

NUT SELECTION BY CAPTIVE BLUE JAYS: IMPORTANCE OF AVAILABILITY AND IMPLICATIONS FOR SEED DISPERSAL

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Abstract. We assessed dietary preference of 14 captive Blue Jays (*Cyanocitta cristata*) for different food types under different conditions of availability. In four separate feeding trials, we provisioned jays with the following: Trial 1, two nuts each of white oak (*Quercus alba*), pin oak (*Q. palustris*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), and shagbark hickory (*Carya ovata*); Trial 2, two small and two large red oak acorns; Trial 3, two germinating and two nongerminating white oak acorns; and Trial 4, one large red oak acorn, one large white oak acorn, and one shagbark hickory nut. We used discrete choice models to describe selection under conditions of changing choice sets. Blue Jays displayed a clear preference for pin oak and strong avoidance of red oak acorns when alternative foods were available. White oak and black oak acorns were selected intermediately. Shagbark hickory nuts were never used. Correlation coefficients suggested that preference was inversely related to seed size and the proportion of seed consisting of hard seed coat. In the absence of alternative food items, small red oak acorns were readily taken, whereas large red oak acorns were mostly avoided but still used by some birds. These results highlight the importance of considering food availability when making conclusions about preference, and lend support to the hypothesis that Blue Jays can be important dispersers of even less-preferred oak species. We discuss the potential as well as the limitations for Blue Jays to act as seed dispersers, with respect to postglacial range expansion of fagaceous tree species, and in the context of present-day dispersal in regions where forests are highly fragmented.

Key words: *Cyanocitta cristata*, discrete choice model, jays, oaks, selection.

Selección de Bellotas por *Cyanocitta cristata* en Cautiverio : Importancia de la Disponibilidad e Implicancias para la Dispersión de Semillas

Resumen. Determinamos las preferencias de dieta en condiciones de cautiverio para 14 individuos de la especie *Cyanocitta cristata* para cuatro tipos de alimento bajo diferentes condiciones de disponibilidad. En cuatro pruebas de alimentación, ofrecimos a las aves las siguientes combinaciones: Prueba 1, dos bellotas de *Quercus alba*, *Q. palustris*, *Q. velutina*, *Q. rubra* y *Carya ovata*; Prueba 2, dos bellotas grandes y dos pequeñas de *Q. rubra*; Prueba 3, dos bellotas germinadas y dos no germinadas de *Q. alba* y Prueba 4, una bellota grande de *Q. rubra*, una bellota grande de *Q. alba* y una bellota de *C. ovata*. Utilizamos modelos discretos de elección para describir la selección bajo condiciones cambiantes de los grupos de alimento ofrecidos. Las aves mostraron una clara preferencia por bellotas de *Q. palustris* y un fuerte rechazo por bellotas de *Q. rubra* cuando existía disponibilidad de alimentos alternativos. Las bellotas de *Q. alba* y *Q. velutina* fueron seleccionadas de manera intermedia. Las bellotas de *C. ovata* nunca fueron utilizadas. Los coeficientes de correlación sugirieron que la preferencia está inversamente correlacionada con el tamaño de la semilla y con la proporción de la semilla que representa su cubierta dura. En la ausencia de ítems alimenticios alternativos, las bellotas de *Q. rubra* de pequeño tamaño fueron ingeridas frecuentemente, mientras que las semillas de *Q. rubra* de gran tamaño fueron evitadas en la mayoría de los casos, aunque fueron utilizadas por algunos individuos. Estos resultados resaltan la importancia de considerar la disponibilidad de alimento al sacar conclusiones sobre las preferencias alimenticias, y apoyan la hipótesis de que *C. cristata* puede ser un dispersor importante incluso de las especies de *Quercus* menos preferidas. Discutimos el potencial y las limitaciones que *C. cristata* puede presentar como dispersor de semillas con relación a la expansión postglacial de las especies de árboles fagáceas y en el contexto de la dispersión actual en regiones en que el bosque se encuentra altamente fragmentado.

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INTRODUCTION

Blue Jays (*Cyanocitta cristata*) are credited as the primary avian disperser of eastern hardwood trees of the family Fagaceae. In autumn, individual birds may remove several thousand seeds from nut-bearing trees (Darley-Hill and Johnson 1981, Johnson and Adkisson 1985) and cache them in a way that is favorable for seedling establishment (if seeds are not later retrieved for consumption). Specifically, jays typically bury or cover seeds in shallow soil and leaf litter, and selectively cache them in early successional habitats such as woodland-grassland edges where light requirements for regeneration are more likely to be met (Johnson et al. 1997). Other birds, such as Wild Turkeys (*Meleagris gallopavo*) and woodpeckers, also consume acorns, but do not serve the dual role of disperser because of the manner in which they handle or store seeds (Steele and Smallwood 2002). Moreover, unlike mammalian dispersers (e.g., tree squirrels [*Sciurus* spp.]) that cache nuts over relatively short distances (<150 m; Stapanian and Smith 1986), Blue Jays are known to disperse seeds up to several kilometers from a source (Darley-Hill and Johnson 1981, Johnson and Adkisson 1985), thus facilitating tree dispersal across isolated habitat patches in fragmented regions and possibly explaining rapid postglacial expansion of fagaceous trees during the late Quaternary period (Johnson and Webb 1989, Clark et al. 1998, Powell and Zimmerman 2004).

Evidence of seed consumption or dispersal by Blue Jays is strong for tree species that produce relatively small nuts such as pin oak (*Quercus palustris*), willow oak (*Q. phellos*), and American beech (*Fagus grandifolia*, Darley-Hill and Johnson 1981, Johnson and Adkisson 1985, Scarlett and Smith 1991, Steele et al. 1993). However, the potential role of jays as dispersers of larger nuts (within Fagaceae or other plant families) has been less well demonstrated. Darley-Hill and Johnson (1981) reported that Blue Jays in Virginia did not use acorns of northern red oak (*Q. rubra*) or white oak (*Q. alba*), and Scarlett and Smith (1991) similarly observed almost no utilization of these two species in Arkansas. Johnson et al. (1997) observed jays in Iowa using white oak, but not red oak or bur oak (*Q. macrocarpa*). However, none of these studies tested whether

seemingly avoided species would be used by jays in the absence of preferred smaller acorns. This is an important consideration, because annual mast production is highly variable across species (Koenig and Knops 2002), resulting in some years in which nuts of preferred species are rare or absent. Also, tree species that produce smaller nuts may not occur in some geographic areas, and seed size within a species is known to vary throughout its range (Aizen and Woodcock 1992). Thus, a species not used in one geographic area may be heavily used in another. Vaughan (1991) described dispersal of red oak acorns by Blue Jays in central Maine, where other oak species did not occur and where red oak acorns were considerably smaller than those in other parts of the range (Scarlett and Smith 1991, Aizen and Woodcock 1992, this study).

We conducted four laboratory feeding trials with captive Blue Jays to evaluate relative preferences for, and potential use of, nuts from four species of *Quercus* (pin, red, white, and black [*Q. velutina*]) and one species of hickory (shagbark: *Carya ovata*, Juglandaceae). We acknowledge that selection of seeds for consumption may not be synonymous with selection for caching (and hence with dispersal potential). However, seeds not eaten by birds seem unlikely to be cached, and seeds that are selected for feeding but not ever cached may still be dispersed via germination of partially eaten nuts (Steele et al. 1993) or accidental dropping (Webb 1986). Therefore, understanding which nut characteristics influence feeding should provide useful insight into which nut trees are likely to derive dispersal benefits from jays. Specifically, we addressed the following questions in this study: Trial 1—Given a choice among nuts from five tree species, which did Blue Jays prefer and avoid? Which nuts were selected as the most preferred items became unavailable? Trial 2—Would Blue Jays in our study region consume acorns of northern red oak when other food types were not available, and if so, did birds prefer smaller red oak acorns to larger ones? Trial 3—Did Blue Jays prefer nongerminating white oak acorns to germinating ones? Trial 4—How capable were Blue Jays of utilizing large nuts (large red oak acorns, large white oak acorns, and shagbark hickory nuts) when smaller food items were not available?

Did birds show a preference for large nuts of one species over another?

All tree species used in feeding trials were common in our study region, except pin oaks, which were present but rare (JEM and RKS, unpubl. data). We included pin oak acorns to evaluate selection of locally common species in comparison with this rare but preferred food species (Scarlett and Smith 1991). We did not expect jays to consume the large nuts of shagbark hickory, but included them in trials because Tarvin and Woolfenden (1999) suggested that hickory nuts may be among the thousands of nuts cached by individual jays each year, and because stomach-content analyses (Beal 1922) suggested Blue Jays may consume at least some species of *Carya* besides pecan (*C. illinoensis*), a known food for jays (Batcheller et al. 1984). Trials allowed us to assess selection of various seed types by Blue Jays under different conditions of availability, and revealed limitations in the abilities of jays to handle large seeds with hard shells, thus providing insight into the potential for jays to act as dispersers of ostensibly avoided species.

METHODS

We captured 14 Blue Jays in Tippecanoe County, northern Indiana, between 8 December 2003 and 8 February 2004, using 15 × 15 × 48 cm Tomahawk Live Traps (Tomahawk, Wisconsin) baited with peanuts. The region in which we conducted our study, the Upper Wabash River basin, is dominated by agriculture (mostly corn and soybeans), and native habitats such as deciduous forest are highly fragmented (see Swihart and Slade [2004] and Moore and Swihart [2005] for full descriptions of the study region).

We housed Blue Jays indoors at a constant temperature (~21°C) for nine days, and provided artificial lighting from dawn to dusk. Jays held at the same time were kept in the same room, but in separate metal cages (61 × 61 × 46 cm) with solid sidewalls and ceilings so birds could not see each other. The latter point was to reduce the likelihood of birds influencing each other's feeding behavior. We provided each bird with a wooden perch and a water bowl, which we cleaned and filled daily. To the inside of each water bowl we mounted a small (4 × 3.5 × 2 cm) wooden block to facilitate the opening of nuts. Jays perched on the edges of the bowls

and held nuts against the tops of the blocks with their feet while hammering the nuts with their bills to break the shells. We performed four different 4-hr feeding trials with each bird, each beginning between 08:00 and 10:00 on days 3, 5, 7, and 9 of a bird's captive period. After the completion of trials 1–3, and on days between trials, we fed birds a maintenance diet of squirrel food (e.g., peanuts, cracked corn, and sunflower seeds) and canned dog food. We removed the maintenance diet from each bird's cage during the afternoon before a feeding trial. At the end of trial 4, birds were immediately released at their site of capture.

For each trial, we inserted into the cage a plastic tray that was divided into small dishes, each dish containing the same number of nuts for each seed type. For each bird undergoing a given trial, we haphazardly varied the placement of seed types in the different dishes. We used video camcorders to record the order of seed use during each 4-hr trial. We considered a seed to be used when it was successfully opened and at least partially consumed.

TRIAL 1

We provided two nuts from each of the five species: black oak (BLO), northern red oak (NRO), pin oak (PIO), white oak (WHO), and shagbark hickory (SHH). Except for pin oak acorns, which were commercially ordered (F. W. Schumacher Co., Sandwich, Massachusetts, and Sheffield's Seed Co., Locke, New York) from the autumn 2002 crop and kept in cold storage until feeding trials, all seeds for this trial were collected locally in autumn 2003 and held in cold storage before use. In all trials, we provided acorns without caps and hickory nuts without husks. We carefully selected sound acorns for our experiments by removing nuts that showed signs of damage by insects (e.g., *Curculio* weevil larvae), fungi, or mold.

We analyzed our data using a discrete choice model (McCracken et al. 1998, Cooper and Millsbaugh 1999, Manly et al. 2002) and program DISCCHSE (Western Ecosystems Technology, Inc., Cheyenne, Wyoming). Discrete choice models assume that a unique set of choices (called the choice set) is available to one or more individuals each time they select a resource item (e.g., food item or habitat patch), and that the conditional probability of a given resource unit being selected from

a particular choice set depends on the relative “utility” of that unit compared to the utility of other available units (Cooper and Millspaugh 1999). In our study the choice set changed whenever a Blue Jay used a nut because only a subset of the original seeds were available to choose from in subsequent choices. This model thus allowed us to evaluate selection of less preferred seed types when the most preferred seed type was absent. The utility that an animal derives by selecting the j th resource unit available during the i th choice is estimated by

$$U_{ij} = \beta_1 x_{ij1} + \beta_2 x_{ij2} + \dots + \beta_p x_{ijp},$$

where $\beta_1, \beta_2, \dots, \beta_p$ are unknown parameters corresponding to p variables (x_{ijp}) describing each resource unit. In our case, U_{ij} simply depended on the categorical variable “seed type” (i.e., tree species), so the x_{ijp} were p binary indicator variables to code the $p + 1$ seed types we used. The resource selection function (RSF) gives the relative probability of use for different resource units, and is estimated as $\exp(U_{ij})$ (Manly et al. 2002). The probability of selecting unit j during the i th choice is then described by the resource selection probability function:

$$p_{ij} = \exp(U_{ij}) / \sum_{k=1}^n \exp(U_{ik}),$$

where $k = 1, 2, \dots, n$ are all the resource units available in the choice set. Parameters $\beta_1, \beta_2, \dots, \beta_p$ are estimated by maximizing the likelihood for a multinomial logit function (McCracken et al. 1998, Manly et al. 2002), and Akaike’s information criterion (AIC) may be used to select the model that most parsimoniously describes selection data. We used a small-sample corrected AIC (AIC_c ; Burnham and Anderson 2002) because n (number of choices observed) was only 34, and we calculated each model’s AIC_c weight (w_i), which indicates the probability that model i is the best model in the set of candidate models. The discrete choice model assumes all choices are statistically independent, but since multiple observations came from the same individuals, we recommend caution in extrapolating inference from our sample to the entire Blue Jay population in our study area. Other discrete choice studies in the ecological literature also

used repeated measures of resource selection by the same individuals (Arthur et al. 1996, McCracken et al. 1998, Cooper and Millspaugh 1999, Manly et al. 2002), and we are not aware of available tools to more appropriately model possible autocorrelation.

Shagbark hickory nuts were never successfully utilized by any bird, so we did not include this species in model selection. Thus, we initially compared a null model of no selection between pin oak (PIO), white oak (WHO), black oak (BLO), and northern red oak (NRO) to a model in which the resource selection function (RSF) was estimated separately for these four species. Results of this comparison clearly revealed avoidance of northern red oak, but interpretation of whether the RSF differed between the other three species was ambiguous (i.e., confidence intervals for β_{PIO} , β_{WHO} , and β_{BLO} overlapped). Therefore, we additionally fit two *post-hoc* models: (1) RSF was lower for red oak, but was the same for remaining food types, i.e., $\beta_{PIO} = \beta_{WHO} = \beta_{BLO} > \beta_{NRO}$, and (2) RSF was highest for pin oak, intermediate for white oak and black oak, and lowest for red oak, i.e., $\beta_{PIO} > \beta_{WHO} = \beta_{BLO} > \beta_{NRO}$.

To gain insight into why different seed types were selected or avoided, we measured size characteristics of 15–20 randomly drawn seeds of all five seed types, and we summarized published information about nutritional characteristics (Table 1). We measured seed mass of whole seeds (including the shell) and of the seed kernel after drying seeds for 48 hr at 100°C. We calculated Spearman rank correlations between seed characteristics and their estimated resource selection probability (\hat{p}_{ij}) when all types were available in equal numbers.

TRIAL 2

Because most previous studies have reported avoidance of northern red oak acorns by Blue Jays (and Trial 1 in our study also suggested avoidance of red oak), we provided birds with only two nuts each of small red oak acorns (length: 18.6 ± 1.7 mm [mean \pm SD]; width: 18.9 ± 0.7 mm) and large red oak acorns (length: 23.6 ± 1.1 mm; width: 21.9 ± 1.0 mm). This was to determine whether Blue Jays in our region would consume red oak acorns when they were the only food source available, and if so, whether this depended on the size of nuts available. Large acorns were collected locally in

TABLE 1. Size and nutritional characteristics of seed types given to 14 captive Blue Jays in feeding trial 1, December 2003–February 2004, Tipton County, Indiana. Size data are based on a random sample of 15–20 nuts drawn from the same sources as those used during trials. Nutrient data are from previously published studies. Values reported are means (\pm SD when available).

	White oak (<i>Quercus alba</i>)	Black oak (<i>Q. velutina</i>)	Pin oak (<i>Q. palustris</i>)	Northern red oak (<i>Q. rubra</i>)	Shagbark hickory (<i>Carya ovata</i>)
Length (mm)	25.0 \pm 1.4	16.8 \pm 1.2	14.7 \pm 1.1	23.3 \pm 1.1	25.4 \pm 1.1
Width (mm)	16.8 \pm 1.2	16.0 \pm 0.9	16.1 \pm 1.4	19.2 \pm 1.2	22.2 \pm 0.8 16.3 \pm 0.7 ^a
Total dry mass (g)	2.43 \pm 0.40	1.64 \pm 0.30	1.27 \pm 0.25	5.15 \pm 0.77	4.80
Kernel dry mass (g)	1.78 \pm 0.33	1.18 \pm 0.18	1.00 \pm 0.24	3.45 \pm 0.53	1.68
% kernel	72 \pm 5	72 \pm 3	74 \pm 5	67 \pm 2	35 ^b
kJ per g (kernel) ^c	18.12	21.60	21.60	21.60	29.56
kJ per kernel	32.33	25.55	21.64	74.65	49.64
% lipid (kernel) ^d	6.4	15.3	11.7	18.4	29.3
g lipid per kernel	0.11	0.18	0.12	0.64	0.49
% protein (kernel) ^e	5.2	5.9	6.1	5.8	16.4
g protein per kernel	0.09	0.07	0.06	0.20	0.28
Tannin (z) ^f	-0.68	1.60	0.14	1.03	-0.53

^a Width of shagbark hickory nuts was measured in two dimensions because they are flattened along the longest axis.

^b Average of values reported by Smith and Follmer (1972) and Ivan and Swihart (2000).

^c Values of kJ per g for black oak, pin oak, and northern red oak represent average of reported values for northern red and shumard oak (*Q. shumardii*), also in the “red oak group.”

^d From Smith and Follmer (1972), Short (1976), Briggs and Smith (1989), and Servello and Kirkpatrick (1989).

^e From Smith and Follmer (1972), Short (1976), Stapanian and Smith (1984), Briggs and Smith (1989), Servello and Kirkpatrick (1989), and Ivan and Swihart (2000).

^f Various tannin metrics have been reported in the literature (e.g., phenols, % tannin, tannic acid equivalents), so we converted the value for each species within a comparative study (i.e., where multiple species were evaluated) to a z-score, which we then averaged across studies (if multiple studies existed). Higher z-scores indicate higher relative tannin content. Data are from Briggs and Smith (1989), Servello and Kirkpatrick (1989), and Ivan and Swihart (2000).

autumn 2003, but small acorns were ordered commercially from the autumn 2002 crop and held in cold storage until use. This could have affected seed choice by Blue Jays, particularly if age affected acorn chemistry. However, Dixon et al. (1997) and Smallwood et al. (2001) found no decline in tannin levels for northern red oak acorns with time, and jays would not have had prior knowledge of any differences in chemistry between small and large red oak acorns in this trial, so initial choices should have been based on other cues (e.g., appearance, size, and shell hardness).

TRIAL 3

Several species of oak in the subgenus *Leucobalanus*, including white oak, have seeds that do not have a dormancy period and germinate soon after they fall. Food reserves stored in the seedling taproot of white oak are not useful to seed consumers (Smith and Follmer 1972, Fox 1982, Steele and Smallwood 2002). We pro-

vided Blue Jays with two nuts each of similar size (length: 25.0 \pm 1.4 mm [mean \pm SD]; width: 16.8 \pm 1.2 mm) of both germinating and nongerminating white oak acorns to determine whether birds exhibited a preference for nongerminating acorns, in which a higher proportion of nutrient stores should have been available to the birds. We analyzed these data using a discrete choice model, as in Trial 1. We also noted whether birds consumed or avoided the apical portion of germinating acorns. Steele et al. (1993) observed that Blue Jays, gray squirrels (*Sciurus carolinensis*), and Common Grackles (*Quiscalus quiscula*) avoided the apical portion of willow oak acorns, and found that the apical portions of acorns were higher in tannin content.

TRIAL 4

To assess the limits of ability of Blue Jays to consume difficult-to-use food items in the absence of preferred food types, we presented

TABLE 2. Number of nuts at least partially consumed by 14 Blue Jays during captive feeding trials, December 2003–February 2004, Tippecanoe County, Indiana. PIO = pin oak, WHO = white oak, BLO = black oak, NRO = northern red oak. See text for description of each trial.

Bird	Trial 1				Trial 2		Trial 3		Trial 4	
	PIO	WHO	BLO	NRO	Small NRO	Large NRO	Germinating WHO	Nongerminating WHO	Large NRO	Large WHO
1	1	–	–	–	2	–	1	–	–	–
2	1	–	–	–	1	–	2	2	–	–
3	2	1	2	–	2	–	2	1	1	1
4	–	1	1	–	–	–	2	1	–	1
5	1	1	1	–	1	–	1	1	–	1
6	2	–	–	–	–	–	1	1	–	–
7	2	–	–	–	1	–	1	1	–	1
8	–	1	–	1	1	–	2	1	1	1
9	1	–	2	–	2	–	2	1	–	1
10	1	1	–	–	–	–	2	2	–	1
11	2	1	–	–	2	1	2	2	–	1
12	–	2	1	–	–	–	2	1	–	1
13	2	–	–	–	1	–	2	2	1	1
14	1	1	–	–	1	–	2	1	1	1

birds with only one large northern red oak acorn (length: 23.6 ± 1.1 mm [mean \pm SD]; width: 21.9 ± 1.0 mm), one large white oak acorn (length: 28.4 ± 1.5 mm; width: 20.9 ± 1.1 mm), and one shagbark hickory nut (length: 25.4 ± 1.1 mm; width: 22.2 ± 0.8 mm; breadth: 16.3 ± 0.7 mm). We recorded which seeds were taken, and in what order.

RESULTS

TRIAL 1

Twenty-eight nuts of each species were offered to 14 Blue Jays. Of these, birds at least partially consumed 16 (57%) pin oak acorns, nine (32%) white oak acorns, seven (25%) black oak acorns, and only one (3.6%) red oak acorn

(Table 2). No birds successfully opened a shagbark hickory nut, although several birds attempted to do so. Based on AIC_c scores and model weights, the most strongly supported discrete choice model ($w_i = 0.64$) suggested that pin oak acorns were selected above other food types, that selection for black oak and white oak acorns was less than for pin oak acorns but similar to each other, and that red oak acorns were avoided (Table 3, 4). Some support ($w_i = 0.29$) existed for the model suggesting that the utility (U_{ij}) and hence resource selection function (RSF) for white oak was greater than for black oak (as indicated by larger β for black oak), but because of the relatively low number of birds involved and probable nonindependence among some choices, we chose to adopt

TABLE 3. Results of discrete choice model selection for feeding trials 1 and 3, using 14 captive-held Blue Jays from Tippecanoe County, Indiana, December 2003–February 2004. ΔAIC_c is the difference in AIC_c between model i and the model with lowest AIC_c . Model weight (w_i) describes relative support of each model. The number of estimated parameters, K , is 0 for the null model because models do not include an intercept term (i.e., $\beta_0 = 0$). PIO = pin oak, WHO = white oak, BLO = black oak, NRO = northern red oak, “germ” = germinating white oak; “nongerm” = non-germinating white oak.

Model	$\log(\mathcal{L})$	K	ΔAIC_c	w_i
Trial 1				
$\beta_{PIO} > \beta_{WHO} = \beta_{BLO} > \beta_{NRO}$	–54.78	2	0.00	0.64
$\beta_{PIO} > \beta_{WHO} > \beta_{BLO} > \beta_{NRO}$	–54.39	3	1.62	0.29
$\beta_{PIO} = \beta_{WHO} = \beta_{BLO} > \beta_{NRO}$	–58.14	1	4.46	0.07
$\beta_{PIO} = \beta_{WHO} = \beta_{BLO} = \beta_{NRO}$	–66.21	0	18.47	<0.01
Trial 3				
$\beta_{germ} = \beta_{nongerm}$	–20.80	0	0.00	0.50
$\beta_{germ} \neq \beta_{nongerm}$	–19.72	1	0.01	0.50

TABLE 4. Parameter estimates from the most parsimonious discrete choice model (Table 3) for feeding trial 1, based on data from 14 captive-held Blue Jays in Tippecanoe County, Indiana, December 2003–February 2004. Slope coefficients ($\hat{\beta}_j$) represent the utility (U_{ij}) of each food type because no other variables were measured for resource units. The resource selection function (RSF) is equal to $\exp(U_{ij})$ and gives the relative probability of selecting one food type over another when both are available. Here, \hat{p}_{ij} is the estimated probability of selecting a given food type when an equal number of all types is available. \hat{p}_{ij} for shagbark hickory nuts is 0.

Seed type	$\hat{\beta}_j \pm SE$	RSF	\hat{p}_{ij}
Pin oak (<i>Quercus palustris</i>)	3.27 \pm 1.04	26.31	0.56
Black oak (<i>Q. velutina</i>)	2.27 \pm 1.03	9.68	0.21
White oak (<i>Q. alba</i>)	2.27 \pm 1.03	9.68	0.21
Red oak (<i>Q. rubra</i>)	0.00	1.00	0.02

the conservative interpretation that the RSFs of black oak and white oak acorns to Blue Jays were at least similar, if not the same.

Resource selection probabilities (\hat{p}_{ij} ; Table 4) were strongly positively correlated with the percentage of seed mass comprising edible seed kernel ($r_s = 1.00$; Table 5). Seed mass also seemed important ($r_s = -0.87$, $P = 0.05$), with birds preferring smaller seeds. Thus, larger seeds with thicker, heavier shells were less favored. Other correlations between \hat{p}_{ij} and seed characteristics were not statistically evident, although small sample size ($n = 5$ seed types) and strong correlations between seed characteristics (Table 5) preclude strong inference about most of these.

TRIAL 2

Nine of the birds consumed one or two of the small red oak acorns but none of the large red oak acorns offered to them (Table 2). Only one

bird consumed any of the large red oak acorns, and it did so after first consuming both small acorns. Four birds (29%) did not consume any nuts during this trial. These results are consistent with those of trial 1, in which small nuts were favored over large nuts and locally collected red oak acorns were almost entirely avoided. Nearly one-third of Blue Jays did not consume even small red oak acorns in this trial, providing further evidence of avoidance of this food species.

TRIAL 3

We found no evidence that Blue Jays preferred nongerminating white oak acorns to germinating acorns. In fact, jays in our sample may have displayed a slight preference for germinating nuts, which may have been easier to open from the apical end than nongerminating nuts. Of 28 nuts of each type offered to the 14 birds, 24 (86%) germinating nuts were eaten, compared to 17 (61%) nongerminating nuts (Table 2). Based on AIC_c scores, model support (w_i) was equal for the null model of no difference in resource selection function between the two acorn types, and a model in which RSF differed for the two types (Table 3).

TRIAL 4

Eleven of 14 Blue Jays consumed the large white oak acorns that were presented, and four of these 11 birds also proceeded to consume at least part of the large red oak acorns available (Table 2). Three birds did not utilize any nuts in this trial, and no birds succeeded in opening a shagbark hickory nut. These results are consistent with those of trials 1 and 2; white oak acorns were preferred to those of red oak, shagbark hickory nuts were too difficult for

TABLE 5. Spearman rank correlations between size and nutritional attributes of five seed types used in Trial 1 and their estimated resource selection function probabilities (\hat{p}_{ij} ; Table 4) under the most parsimonious selection model.

	Total mass (g dry)	% kernel	kJ g ⁻¹ (kernel)	% lipid (kernel)	% protein (kernel)	Tannin (z)
\hat{p}_{ij}	-0.87*	1.00*	-0.57	-0.82	-0.21	0.10
Dry mass total (g)		-0.87*	0.22	0.60	-0.20	-0.10
% kernel			-0.57	-0.82	0.21	0.10
kJ g ⁻¹ (kernel)				0.89*	0.89*	0.22
% lipid (kernel)					0.60	0.30
% protein (kernel)						0.10

* Statistically significant at $\alpha = 0.05$ for one-tailed test.

Blue Jays to open, and few birds consumed the locally collected red oak nuts.

DISCUSSION

Our results demonstrate the influence that availability can have on selection of nuts and, taken in concert with other studies of Blue Jay foraging, suggest that the tree species most utilized by Blue Jays for food vary considerably throughout the bird's geographic range. In the only previously reported diet choice experiment with Blue Jays, Scarlett and Smith (1991) observed that birds in Arkansas largely avoided eating or caching nuts from black oak, white oak, or red oak, favoring instead the smaller acorns of pin, post, and willow oak. In contrast, we found that captive-held Blue Jays in northern Indiana readily consumed black oak and white oak acorns even when pin oak acorns were present, although pin oak acorns were more strongly favored. Our results may have differed from the findings of Scarlett and Smith (1991) because preferred food items (i.e., pin oak acorns) are less available under natural conditions to birds in our study, or because black oak and white acorns collected at our study site were smaller than in their study. Their black oak acorns had mean length and width of 22.4 mm and 18.8 mm, respectively, and their white oak acorns had mean length and width of 26 mm and 21.2 mm, respectively, compared with our black oak acorns of 16.8 × 16.0 mm and white oak acorns of 25.0 × 16.8 mm. Differing choice sets and spatial variation in seed size are thus important considerations when making conclusions about nut species selected for food.

Scarlett and Smith (1991) also concluded that acorns from the subgenus *Erythrobalanus* (red or black oak group) were favored by Blue Jays over acorns from *Leucobalanus* (white oak group). However, size and subgenus were confounded in their study. The two most preferred species in their spring choice trials (*Q. phellos* and *Q. palustris*, both "red oaks") were also the two smallest species, and preference of jays for smaller acorns has been noted elsewhere (Darley-Hill and Johnson 1981, Johnson et al. 1997). We also observed seed size and shell thickness to correlate most closely with preference, suggesting limitations in the ability of jays to make efficient use of larger seeds. Although we did not quantify handling

time for different seed types, personal observations (JEM) suggest that birds were much more efficient at opening small pin oak acorns than larger red oak acorns.

Given seeds of comparable size, we would expect nutritional characteristics such as tannin content to be important determinants of seed selection. Experimental studies with Blue Jays (Johnson et al. 1993, Dixon et al. 1997), Western Scrub-Jays (Koenig and Heck 1988, Fleck and Tomback 1996), and Acorn Woodpeckers (Koenig 1991) have demonstrated the negative effect of acorn tannins on digestion and weight maintenance. In Scarlett and Smith's (1991) study, Blue Jays preferred seeds of willow oak and pin oak, which had relatively low tannin content compared to other species in the same subgenus.

In our study, we found no difference in selection between white oak and black oak acorns; in fact, white oak may have been slightly preferred. If selection by jays was strictly size-dependent, or based on higher per-gram content of lipids or energy, then the smaller black oak acorns should have been preferred over white oak acorns in our study. However, black oak acorns have high tannin content, even for species in *Erythrobalanus* (Briggs and Smith 1989), which may have deterred some birds from selecting this species over white oak acorns, which have lower percent fat and per-gram energy content but also lower tannin content. Further, the large white oak acorns in trial 4 were of similar width to large red oak acorns in the same trial, and were considerably larger in both dimensions than the small red oak acorns provided in trial 2, yet the number of birds utilizing large white oak acorns in trial 4 was much higher than the number using large red oak acorns, and similar to the number of birds that used small red oak acorns in trial 2 ($n = 10$). Three of the four birds that avoided even small red oak acorns in trial 2 used larger white oak acorns in trial 4. Given that large red oak acorns contained substantially more energy (means from 15–20 randomly selected seeds = 74.6 kJ vs. 45.0 kJ, red vs. white oak, respectively), lipids (0.64 g vs. 0.16 g), and protein (0.20 g vs. 0.13 g) than comparably sized white oak acorns in trial 4, these observations indicate birds may prefer lower tannin content. Alternatively, the birds may simply have limited abilities to open large

red oak acorns, which have harder shells than white oak acorns (Ivan and Swihart 2000), but this does not explain why birds seemed equally inclined to use large white oak acorns and small red oak acorns, or why birds who were able to use both types in trial 4 showed a preference for white oak acorns. Sensitivity of jays to high tannin content also was supported by our observations that they discarded the apical end of germinating white oak acorns in trial 3 (also see Steele et al. 1993). We note, however, that we were principally evaluating feeding decisions of birds in winter. These may differ somewhat from autumn caching decisions, during which birds may prefer less perishable seeds with higher tannin content.

Although several studies have reported avoidance by Blue Jays of larger acorns such as those of northern red oak and bur oak, our results lend empirical support to the speculation of Johnson and Webb (1989) that all species of Fagaceae may at least occasionally be dispersed by jays, and to their suggestion that Blue Jays were responsible for the rapid northward expansion of all eastern North American oak species following the last Ice Age. We found that red oak acorns were clearly avoided by jays in the presence of more preferred food species, but in the absence of alternatives, smaller red oak acorns in trial 2 were readily used by most birds, and even the large red oak acorns in trial 4 were used by some individuals. These trials may have somewhat mimicked the situation Blue Jays face in years when northern red oak acorns are abundant but other species yield poor seed crops. Furthermore, Aizen and Woodcock (1992) documented a latitudinal trend in acorn size of eastern oaks, whereby trees within the same species produce smaller acorns at higher latitudes. Presumably, this latitudinal trend in acorn size would have increased the likelihood of Blue Jays dispersing large-acorn species along the northern extent of their expanding range, providing a possible explanation for how jays might have dispersed species such as bur oak, basket oak (*Q. michauxii*), and chestnut oak (*Q. prinus*), whose acorns are considerably larger than acorns of northern red oak (Aizen and Woodcock 1992) and which are probably avoided by jays in most areas. Indeed, red oak acorns were commonly dispersed by Blue Jays in central Maine (Vaughan 1991); these acorns were of a similar

size (~17.5–19 mm long and 16–16.2 mm wide) as black acorns in our study and much smaller than our white oak or red oak acorns.

Food handling behavior by Blue Jays also may have important consequences for dispersal of seeds, especially for seed types that are more difficult for birds to handle. Captive jays in our study frequently dropped seeds from their perches while trying to open them. In a forest setting, such seeds probably would be lost on the forest floor and subsequently covered by leaf litter in autumn. Thus, it is possible that Blue Jays may disperse seeds by means other than failing to retrieve caches.

While Blue Jays have no doubt been important contributors to postglacial expansion of fagaceous species, we hesitate to give jays sole credit for rapid nut-tree migration. Johnson and Webb (1989) acknowledged that observed caching distances of Blue Jays are too short to explain the postglacial migration rate of *Fagus*. It is possible that in rare and unobserved instances seeds may be cached at greater distances than those recorded, and such rare long-distance dispersal events are important for explaining rapid postglacial expansion (Clark 1998, Clark et al. 1998, 2001, Powell and Zimmerman 2004). Nevertheless, our study suggests that Blue Jays probably cannot utilize shagbark hickory nuts, which are fairly typical in size among *Carya* species (Young and Young 1992). Yet the postglacial expansion rate of *Carya* is comparable to that of other fagaceous and wind-dispersed genera (Davis 1981, 1983). Of course, we cannot rule out that Blue Jays disperse hickory nuts, even if they are unable to subsequently consume them. Jays in our trials often attempted to open hickory nuts, and shagbark hickory nuts were removed from feeding stations utilized only by Blue Jays and woodpeckers (N. Lichti, Purdue University, pers. obs.), so perhaps some birds rarely cache them. Additional field studies are required to more unequivocally answer this question. If Blue Jays are not important dispersers of hickory, then this points to additional sources of dispersal for such large-seeded tree species. Humans were in eastern North America at least throughout the Holocene and possibly for the past 20 000 years or longer (Gibbons 1996, Goodyear 2004), and may have influenced forest composition by cultivating or inadvertently dispersing nut trees (Delcourt et al. 1986,

Delcourt 1987, Delcourt and Delcourt 1987, Wykoff 1991). The extinct Passenger Pigeon (*Ectopistes migratorius*) has also been suggested as a possible long-distance dispersal agent of *Quercus* spp., including species with large acorns such as red oak (Webb 1986, Ellsworth and McComb 2003); however, Passenger Pigeons likely did not disperse hickory nuts. Alternatively, Clark et al. (1998, 2001) have suggested that some taxa (e.g., *Carya*) may have simply been more widespread during the Pleistocene than is currently inferred from the pollen record, in which case contemporary distributions can be explained by slower migration rates.

In highly fragmented landscapes of the contemporary eastern U.S., and particularly in the central hardwoods forest region of the Midwest, successful interpatch dispersal and recruitment of nut trees depends on animal dispersers that can readily cross forest gaps, usually through expansive agricultural fields. Thus, for a given area over contemporary time scales, Blue Jays may play an important role in maintaining tree biodiversity within isolated forest remnants. Our data suggest that in the Upper Wabash River basin of northern Indiana, Blue Jays are likely to be important dispersers of white oak, black oak, and species with smaller nuts, such as pin oak. Northern red oak may receive some dispersal benefit from Blue Jays, but we expect this benefit to be much lower than for other species for several reasons. First, our data suggest that red oak acorns will be avoided in years when alternative acorn types are available. Second, there appears to be regional synchrony in acorn production among species whose acorns require the same number of years (one or two) to develop (Mohler 1990, Koenig and Knops 2002). Thus, it is probably uncommon for red oak acorns to be abundant and acorns from black oak, pin oak, and other species on a two-year cycle to all be rare at the same time. Finally, our data suggest that Blue Jays taking red acorns in our region are likely to select smaller nuts, which probably have lower seedling establishment rates than larger nuts (McComb 1934, Tripathi and Khan 1990). Moreover, seed survival rates are lower in years when mast is less abundant (JEM and RKS, unpubl. data; also see review by Kelly and Sork 2002) and when jays are therefore more likely to utilize less-preferred food sources. Sork et al.

(1983) recorded extremely low use of red oak trees in Missouri by Blue Jays (and other vertebrates) in a year when production was moderate for red oak and low for other oak species, although sampling design in this study may have prevented robust inference from their results (Johnson and Adkisson 1985). Trees that bear larger nuts, such as black walnut (*Juglans nigra*), *Carya* species, and oak species that have large acorns and are in the southern portion of their range (where within-species acorn size is largest), should not benefit from Blue Jay foraging behavior. Further field experiments should seek to identify long-term consequences of forest fragmentation for nut trees that cannot be dispersed by Blue Jays in all or part of their geographic range.

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