Tree-Species Preferences of Foraging Insectivorous Birds: Implications for Floodplain Forest Restoration

AARON P. GABBE,*§ SCOTT K. ROBINSON†, AND JEFFREY D. BRAWN‡

*Department of Natural Resources and Environmental Sciences, 515 Morrill Hall, University of Illinois, Urbana-Champaign, 505 South Goodwin Avenue, Urbana, IL 61801-3799, U.S.A.
†Department of Ecology, Ethology and Evolution, 515 Morrill Hall, University of Illinois, Urbana-Champaign, 505 South Goodwin Avenue, Urbana, IL 61801-3799, U.S.A.
‡Illinois Natural History Survey and Department of Natural Resources and Environmental Sciences, University of Illinois, 607 East Peabody Drive, Champaign, IL 61820, U.S.A.

Abstract: *The tree-species composition of forests can be an important component of habitat selection by breeding birds. We examined tree-species use by observing the foraging behavior of 13 species of foliage-gleaning birds in floristically diverse floodplain forests in southern Illinois in 1997 and 1998. Twelve of 13 bird species foraged selectively with respect to tree species. The Yellow-throated Warbler (*Dendroica dominica*) and Cerulean Warbler (*D. cerulea*) were the most selective species, whereas the Yellow-throated Vireo, Red-eyed Vireo, and Eastern Tufted Titmouse (* Vireo flavifrons, V. olivaceus, and Baeolophus bicolor, *respectively) were the least selective. Three tree species were strongly preferred by most of the bird community: kingnut hickory, bitternut hickory, and silver maple (*Carya laciniosa, C. cordiformis, *and* Acer saccharinum, *respectively). Less common bird species tended to be more selective foragers than the more abundant bird species. The four most preferred trees were relatively uncommon where we sampled. Heavy-seeded hickories are slow to recolonize forests traditionally restored with common oak species (*Quercus *spp.). Therefore, restoring floristically diverse floodplain forests by planting preferred heavy-seeded and uncommon trees will enhance habitat quality for birds in these forests.*

Preferencia de Aves Forrajeras Insectívoras por Especies de Árboles: Implicaciones en la Restauración de Bosques de Llanuras Inundables

Resumen: *La composición de especies de árboles de un bosque puede ser un componente importante de la selección de hábitat por aves que están reproduciéndose. Examinamos el uso de las especies de árboles mediante la observación de la conducta de forrajeo de 13 especies de aves recolectoras de follaje en bosques de llanuras de inundación florísticamente diversos del Sur de Illinois en 1997 y 1998. Doce de las 13 especies de aves forrajearon selectivamente con respecto a la especie de árbol. El Chipe Pecho Amarillo (*Dendroica dominica*) y el Chipe Cureleano (*D. curelea*) fueron las especies más selectivas, mientras que el Vireo Pecho Amarillo, el Vireo Ojirojo y el Paro Copetudo del Este (*Vireo flavifrons, V. Olivaceus *y* Baeolophus bicolor, *respectivamente) fueron los menos selectivos. Tres especies de árboles fueron altamente preferidas por la mayoría de la comunidad de aves: El nogal nuez-rey, el nogal de nuez amarga y el arce plateado (*Carya laciniosa, C. Cordiformis *y* Acer saccharinum, *respectivamente). Las especies de aves menos comunes tendieron a ser forrajeros más selectivos que las especies de aves más abundantes. Los cuatro árboles más preferidos fueron relativamente poco comunes en los sitios muestreados. Los nogales altamente cargados de semillas son lentos para recolonizar bosques tradicionalmente restaurados mediante la siembra de especies comunes de robles (*Quercus *spp). Por lo tanto, la restauración de bosques de llanuras de inundación florísticamente diversos mediante la siembra de árboles con muchas semillas y poco comunes enriquecerá la calidad del hábitat para las aves de estos bosques.*

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§Current address: Department of Environmental Studies, University of California, Santa Cruz, CA 95064, U.S.A., email gabbe@cats.ucsc.edu

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Introduction

Conservation efforts for breeding forest birds in North America have focused on habitat loss and the adverse effects of habitat fragmentation on reproductive success (e.g., Robbins et al. 1989; Robinson 1992; Robinson et al. 1995). To alleviate the deleterious effects of habitat loss and degradation, restoration has become increasingly necessary (e.g., Koebel 1995; Kus 1998; Holl 1999). For forest ecosystems, little attention has been given to the effects of internal components such as floristic composition and vegetative structure—which are directly affected by restoration processes (Palmer et al. 1997)—on bird conservation.

The perceived importance of vegetation structure on the distribution and abundance of birds (Holmes & Robinson 1981) has long overshadowed the effects of floristic composition on avian community structure. Many studies have correlated avian abundance and diversity with specific structural characteristics such as foliage height diversity and stem density (e.g., MacArthur & MacArthur 1961). Indeed, changes in forest structure from natural succession (Odum 1950; Holmes et al. 1986; Hunt 1998), logging (Titterington et al. 1979; Thompson & Capen 1988; Greenberg et al. 1995), and browsing by herbivores (Mountainspring et al. 1990; DeGraaf et al. 1991; Decalesta 1994) can lead to changes in populations of species. The long-term decline of the Least Flycatcher (*Empidonax minimus*) and Philadelphia Vireo (*Vireo philadelphicus*) at the Hubbard Brook forest in New Hampshire and declines in American Redstart (*Setophaga ruticilla*) populations in Vermont and New Hampshire were attributed to successional changes in habitat structure (Holmes et al. 1986; Hunt 1998).

Tree-species composition can affect avian community structure, however (Franzreb 1978; Holmes & Robinson 1981; Rice et al. 1984; Robinson & Holmes 1984; Peck 1989). Morphological and behavioral adaptations for procuring food and differences in prey abundance among tree species may lead to foraging preferences for certain tree species, which can, in turn, dictate the distribution and abundance of birds (Holmes & Robinson 1981; Whelan 1989; Parrish 1995*a*, 1995*b*). Holmes and Robinson (1981) found that rare, patchily distributed birds are more selective foragers than common birds, and that some relatively rare tree species are strongly preferred by birds. Identifying tree-species preferences of foraging birds is therefore potentially important for land managers involved in conservation, particularly habitat restoration, to provide high-quality habitat for the avian community.

We studied tree-species use by foraging birds to help guide floodplain forest restoration within the Lower Mississippi River Alluvial Valley (LMRAV). The LMRAV historically contained approximately 9.8 million ha of floodplain forest. By 1978, conversion to agricultural land, flood-control projects, and urbanization had reduced this rich and diverse ecosystem to approximately 2.2 million ha of fragmented forests (MacDonald et al. 1979). Although much effort has been directed toward restoring native terrestrial plant communities and ecosystems such as grasslands (e.g., Howe 1994; Wilson & Gerry 1995; Knapp & Rice 1996) and forests (e.g., Guariguata et al. 1995; Lamb 1998), less has been done to examine habitat restoration for avian communities (but see Bradley & Bradley 1993; Weller 1995; Kus 1998). Specifically, we addressed the following questions: (1) Do foraging birds that breed on our study sites in the LMRAV have foraging preferences for tree species? (2) If so, do certain tree species play a disproportionate role in the overall foraging ecology of the avian community? (3) What is the association between tree-species selectivity and local abundance of birds? (4) How can data on tree-species preference be integrated into floodplain restoration and management?

Methods

Study Areas

Located in southern Illinois within the floodplain of the Mississippi and Ohio Rivers, the Cache River Wetlands project is a large-scale effort to preserve and restore 24,000 ha (8000 ha of which are already forested) to bottomland hardwood forest. Over 70% of the Cache watershed (1909 km^2) has been converted to agriculture, with forested wetlands remaining as fragments throughout the floodplain (Cache River Area Assessment 1997). Currently, the agricultural landscape is being reforested by replanting and allowing fields to return to forest through natural succession.

Forest composition within the Cache River floodplain is strongly influenced by hydrology and topography. Different forest types are dispersed throughout the study sites, as described in the Cache River Area Assessment (1997). Permanently inundated swamps are dominated by bald cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*). Seasonally wet/dry swamps are dominated by bald cypress, tupelo, red maple (*Acer rubrum* var. *drummondii*), pumpkin ash (*Fraxinus profunda*), green ash (*F. pennsylvanica*), and sweetgum (*Liquidambar styraciflua*), with occasional kingnut hickory (*Carya laciniosa*), pin oak (*Quercus palustris*), Shumard's Oak (*Q. shumardii*), and overcup oak (*Q. lyrata*). Wet floodplain forests are dominated by red maple, sugarberry (*Celtis laevigata*), overcup oak, and swamp chestnut oak (*Q. michauxii*), with occasional pin oak, sweet gum, cherrybark oak (*Q. pagodaefolia*), American elm (*Ulmus americana*), bitternut hickory (*C. cordiformis*), kingnut hickory, and box elder (*Acer negundo*).

To obtain a representative sample of floodplain forests within the Cache watershed, we established seven study sites in seven forest fragments in the Cache River floodplain. The largest study plot was 2500 ha; the others ranged from 22 to 700 ha. The largest site was composed of primary forest with a limited history of selective logging of bald cypress. The other six sites were composed of mostly mature (>70 years old) second-growth forest. The three forest types—permanently inundated swamps, seasonally wet/dry swamps, and wet floodplain forests — were represented in each study site.

Surveys

Two researchers observed the foraging behavior of foliage insectivores from the last week in April to the last week in July 1997. One researcher repeated this effort over the same time period in 1998. Each of the six smaller plots was visited an average of once every 10 days. The larger plot was divided into thirds, and each third was visited on average 1 out of every 10 days. Researchers systematically searched each plot for foraging birds. Search effort was evenly distributed throughout each plot to minimize sampling bias. Consequently, the tree species and forest types specified above were sampled in proportion to availability within study sites. Most birds were initially located by sound and then quickly located visually. Individual trees were thoroughly searched to minimize potential bias. Although biases in the detectability of birds on different tree species may exist, we were unable to identify any.

Once a foraging bird was located, it was observed for up to 5 minutes. We described and categorized foraging behavior using standard terminology from Remsen and Robinson (1990). For each foraging bout, we recorded the bird species and the tree species on which the bird was foraging. Observations were recorded on a microcassette for later transcription. To ensure statistical independence of foraging observations, unless more than one individual was clearly identified, we recorded only one foraging observation of a given species and sex within 100 m of another of the same species and sex per day. Only the first tree species used by a bird in a foraging observation was used in the analyses of tree-species selectivity, because observations of additional trees used by bird species in the same foraging bout may not be independent from the initial tree used by bird species in the observation (Bell et al. 1990).

We used the point-quarter technique (Cottam & Curtis 1956) at 480 randomly assigned points to estimate tree-species composition of study sites. Researchers measured diameter at breast height (dbh), density, and frequency for all trees of >2.5 cm dbh. Importance values (IV) for each tree species were calculated: IV = relative frequency + relative density + relative coverage. Coverage was calculated from dbh because dbh is a good indicator of coverage (Whittaker et al. 1974). Importance values for each tree species were converted into percentages of total leaf cover (importance percentage) to characterize the proportion of leaf coverage for each tree species available for foraging birds (Holmes & Robinson 1981).

To determine whether birds foraged on each tree species in proportion to availability, we comparred observed frequencies with expected frequencies (Holmes & Robinson 1981) for each tree species. We calculated expected frequencies by multiplying IVs by the total number of observations for each bird species. We used a chi-square goodness-of-fit exact test to identify statistical differences between observed and expected frequencies. Monte Carlo estimates of exact p values were used to generate probability values using StatXact (Mehta & Patel 1995). Exact tests were derived because all bird species had an expected value of <5 for one or more tree species (Sokal & Rohlf 1995).

Tree species used in frequency analyses were limited to the 19 trees with an importance percentage of >1.3%, because all trees with an importance percentage of <1.3% were too rare to register more than one or two foraging observations for only a few species of birds (Fig. 1). All trees with an importance percentage of >1.3% were sufficiently abundant to be used as a foraging substrate by enough individuals for meaningful analysis.

To quantify tree-species foraging selectivity for each bird species, we used a preference index similar to that used by Holmes and Robinson (1981). A preference index (PI) value for a species of bird is the sum of the absolute values of the percent deviations of observed values from IVs for all tree species. This value represents the bird's foraging selectivity. The greater the PI value, the more selective the species of bird. Preference for a given species of tree by a bird is referred to as either the preference value or aversion value, the difference between a percent observed value from a percent IV.

To estimate the abundance of birds, each study site was surveyed once each breeding season from the last week in April to the third week in June in 1997 and 1998. We surveyed birds using 6-minute, 70-m, fixed-radius point counts (Robinson 1992) on all study sites. For a thorough and systematic coverage of each study site, 163 points were distributed along transects throughout the study sites. Points were separated by 150 m in the four cardinal directions. We pooled survey data from all sites for both years to derive indices of abundance. Abundance indices were the mean number of males per point estimated from numbers of singing males. Spearman rank correlations were derived to estimate the strength of association between bird abundance and preference index.

Results

We included in this study 13 arboreal foliage insectivores that bred on the study sites (Table 1). With one

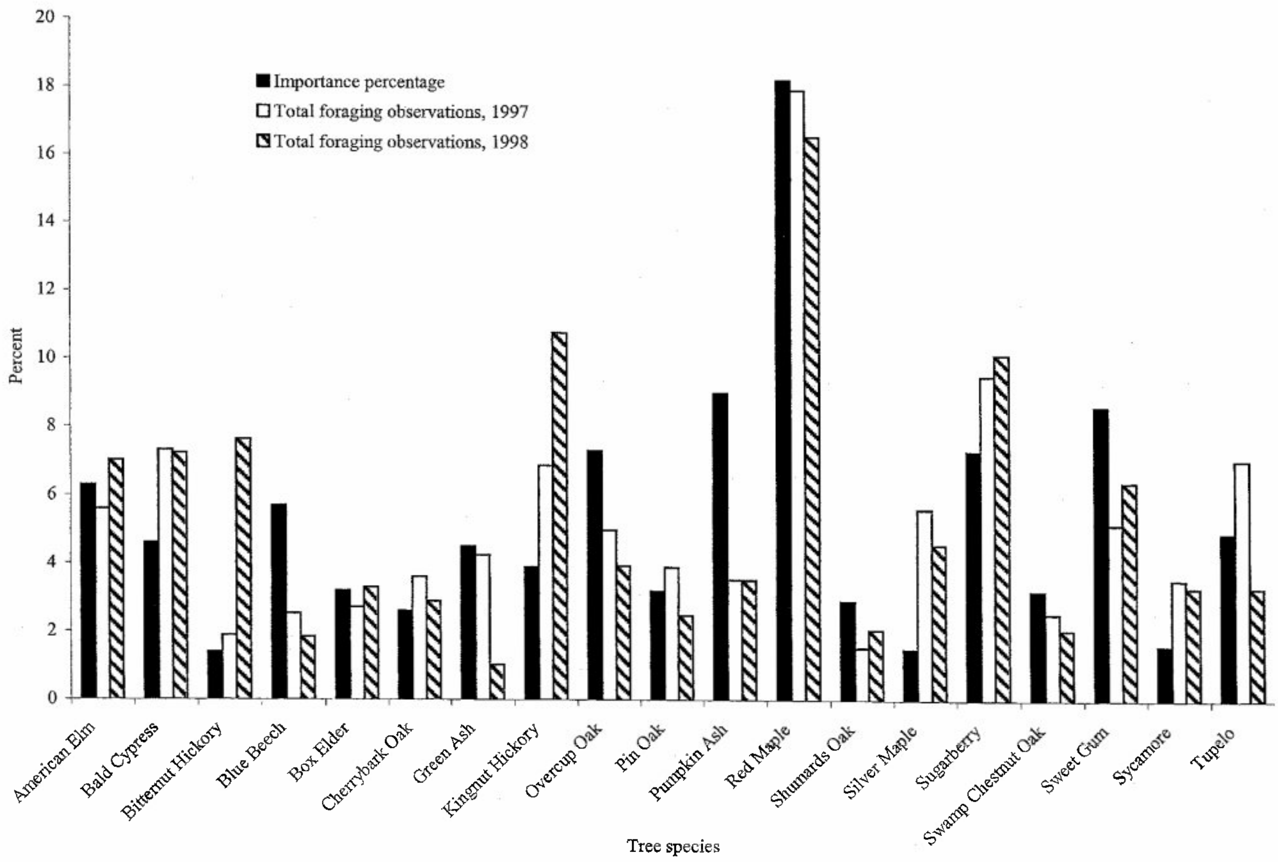

Figure 1. Use of tree species by all foraging birds combined in the Cache River study sites for 1997 and 1998.

exception, these species were observed in every study site. The Cerulean Warbler (*Dendroica cerulea*) was restricted to the largest study area. Consequently, Cerulean Warbler foraging data were compared with tree-species data from only the largest study site.

For all bird species combined, with few exceptions, birds used tree species in similar proportions in 1997 and 1998 (Fig. 1). Use of bitternut and kingnut hickory increased from 1997 to 1998: 2% to 7.6% for bitternut hickory and 7% to 11% for kingnut hickory. Conversely,

Table 1. Chi-square goodness-of-fit exact tests comparing observed and expected frequencies of use of tree species by birds (preference index [PI]) and abundance estimates for 13 species of birds in the Cache River floodplain.

Species (code)	n	*df*	χ^2	p[a]	*PI*[b]	*Abundance*[c]
Acadian Flycatcher (ACFL)	153	18	120.4	< 0.0001	62.8	1.79
Blue-gray Gnatcatcher (BGGN)	281	18	128.2	< 0.0001	58.2	1.59
Carolina Chickadee (CACH)	209	18	136.6	< 0.0001	59.7	1.27
Cerulean Warbler (CERW)	77	18	317.4	< 0.0001	107.6	0.06
Northern Parula (NOPA)	187	18	286.5	< 0.0001	78.1	0.69
Prothonotary Warbler (PROW)	38	18	93.0	< 0.0001	68.7	1.07
Red-eyed Vireo (REVI)	127	18	69.6	< 0.0001	50.5	0.64
Scarlet Tanager (SCTA)	28	18	72.3	0.0002	87.9	0.03
Summer Tanager (SUTA)	28	18	43.9	0.0031	83.5	0.08
Eastern Tufted Titmouse (ETTI)	187	18	75.1	< 0.0001	51.2	1.14
Yellow-billed Cuckoo (YBCU)	46	18	95.5	< 0.0001	61.0	0.49
Yellow-throated Vireo (YTVI)	59	18	25.2	0.1236	42.9	0.26
Yellow-throated Warbler (YTWA)	71	18	441.9	< 0.0001	130.9	0.10

[a] *Monte Carlo estimate.*
[b] *Preference index represents foraging selectivity; higher PIs indicate greater selectivity.*
[c] *Mean densities (numbers of males/point) from summers of 1997 and 1998*

use of green ash and tupelo decreased from 1997 to 1998: 4% to 1% for green ash and 7% to 3% for tupelo. These differences may be attributed to a varying abundance of arthropods and other prey on specific tree species. Bird use of all other tree species deviated by less than ±1.5% between years. Therefore, foraging observations for both years were pooled by bird species to increase sample sizes. For four bird species with a large enough sample size for comparison—Carolina Chickadee (*Parus carolinensis*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Northern Parula (*Parula americana*), and Eastern Tufted Titmouse (*Baeolophus bicolor*)—yearly variation in use of tree species generally mirrored the pooled data for all bird species.

Preference indices ranged from 42.9 for the Yellow-throated Vireo (*Vireo flavifrons*) to 130.9 for the Yellow-throated Warbler (*Dendroica dominica*). With the exception of the Yellow-throated Vireo ($\chi^2 = 25.2$, $p = 0.1236$) all species were selective in their choice of foraging substrate ($p < 0.001$). The two most selective foragers were the Yellow-throated Warbler and Cerulean Warbler, whereas the Yellow-throated Vireo, Red-eyed Vireo (*Vireo olivacea*), and Eastern Tufted Titmouse were comparatively generalized foragers (Table 1).

Preference for tree species varied greatly among bird species (Table 2). Selective foragers were characterized by strong preference for one tree species (Figs. 2 & 3). Yellow-throated Warblers exhibited a strong preference for bald cypress, followed by tupelo, and they generally avoided other tree species, especially red maple. Cerulean Warblers exhibited a strong preference for kingnut hickory and avoided red maple. Other birds also showed preferences: Northern Parulas preferred kingnut hickory, Scarlet Tanagers (*Piranga olivacea*) preferred cherrybark oak and kingnut hickory, Yellow-billed Cuckoos (*Coccyzus americanus*) preferred silver maple (*Acer saccharinum*), Red-eyed Vireos and Carolina Chickadees preferred sugarberry, and Acadian Flycatchers (*Empidonax virescens*) and Prothonotary Warblers (*Protonotaria citrea*) preferred red maple.

Of the 19 tree species we considered, three were strongly preferred by foraging birds (subjectively defined as having five bird species with preference values of >5, none with aversion values below -5): kingnut hickory, bitternut hickory, and silver maple. Three tree species were strongly avoided by foraging birds (five birds with aversion values below -5, none with preference values of >5): blue beech (*Carpinus caroliniana*), pumpkin ash, and sweet gum.

Relatively rare tree species emerged as important foraging substrates. Of the 19 trees ranked by importance percentage (Fig. 1), three strongly preferred trees—kingnut hickory, silver maple, and bitternut hickory—ranked eleventh, eighteenth, and nineteenth, respectively. Conversely, four generally avoided trees—pumpkin ash, sweet gum, overcup oak, and blue beech—were common, ranking second, third, fourth, and seventh in importance percentage, respectively.

Estimated bird abundances (Table 1) in the study were negatively correlated with PI, although this was marginally significant ($r = -0.533$, $p = 0.061$; Fig. 4). Less abundant birds tended to be more selective foragers. One exception was Yellow-throated Vireos, an uncom-

Table 2. Tree-species preferences of foraging birds.[a]

	Bird species[b]												
Tree species	*ACFL*	*BGGN*	*CACH*	*CERW*	*NOPA*	*PROW*	*REVI*	*SCTA*	*SUTA*	*ETTI*	*YBCU*	*YTVI*	*YTWA*
American Elm	6.73	-2.07	-0.60	-0.08	-3.13	0.18	-0.04	-6.34	0.80	3.82	-4.17	2.14	-6.34
Bald Cypress	-3.27	7.88	4.99	-2.50	-4.04	-2.41	-1.43	-4.58	2.56	-1.91	-2.41	3.90	48.94
Bitternut Hickory	-0.14	1.04	1.90	7.65	4.97	-0.72	-0.66	5.69	9.27	0.69	5.07	1.94	-0.04
Blue Beech	1.46	-5.37	-4.77	-8.82	-4.12	2.24	-4.94	-2.16	-5.73	-3.59	-3.55	-2.34	-5.73
Box Elder	3.96	-1.45	-2.28	-5.54	-1.10	4.01	1.49	-3.23	0.34	-1.63	1.11	0.16	-3.23
Cherrybark Oak	-0.60	0.99	-2.09	-1.47	5.99	-2.57	-0.99	18.86	1.01	1.71	3.96	2.52	0.25
Green Ash	-2.54	-2.01	-2.11	3.64	0.31	-1.60	0.23	-0.93	-0.93	-1.82	2.02	-1.11	-3.09
Kingnut Hickory	0.70	1.11	4.26	32.81	10.03	-3.15	0.85	10.41	6.84	5.22	0.48	-0.48	-1.06
Overcup Oak	-5.32	3.75	-2.98	3.13	-6.21	-3.66	-5.71	-7.28	-3.71	-0.33	-2.94	-3.89	-4.47
Pin Oak	-2.55	1.42	-1.77	-0.45	3.21	-2.48	4.67	0.37	-3.20	-0.53	-1.03	6.96	-1.80
Pumpkin Ash	-7.00	-6.82	-2.26	-5.28	-4.68	-6.78	-5.81	-5.39	-8.96	-6.82	1.91	-3.87	-3.32
Red Maple	9.87	-6.49	0.90	-17.61	-3.26	11.47	-0.91	-0.38	-3.95	3.15	-3.02	-2.98	-15.42
Shumards Oak	-1.62	-1.50	-1.49	-4.95	-1.32	-2.92	0.23	0.65	-2.92	-1.32	-2.92	0.47	-2.92
Silver Maple	7.63	1.33	4.23	4.05	6.51	5.01	0.85	5.63	5.63	1.69	15.88	-1.52	-0.11
Sugarberry	-0.75	-2.66	9.94	-1.28	-5.68	9.38	14.76	-7.28	-3.71	9.29	-2.94	-0.50	-5.87
Swamp Chestnut Oak	0.70	-0.73	-1.78	-5.81	-2.15	1.13	-1.64	0.35	7.49	-0.55	-3.22	0.17	-3.22
Sweet Gum	-6.65	4.20	-7.18	1.48	-2.19	-7.16	-3.10	-1.47	-8.61	-2.19	0.08	-5.22	-8.61
Sycamore	0.36	1.60	3.66	0.48	8.02	-0.88	0.76	1.97	1.97	-1.07	-1.60	3.48	-0.19
Tupelo	-0.98	5.78	-0.59	0.55	-1.15	0.90	1.40	-4.90	5.82	-3.83	-2.72	0.19	16.23

[a] *Values are preference and aversion values.*
[b] *See Table 1 for species codes.*

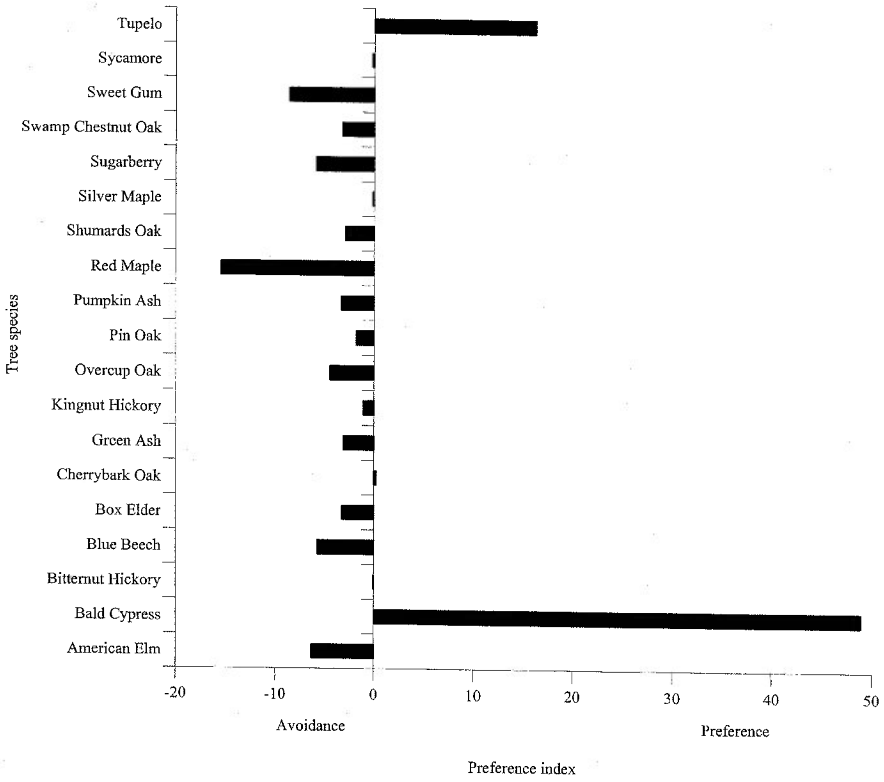

Figure 2. Tree-species preference and avoidance for the Yellow-throated Warbler. Positive values indicate usage greater than expected; negative values indicate usage less than expected.

mon bird with the lowest PI among the 13 birds in this study. The four rarest birds, the Scarlet Tanager, Cerulean Warbler, Summer Tanager (*Piranga rubra*), and Yellow-throated Warbler, had the four highest PI values. The Yellow-throated Warbler was also the most patchily distributed bird, being limited to patches of floodplain with bald cypress.

Discussion

In the Cache River floodplain, birds had strong preferences for a diverse set of tree species. Except for Yellow-throated Vireos, all foraging bird species were selective of tree species. Certain tree species were clearly preferred by the arboreal foliage insectivorous guild, whereas others were generally avoided or used in proportion to availability. Tree species composition may therefore be an important component in forest restoration projects that seek to restore both plant and wildlife communities.

Two of the tree species preferred by the avian community are heavy-seeded. Kingnut and bitternut hickories produce large seeds with relatively short-distance dispersal qualities. In a comparative study of tree regeneration in 4- to 8-year-old replanted bottomland forests in Mississippi, Allen (1997) found that invading, heavy-seeded *Carya* and *Quercus* species are notably low in abundance in stands planted with common *Quercus* species. Shear et al. (1996) also found that in bottomland stands 50 years after planting, heavy-seeded species in the genera *Carya* and *Quercus* are poorly represented. Natural regeneration alone may not be a reliable means for replacement of heavy-seeded species (Shear et al. 1996) or even for some wind-dispersed species 50 years after planting (Allen 1997).

Rather than relying on natural processes such as succession to restore a diverse forest represented by tree species important to the bird community, the restoration process should include active planting of heavy-seeded species and other species important to birds such as silver maple. Until tree species important as foraging substrates for selective birds become established in the forest canopy, forests restored by planting of only common oak species may not be adequate for restoration of a diverse avian community. It is unknown how long natural processes will take to restore a diverse floodplain forest, particularly in a fragmented landscape where seed dispersal may be limited, but evidence indicates that it may take much longer than 50 years (Shear et al. 1996; Allen 1997).

It remains to be tested whether forests of similar structure, but lacking preferred tree species, support similar avian communities. Our results indicate, however, that restored forests lacking preferred trees may be suboptimal for selective foragers and may limit constituent bird

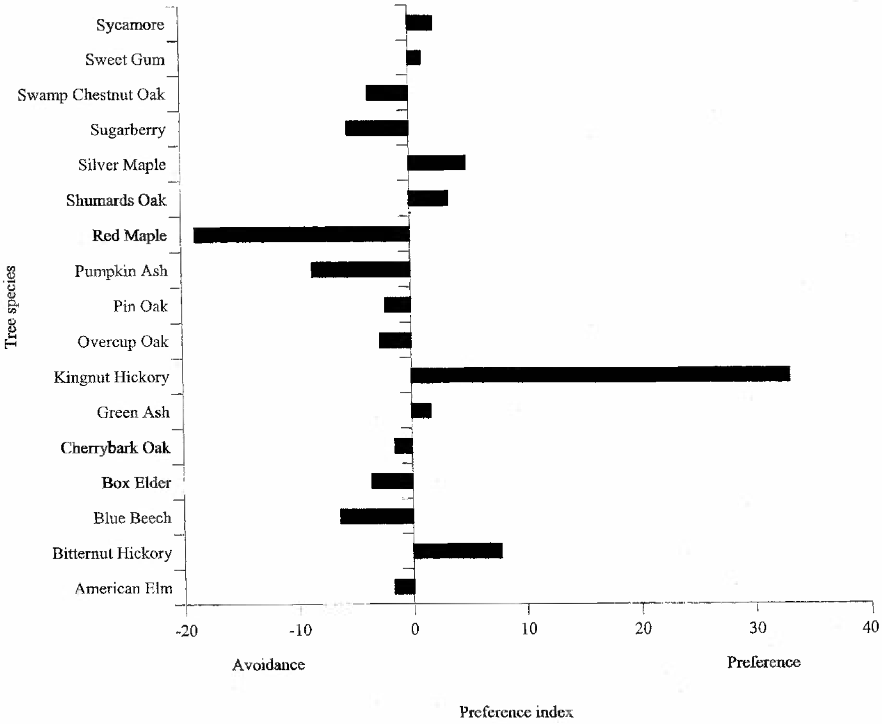

Figure 3. Tree-species preference and avoidance for the Cerulean Warbler. Positive values indicate usage greater than expected; negative values indicate usage less than expected.

populations to only common, nonselectively foraging birds. This result is similar to that of Holmes and Robinson (1981), who found a significant negative correlation between an index of tree species preference and mean bird densities ($r = -0.789, p < 0.01$).

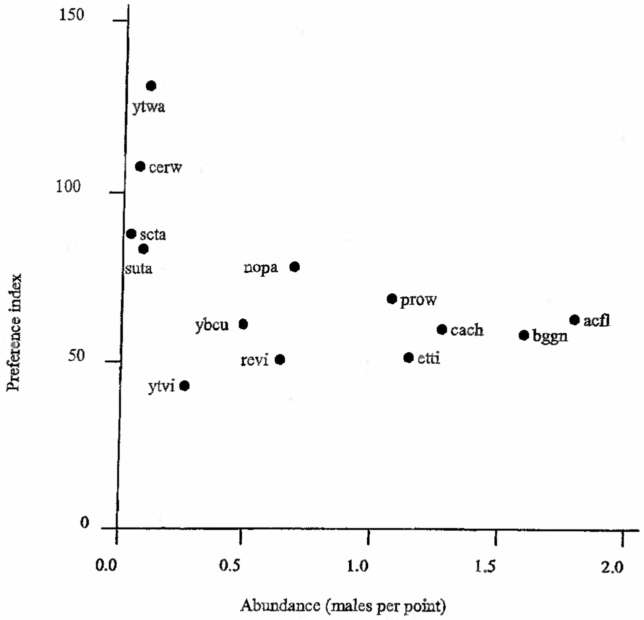

Figure 4. Relationship between avian abundance (number of males per point) and preference index ($r = -0.544$, $p = 0.055$). See Table 1 for species codes.

Yellow-throated Warblers, for example, which are virtual specialists on bald cypress in the Cache River floodplain, would likely decline drastically if bald cypress were removed. Presently, this warbler is relatively uncommon in the Cache, probably because of past selective logging of bald cypress and the rarity of sycamore (*Platanus occidentalis*), a preferred tree in other parts of its range and within Illinois (Dunn & Garrett 1997; A.P.G., personal observation). Furthermore, the disproportionate use of uncommon tree species such as silver maple and bitternut hickory, the high diversity of preferred trees, and specific preferences for rare tree species by certain species of birds—such as the Northern Parula for sycamore—suggest that high tree-species diversity may help maintain bird species diversity. A more rigorous evaluation of the relationship between forest tree-species composition and avian abundance is needed to determine the effects of tree-species composition on avian community structure.

Many other habitat characteristics undoubtedly play a role in determining local avian abundance. Forest structure and successional stage, for example, may limit the abundance of Yellow-billed Cuckoos. Relatively uncommon, Yellow-billed Cuckoos are associated with dense, early-successional forests and natural edges created by streams and rivers (Hughes 1999). Early successional forests were absent from our study sites, and natural edges made up a very small proportion of them.

Preference for certain features of habitat structure can confound tree-species preference. The habitat associations of the Yellow-billed Cuckoo may explain its preference for silver maple, often located along disturbed edges such as riverbanks. Preference for red maple by the Acadian Flycatcher and Prothonotary Warbler is likely a consequence of preference for the flooded habitat of seasonal wet/dry swamps, in which red maple dominates the lower strata. This relatively open microhabitat is suitable for the Acadian's aerial foraging maneuvers of plucking prey off leaves. Prothonotary Warblers, in contrast, prefer to nest in cavities over standing water (Petit 1999) in these seasonal wet/dry swamps

Our results also have implications for areas of the LMRAV outside of active restoration sites. In addition to selective logging, changes in floodplain hydrology in the LMRAV may lead to changes in floodplain tree-species composition (Pezeshki & Anderson 1997) and avian habitat quality. Channelization, dredging, and damming has changed floodplain hydrology, altering the natural flood regime and water table (Cache River Area Assessment 1997). Channelization in the Cache has effectively deepened channels and lowered water tables, leading to increased drainage of floodplain forests and bald cypress–tupelo swamps (Shear et al. 1996; Cache River Area Assessment 1997). The subtle desiccation of floodplains could lead to a gradual replacement of hydrophilic tree species such as bald cypress and tupelo by mesic and upland species. Furthermore, changes in floodplain hydrology such as excessive sedimentation can alter flood frequency and intensity (Cache River Area Assessment 1997), resulting in a more severe disturbance regime. Consequently, early successional tree species could gain importance in the floodplain to the detriment of late-successional tree species. The specific effects of hydrological alterations on floodplain forest tree species are unclear. Declines of tree species important to birds could lead to population changes in the avian community, however, through changes in either tree-species composition and/or habitat structure.

As a vital component of ecosystems, birds are important seed dispersers (Willson 1986), pollinators (Brown & Hopkins 1996), and predators of insects (Holmes 1990; Marquis & Whelan 1994); they should not be overlooked in habitat restoration projects. Active planting of preferred heavy-seeded and rare tree species might be the most effective means to restore tree species important to forest bird communities. We believe that it is critical to identify the tree-species preferences of foraging birds to help guide the restoration process. Further research needs to be done to elucidate the complex interactions of alterations in floodplain hydrology and changes in forest tree-species composition, and the effects of these interactions on the avian community. Our conclusions may be applicable to other systems. Plant-animal relationships should be taken into consideration when other ecosystems are restored, particularly tropical rainforests, where biological diversity is high and plant-animal interactions are potentially more complex.

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Literature Cited

Allen, J. A. 1997. Reforestation of bottomland hardwoods and the issue of woody species diversity. Restoration Ecology **5:**125–134.

Bell, G. W., S. J. Hejl, and J. Verner. 1990. Proportional use of substrates by foraging birds: model considerations on first sightings and subsequent observations. Pages 161–165 in Morrison, M. L., C. J. Ralph, J. Verner, and R. J. Joseph Jr., editors. Avian foraging: theory, methodology, and applications. Studies in avian biology 13. Allen Press, Lawrence, Kansas.

Bradley, R. A., and D. W. Bradley. 1993. Wintering shorebirds increase after kelp (*Macrocystis*) recovery. Condor **95:**372–376.

Brown, E. D., and M. J. G. Hopkins. 1996. How New Guinea rainforest flower resources vary in time and space: implications for nectarivorous birds. Australian Journal of Ecology **21:**363–378.

Cache River Area Assessment. 1997. Hydrology, air quality, and climate and living resources. Volume 1. Illinois Department of Natural Resources, Springfield.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology **37:**451–460.

Decalesta, D. S. 1994. Effect of White-tailed Deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management **58:**711–718.

DeGraaf, R. M., W. M. Healy, and R. T. Brooks. 1991. Effects of thinning and deer browsing on breeding birds in New England (USA) oak woodlands. Forest Ecology and Management **41:**179–192.

Dunn, J. L., and K. L. Garrett. 1997. A field guide to the warblers of North America. Houghton Mifflin, New York.

Franzreb, K. E. 1978. Tree species used by birds in logged and unlogged mixed-coniferous forests. Wilson Bulletin **90:**221–238.

Greenberg, C. H., L. D. Harris, and D. G. Neary. 1995. A comparison of bird communities in burned and salvage-logged, clearcut, and forested Florida sand pine scrub. Wilson Bulletin **107:**40–54.

Guariguata, M. R., R. Rheingans, and F. Montagnini. 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. Restoration Ecology **3:**252–260.

Holl, K. D. 1999. Tropical forest recovery and restoration. Trends in Ecology and Evolution **14:**378–379.

Holmes, R. T. 1990. Ecological and evolutionary impacts of bird predation on forest insects: an overview. Pages 6–13 in M. L. Morrison, C. J. Ralph, J. Verner, and R. J. Joseph Jr., editors. Avian foraging: theory, methodology, and applications. Studies in avian biology 13. Allen Press, Lawrence, Kansas.

Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia **48:**31–35.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long term trends at Hubbard Brook. Ecological Monographs **56:**201–220.

Howe, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology **8:**691–704.

Hughes, J. M. 1999. Yellow-billed Cuckoo (*Coccyzus americanus*). Page 408 in A. Poole and F. Gill, editors. The Birds of North America. The Birds of North America, Philadelphia.

Hunt, P. D. 1998. Evidence from a landscape population model of the importance of early successional habitat to the American Redstart. Conservation Biology **12:**1377–1389.

Knapp, E. E., and K. J. Rice. 1996. Genetic structure and gene flow in *Elymus glaucus* (blue wildrye): implications for native grassland restoration. Restoration Ecology **4:**1–10.

Koebel, J. W., Jr. 1995. An historical perspective in the Kissimmee River Restoration Project. Restoration Ecology **3:**149–159.

Kus, B. E. 1998. Use of restored riparian habitat by the endangered least Bell's Vireo (*Vireo bellii pusillus*). Restoration Ecology **6:**75–82.

Lamb, D. A. 1998. Large-scale ecological restoration of degraded tropical forest lands: the potential role of timber plantations. Restoration Ecology **6:**217–279.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology **42:**594–598.

MacDonald, P. O., W. E. Frayer, and J. K. Clauser. 1979. Documentation, chronology, and future projections of bottomland hardwood habitat loss in the Lower Mississippi Alluvial Plain. Volumes 1 and 2. U. S. Fish and Wildlife Service, Vicksburg, Mississippi.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology **75:**2007–2014.

Mehta, C., and N. Patel. 1995. StatXact 3 for Windows. Cytel Software Corporation, Cambridge, Massachusetts.

Mountainspring, S., T. L. C. Casey, C. B. Kepler, and J. M. Scott. 1990. Ecology, behavior, and conservation of the poo-uli (*Melamprosops phaeosoma*). Wilson Bulletin **102:**109–122.

Odum, E. P. 1950. Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology **31:**587–605.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology **5:**291–300.

Parrish, J. D. 1995*a*. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology **76:**1813–1820.

Parrish, J. D. 1995*b*. Experimental evidence for intrinsic microhabitat preferences in the Black-throated Green Warbler. Condor **97:** 935–943.

Peck, K. M. 1989. Tree species preferences shown by foraging birds in forest plantations in northern England. Biological Conservation **48:** 41–58.

Petit, L. J. 1999. Prothonotary Warbler (*Protonotaria citrea*). Number 408 in A. Poole and F. Gill, editors. The Birds of North America. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Pezeshki, S. R., and P. H. Anderson. 1997. Responses of three bottomland species with different flood tolerance capabilities to various flood regimes. Wetlands Ecology and Management **4:**245–256.

Remsen, J. V., and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Pages 144–160 in M. L. Morrison, C. J. Ralph, J. Verner, and R. J. Joseph Jr., editors. Avian foraging: theory, methodolgy, and applications. Studies in avian biology 13. Allen Press, Lawrence, Kansas.

Rice, J., B. W. Anderson, and R. D. Ohmart. 1984. Comparisons of the importance of different habitat attributes to avian community organization. Journal of Wildlife Management **48:**221–238.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences United States of American **86:**7658–7662.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408–418 in J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk **101:** 672–684.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267:**1987–1990.

Shear, T. H., J. L. Thomas, and S. Fraver. 1996. Comparison of restored and mature bottomland hardwood forests of Southwestern Kentucky. Restoration Ecology **4:**111–123.

Sokal, R. R., and J. F. Rohlf. 1995. Biometry. W. H. Freeman, New York.

Thompson, F. R., III, and D. E. Capen. 1988. Avian assemblages in seral stages of a Vermont (U.S.A.) forest. Journal of Wildlife Management **52:**771–777.

Titterington, R. W., H. S. Crawford, and B. N. Burgason. 1979. Songbird responses to commercial clear-cutting in Maine, USA spruce-fir forests. Journal of Wildlife Management **43:**602–609.

Weller, M. W. 1995. Use of two waterbird guilds as evaluation tools for the Kissimmee River restoration. Restoration Ecology **3:**211–224.

Whelan, C. J. 1989. Avian foliage structure preferences for foraging and the effect of prey biomass. Animal Behaviour **38:**839–846.

Whittaker, R.H., F. H. Bormann, G. E. Likens, and T. G. Siccama. 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecological Monographs **44:**233–254.

Willson, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. Pages 223–279 in R. F. Johnston, editor. Current ornithology. Volume 3. Plenum Press, New York.

Wilson, S. D., and A. K. Gerry. 1995. Strategies for mixed-grass prairie restoration: herbicide, tilling, and nitrogen manipulation. Restoration Ecology **3:**290–298.