# FORAGING SUCCESS AND TREE SPECIES USE IN THE LEAST FLYCATCHER

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ABSTRACT.—I examined the effect of tree species morphology on foraging behavior in a hover-gleaning bird species, the Least Flycatcher (*Empidonax minimus*). Birds in four breeding territories in northern Wisconsin displayed nonsignificant differences in an index of foraging success (S) among four tree species of divergent morphology. However, significant variation in S occurred among the three tree species common to all four territories; in addition, multiple comparisons indicated that S values in *Betula papyrifera* were significantly greater than those in *Acer* spp. or *Quercus* spp. Despite its statistical significance, variation in S was not large, and flycatchers used available tree species in general accordance with their abundances. No significant correlation was found between S and tree species use. These results are not immediately consistent with an emerging perspective of avian community structure that predicts that hover-gleaners, unlike gleaners, should be affected little by foliage morphology. Foraging efficiency and prey depletion in initially favored tree species are proximate factors possibly linked to breadth of tree species use. *Received 15 July 1983, accepted 27 February 1985.*

SMALL-BODIED, foliage-gleaning avian insectivores use tree species with foliage morphologies they can exploit efficiently (Holmes and Robinson 1981). In contrast, small-bodied, foliage-hovering avian insectivores show only slight tree species preferences and exploit a comparatively wider variety of foliage morphology (Holmes and Robinson 1981). Thus, given tree species preferences by bird species, variation in tree species composition (TSC) can cause variation in avian community structure among forests (Holmes et al. 1979, Holmes and Robinson 1981, Robinson and Holmes 1982). Tree species preference is a well-documented phenomenon among birds (Hartley 1953; Morse 1968, 1978; Balda 1969; Jackson 1970; Kilham 1970; Willson 1970; Austin and Smith 1972; James 1976, 1979; Franzreb 1978, 1983; Eckhardt 1979; Conner 1980; Holmes and Robinson 1981; Rice et al. 1983).

Holmes and Robinson (1981) argued that foliage morphology may cause such preferences. Gleaning species possibly are restricted to foraging in those tree species with relatively short petioles and small leaf surface area (e.g. yellow birch, *Betula lutea*) because they cannot reach prey in tree species with relatively longer petioles and greater leaf area. In addition, gleaners may select tree species with relatively more leaves/supporting twig (e.g. *B. lutea*) compared to other species (e.g. sugar maple, *Acer saccharum*). In contrast, hover-gleaning species forage in and around foliage regardless of tree species due to their ability to reach prey while in flight.

I studied the influence of foliage morphology on a measure of foraging success in a small-bodied (ca. 10 g) hover-gleaner, the Least Flycatcher (*Empidonax minimus*). In particular, I tested the hypothesis that a hovering species should forage with equal success in tree species of divergent morphology. At the outset I assumed that any tree species, regardless of its foliage structure, should constrain foraging success to a certain degree. The question thus became whether the morphology of a given tree species affects success more than any other(s). Results are interpreted with respect to the proposed relationships among foliage morphology, tree species use, and avian community organization.

## METHODS AND MATERIALS

*Study area.*—This study was conducted in a forested portion of the Chequamegon National Forest on a site 6.4 km south of Pigeon Lake Field Station (University of Wisconsin) in southwest Bayfield County, Wisconsin. A 20-ha study area of second-growth deciduous-coniferous forest was selected that met the

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criteria of subjectively constant tree density and a dense population of breeding Least Flycatchers (171 birds/40 ha, Rogers 1977). Tree species common in the study area were sugar maple, red oak (*Quercus rubra*), pin oak (*Q. ellipsoidalis*), and paper birch (*Betula papyrifera*). White pine (*Pinus strobus*), quaking aspen (*Populus tremuloides*), and red maple (*A. rubrum*) were less common. Dominant understory species were hazelnut (*Corylus americana*) and bracken (*Pteridium aquilinum*). Bird species common in the area (number of birds/40 ha, from Rogers 1977) were the Red-eyed Vireo (*Vireo olivaceus,* 85) and Ovenbird (*Seiurus aurocapillus,* 49); less common species were the Veery (*Catharus fuscescens,* 19), the Black-throated Green Warbler (*Dendroica virens,* 12), and the Eastern Wood-Pewee (*Contopus virens,* 7).

*Selection of study territories and measurement of vegetation.*—Between 21 May and 24 June 1979 I located, captured, and color-banded breeding pairs of Least Flycatchers and marked 15 breeding territories on the basis of male song perch location. I then selected 4 of the 15 territories for detailed study of foraging behavior. Specific boundaries of that portion of the territory defended by the territorial male actually used for foraging by both the male and female were determined during the nestling phase of the breeding cycle (see below). Because the goal of the study was to quantify foraging behavior in morphologically divergent tree species, I chose the 4 study territories to meet the following experimental design. *Corylus americana, Acer* spp. (*A. rubrum, A. saccharum*), *Quercus* spp. (*Q. alba, Q. ellipsoidalis*), and *B. papyrifera* were common to 4, *P. tremuloides* to 3, and *Pinus* spp. (*P. strobus, P. resinosa*) to 2 territories. Six tree species therefore represented unequally replicated treatments, with foraging behavior (see below) as the dependent variable.

I measured TSC and foliage height diversity (FHD = $-\Sigma\, p_i \log p_i$, where $p_i$ categories are 1-m height intervals) in each of the 4 utilized territories which, in all cases, exceeded in area that area defended by the territorial male. Using colored plastic flagging I marked 4 evenly spaced transects in each territory and randomly placed 50 sample points/territory on the transect lines. A random-number table determined distance between sample points. At each sample point I focused a mounted 35-mm camera (Mamiya-Sekor 1000 DTL) equipped with a 250-mm telephoto lens on all foliage occurring in the 5-m upper canopy range. For each leaf in the central spot of the viewfinder, I recorded tree species and height to the nearest meter. Single and groups of leaves seen in the spot were recorded as a single foliage detection (i.e. "leaf"). A 5-m vertical pole similarly measured foliage in the 0- to 5-m height range. Vegetation measurements were made after foliage development was complete.

*Measurement of foraging behavior in different species.*—To avoid a possible seasonal effect on foraging behavior (shown by Sherry 1979 in the Least Flycatcher), I gathered foraging data only during the 10-day nestling phase of the breeding cycle. Daily nest checks verified onset of the nestling phase, which occurred in the same 2-day span in all 4 territories. Each of the 10 sampling days (29 June to 8 July) consisted of 8 45-min observation periods between 0700 and 1600, one in the morning (before 1200) and one in the afternoon in each territory. A random-number table determined order of sampling territories in each half-day period. I followed flycatchers located on regular traverses of utilized territories as long as they remained in sight, usually less than 20 s. Foraging data were collected only when flycatchers were foraging and not also engaged in singing, preening, etc. For each perch chosen I recorded the tree species of perch, whether it was used for foraging, and, if appropriate, the foraging tactic used. These were described by Sherry (1979) as either flycatch (FL), hover at leaf (HL), branch (HB), or trunk (HT). Thus, two types of perches were selected by foraging flycatchers: those foraged from (FL) or at (HL; F perches) and those not foraged from (no tactic; NF perches).

*Determination of foraging success in different tree species.*—A simple index of foraging success was calculated for each utilized tree species by determining the proportion of total chosen perches (sum of F and NF sample populations = F + NF) from or at which a bird foraged. Thus, $S = F/(F + NF)$ for each tree species in each territory. HB and HT tactics were not included in calculations of S because they are not foliage-related. Although S is not a direct measure of foraging success, it probably is correlated with actual foraging success. Because of the clear distinction between F and NF perches, flycatchers showing low S values did not attempt to catch as many prey per perch as did flycatchers showing high S values. Unless flycatchers persisted in unsuccessful foraging attempts differentially in some species of trees, S may be used as an indicator of foraging success.

*Statistical analyses.*—In all statistical analyses involving tree species data, *Acer* spp. is a combination of *A. saccharum* and *A. rubrum, Quercus* spp. is a combination of *Q. rubra* and *Q. ellipsoidalis,* and *Pinus* spp. is a combination of *P. strobus* and *P. resinosa.* These data combinations were necessary due to the difficulty of identifying foliage in these three genera to species while observing rapid foraging movements.

For each territory only 1 randomly chosen foliage detection (leaf) from each of the 50 sample points was used in subsequent statistical analyses involving tree species data. This procedure ensured that vegetation samples were independent, a criterion not satisfied if more than one detection/sample point (often including several detections from the same tree) were included in the data set. The relative frequency of a tree species is defined as its percentage of the 50 foliage detections of all tree species in a particular territory. Hypothetical (expected) frequencies of tree

TABLE 1. Tree species composition and aspects of vegetation structure in the four study territories.

| | Territory | | | |
|---|---|---|---|---|
| Tree species | 4 | 6 | 8 | 11 |
| *Acer* spp. | 0.33 | 0.50 | 0.56 | 0.20 |
| *Quercus* spp. | 0.50 | 0.00 | 0.07 | 0.32 |
| *Pinus* spp. | 0.00 | 0.39 | 0.16 | 0.00 |
| *Betula papyrifera* | 0.17 | 0.11 | 0.22 | 0.48 |
| Total detections[a] | 168 | 190 | 245 | 251 |
| No. detections/sample point[a,b] ($\bar{x} \pm 1$ SE) | 1.69 ± 0.08 | 1.80 ± 0.11 | 1.99 ± 0.14 | 1.00 ± 0.14 |
| FHD (H) ($\bar{x} \pm 1$ SE) | 0.98 ± 0.017 | 1.06 ± 0.018 | 1.05 ± 0.026 | 1.02 ± 0.039 |
| Canopy height (m)[c] ($\bar{x} \pm 1$ SE) | 17.4 ± 0.37 | 16.2 ± 0.41 | 16.8 ± 0.36 | 17.9 ± 0.38 |

[a] Data set from which subsample ($n = 50$) was taken.

[b] Square-root transformed.

[c] All foliage detections $\geq 12$ m.

species use were determined for each tree species in every territory by multiplying relative frequencies of tree species by the total number of selected perches (i.e. F and NF perches added over all tree species within a particular territory). For each territory, I tested the hypothesis that foliage was used randomly using a $2 \times n$ contingency table and $G$-test (observed and expected tree species use as 2 rows vs. number of tree species in the territory as $n$ columns). Variation among tree species in the measure of foraging success, S, was analyzed using Kruskal-Wallis nonparametric analysis of variance and nonparametric multiple comparisons (after Zar 1974). *Corylus americana* and *P. tremuloides* were omitted from Kruskal-Wallis tests and thus also $G$-tests because small F and NF sample sizes do not yield reliable S values in individual territories. Variation among the study territories in TSC ($\chi^2$ $4 \times 4$ contingency table, 4 territories vs. 4 tree species), density of vegetation (one-way analysis of variance of the square root of the number of foliage detections at each of the 50 sample points), and FHD were analyzed. The latter analysis was carried out with a one-way analysis of variance of 10 FHD values per territory. Each FHD value was based on 5 sample points randomly selected from the original 50 sample points per territory.

I used Spearman rank correlations ($r_s$) to relate (1) relative tree species use by flycatchers and relative frequencies of tree species and (2) relative tree species use by flycatchers and S in individual tree species. In these correlations, relative frequencies of tree species are based on the complete set of foliage detections, not on a random subsample of 50 detections as described above. This was done because subsampling excluded *C. americana* and *P. tremuloides*; these two species were necessary to obtain a minimum number of tree species available for correlation. Also, relative to the subsampling method, this procedure was felt to better estimate the abundance of *C. americana*, a relatively rare plant species. In each territory, use of all foliage detections and the subsample method yielded exactly the same rank abundances of tree species.

## RESULTS

*Description of study territories.*—The four study territories differed in tree species composition ($\chi^2 = 92.41$, $P < 0.001$) but not in foliage density ($F = 1.37$, $P > 0.50$) or FHD ($F = 1.90$, $P > 0.20$). Mean canopy height varied little among the study territories (Table 1). For purposes of discussing variation in foraging success among tree species, territories are considered equivalent with respect to each vegetation attribute except TSC.

*General foraging behavior.*—Figure 1 shows the relative frequencies of the four foraging tactics for the 10-day observation period. Flycatching was the most common tactic, followed by hovering at foliage (HL). Least Flycatchers did not hover at foliage as much as reported in other studies (e.g. Sherry 1979), although they nearly always foraged in close association with foliage. Midair flycatches were rare and characterized by short sallies (see also Via 1979).

*Variation in foraging success among morphologically divergent tree species.*—Table 2 lists F and NF sample sizes and S values for each tree species in each territory. Overall S values calculated by combining F and NF sample populations across territories within tree species revealed the following rank order (S value) of decreasing foraging success: *C. americana* (0.62), *B. papyrifera* (0.59), *Quercus* spp. (0.52), *Pinus* spp. (0.48), *Acer* spp. (0.46), and *P. tremuloides* (0.37).

Excluding the two tree species with low sample sizes within territories (*C. americana, P. tremuloides*), S did not vary significantly among

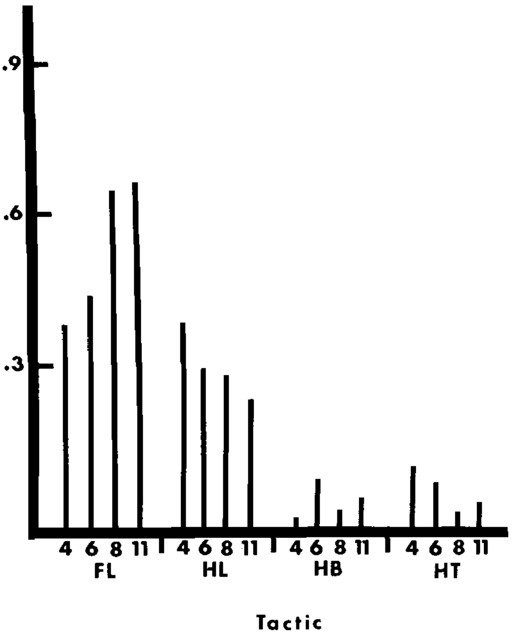

Fig. 1. Foraging tactics used by birds of the four study territories (4, 6, 8, 11) as percentages of total foraging maneuvers; sample sizes in Table 2. FL = flycatch, HL = hover at leaf, HB = hover at branch, HT = hover at trunk.

TABLE 2. Frequencies of perches foraged from (F perches), not foraged from (NF perches), and S values for each tree species in the four territories. Overall values are values combined across territories within tree species.

| Tree species | Territory | F | NF | S |
|---|---|---|---|---|
| *Corylus americana* | 4 | 5 | 12 | 0.29 |
| | 6 | 2 | 5 | 0.29 |
| | 8 | 23 | 1 | 0.96 |
| | 11 | 3 | 2 | 0.60 |
| | Overall | 33 | 20 | 0.62 |
| *Acer* spp. | 4 | 47 | 52 | 0.47 |
| | 6 | 18 | 18 | 0.50 |
| | 8 | 49 | 54 | 0.48 |
| | 11 | 21 | 36 | 0.37 |
| | Overall | 135 | 160 | 0.46 |
| *Quercus* spp. | 4 | 50 | 46 | 0.52 |
| | 6 | 2 | 1 | 0.67 |
| | 8 | 11 | 12 | 0.48 |
| | 11 | 18 | 16 | 0.53 |
| | Overall | 81 | 75 | 0.52 |
| *Pinus* spp. | 4 | — | — | — |
| | 6 | 44 | 56 | 0.44 |
| | 8 | 16 | 10 | 0.62 |
| | 11 | — | — | — |
| | Overall | 60 | 66 | 0.48 |
| *Betula papyrifera* | 4 | 15 | 10 | 0.60 |
| | 6 | 9 | 7 | 0.53 |
| | 8 | 17 | 10 | 0.63 |
| | 11 | 24 | 19 | 0.56 |
| | Overall | 65 | 46 | 0.59 |
| *Populus tremuloides* | 4 | 1 | 0 | 1.00 |
| | 6 | 4 | 9 | 0.31 |
| | 8 | 2 | 3 | 0.40 |
| | 11 | — | — | — |
| | Overall | 7 | 12 | 0.37 |
| All tree species | 4 | 118 | 120 | 0.50 |
| | 6 | 79 | 96 | 0.45 |
| | 8 | 118 | 90 | 0.57 |
| | 11 | 66 | 73 | 0.47 |
| | Overall | 381 | 379 | 0.50 |

tree species (Table 3). However, S varied significantly among the three species common to all four study territories (Table 3). In addition, *Acer* spp. and *Quercus* spp. were not significantly different from each other, but both were significantly different ($P < 0.05$) from *B. papyrifera,* the species with the highest overall and least variable S values (Table 2; see Table 3 for multiple comparisons). Schaffner (1949) recorded more species of leaf-dwelling insects in *B. papyrifera* (15) than in *Q. rubra* (7), *Q. ellipsoidalis* (2), or *Acer* spp. (9). The higher S values in *B. papyrifera* therefore may be due to tree species differences in overall prey density.

The four S values obtained by combining F and NF data across tree species within territories (Table 2) are relatively constant (0.50, 0.45, 0.57, 0.47; $\chi^2 = 5.93$, $P > 0.10$, df = 3 for territories vs. F, NF 4 × 2 contingency table); together with the single S value combining data across territories as well (0.50), these values suggest that approximately half of all chosen perches resulted in a foraging maneuver.

*Patterns of tree species use.*—Figure 2 compares relative frequencies of tree species in territories with their relative use by flycatchers. Contingency table analysis indicated nonrandom use of foliage in all four territories ($G = 15.13$, 16.27, 7.82, and 13.82 in territories 4, 6, 8, and 11; df = 3, 4, 4, 4; all $P < 0.05$). One of the four tree species present was consistently used less than expected by chance (*Pinus* spp.), but this species was present in only two territories. All three dominant tree species on the study site (*Acer* spp., *Quercus* spp., *B. papyrifera*) were used inconsistently, indicating lack of preference for a common species.

TABLE 3. Results of the Kruskal-Wallis analyses and nonparametric multiple comparisons of S values (data in Table 2; * $P < 0.05$; tree species not sharing underlining are significant at $P < 0.05$).

| Analysis | $H_c$ | Multiple comparisons |
|---|---|---|
| All tree species[a] | 6.53 NS | — |
| *Acer* spp.,[b] *Quercus* spp.,[b] *Betula papyrifera*[b] | 6.88* | *Acer* spp., *Quercus* spp., *B. papyrifera* |

[a] *P. tremuloides* and *C. americana* in all territories and *Quercus* spp. in territory 6 were eliminated due to low sample size.

[b] Dominant species found in all four territories; territory 6 excluded to allow multiple comparisons.

When data were combined across territories, foraging success and relative frequency of use were not significantly related (Table 4). Use and relative frequency of tree species were significantly correlated in territory 6 and nearly so in territory 4; coefficients were high and positive but not significant in territories 8 and 11 (Table 4). These variables were significantly correlated when data were combined across territories (Table 4). When probability levels of individual use and relative frequency correlations from territories were combined into a single statistical test (after Sokal and Rohlf 1969; correlations of data combined across territories omitted), use and relative frequency of tree species were significantly related ($\chi^2 = 16.14$, $P < 0.05$). Thus, flycatchers foraged in tree species in proportion to tree species abundances instead of in proportion to foraging success experienced in various tree species.

## DISCUSSION

*Implication for understanding avian community structure.*—These results suggest that tree species morphology is a factor affecting foraging success of a hover-gleaning bird species. However, the influence is not extensive, as S varied only between 0.42 and 0.67 (values from single territories). Unfortunately, no information is yet available concerning how variation in foraging success among different tree species affects habitat selection and subsequent community structure. If an effect exists, Least Flycatchers should occur primarily at forest sites harboring those tree species with high demonstrated S values (e.g. *B. papyrifera*). Bent (1963) describes the Least Flycatcher nesting in at least 22 tree species of 18 genera in coniferous, deciduous, and mixed forests. High population densities (numbers in parentheses are number of birds/40 ha) have been reported for aspen (271, MacQueen 1950), oak-chestnut (*Castanea*, 60; Davis 1959), mixed oak-maple-birch (60, Davis 1959; 85, Rogers 1977 for the population of the present study), and maple-beech (*Fagus*, 56; Holmes and Robinson 1981) forests. In the latter study, flycatchers showed only slight tree species preferences in a mixed deciduous-coniferous forest in New Hampshire. Data from the present study (Table 4) further suggest that this species is broad-niched with respect to tree species use.

Thus, moderate variation in foraging success among tree species does not appear to translate into selection of habitats offering potentially high rates of prey capture. Indeed, it appears that the Least Flycatcher uses a foraging strategy that allows efficient resource exploitation in morphologically divergent tree species and a concomitant ability to breed in forests of different TSC. By this reasoning, TSC has no effect on avian community structure within the hover-gleaner guild. This result is expected under the perspective of community organization in forest birds presented at the beginning of this report. Under this view, hover-gleaning species are distributed over forest habitat without respect to TSC because these species can efficiently exploit a wide range of foliage morphology (Holmes and Robinson 1981). In contrast, species that glean prey from a stationary position are restricted to using tree species and hence forest sites offering favorable foliage morphologies.

On the other hand, the significant variation in S demonstrated in this study is consistent with recent evidence that indicates a moderate effect of foliage morphology on foraging behavior of hover-gleaning bird species (Robinson and Holmes 1984); this effect is greater, however, in gleaning species (Holmes and Robinson 1981). Collectively, results of this study and others point to the conclusion that foraging behavior (in the present case, foraging success) in both the hover-gleaner and

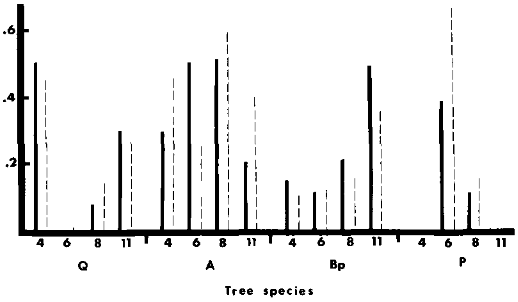

Fig. 2. Relative frequencies of tree species in the four study territories (4, 6, 8, 11; solid lines) and relative frequency of tree species use expressed as percentages of total foraging maneuvers (dashed lines; sample sizes in Table 2). Q = *Quercus* spp., A = *Acer* spp., Bp = *Betula papyrifera*, P = *Pinus* spp.

gleaner guilds is affected by foliage morphology (e.g. Table 3), although the former guild is relatively less affected than the latter. The impact of this differential effect seems clear: in a New Hampshire forest, degree of tree species preference (low in hover-gleaners, high in gleaners) and avian abundance were inversely related (Holmes and Robinson 1981). This correlation helps explain why bird species diversity (BSD) can vary among forests alike in FHD (shown by Willson 1974), a factor long held to be an important regulator of bird communities (MacArthur and MacArthur 1961). An important and testable prediction is that the distribution of gleaners, not hover-gleaners, is largely responsible for variation in BSD among forest habitats alike in FHD (shown by Willson 1974).

Finally, a caveat is in order. In the absence of data on density of invertebrate prey in utilized tree species, results of this study should be considered suggestive rather than conclusive. To illustrate, consider a case where one tree species harbors half the prey density of a second tree species, but foliage morphology makes prey capture in the second tree species twice as difficult as in the first tree species. If a bird makes the same number of attack maneuvers per nonforaging maneuver in both species, such data would generate S values leading to the incorrect conclusion of a lack of influence of foliage morphology on foraging success. The opposite case is clearly possible: foliage morphology and prey density may combine to exaggerate differences in S among tree species. Observed patterns of S within a given group of tree species are realistic only if prey density is constant or nearly so. The preferred prey of the Least Flycatcher is relatively mobile (mainly consisting of adult insects of the orders Diptera, Hymenoptera, and Coleoptera), suggesting that prey need not covary closely with tree species (Robinson and Holmes 1982). However, such independence may not be true of all hover-gleaning species. At least one population of the Acadian Flycatcher (*Empidonax virescens*) strongly prefers beech trees, perhaps due to the presence of a unique prey base there (Maurer and Whitmore 1981).

*Proximate factors related to patterns of tree species use.*—I argued above that the Least Flycatcher is able to exploit a wide variety of tree species with generally equivalent foraging success among them. At least two proximate factors are potentially responsible for such a foraging

TABLE 4. Spearman rank correlation coefficients ($r_s$) of (1) foraging success (S value) in and relative frequency of use of tree species and (2) relative frequency of use and relative frequency of tree species in the four study territories.

| | Correlation | | | | | |
|---|---|---|---|---|---|---|
| | S and relative use[a] | | | Relative frequency and use[b] | | |
| Territory | $r_s$ | $P$ | $n$ | $r_s$ | $P$ | $n$ |
| 4 | — | — | — | 0.80 | 0.10 | 5 |
| 6 | — | — | — | 0.98 | 0.05 | 6 |
| 8 | — | — | — | 0.49 | 0.25 | 6 |
| 11 | — | — | — | 0.70 | 0.25 | 4 |
| Overall | −0.10 | 0.50 | 6 | 0.90 | 0.05 | 6 |

[a] Correlations within territories were not possible due to low F and NF sample sizes in *C. americana* and *P. tremuloides*; overall correlations are those derived from data combined across territories, a procedure that increased sample sizes from these two species.

[b] *C. americana* and *P. tremuloides* included to increase number of tree species in correlations (see Methods).

strategy. First, it may be inefficient to pass through or by resource-laden patches (trees) that differ only in foliage morphology, assuming variation in prey density among patches is negligible. Increased foraging efficiency gained by exploiting the complete set of available tree species in a given territory would favor continued use of all tree species. Second, decreasing prey density in initially favored tree species would cause switching from these to other tree species present. This mechanism could explain the lack of correlation between S and relative use of tree species (Table 4). The species with the highest S values, *B. papyrifera,* was also an uncommon species (compared to the other two dominant species, *Acer* spp. and *Quercus* spp.) in the study territories. Limiting foraging to a relatively uncommon tree species soon would exhaust available prey there, necessitating a switch to a more common species conferring acceptable but lower S values.

This possibility is only partially consistent with optimal foraging theory. Simple foraging theory predicts that birds will forage in patches in direct proportion to prey density encountered in the patches. I consider different tree species analogous to different patches and variation in S among tree species analogous to variation in prey density among patches. Use of all available tree species by flycatchers concords with theory, but the lack of a significant relation between tree species use and S (Table 4) does not. However, variation in patch size (i.e. tree species abundance) within a given territory is an additional factor that may cause switching among tree species, resulting in a nonsignificant relationship.

These arguments preassume evolved morphological (e.g. bill dimensions, wing-loading) and behavioral (e.g. propensity to engage in hovering flight) adaptations for hovering in and around foliage. Ultimate factors responsible for them remain unknown. It is possible, however, that proximate factors linked with a broad foraging strategy are also ultimate evolutionary forces responsible for adaptations associated with hovering.

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## ERRATUM

There is an error in the caption of Fig. 9 of Kålås and Byrkjedal (1984, Auk 101: 838-847). The ratio in the legend should be inverted to read [(weight/wing length) × 100].