarders (Lichti et al. 2014, Pesendorfer et al. 2016b).

The first step in the scatter-hoarding process is seed selection. A number of studies have shown that seed selection is non-random, and animals exhibit preferences based on seed traits, including nutritional reward (Wang and Chen 2012), palatability (Steele et al. 1993), perishability (Smallwood et al. 2001), shell thickness (Moore and Swihart 2006), and size (Bossema 1979, Pons and Pausas 2007). As chestnuts have been functionally extinct for nearly a century, we have very little information on whether animals preferred chestnuts compared to other tree nuts, though they are often assumed to have been a favored food, and valuable to wildlife, due to several key characteristics including low tannin content, nutritional reward, and thin/soft shells (Table S1). Perhaps most importantly for wildlife populations, chestnut trees provided an abundant and consistent crop of tree nuts every year (Diamond et al. 2000), as opposed to most oaks which go through cycles of low and high acorn abundance (Koenig and Knops 2000). The consistency of chestnut mast likely buffered against dramatic wildlife population declines in years of oak mast failure. Indeed, it is estimated that total hard mast production in a southern Appalachian forest declined by 34% after the loss of mature chestnut trees (Diamond et al. 2000), with declines as high as 95% when production by other species was lacking.

Despite the many benefits of chestnuts, recent studies that investigated the preference of scatter-hoarding rodents (*Sciurus* genus) found that large tree nuts like walnuts (*Juglans nigra*) and hickory (*Carya* spp.) nuts were preferred over chestnuts (Blythe et al. 2015). When compared with similar-sized acorns, however, preference was less clear, but chestnuts appeared more likely to be cached when encountered alongside white oak (*Quercus alba*) acorns, which are preferentially consumed (likely due to their lack of dormancy; Lichti et al. 2014). Scatter-hoarding birds, on the other hand, are likely to play a more important role in the dispersal of reintroduced chestnuts to new habitat patches, as they transport seeds much farther than rodents (Pesendorfer et al. 2016a), but no studies have yet assessed the preference of these species for chestnut. In the former range of chestnut, several scatter-hoarding birds could potentially play a role as dispersal agents. These include, for instance, the Tufted Titmouse (*Baeolophus bicolor*) and woodpeckers in the genus *Melanerpes*. However, the effectiveness of these birds as dispersers may be limited due the preference of woodpeckers for caching in trees, and the shallowness of caching depths by titmice (Sipes et al. 2013). On the other hand, the preference of Blue Jays (*Cyanocitta cristata*) is particularly relevant, since they are often considered the most important disperser of small tree nuts in eastern deciduous forests. Jays are scatter-hoarders that can carry multiple seeds at once (Bartlow et al. 2011), cache seeds in the soil, and transport seeds hundreds to thousands of meters from the parent tree (e.g., Darley-Hill and Johnson 1981, Johnson and Adkisson 1985). They are thought to be largely responsible for the rapid northward expansion of oaks and American beech (*Fagus grandifolia*) following the last ice age (Johnson and Webb 1989), as they are the only species known to regularly transport seeds multiple kilometers. In addition, one recent study found that jays readily consumed and transported chestnuts in Maine when the crop of beech nuts failed (Heinrich 2014). Given these observations, jays are expected to be key dispersers of chestnuts and may provide critical ecosystem services to establishment of chestnut across their former range.

Previous studies of Blue Jay preference have found they generally prefer the smallest seeds available (e.g., Richardson et al. 2013), but may use larger, less preferred seeds in the absence of smaller seeds (Moore and Swihart 2006). In addition, it has been suggested that their preference may be influenced by both familiarity with a seed species and palatability (Steele et al. 1993). It is unknown to what degree background mast availability may influence seed preference. As most eastern oak species undergo masting cycles, the availability of particular species of acorns, and thus the familiarity of local jays with those acorns, will vary annually. In addition, acorn availability varies over the course of a single fall season, as acorns drop from trees and are consumed or cached by wildlife. If birds select different seeds for caching and consumption, then seed preference may differ even over the space of a month, as caching behavior occurs more often when acorns are abundant and have not dropped from trees (Johnson et al. 1997).

Here, we assess preference of several species of seed-caching birds, with a particular focus on Blue Jays, for American chestnut seeds compared to two oak acorn species common to the central Appalachians, black oak (*Q. velutina*) and white oak. In order to measure their preferences, we presented these three seed species to wild birds in a series of six seed selection trials at feeding platforms in a central Appalachian forest. In general, we predict that jays will consistently prefer the smallest seeds available (Moore and Swihart 2006), and titmice and nuthatches the smaller and softer-shelled seeds (Richardson et al. 2013). We do not make specific predictions regarding woodpecker preference, given the lack of existing information on their seed preferences. By performing these selection trials over three years and two “seasons,” we attempt to quantify the context-dependence of birds’ preferences (Pesendorfer et al. 2016b) in relation to changing mast availability, and discuss the implications of our findings.

2. Methods

2.1. Study site and species

We conducted this study at two sites in Vinton County, southeast Ohio, from October to December over three years, 2018–2020. The primary site, Vinton Furnace State Experimental Forest (39.2°N, 82.4°W), is characteristic of the unglaciated Allegheny Plateau with narrow ridge and valley topography and low relief (<100 m). The secondary site, the Biological Station at Lemay (39.3°N, 82.3°W), is located on private property ~ 14 km northeast of the primary site, with similar topographic features. Soils at these sites are predominantly unglaciated silt loam derived from sandstone, siltstone, and shale. Both sites consist of mature, second-growth oak-hickory to mixed-mesophytic forest communities interspersed with patches of early- and mid-successional forests (Iverson et al. 2018). Before the chestnut blight epidemic, American chestnut was a dominant canopy tree in the region, particularly on ridgetops and slopes underlain with sandstone (Sears 1925, Heffner 1939). The historical occurrence of chestnut in the area is further evidenced by its continued presence in the understory as small saplings (JRW personal observation). To estimate change in background acorn abundance over a season and between years, we performed acorn surveys of 9 white and 9 black oak trees (3 trees at each platform site) every week from early September to early December, by scanning the crown with binoculars and counting as many acorns as possible in 30 s (Koenig et al. 1994). To reduce observer bias across years, JRW trained all observers and supervised most surveys. We compare the mean acorn counts by species and year (Table 1) for the second week of October (early season) and first week of December (late season).

Several species of birds that store seeds were present and common at our study sites. These included species that cache seeds above ground in

Table 1
Mean background acorn abundance of black and white oak trees at Vinton Furnace State Experimental Forest in southeast Ohio by year (2018–2020) and season (early/late), and mean and standard deviation (in parentheses) of seed sizes for the species used in the study. Due to the flattened shape of chestnuts, these seeds have an additional dimension of measurement.

Species	Year	Acorn abundance		Seed size			
		Early	Late	Mass (g)	Length (mm)	Width (mm)	Depth (mm)
Black oak	2018	8.4	1.5	2.1 (0.6)	16.9 (1.3)	16.0 (1.7)	
	2019	20.8	0.3	2.5 (0.7)	16.9 (1.2)	14.5 (1.7)	
	2020	52.5	2.4	2.5 (0.3)	16.5 (0.6)	15.4 (0.7)	
White oak	2018	8.3	0.1	3.3 (0.8)	20.8 (1.2)	16.0 (1.8)	
	2019	0.4	0	4.0 (0.9)	22.6 (2.2)	16.9 (2.1)	
	2020	7.3	0	5.0 (1.0)	23.3 (1.9)	18.6 (1.5)	
Chestnut	2018			3.7 (0.9)	20.2 (1.4)	21.3 (2.0)	13.5 (1.7)
	2019			4.5 (1.0)	21.4 (1.4)	23.8 (1.9)	14.3 (1.6)
	2020			4.2 (1.2)	20.9 (1.5)	22.9 (2.6)	14.0 (2.3)

trees, such as Red-bellied Woodpecker (*Melanerpes carolinus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), and White-breasted Nuthatch (*Sitta carolinensis*). Outside of occasionally dropping nuts, these species are not effective dispersers and primarily act as seed predators. Two species at our site cache seeds in the ground and thus serve as better dispersal agents, namely Blue Jays and Tufted Titmouse. Although titmice can be good dispersal agents, they are more limited in the size and thickness of nuts they can handle, and typically do not transport nuts as far or bury them as deep as jays (Sipes et al. 2013). To determine how seed preference may vary across individuals of a species, we captured jays (n = 114) and titmice (n = 67) in baited walk-in traps and mist nets. We banded birds with numbered U.S. Geological Survey aluminum bands and unique combinations of plastic color bands, and used videos (see below) to identify individuals. All capture and banding methods were approved by the Institutional Animal Care and Use Committee of the Ohio State University (protocol # 201500000028-R2).

2.2. *Seed collection*

We collected seeds and stored them in plastic bags at 4 °C until selection trials. Each year we recorded mass, length, and width (and depth for chestnuts) for 100 seeds of each species (Table 1). As Blue Jays are known to exhibit acorn preference based on size, we endeavored to control for size within a species by discarding small or large seeds to retain focus on mean seed size by species. As a result of changing mast conditions across years, we were not always able to collect seeds from consistent sources, and the average size of acorns and chestnuts varied between years (see Table 1). We report the percentage differences in mass across years below. Black oak acorns were collected from the ground at the primary field site from 5 to 10 trees, and variation across years was within 11% of the mean. White oak acorns were collected from the ground at the primary field site from 5 trees in 2018, and from 5 trees in central Columbus, Ohio, (~100 km northwest of the field site) in 2019 and 2020. Variation across years was within 22% of the mean. American chestnuts were collected with help from The American Chestnut Foundation and associated orchards. In 2018, we used blight-resistant (BC_3F_2 and BC_3F_3) hybrid chestnuts that were collected from chestnut orchards in Pennsylvania; in 2019, we collected pure American open-pollinated chestnuts from Indiana; and in 2020, we collected American open-pollinated chestnuts from West Virginia, which may have included some hybrid pollinated seeds. Variation in mass across years was within 10% of the mean. Although relying on three chestnut sources across years is a limitation which introduces noise within our chestnut sample, our aim here was to compare across species in an oak-dominated landscape. In future studies, working with multiple mother trees at a chestnut orchard site would afford a more controlled and representative chestnut sample. Before selection trials each year, we used the float method and visual inspection to discard unsound acorns and chestnuts. In 2018, however, many acorns that appeared sound were later found to have weevil (*Curculio* sp.) larvae. Therefore, in 2019 and 2020, we also heat-treated the sound acorns and chestnuts, by soaking seeds in 49 °C water for 20 min, to kill potential weevil eggs/larvae but maintain the viability of the seeds (Bonner and Karrfalt 2008).

2.3. *Study design*

To examine seed preferences of wild birds, we adapted methods developed by Richardson et al. (2013). We established 6 plywood feeding platforms (0.6 m × 0.6 m) mounted on wooden fence posts (1.5 m high) across the two study sites: five platforms at Vinton Furnace and one platform at Lemay. We attempted to disperse platforms evenly throughout the forest, but had little success enticing birds to platforms that were not on forest edges. Thus, all platforms were located at broadleaf forest edges, with mature forest on one side and early- or mid-successional forest on the other. In addition, all platforms were located > 600 m apart to prevent individual birds from visiting multiple platforms.

We mounted three Browning trail cameras (model Strike Force HD 2015) on each platform, secured with 1.5 m long half-inch aluminum conduit bolted to the platform. Two cameras were set to record 30-second videos when motion-activated, mounted horizontally (hereafter “side camera”) and at a 45-degree angle (hereafter “angled camera”) above the platform. The third camera was mounted directly above the platform (hereafter “top camera”) looking down, and set to record one photo every 10 s for daylight hours. The side and angled cameras recorded behavioral interactions, particularly seed sampling and selections of color-banded individuals, while the top camera recorded selections and the choice set for each selection. Beginning in mid-August every year, we baited platforms with peanuts to attract birds until they were visiting on a regular basis. When birds were visiting platforms multiple times a day, we began seed selection trials. As in Richardson et al. (2013), most trials consisted of presenting the three species of seeds on plywood trays drilled with a grid of 225 numbered cells (2.5 cm diameter by 2 cm deep), organized in nine 5 × 5 sectors (Fig. 1). Each sector contained one seed species, and each seed species was in three color-coded sectors (white, light gray, and dark gray), thus birds were presented with 75 seeds of each species. The three sectors of each species were never adjacent, and the species were randomly assigned to a sector set, so the location of seeds on the platform varied throughout the trials.

In 2019 and 2020, we performed two trials per year, separated by one month. The first trial was performed in late October to early November (early season), when acorns were still dropping from trees. The second trial was performed in early December (late season), when very few acorns remained on trees (Table 1). We performed trials concurrently at all 6 platforms, and ended trials when the platform was cleared of all seeds or birds stopped visiting. As 2018 was the pilot year of the study, the selection trials in this year varied in several ways. First, the two trials were performed in the first and second week of December (i.e., late season only). Second, these were two-species trials, where the first trial presented only black oak and chestnut, and the second trial presented only white oak and chestnut. Lastly, only two cameras were mounted on each platform this year (top and side cameras), both set to motion-activation, so more selection events were missed when cameras were not triggered compared to the 2019 and 2020 trials.

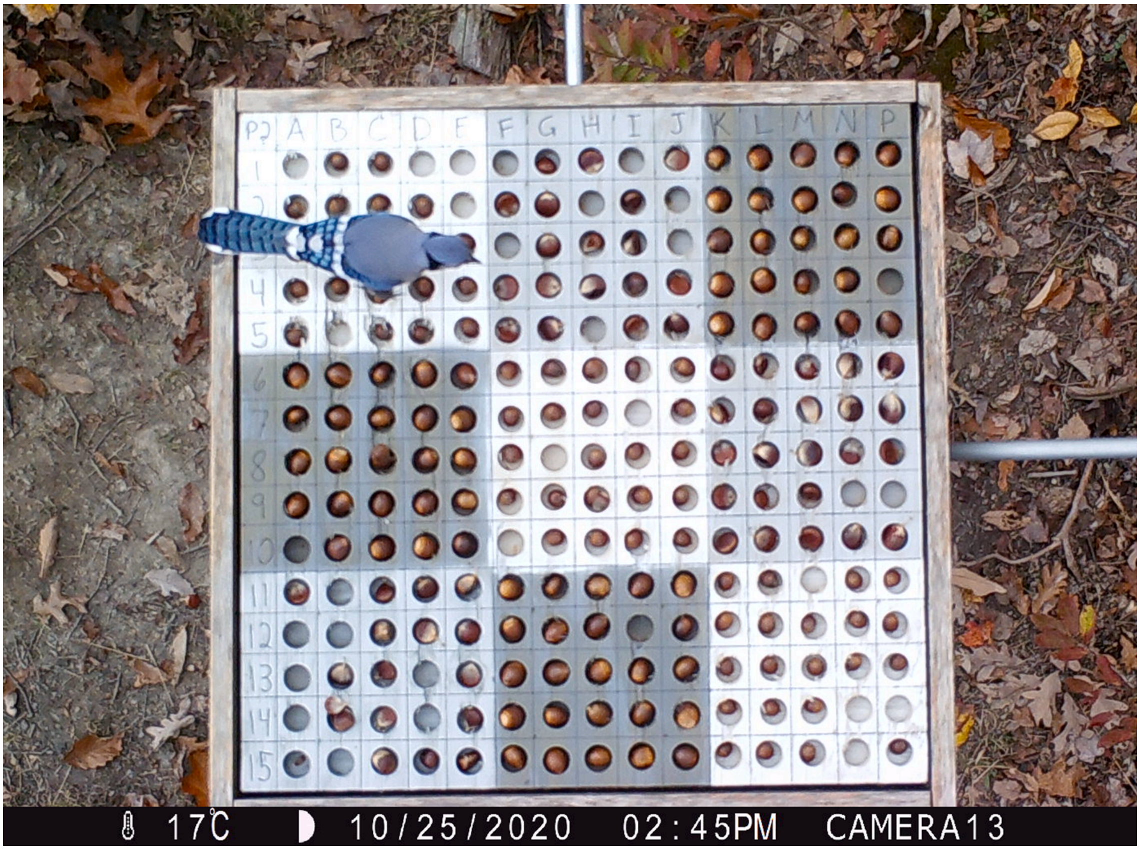

Fig. 1. Photo of Blue Jay on feeding platform with seed selection tray from top camera, at Vinton Furnace State Experimental Forest, southeast Ohio.

To standardize data collection, one observer analyzed all videos and time-lapse photos of the trials. When a bird visited the platform, we recorded the species, color-band combination if present, date/time, seed species selected, choice set, and number of seeds "sampled" (i.e., handled but not selected, see supplementary materials). Jays occasionally took more than one seed in a single visit, storing the first seed in their gular pouch and the second or third in their bill. These were treated as separate selections (Richardson et al. 2013), as the available choice set changed. Visits where no selection was made or the bird identity was obscured due to camera malfunction/precipitation were not included in analyses. Although we color-banded 67 titmice, the videos were often too blurry to accurately record the color combination, so we were unable to quantify individual-level selection data for titmice. Jay color bands were larger and easier to see, however, so we were able to record selections from 26 marked individuals out of 114 banded birds across the three years. For purposes of statistical analysis, when modeling individual-level selection we only include birds that made 10 or more selections. Color-banding individuals also provided support for our assumption that the distance between platforms was sufficient to ensure individuals were not visiting multiple platforms, as no banded birds were seen making selections at more than one platform.

2.4. Statistical analysis

2.4.1. 2.4.1. Seed preference of bird species

We modeled seed preference using Bayesian discrete choice models (Manly et al. 2002) for each bird species in the jagsUI package (Kellner 2021) in Program R (R Core Team 2021), including only those selections where the choice set included more than one seed species. These models, described in Richardson et al. (2013), account for the changing choice set of seed abundance for each selection by incorporating a relative abundance parameter into the multinomial mixed effects logistic regression model. For bird species with sufficient selection data across multiple platforms, seasons (early and late), and years (2019 and 2020), we compared five models: 1) a null model of selection proportional to availability; 2) a mean selection model, where platform is a random effect (η_P: this term was retained in all remaining models); 3) a "season model," with fixed effect of season ($\eta_P + \beta_S$); 4) a "year model," with fixed effect of year ($\eta_P + \beta_Y$); and 5) a full model with fixed effects of season and year ($\eta_P + \beta_S + \beta_Y$). Platform was included as a random effect because selections within a platform may be autocorrelated, as many selections at a given platform were made by few individuals which may each have strong preferences that differ. In all models, we set chestnut as the reference level. We used the deviance information criterion (DIC) to compare models (Spiegelhalter et al. 2002), and chose the final "preference model" as the most parsimonious model with the lowest DIC, where $\Delta DIC < 5$. We compared these models for Blue Jay, Tufted Titmouse, and Red-bellied Woodpecker selections. Jay and titmouse selections during the pilot year (2018) were analyzed separately with a mean selection model due to differences in trials described above. Sample sizes were not sufficient to analyze the pilot year separately for Red-bellied Woodpecker. For Red-headed Woodpecker and White-breasted Nuthatch, where we had limited selection data for only 2 trials at ≤ 2 platforms, we only compared a null model and a mean selection model (η_M) with no random effect of platform. For all models we report the "preference coefficients" in Table 2, which are calculated by adding the appropriate β terms to the baseline η term for that model. Positive values indicate preference for the first species compared to chestnut, negative values indicate selection against that species compared to chestnut. We consider preference strong if $> 95\%$ of the posterior distribution falls on the same side of zero as the coefficient, moderate if this proportion is between 85 and 95%, and weak or no preference if $< 85\%$. Preference coefficients for black oak versus white oak acorns can be found by subtracting the BO:CH and WO:CH coefficients.

Table 2

Mean, standard deviations, and 95% credible intervals of preference coefficients (η) and group-level variances (σ) derived from the best discrete choice "preference model" for each bird species. The proportion of the posterior distribution with the same sign as the mean ($P \lesssim 0$) is shown for each estimated coefficient; values of ($P \lesssim 0$) < 0.85 suggest weak or no preference. Positive coefficients indicate preference for the first species compared to the second, while negative coefficients show the inverse. Note that 2018 trials for Blue Jay and Tufted Titmouse were analyzed separately and not included in selection models (see text for details). BO = black oak; CH = chestnut, WO = white oak.

Species and selection model	Preference	Coefficient	Mean	SD	95% C.I.	$P \lesssim 0$
Blue Jay						
Season model (2019–2020)	BO:CH	η_{2018}	−0.15	1.02	(-2.23, 1.96)	0.56
		σ_{2018}	2.46	1.37	(0.98, 5.93)	1.00
		η_{Early}	1.20	0.60	(-0.07, 2.38)	0.97
		η_{Late}	2.84	0.60	(1.59, 4.02)	1.00
		σ_P	1.42	0.63	(0.66, 2.99)	1.00
	WO:CH	η_{2018}	1.24	0.99	(-0.92, 3.11)	0.91
		σ_{2018}	2.55	1.55	(0.93, 6.44)	1.00
		η_{Early}	−1.58	0.50	(-2.47, −0.49)	0.99
		η_{Late}	−1.25	0.46	(-2.06, −0.22)	0.99
		σ_P	0.92	0.45	(0.38, 2.02)	1.00
Tufted Titmouse						
Year model (2019–2020)	BO:CH	η_{2018}	−3.43	0.75	(-5.14, −2.22)	1.00
		σ_{2018}	1.19	0.91	(0.24, 3.56)	1.00
		η_{2019}	0.38	0.92	(-1.50, 2.15)	0.67
		η_{2020}	−0.25	0.87	(-2.03, 1.46)	0.62
		σ_P	2.36	0.94	(1.20, 4.75)	1.00
	WO:CH	η_{2018}	−3.03	1.07	(-5.36, −1.20)	1.00
		σ_{2018}	1.01	0.88	(0.22, 3.37)	1.00
		η_{2019}	0.89	0.58	(-0.28, 2.03)	0.94
		η_{2020}	−0.60	0.49	(-1.58, 0.37)	0.90
		σ_P	1.07	0.49	(0.48, 2.31)	1.00
Red-bellied Woodpecker						
Year model	BO:CH	η_{2018}	1.23	1.49	(-1.87, 4.01)	0.80
		η_{2019}	1.60	1.73	(-2.07, 4.73)	0.83
		η_{2020}	0.52	1.62	(-3.00, 3.44)	0.66
		σ_P	4.73	4.01	(1.56, 14.07)	1.00
	WO:CH	η_{2018}	−0.39	1.20	(-2.77, 1.95)	0.63
		η_{2019}	−2.68	1.30	(-5.32, −0.19)	0.98
		η_{2020}	−1.44	1.24	(-3.83, 1.11)	0.88
		σ_P	3.06	1.65	(1.24, 7.23)	1.00
Red-headed Woodpecker						
Mean model	BO:CH	η_M	3.08	0.47	(2.31, 4.17)	1.00
	WO:CH	η_M	−1.31	0.44	(-2.24, −0.53)	1.00
White-breasted Nuthatch						
Mean model	BO:CH	η_M	−1.85	0.81	(-3.77, −0.58)	1.00
	WO:CH	η_M	−3.22	0.91	(-5.28, −1.70)	1.00

When parameterizing models, we used weakly informative prior distributions, based on the variance of selection results reported in Richardson et al. (2013). These informative priors prevent Markov-chain Monte Carlo (MCMC) draws from exploring unreasonably large parameter space, which helps improve model convergence and predictive performance (Lemoine 2019). For β coefficients of season, year, and the group-level means (η_P and η_M), we used normal (0, 2) prior distributions, while for the group-level standard deviations (σ_P for platform, σ_M for overall), we used uniform (0, 3) prior distributions. We ran the models on 3 MCMC chains of 10,000 iterations each. To evaluate model convergence, we used the Gelman-Rubin statistic, where values < 1.1 indicate convergence (Gelman et al. 2004). We evaluated model fit by estimating the proportion of seed selections that would be correctly predicted (CP; following Richardson et al. 2013) by the given model, by generating 100 simulated datasets from the model and comparing simulated predictions to the actual dataset. We calculated the mean proportion of predictions that agreed with the actual selections across the 100 simulated datasets, and report the mean CP for each model, as well as percent improvement over the null model for that species.

2.4.2. 2.4.2. Variation in individual seed preference

The majority of Blue Jay seed selections were by unmarked individuals, so we were unable to incorporate individual preference into the full dataset. However, cameras recorded 356 selections for 26 marked birds, 13 of which made > 10 selections. Since 11 of these birds were from 2020 in the late season trial, we excluded the two birds from 2018 to control for year and season. We analyzed selection for these 11 individuals with a Bayesian discrete choice model as above, comparing a null model to a model with individual as a random effect. We report the group-level mean preference (η_{Bird}) and standard deviation (σ_{Bird}), as well as the estimated individual preferences (β_1 to β_{11}; Table 3) to clearly illustrate the differences in individual seed preference.

3. Results

Across the 6 selection trials and 6 platforms, our cameras recorded information on 3,382 visits of the five focal species, including 2,469 selections (Table S2). Of the recorded selections, 1,461 were by Blue Jays, 636 by Tufted Titmouse, 252 by Red-bellied Woodpecker, 91 by Red-headed Woodpecker, and 29 by White-breasted Nuthatch. Due to camera failure or obstructions, cameras missed recording 296 selections (64 black oak, 126 chestnut, 106 white oak seeds), 50% of which were during 2018 pilot season trials.

All species selection models (Table 2) performed better than null models (CP values and percent improvement: BLJA = 0.62, 98%; TUTI = 0.55, 67%; RBWO = 0.63, 68%; RHWO = 0.67, 127%; WBNU = 0.64, 123%). For titmouse and Red-bellied Woodpecker, the year model best explained variation in preference, whereas for jays the season model explained the most variation (Table S5). Jays generally preferred black oak acorns over chestnuts, but the strength of this preference increased from early ($\eta = 1.12$) to late ($\eta = 2.84$) season trials (Fig. 2). Odds ratios calculated from these coefficients indicate that jays are between 3.3 and

17.2 times more likely to choose black oak over chestnut. Chestnuts were preferred over white oak acorns, with a marginal reduction in strength from early ($\eta = -1.58$) to late ($\eta = -1.25$) season, indicating jays are between 3.5 and 4.9 times more likely to choose chestnut over white oak. Pilot season data also performed well (CP = 0.67, 28% improvement) but were less conclusive, showing no preference for black oak compared to chestnut and a moderate preference for white oak over chestnut. For titmice, selection was less defined, with no preference for black oak versus chestnut and variable preference for or against white oaks compared to chestnut (Table 2). During the pilot season (n = 47 selections), titmice showed very strong preference for chestnuts over both black and white oak acorns. Both Red-bellied and Red-headed Woodpeckers echoed Blue Jay preference of black oak over chestnut, and chestnut over white oak. Note, however, the larger standard deviation across platforms in woodpeckers and titmice compared to jays, indicating that preference among individuals of these species was less consistent than for jays. Finally, nuthatches strongly preferred chestnuts over both black and white oak acorns, though these results are based only on 26 observations.

For the 11 uniquely marked birds included in individual selection analyses, cameras recorded 263 selections. Sample sizes for individual birds ranged from 10 to 43 selections (mean = 23.9 selections). The model of selection performed well (CP = 0.75; improvement = 58%), and reflected the larger dataset of jay selections. Overall, the marked birds strongly preferred black oak over chestnut, and chestnut over white oak, but the individual preference coefficients show substantial variation (Table 3), with birds ranging from no apparent preference to very strong preference (e.g., up to 822 times more likely to choose black oak over chestnut). Although the small sample sizes per individual are largely responsible for several unusually strong preference coefficients, it is important to note that nearly all birds at least retained the same order of preference (black over chestnut over white oak).

Table 3

Mean, standard deviation, and 95% credible intervals for group-level mean (η_{Bird}) and variance (σ_{Bird}) of preference, as well as individual (β_X) preference coefficients for uniquely marked Blue Jay individuals during the late season 2020 selection trial. The proportion of the posterior distribution with the same sign as the mean ($P \lesseqgtr 0$) is shown for each estimated coefficient. BO = black oak; CH = chestnut, WO = white oak.

Preference	Coefficient	Mean	SD	95% C.I.	$P \lesseqgtr 0$
BO:CH	η_{Bird}	2.39	0.91	(0.52, 4.15)	0.99
	σ_{Bird}	3.14	1.13	(1.68, 5.90)	1.00
	β_1	−0.22	0.49	(-1.22, 0.69)	0.67
	β_2	6.33	2.15	(3.44, 11.62)	1.00
	β_3	−0.35	0.61	(-1.61, 0.77)	0.72
	β_4	5.24	2.29	(2.07, 10.68)	1.00
	β_5	0.43	0.56	(-0.68, 1.53)	0.78
	β_6	3.94	0.97	(2.36, 6.11)	1.00
	β_7	0.67	0.61	(-0.57, 1.87)	0.87
	β_8	4.05	1.09	(2.20, 6.47)	1.00
	β_9	1.90	0.97	(0.10, 3.94)	0.98
	β_{10}	6.71	2.11	(3.89, 11.79)	1.00
	β_{11}	5.04	1.04	(3.32, 7.42)	1.00
WO:CH	η_{Bird}	−2.35	0.49	(-3.23, −1.28)	1.00
	σ_{Bird}	1.13	0.63	(0.30, 2.67)	1.00
	β_1	−3.86	0.82	(-5.87, −2.58)	1.00
	β_2	−2.47	1.29	(-5.18, 0.06)	0.97
	β_3	−2.88	0.78	(-4.65, −1.54)	1.00
	β_4	−2.01	1.00	(-3.86, 0.08)	0.97
	β_5	−2.20	0.60	(-3.37, −1.04)	1.00
	β_6	−0.95	1.31	(-2.96, 1.95)	0.78
	β_7	−2.55	0.46	(-3.47, −1.64)	1.00
	β_8	−3.33	1.13	(-6.12, −1.72)	1.00
	β_9	−2.15	0.75	(-3.61, −0.64)	1.00
	β_{10}	−2.42	0.51	(-3.47, −1.47)	1.00
	β_{11}	−2.18	0.76	(-3.64, −0.64)	1.00

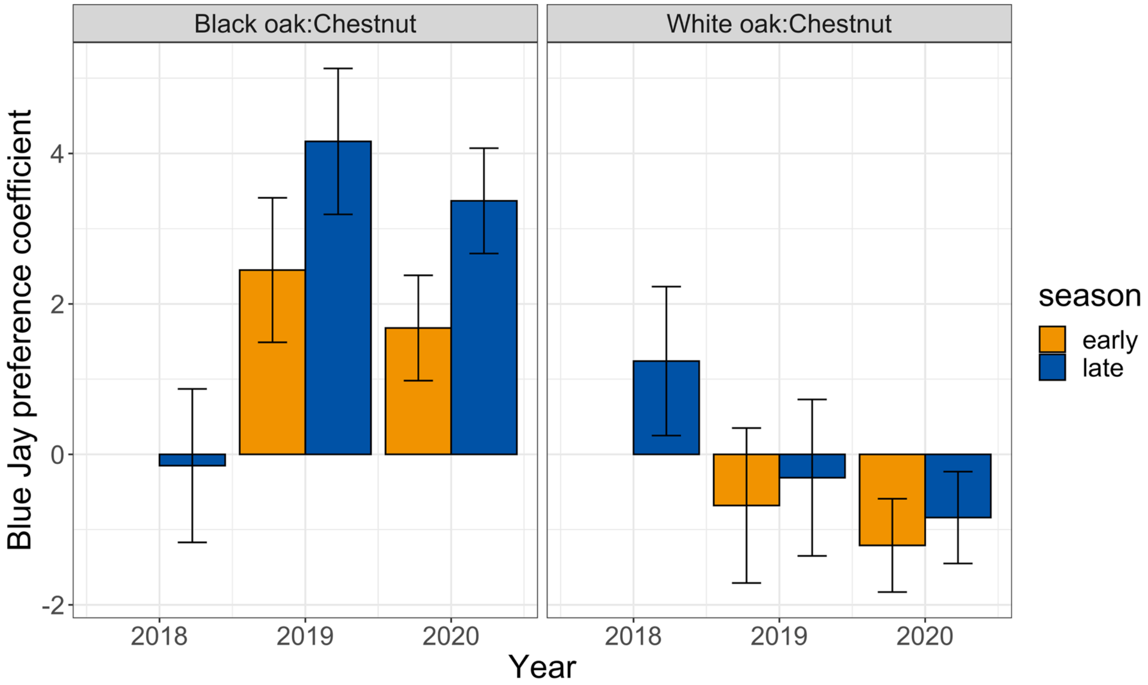

Fig. 2. Bar chart of preference coefficients and 95% credible intervals across years and seasons for Blue Jays. Note that 2018 was analyzed separately and only contained late season trials (see text for details), and the final preference model for 2019–2020 trials (Table 2) only included a significant effect of season. Positive coefficients indicate preference for the acorn species compared to chestnut, while negative coefficients show preference for chestnut compared to the acorn species.

4. Discussion

Our study has shown that seeds of American chestnut are readily selected by avian nut predators, despite being absent from the landscape for nearly a century. In fact, the most important dispersal agents, Blue Jays, appear to prefer chestnuts over similarly sized white oak acorns. Other species showed a variety of preferences, ranging from irregular or no preference to strong preference for chestnut over both acorn species we tested. These results support the idea that chestnuts will be a popular food choice when returned to the landscape, and avian seed-hoarders may indeed facilitate chestnut dispersal, particularly in years of black oak mast failure.

As in past studies of avian seed preference, seed size likely played an important role in selection. Black oak acorns were the smallest in our study, and were strongly or moderately preferred by jays and the two woodpecker species. Jays often took 2 or 3 black oak acorns in a single visit (n = 80 visits with multiple selections; see Bartlow et al. 2011), but due to the larger size of chestnuts and white oak acorns we collected, birds were not able to transport multiple seeds of these species. There were, however, several instances of birds transporting one black oak acorn in their gular pouch and one chestnut in their bill (see Pons and Pausas 2007 for discussion of throat limitations). For nuthatches, shell thickness (as suggested in Richardson et al. 2013), rather than size, may have played a role in their preference for chestnut, as chestnut shells are considerably thinner and softer (Sundaram et al. 2015; Table S1) than the acorn species we tested. Chestnut and white oak acorn size was annually variable in our study, which may have driven differences in preference coefficients between years for titmice and Red-bellied Woodpeckers. White oak acorns were lighter than chestnuts in 2019 and preferred by titmice, but this preference reversed in 2020 when white oak acorns were heavier than chestnuts. It is important to note that due to the flattened shape of chestnuts, they always had a smaller dimension (depth) than white oak acorns, requiring a smaller bill gape to handle. This may explain why jays and Red-bellied Woodpeckers consistently preferred chestnuts over white oak acorns despite the inverted relationship of mass between years. Interestingly, titmice were often seen to grasp and transport chestnuts by the narrow tassel-like remnant of the flower style, allowing them to transport nuts that would otherwise be too large to handle. Since seed size was confounded with year in our study, we cannot yet draw any conclusions regarding the effect of background acorn abundance or other annually changing conditions on seed preference. Additionally, we acknowledge that the small number of mother trees used in seed collections and the imprecise size selection method may have biased our results, given seed size can vary substantially across chestnut and oak families (Bonner and Karrfalt 2008, Clark et al. 2012, Pinchot et al. 2015). Despite that bias, the change in relative size between white oak acorns and chestnuts over the years presented an opportunity to assess how seed size influenced species preference.

The pilot year showed significant differences in preference compared to other years, and the smaller size of both white oak and chestnut seeds in 2018 may have played a role in these differences. However, it is likely that weevil infestation of black oak acorns is the primary driver of these differences, as we did not heat-treat seeds this year (see Methods). In addition, average black oak acorns were 0.4 g lighter this year than the following years, despite being slightly larger in width, suggesting that the cotyledons may have been partly consumed by weevil larvae. Blue Jays are typically able to detect unsound nuts, even without visual cues, and prefer uninfested nuts (Dixon et al. 1997). Our pilot season results, therefore, are likely confounded by weevil infestation, and should be interpreted with caution.

For Blue Jays, seed preference did not vary by year, but rather by season. The key change in jay selection between seasons was the strength of black oak preference (greater in late season). One contribution to this amplification of selection may be a stronger preference for a favored species when it is less abundant (Lichti et al. 2017). As all acorns are scarcer in late season, jays may be more likely to focus on their favored food when it is presented to them, because they cannot rely on finding more in another location. Another possible reason for selecting more black oak acorns in late season trials is a change in birds' nutritional needs. As temperatures drop with the onset of winter, birds will need more energy to maintain body temperature (Liknes et al. 2002), particularly more calories from fat (Rogers and Reed 2003). Of the three seed species presented in this study, black oak acorns have the greatest energy and lipid concentrations (Table S1; Steele et al. 2005, Sundaram et al. 2015), so are more likely to satisfy energetic requirements in colder weather. The increased need for efficiency in late season is also evident in our visiting/sampling rates. The proportion of Blue Jay visits that resulted in no seed selection fell from 21.2% to 13.5% from early to late trials (Table S2), and the proportion of visits where no seed was sampled before a selection was made (i.e., rapid choice without handling multiple seeds) rose from 30.5% to 40.8% (Table S3). Although the effect of season did not change the order of preference for jays (black oak > chestnut > white oak), the observed change in behavior and strength of preference suggests that future studies should consider seasonal energetic requirements when evaluating preference.

Another key difference between early and late season trials may be the intended use of the seeds that were taken from our platforms. Birds could either cache or immediately consume seeds, and they may cache or consume at different rates between early and late trials (Pesendorfer et al. 2016b, Lichti et al. 2017). We did not track the fates of seeds in this study, so cannot say whether this behavioral change existed for our birds. However, the predator satiation hypothesis states that satiated scatter-hoarders will cache more seeds when acorn abundance is high (early season in our study), and consume more when food is scarce (late season; Kelly and Sork 2002, Greenberg and Zarnoch 2018). Thus, if birds alter their selection based on the intended use of the seed, then we would expect less perishable seeds to be selected in early season and more palatable seeds to be selected in later season. Black oak acorns have a long dormancy period and relatively high tannins (Steele et al. 2005, Sundaram et al. 2015), so this species is less palatable and less perishable. White oak acorns, on the other hand, have no dormancy and lower tannins, making them both more palatable and perishable (Sundaram et al. 2015). Finally, chestnuts have both a dormancy period and no tannins (Steele et al. 2005), making them a good choice for both caching and consumption. Thus, we would expect black oak acorns to be selected more in early season and less in late season if palatability and perishability were a concern. As we observed the opposite effect, we do not have evidence that these variables impacted preference, even if birds did cache or consume at different rates.

One crucial limitation of our study is that seed selection at a feeding platform is ultimately an artificial setting, and true selection in the wild occurs on trees that are actively producing acorns and chestnuts. Thus, additional variables will influence true preference, such as perceived competition with mammalian seed predators and ease of dislodging nuts from trees. The latter variable is particularly likely to influence selection and dispersal of chestnuts, since these seeds mature in a different way than acorns. Chestnuts are protected by spiny burs until they mature, when burs then open and quickly drop their seeds to the ground (Steele et al. 2005). As jays are less likely to take seeds from the ground (Darley-Hill and Johnson 1981, Vander Wall 2001), and fallen seeds are also then available to all seed predators for consumption, this limits availability for avian consumption. Acorns, on the other hand, mature in the open with essentially no protection from seed predators, so they are available for avian caching and consumption for a longer period of time. Despite this evident disadvantage to chestnut dispersal by birds, however, jays will still readily transport mature chestnuts from trees given the opportunity (Heinrich 2014), so the spiny bur does not appear to pose a large barrier to selection and dispersal once the bur has opened. Nevertheless, a promising avenue for future research would be to perform avian selection and dispersal studies at sites more akin to future restoration plantings, such as chestnut orchards surrounded by oak forests.

4.1. Conclusions

Overall, the results of our study show promising evidence that key scatter-hoarding birds will provide an important dispersal service for reintroduced chestnuts. Chestnuts were never the least preferred species, and are generally of intermediate preference for the birds we studied. In particular, our results suggest that in black and white oak dominated stands, chestnuts could be an important, preferred resource in years of black oak mast failure, providing further evidence that widespread chestnut restoration will be a great boon for populations of granivorous wildlife. Of course, the seeds we studied do not represent all the species that will compete with chestnut for avian attention, and relative size and abundance of other seed species will likely impart heterogeneity in chestnut use. However, as several other preferred species have pronounced masting cycles (e.g., pin oak [*Q. palustris*] and beech; Johnson and Adkisson 1985, Richardson et al. 2013) the availability of chestnut seeds could buffer against these periodic declines. Furthermore, chestnut could be an important resource buffer for wildlife from overall population declines of seed-producing trees caused by both environmental change (e.g. oak mesophication; Nowacki and Abrams 2008) and disease (e.g. beech leaf disease; Reed et al. 2022).

Pesendorfer et al. (2016a) highlight several instances in which land managers have used scatter-hoarding corvids (e.g., Eurasian Jays [*Garrulus glandarius*] and Clark's Nutcrackers [*Nucifraga Columbiana*]) as critical, cost-effective tools in restoration efforts for threatened oak and pine forests. Our results suggest that this strategy may be successfully employed with Blue Jays and chestnuts to inform site selection approaches for chestnut reintroduction. To encourage selection and potential dispersal of chestnuts by jays, restoration plantings can be located in suitable areas where preferred acorns like black oak are scarce, so birds will be more likely to transport chestnuts. Likewise, a study of rodent dispersal effectiveness found that chestnuts were more likely to be cached, and thus survive overwinter, when paired with perishable white oak acorns (Lichti et al. 2014). Taken together, it would appear that locating restoration plantings in areas that are both suitable for American chestnut, based on historical abundance or predictive modeling, and dominated by white oak may be a successful strategy for encouraging dispersal. Note, however, that important scatter-hoarders like jays should first be present at the site, which may not be the case if no preferred oaks are present. Thus, it may be that ideal sites for maximizing likelihood of jay occupancy and establishment/dispersal of chestnuts will (1) be areas where chestnuts previously occurred, (2) have a low to moderate abundance of preferred oaks, and (3) have a greater abundance of less preferred, perishable seed species. Whether or not this strategy will prove effective, it will be important to survey local wildlife populations prior to restoration plantings, both to predict dispersal potential and to monitor the impact of chestnut restoration on wildlife communities (Jacobs et al. 2013).

Authorship Statement

Conceived the study and acquired funding: JRW, SNM, CCP, CMT. Supervised the study: SNM, CCP, CMT. Implemented the study, analyzed data, and wrote first draft of manuscript: JRW. Provided input on further manuscript drafts: JRW, SNM, CCP, CMT.

CRediT authorship contribution statement

James R. Wright: Conceptualization, Funding acquisition, Writing – review and editing, Formal analysis, Methodology, Writing – original draft. **Stephen N. Matthews:** Conceptualization, Funding acquisition, Writing – review and editing, Supervision. **Cornelia C. Pinchot:** Conceptualization, Funding acquisition, Writing – review and editing, Supervision. **Christopher M. Tonra:** Conceptualization, Funding acquisition, Writing – review and editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120133.

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