NEST SITE SELECTION IN EASTERN AND WESTERN KINGBIRDS: A MULTIVARIATE APPROACH

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ABSTRACT.—Nest site selection by Eastern and Western kingbirds (*Tyrannus tyrannus* and *T. verticalis*) was studied at Delta Marsh, Manitoba, and results were analyzed using multivariate techniques. Principal component analysis of overstory vegetation characteristics for randomly selected plots defined the habitat space of the study area in terms of the major components of variation in the vegetation. Discriminant function analysis of the random plots identified the major trend in the vegetation (corresponding roughly to a north-south topographical gradient), and characterized the differences between north- and south-zone habitat types.

Principal component analysis of the vegetation characteristics of kingbird nest sites determined the relative position of each species in the habitat space. Virtually all of the Western Kingbird sites and most of the Eastern Kingbird sites appeared to be situated in that portion of the habitat space considered to represent north-zone habitat. Projection of the nest site data onto the random plot discriminant axis indicated that Eastern Kingbird nest sites were more evenly distributed than those of Western Kingbirds along the major trend of variation in the forest vegetation. Discriminant function analysis of the nest sites identified the variables most important in characterizing the difference between the nest sites of the two species. Western Kingbird sites were characterized by fewer but larger trees than Eastern Kingbird sites. Western Kingbird nest trees were larger and taller, and Western Kingbird nests were placed higher than those of Eastern Kingbirds.

Eastern Kingbirds behaved as habitat generalists, selecting nest sites from both available habitat types, and selecting nest trees from a wide range of tree sizes. Western Kingbirds behaved as specialists, selecting sites in only the north-zone habitat type, and nest trees from the larger sizes.

The Eastern Kingbird (*Tyrannus tyrannus*) and the Western Kingbird (*T. verticalis*) are sympatric over much of western North America (Fig. 1). The area of sympatry constitutes 35% of the breeding range of the Eastern Kingbird, and 60% of that of the Western Kingbird. Within their common range, where one species is abundant the other is usually much less so, and there is also regional variation as to which species exploits the wider range of habitats (Hiatt 1942, Hamilton 1962, Smith 1966, Tatschl 1973).

Over much of its range the Eastern Kingbird nests along the edges of woodlots, in orchards, near marshes, and frequently in riparian communities (Bent 1942, Smith 1966). In the parts of its range where woods are scarce, the Eastern Kingbird inhabits open country, often nesting in low shrubs.

The Western Kingbird is typical of dry grassland areas, but over much of its range its distribution appears to depend on the presence of at least a few trees for nesting. It is, therefore, a common inhabitant of prairie riparian woodlands, where it often reaches high nesting densities (e.g., see Carothers et al. 1974). This preference for trees or other tall structures (e.g., utility poles) for nesting suggests that the recent expansion of the breeding range of the Western Kingbird (since 1900) may have been influenced by the planting of trees and erection of man-made structures which accompanied settlement of the plains at the turn of the century (see Nice 1924).

The association of these species in Manitoba is the result of this recent breeding range expansion of the Western Kingbird (Taverner 1927). Analysis of census data from the Breeding Bird Survey (Robbins and Van Velzen 1967) for the period 1970–1975 revealed that the Eastern Kingbird was four times as abundant as the Western Kingbird in Manitoba. Both species breed in high densities on the forested dune ridge

at Delta Marsh, Manitoba. There the Eastern Kingbird is about three times as abundant as the Western Kingbird (Smith 1966; MacKenzie, pers. observ.). Both species are primarily insectivorous (Beal 1912) and are sustained by an abundant food supply, chiefly chironomids (MacKenzie, unpubl. data). The availability of suitable nest sites, however, could be an important factor limiting the population of one or both species.

Birds are generally believed to select their habitat according to visual aspects of the vegetation configuration (Shugart and Patten 1972, Smith 1977). Lack (1933) and Lack and Venables (1939) emphasized the *Gestalt* nature of habitat selection in birds. Lack (1937) suggested that a species may select specific habitats on the basis of "psychological preferences," even though the presence of the preferred features is not necessarily essential to its existence. One might argue, by corollary, that the availability of the preferred features in a given habitat could, in fact, limit the population size of a species in that habitat (see Miller 1942). A stenotypic response by the Western Kingbird to the available habitat, in terms of the perceived number of suitable nest sites, could be a factor contributing to the much smaller population of this species compared to that of its more ubiquitous congener at Delta Marsh. Such a response would be consistent with the stenotypic behavior of a species at the periphery of its range.

James (1971) introduced the term "niche-gestalt" to describe that combination of habitat factors that characterizes the occurrence of a species. She emphasized the multivariate nature of *Gestalt* perception as an individual's response to an organized perceptual field. Accordingly, we applied multivariate analyses to nest site selection by Eastern and Western kingbirds in an attempt to characterize the nest sites of each species and thereby to determine interspecific differences.

STUDY AREA

The study was carried out on a 2-km segment of the forested dune ridge that separates the south shore of Lake Manitoba from Delta Marsh (50°11'N, 98°19'W) (see Sealy 1980 for a map and photograph of the study area). The ridge is a remnant shoreline of glacial Lake Agassiz (Walker 1965, Sproule 1972) formed by wind, wave, and ice action (Löve and Löve 1954). The dune formation, itself, averages 2.5 m in height and seldom exceeds 30 m in width on the study area. However, the ridge forest averages 80 m in width.

The vegetation of the ridge forest has been described by Löve and Löve (1954), Walker (1965), and MacKenzie (in press). The common trees on the study area
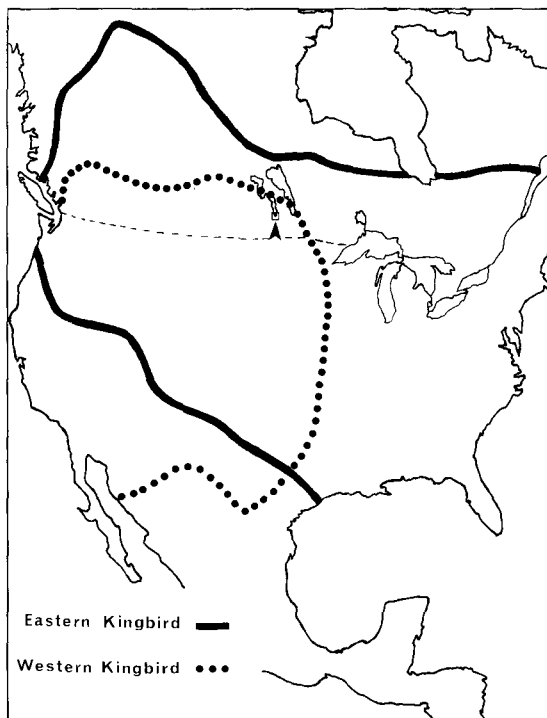

FIGURE 1. Breeding distributions of Eastern and Western kingbirds. Arrow indicates the location of the study area at Delta Marsh, Manitoba. Map based upon the A.O.U. Check-list (1957), Godfrey (1966), and the Breeding Bird Survey for 1975.

are peach-leaved willow (*Salix amygdaloides*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and cottonwood (*Populus deltoides*). The common shrubs include sandbar willow (*Salix interior*), red-berried elder (*Sambucus pubens*), and red osier (*Cornus stolonifera*).

Seven species of birds in addition to the kingbirds nest in the ridge forest in high numbers: Mourning Dove (*Zenaida macroura*), Least Flycatcher (*Empidonax minimus*), Northern Oriole (*Icterus galbula*), Warbling Vireo (*Vireo gilvus*), Yellow Warbler (*Dendroica petechia*), Gray Catbird (*Dumetella carolinensis*), and American Robin (*Turdus migratorius*).

METHODS

SAMPLING PROCEDURES

Kingbird nests were located through intensive searching of the study area during the 1976 and 1977 breeding seasons. We monitored the nests throughout the breeding season and, where possible, examined the contents of each nest at least once a week. Some nests were not reached because of either their height and position in the nest tree, or the condition of the nest tree. Others were reached only with much time spent in the nest tree and, as a consequence, much disturbance to the nesting birds. Therefore, we made no attempt to relate nest site selection to breeding success.

Once the young had fledged from the nests, we analyzed the vegetation around each nest site at three levels of resolution: macrosite, microsite, and nest tree. Changes in the vegetation over the breeding season were restricted primarily to the understory, particular-

ly the herbaceous layer. Because both kingbird species perched and nested high, we did not consider characteristics of the understory vegetation to be relevant to nest site selection. Thus, the configuration of the vegetation in terms of the components deemed important to nest site selection by kingbirds remained essentially constant throughout the breeding season. We established concentric circular plots, 0.07 ha (macrosite) and 0.01 ha (microsite), with the position of the nest as their center. We used macrosite plots to sample the vegetation surrounding the nest to detect large-scale habitat differences. Because both species foraged to a large extent off the ridge, they frequently had the opportunity to view the ridge vegetation from a distance. The perspective provided by this distance could have allowed the kingbirds to perceive large-scale habitat differences that might have been imperceptible to species lacking this added perspective. We employed the microsite plots to achieve a finer resolution of vegetation analysis around the nest sites, in case subtler differences proved important, and to provide a nest site sampling unit, which would be comparable in area to the random plots used to sample the study area vegetation.

In both the macrosite and microsite plots every tree greater than or equal to 5 cm in diameter at breast height (dbh) was identified to species and was recorded in the appropriate size class (intervals of 5 cm dbh). From these data 13 variables were calculated: total density of stems; total basal area of stems; stem densities in seven size classes; densities of box elder, green ash, peach-leaved willow, and sandbar willow stems. The use of several size classes ensured that even subtle structural differences in nest site composition would be identified. Because kingbirds tended to nest in the canopy, we considered stems less than 5 cm dbh too small to be selected as nest trees, and too short to constitute an important influence on nest site selection. Stems greater than 35 cm dbh were so few (less than 5% of total stems occurred in any larger size class) that they were combined in one size class. The major tree species were included as potentially important variables because their life forms represent different structural configurations, and as such could elicit different responses from the kingbird species (see Smith 1977).

At each nest tree five characteristics were measured: distance of the nest from the north edge of the ridge forest (a measure of the distribution of the nests across the width of the ridge forest); nest tree height and nest height (measured with a Haga altimeter); nest tree dbh; and nest tree crown volume (calculated using the formula for an elliptical cylinder. Two more variables were then calculated: relative nest tree height (i.e., relative to the average tree height in the macrosite, determined from the heights of ten randomly selected trees); and relative nest height (i.e., relative to the height of the nest tree).

The overstory vegetation was sampled in order to characterize the floristic and structural composition of the study area. Rectangular quadrats (random plots), 5 × 20 m (0.01 ha), were set according to a partial random sampling scheme (MacKenzie in press). In each plot all trees greater than or equal to 5 cm dbh were identified to species and were recorded in the appropriate size class. From these data the 13 variables used in the nest site analyses were calculated. This permitted the detection of any vegetation patterns with which the distribution of kingbird nests might be correlated. Our sampling method thus objectively evaluated the variation in community structure by avoiding the a priori arbitrary designation of synecological units (cf. Smith 1977).

STATISTICAL ANALYSIS

Because our samples were small, particularly of Western Kingbird nest sites, we combined the samples from both years for each species in the analyses. Student's t-tests were performed on the 37 individual variables for each species to test the null hypothesis of no difference between years. For the Eastern Kingbird nest sites only two variables, relative nest tree height and nest tree dbh, were significantly different ($P < 0.05$). For Western Kingbird nest sites, all variables showed non-significant differences ($P > 0.05$). Thus, lumping of the samples was considered justified. We performed t-tests on all variables to evaluate the null hypothesis of no difference between species means. Where the variances of any variable were unequal between two samples, a t-test for unequal variances was used.

Principal component analysis (PCA) was performed to identify the major axes of variation in the vegetation data, and to project the points representing the plots (nest site and random) onto these axes. In this manner we determined whether the patterns of variation in the ridge vegetation were reflected in the nest site data, or whether the distribution of nests was being influenced by factors other than those characterizing the ridge vegetation. The 13 habitat variables of the macrosite plots of both species were subjected collectively to PCA to discover the relative position of each kingbird in the habitat space defined by the axes. The principal components were varimax-rotated to "simple structure" (Thurstone 1947) in order to improve the interpretation of the axes. This procedure was repeated using the microsite data. The resulting ordinations were compared to an ordination derived from varimax-rotated axes of the random plot analysis for the same set of variables.

While PCA is very useful in reducing the dimensionality of the original data to a conceptually meaningful level, it does not necessarily identify those variables which are most important in contributing to the statistical separation of groups. Discriminant function analysis (DFA) provides a mathematically objective method for separating groups, and for assessing the relative importance of each variable to the separation. The latter is determined by examining the standardized discriminant function coefficient for each variable.

The null hypothesis of no difference between group means in each data set was tested a priori using Hotelling's T^2-test. In the random plot analysis, north and south groups of plots were compared. In the nest site analyses, Eastern Kingbird and Western Kingbird groups were compared at three levels: macrosite, microsite, and nest tree. DFA was performed on all data sets for which the difference between group means was significant ($P < 0.05$).

The null hypothesis of homogeneity of within-group dispersion matrices was tested using Box's (1949) test. For each pair of groups tested, the matrices showed significant heteroscedasticity ($P < 0.05$). All variables were then tested individually for homogeneity of variances between groups using Levene's (1960) test. This test was used in preference to Bartlett's (1937) test because of its robustness to departures from normality (Brown and Forsythe 1974). No variables had significantly heterogeneous variances between groups ($P > 0.05$), and thus, the heteroscedasticity of the dispersion matrices was not considered serious enough to invalidate the discriminant analyses. We followed Dueser and Shugart (1979) in proceeding with DFA in spite of significant heteroscedasticity because, in each case, the discriminant function was interpretable ecologically and contributed meaningfully to the separation of groups.

To test the hypothesis that the kingbird species were separating along the major axis of habitat variation, we multiplied the macrosite data for all nest sites by the discriminant function coefficients obtained from the random plot DFA; we then summed the products to produce a discriminant score for each nest site. The null hypothesis of no difference in mean scores between the species was tested using the t-test. For this analysis the macrosite data were scaled by dividing the data matrix by 3. Inspection of the variance structure of both the macrosite and random plot data sets had revealed that the variances of the macrosite variables were larger by a factor of 3. The purpose of this ad hoc procedure was to make the variance-covariance matrix of the macrosite data comparable to that of the random plot data without affecting the interrelationship of the variables within the matrix (K. Subrahmaniam, pers. comm.). Statistical analyses were performed at the University of Manitoba and the University of Toronto, using programs from the SPSS (Nie et al. 1975) and BMDP (Dixon and Brown 1979) packages.

RESULTS

DISTRIBUTION OF NESTS

Twenty-seven Eastern Kingbird nests and 12 Western Kingbird nests were located in 1976; 31 Eastern Kingbird and 10 Western Kingbird nests were found in 1977. Although the breeding chronology was not identical in both species (Fig. 2), the high degree of overlap during both seasons indicated an absence of temporal partitioning of nest sites.

The nests of both species showed similar distributions along the length of the study area. However, there was a marked difference in their distribution across the study area. The null hypothesis of equal distribution of nests in both the north and south halves of the ridge forest was tested for each species using the χ^2-test for deviations of observed frequency from expectation (Sokal and Rohlf 1973). Most Western Kingbird nests were situated in the north half ($P <$
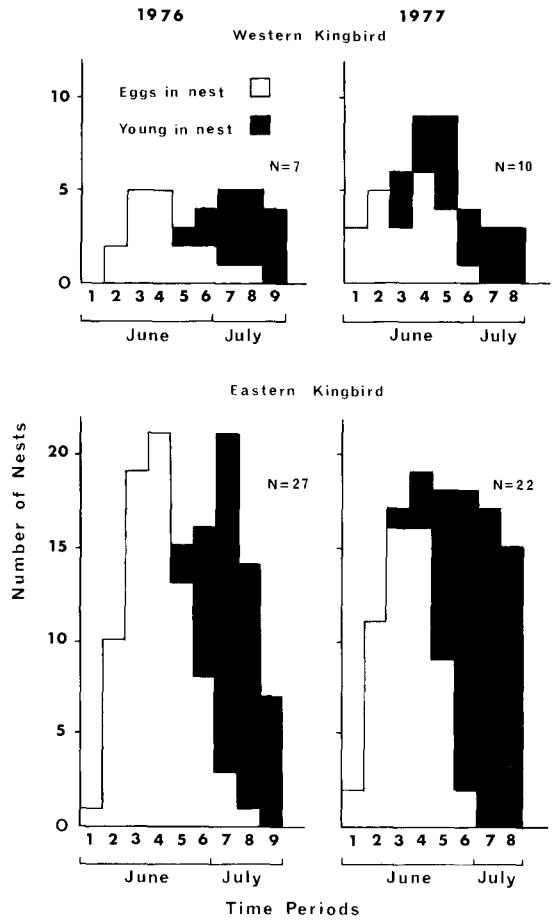

FIGURE 2. Nesting chronology of Eastern and Western kingbirds at Delta Marsh. Time intervals correspond roughly to weekly visits to the nests.

0.01), whereas Eastern Kingbird nests were distributed over both halves with almost equal frequency ($P > 0.05$). This difference led us to hypothesize that the habitat of the ridge forest varied from north to south, and

TABLE 1. Correlations of habitat variables with the first two varimax-rotated factors from the random plot and kingbird macrosite and microsite analyses. High correlations appear in bold-faced type.

| Habitat variables	Random plot		Macrosite		Microsite	
	I	II	I	II	I	II
Total stems	**.94**	.06	**.90**	.08	.00	**.86**
Total basal area	.02	**.89**	−.06	**.57**	**.93**	−.02
Stems 5–10 cm dbh	**.95**	−.13	**.94**	−.23	.48	**.83**
Stems 10–15 cm dbh	.11	−.05	.15	−.00	**.90**	.12
Stems 15–20 cm dbh	.09	.07	−.10	**.52**	.33	−.06
Stems 20–25 cm dbh	−.05	.35	−.14	**.91**	.19	−.04
Stems 25–30 cm dbh	−.13	.01	−.08	**.92**	−.00	−.05
Stems 30–35 cm dbh	−.07	**.67**	−.32	.47	.02	.02
Stems >35 cm dbh	−.12	**.85**	−.17	−.08	−.09	−.34
Box elder	.05	−.01	.22	−.04	**.79**	.29
Green ash	−.19	−.24	−.15	.14	**.84**	−.09
Peach-leaved willow	.44	.48	.13	.14	−.11	.12
Sandbar willow	**.75**	−.22	**.86**	−.22	−.08	**.84**
Variance explained (%)	20.4	18.8	20.8	20.2	26.2	18.3
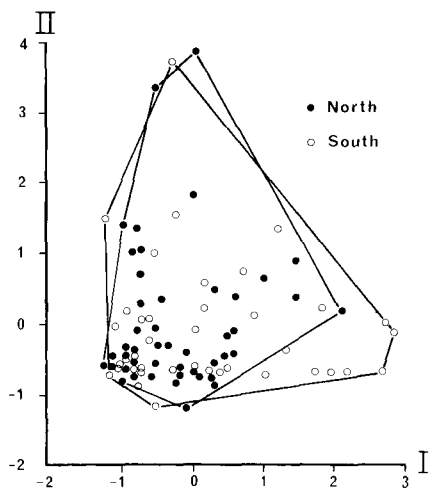
FIGURE 3. Ordination of random plots along the first two rotated axes from the principal component analysis. See Table 1 for interpretation of axes.

that the difference in nest distribution between the species was related to floristic and/or structural differences in the pattern of the vegetation. Accordingly, we assigned the random plots to north and south groups based on their location in either the north or south half of the forest, and without regard to their vegetation characteristics.

CHARACTERISTICS OF RIDGE FOREST

PCA performed on a correlation matrix of the combined random plot samples produced four eigenvectors with eigenvalues greater than 1.0, and accounting for 68.2% of the total variance. The varimax-rotated factors showed high loadings for only a few variables, presumably those most important in explaining the community patterns.

Factor I accounted for 20.4% of the total variance, and was characterized by high positive loadings for total density of stems, density of stems 5–10 cm, and density of sandbar willow stems (Table 1). Thus, it was considered a density factor, emphasizing the number of small stems.

Factor II, accounting for 18.8% of the total variance, showed high positive loadings for total basal area of stems, density of stems in the largest size classes, and density of peach-leaved willow stems. It therefore represented a size or dominance component, emphasizing the presence of large stems, particularly of peach-leaved willow, the quantitatively dominant species on the study area (MacKenzie in press).

Factor III accounted for an additional 15.6% of the variance and showed high pos-

itive loadings for density of stems 10–15 cm and density of box elder. Factor IV, which explained 13.4% of the variance, showed high positive loadings for the middle size classes. These factors were not easily interpretable.

The first two factors were used to construct an ordination of random plots to serve as a model of the habitat space of the ridge forest (Fig. 3). Along the first axis, 63% of north-zone plots fell to the left of the origin, while the south-zone plots were relatively evenly distributed on both sides of the origin. The clustering of the north-zone plots on the left, although not significant (χ^2-test; $P > 0.05$), together with the smaller range of variation in the north-zone group, indicated the relatively greater distinctness of the north-zone group. Predictably, many of the south-zone plots located to the left of the origin showed the influence of the dune substrate, characteristic of the north zone of the ridge forest (MacKenzie in press), and contained a substantial peach-leaved willow component. Thus, the left half of the ordination was considered to represent the north-zone habitat type, characterized by fewer but larger stems, and the right half the south-zone type, characterized by more but smaller stems, largely of sandbar willow. The second axis did not form the basis of any separation of north- and south-zone groups.

Hotelling's T^2-test indicated a significant difference ($P < 0.01$) between the centroids of north and south groups. DFA was then performed to evaluate the relative power of each of the variables to discriminate between the groups. Density of stems 5–10 cm, total density of stems, density of sandbar willow, and density of stems 10–15 cm were, respectively, the most important contributors to the separation of the groups. The discriminant function closely resembled the principal component model in emphasizing the structural dichotomy between north and south zones—large stems in the north, and small stems with a strong sandbar willow component in the south. A stepwise discriminant analysis identified density of sandbar willow, density of stems 5–10 cm, density of peach-leaved willow, and density of stems greater than 35 cm as the subset of variables that achieved the maximum discrimination between groups. The discriminant function classified 83% of north-zone plots and 38% of south-zone plots as belonging to the north zone, indicating the greater abundance of habitat typical of the north zone.

CHARACTERISTICS OF MACROSITES

A PCA performed on a correlation matrix of the combined kingbird species macrosite plots produced five eigenvectors with eigenvalues greater than 1.0, and explaining 82.1% of the total variance. Varimax rotation improved the interpretability of the factors.

Factor I accounted for 20.8% of the total variance, and showed high positive loadings for total density of stems, density of stems 5–10 cm, and density of sandbar willow (Table 1). Thus, it represented the same density continuum as Factor I of the random plot analysis.

Factor II accounted for 20% of the variance, and showed high positive loadings on the larger stem size classes, particularly stems 20–25 cm and 25–30 cm, and total basal area of stems. It resembled the size component represented by Factor II of the random plot analysis.

Factors III and IV represented additional aspects of the dominance trend of Factor II. Factor III showed high positive loadings for total basal area and the two largest size classes. Factor IV had high positive loadings for density of peach-leaved willow and small to medium size classes. Factor V represented a contrast between box elder and green ash on the one hand, and peach-leaved willow on the other.

The first two factors were used to construct an ordination of the macrosite plots for comparison with the random plot reference model (Fig. 4). A significant number of Western Kingbird plots (86%) fell to the left of the origin (χ^2-test; $P < 0.01$), while only 55% of the Eastern Kingbird plots were located to the left. Thus, the distribution of the plots in the ordination matched very closely the distribution of nests across the width of the ridge forest. The stenotypic response of the Western Kingbird to the range of variation in the vegetation was suggested by the concentration of the plots in a relatively small portion of the ordination. Their distribution along the first axis was particularly compressed, suggesting the relative sparseness of trees around Western Kingbird nest sites. By contrast, the Eastern Kingbird showed a broad range of response along both axes, suggesting that it exploited a greater range of habitat variation than the Western Kingbird.

Hotelling's T^2-test indicated that the difference between Eastern and Western kingbird macrosites was significant ($P < 0.05$). Therefore, DFA was performed to evaluate the contribution of each variable to the discrimination between the macrosites of the
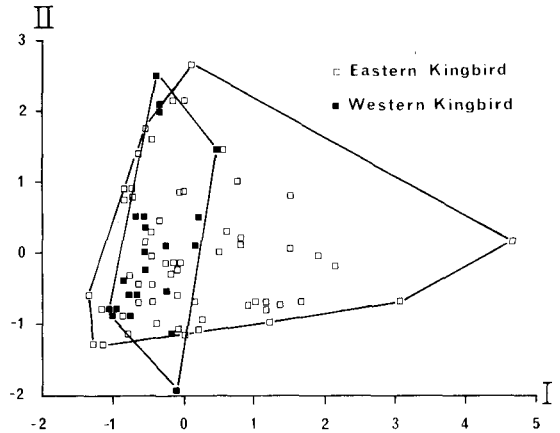

FIGURE 4. Ordination of kingbird macrosite plots along the first two rotated axes from the principal component analysis. See Table 1 for interpretation of axes.

two species. The analysis identified density of stems greater than 35 cm, density of sandbar willow, density of stems 5–10 cm, and total density of stems as, respectively, the four most important contributors to the separation of the species.

An ordination in the form of a frequency distribution of discriminant scores (Fig. 5) showed a pattern consistent with that of the PCA ordination: Eastern Kingbird macrosites showed a broader range of variation than Western Kingbird sites.

To test the hypothesis that the factors separating Eastern and Western kingbird sites were the same as those which were important in discriminating between north and south zones, we derived discriminant scores by multiplying the macrosite data by the discriminant coefficients from the random plot DFA. These discriminant scores would reflect the response of the kingbirds to the factors important in separating the zones. Student's t-test indicated that the mean discriminant scores were not significantly different between the species ($P > 0.05$). We interpreted this to mean that although the separation of Eastern and Western kingbird macrosites paralleled the separation of the zones, the combination of factors important in separating north and south zones was not sufficient to achieve a significant separation of the species' macrosites.

CHARACTERISTICS OF MICROSITES

PCA of the kingbird microsite plots produced five eigenvectors with eigenvalues greater than 1.0, and accounting for 82% of the total variance. Factor I, accounting for 26.2% of the total variance, showed high positive loadings for total basal area, density
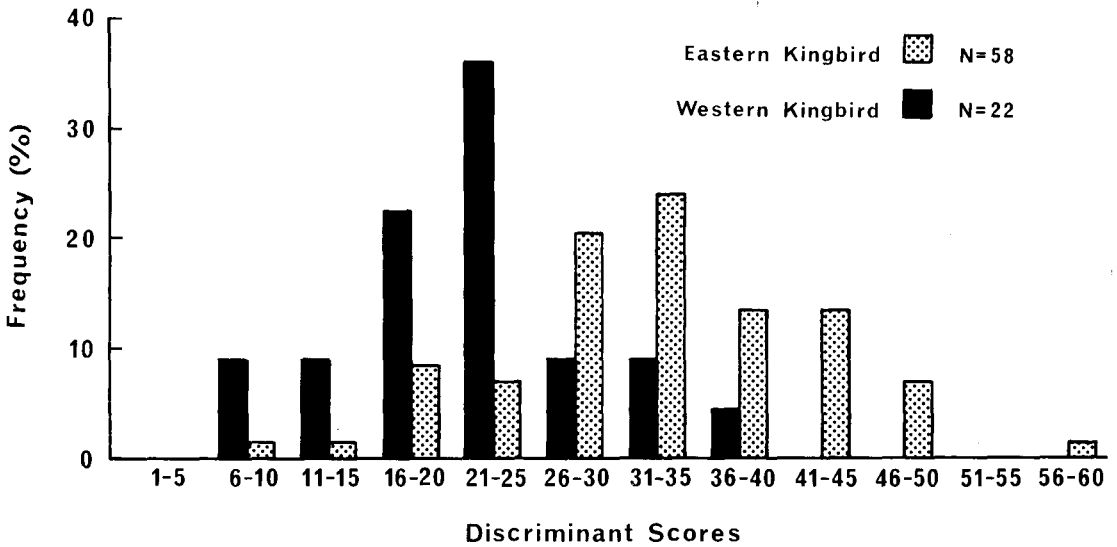
FIGURE 5. Frequency distribution of discriminant scores derived from analysis of the kingbird macrosite data.

of stems 10–15 cm, and densities of box elder and ash. Factor II, explaining 18.3% of the variance, showed high loadings for total density of stems, density of stems 5–10 cm, and density of sandbar willow. Thus, Factor II represented the same trend as that represented by Factor I of both the macrosite and random plot analyses.

In the ordination based on the first two factors, the distributions of the plots of both species along the first axis were clustered about the origin (Fig. 6). Thus, Factor I did not form the basis of any separation of the species. However, the pattern along the second axis resembled that along the first axis of the macrosite ordination. Once again, 86% of the Western Kingbird plots fell to the negative side of the origin, compared with 52% of the Eastern Kingbird plots. Western Kingbird plots again formed a tight cluster (even tighter than in the macrosite ordination), indicating a narrow range of variation. A substantial proportion of Eastern Kingbird plots fell within this cluster, as well. Predictably, Hotelling's T^2-test indicated that the microsites of the two species were not significantly different ($P > 0.05$).

Hotelling's T^2-test did reveal that the microsites of the combined species were significantly different from the random plots ($P < 0.001$). Kingbirds selected sites with fewer small stems and more large stems, more ash, and less sandbar willow than in the random plots. T^2-tests also indicated that Eastern Kingbird microsites were significantly different from random plots ($P = 0.01$), and that Western Kingbird microsites were significantly different from north-zone random plots ($P < 0.01$). Thus, both species appeared to select nest sites non-randomly, at least at the microsite level, even though the difference between the species was not significant.
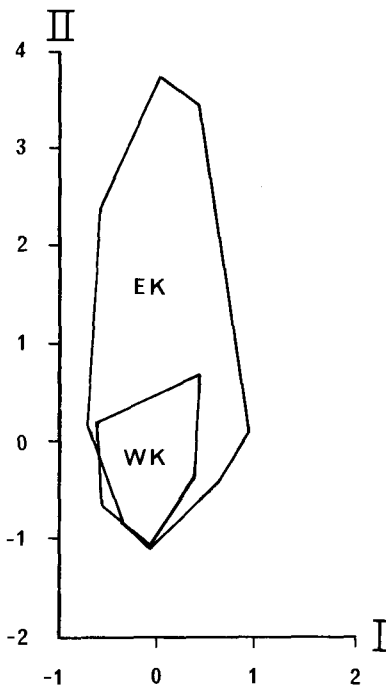

FIGURE 6. Ordination of kingbird microsite plots along the first two rotated axes from the principal component analysis. See Table 1 for interpretation of axes.

CHARACTERISTICS OF NEST TREES

Hotelling's T^2-test indicated a highly significant difference between the centroids of the nest tree data sets for the two species
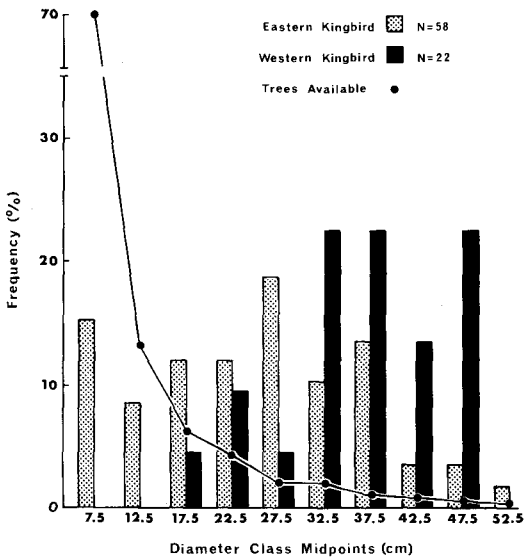
FIGURE 7. Frequency distribution of tree size classes (all species) selected as nest trees by Eastern and Western kingbirds, in relation to their relative availability on the study area.

FIGURE 8. Frequency distribution of Eastern and Western kingbird nest heights in the ridge forest at Delta Marsh.

$(P < 0.001)$. Nest tree height, nest tree dbh, and nest height were all significantly lower for Eastern Kingbirds (Table 2). Only relative nest tree height was not significantly different $(P > 0.05)$. Thus, Western Kingbirds chose, on average, larger, taller nest trees, and nested higher in terms of both absolute and relative nest height. Predictably, Western Kingbird nests, situated in the north zone for the most part, were significantly closer to the north edge of the ridge forest.

Ash and peach-leaved willow were selected as nest trees most frequently by both species. The frequency of selection of these tree species by the kingbird species was not significantly different $(\chi^2$-test; $P > 0.05)$. Structurally, the difference between the nest trees of the two species was quite marked. Eastern Kingbirds selected nest trees from virtually the entire range of tree siz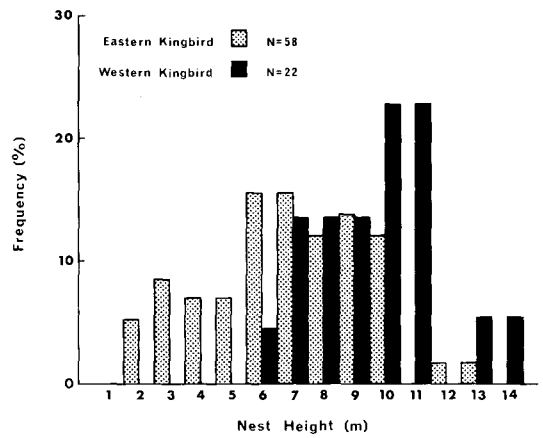es, whereas most Western Kingbird nest trees were selected from the largest size classes (Fig. 7). Trees larger than 30 cm dbh represented only 4.6% of the trees on the study area (as determined from the random plot analysis); yet, 82% of Western Kingbird nest trees were selected from this range of sizes, compared to 33% of Eastern Kingbird nest trees. Both of these frequencies of selection represented significant deviations from expectation $(\chi^2$-test; $P < 0.01)$, but the frequency of selection by Western Kingbirds from this range was also significantly higher than that by Eastern Kingbirds $(\chi^2$-test; $P < 0.01)$.

DFA performed on the variables associated with the nest tree identified nest height, nest tree height, and relative nest height as, respectively, the three best discriminators of kingbird nest trees. This emphasis on height as a discriminator led us to hypothesize that nest height was an important contributor to the vertical separation of these species elsewhere in sympatry. Accordingly, we compared the frequency distribution of nest heights in the study area (Fig. 8) with that of 231 Eastern Kingbird $(\bar{x} = 2.5 \ \text{m} \pm 0.14 \ \text{SE})$ and 103 Western

TABLE 2. Means, standard errors, and results of t-tests for the significance of differences between the variables associated with nest trees of Eastern and Western kingbirds.

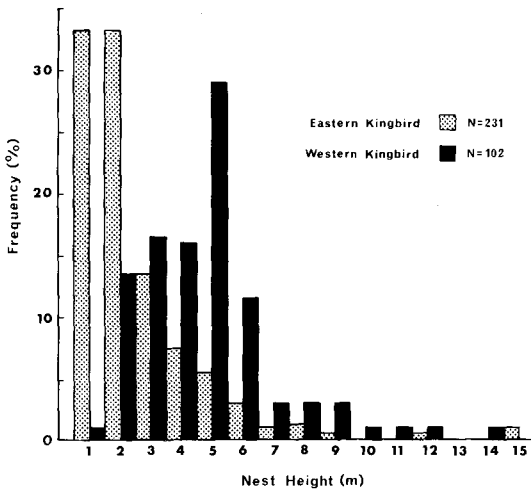| Variables	Eastern Kingbird (N = 58)	Western Kingbird (N = 22)	Significance level[a]
Nest tree height (m)	12.1 (0.55)	15.3 (0.59)	0.001
Relative nest tree height	1.2 (0.47)	1.3 (0.52)	n.s.
Nest height (m)	6.8 (0.33)	9.6 (0.43)	0.001
Relative nest height	0.57 (0.02)	0.64 (0.02)	0.05
Nest tree diameter (cm)	24.6 (1.59)	36.2 (1.97)	0.001
Nest tree crown volume (m³)	87.3 (10.89)	142.6 (20.69)	0.05
Distance to north edge (m)	41.2 (2.63)	30.5 (2.71)	0.01

[a] n.s. = not significant.

FIGURE 9.   Frequency distribution of Eastern and Western kingbird nest heights from Manitoba, Saskatchewan, and Alberta, recorded in the Prairie Nest Records Scheme.

Kingbird (4.7 ± 0.22) nests from Manitoba, Saskatchewan, and Alberta that were reported to the Prairie Nest Records Scheme (Fig. 9). Student's t-test indicated that Western Kingbird nests were significantly higher than Eastern Kingbird nests ($P < 0.001$). Thus, the difference in nest height in the ridge forest at Delta Marsh was consistent with the vertical separation shown by these species elsewhere in sympatry.

DISCUSSION

RESPONSE TO HABITAT HETEROGENEITY

Analyses of the random plot data revealed the existence of two types of habitat, corresponding roughly to the north and south halves of the ridge forest. The north-zone habitat type appears to be more abundant than the south-zone type, the former invading the south half of the ridge in places (MacKenzie in press). Therefore, the ridge forest may be described more accurately, perhaps, as a mosaic of the two habitat patch types, rather than as two distinct zones.

Eastern and Western kingbirds responded differently to the heterogeneity of the ridge forest habitat in the distribution of their nest sites. Eastern Kingbird nests were more abundant and more uniformly distributed in the forest than were those of Western Kingbirds.

The PCA ordinations of the nest sites indicated that Eastern Kingbirds exploited a broader range of habitats than Western Kingbirds, at both the macrosite and microsite levels. Eastern Kingbird nest sites were distributed more uniformly than Western Kingbird sites along both principal com-

ponent axes. Western Kingbird sites were clumped in both ordinations, particularly along the major gradient in the ridge forest vegetation.

Ordination of the macrosites along the discriminant axis of the random plot analysis revealed that, although the species' patterns of response were similar to those in the macrosite ordination, the former resulted in far less pronounced separation of the species. Yet, analysis of the nest sites indicated that the difference between the kingbirds was best characterized by a set of variables similar to those that best characterized the difference between north and south habitats. The major exception to this general similarity was in the importance accorded stems greater than 35 cm dbh. The presence of significantly more large stems around Western Kingbird nest sites appears to be an important difference between the species.

Within the range of habitat types available in the ridge forest, the Eastern Kingbird showed the fine-grained response of a generalist (see Wiens 1976) in its selection of nest sites. It occupied the two major habitat types roughly in proportion to their availability. The Western Kingbird, on the other hand, exploited only the north-zone habitat, resembling a specialist in its coarse-grained response to the habitat heterogeneity.

Rosenzweig (1974) proposed a theory for the evolution of habitat selection which predicts that in a habitat consisting of unequally abundant patch types, two phenotypes (here, congeneric species) will be able to coexist successfully if one, the specialist, uses only the more abundant patch type, and the other, the generalist, uses the given mixture of patch types (see also Dueser and Shugart 1978). Under these conditions the niche of the specialist will be nested within that of the generalist. The theory also predicts that intertypic (here, interspecific) territoriality may evolve, and that intertypic competition should be substantial.

Nest site selection in Eastern and Western kingbirds is largely consistent with Rosenzweig's theory. Principal component ordinations of the nesting habitats of the two species depict the habitat niche of the Western Kingbird as more or less a subset of that of the Eastern Kingbird. Yet, contrary to the predictions of Rosenzweig's theory, our field observations of the two species indicated very little interspecific interaction. The only form of interspecific aggression observed during the study involved the

very infrequent intrusion of a bird of one species into the nest tree of the other. This was in contrast to the strong intraspecific aggression involving members of either species in the general vicinity of a nest. Such a pattern of behavior is inconsistent with interspecific territoriality, and does not suggest substantial interspecific competition for nest sites. Interestingly, we saw no instances of interspecific defense of feeding areas throughout the study either.

We know of no other studies of nest site selection in sympatric Eastern and Western kingbirds for comparison with our findings. Hespenheide (1964) concluded that interspecific territoriality between Western Kingbirds and Cassin's Kingbirds (*T. vociferans*) in Arizona apparently did not exist. Ohlendorf (1974), studying the same two species in Texas, reported some interspecific aggression in defense of nest sites by both species, but more so by Cassin's Kingbirds. Both studies reported frequent intraspecific territorial interactions in Western Kingbirds. Davis (1941) observed that aggression between Eastern Kingbirds and other species, including Western Kingbirds, occurred only in the immediate vicinity of the nest tree, and involved only birds entering or moving around within the nest tree. He also pointed out that interspecific encounters involving Eastern Kingbirds lacked the violence of intraspecific interactions of this species. Our observations are consistent with those of Davis.

The emphasis on the importance of the nest tree, itself, suggests an explanation for the apparent lack of substantial interaction between the species, despite the overlap at the habitat level. Western Kingbirds selected significantly different nest trees than Eastern Kingbirds, even if only the north-zone Eastern Kingbird nests were considered (T^2-test; $P < 0.05$). Western Kingbird nest trees were taller and larger than Eastern Kingbird nest trees, and Western Kingbird nests were higher. The emphasis placed on height by DFA of the nest tree data is given further support by the finding that across the prairies Western Kingbird nests were significantly higher than those of Eastern Kingbirds. It would appear, then, that vertical separation is a basis for nesting habitat resource partitioning between these species. Thus, at the level of the nest tree, the habitat niche of the Western Kingbird is not a subset of that of the Eastern Kingbird, and thus, only the occasional conflict would arise between members of the two species at a nest site.

NEST SITE SELECTION

Wiens (1973) pointed out that distinct bird-vegetation relationships can be discovered at the within-habitat level, but that these patterns may be of a very fine spatial scale. This is the case with Eastern and Western kingbird nest site selection in the ridge forest at Delta Marsh. The total range of variation in the vegetation, both structural and floristic, is small, and thus the differences in nest sites of congeneric species will be subtle, at best.

The question remains whether the distribution of the nests of each species represents true nest site *selection*, or merely nest site *correlation* (Wiens 1976). Does the distribution of nests represent an active preference on the part of either or both species, or is the correlation of a species' presence with certain habitat factors the result of the operation of extrinsic forces? If the former alternative applies, on what basis are nest sites chosen? The results of this study are only correlational, and such questions cannot be answered conclusively without experimental manipulation of the system. Nevertheless, some evidence points toward true nest site selection.

Western Kingbirds were seen in the ridge forest a few days earlier than Eastern Kingbirds each year. They therefore had the advantage of a few days to select their nest sites. Since our observations indicated that a nest was usually located where a pair had been observed first, it would appear that Western Kingbirds were not displaced from their preferred habitats by the later arriving Eastern Kingbirds. Also, Western Kingbirds in the ridge forest showed the same tendency that they showed across the prairies to nest significantly higher than Eastern Kingbirds. Since the average tree height, nest tree height, and nest height were significantly higher at Western Kingbird sites than at Eastern Kingbird sites, it would appear, again, that Western Kingbirds were not displaced by Eastern Kingbirds.

The similarity of north-zone Eastern Kingbird and Western Kingbird nest sites would suggest that the presence of Western Kingbirds in the north zone could have resulted in the displacement of some Eastern Kingbirds from preferred habitat in the north zone to south-zone habitat. This may have occurred, but our observations indicated that some of the earliest Eastern Kingbird nest sites were situated in south-zone habitat in both years. These sites obviously were not exploited by late arrivers or by

birds that had been unsuccessful in obtaining north-zone sites. In any case, the high degree of intraspecific aggression, compared with the infrequent instances of interspecific aggression, would suggest that intraspecific interactions exerted a greater influence on the distribution of nests of both species. Assuming, then, that nest sites were actively selected by both species, the basis for differential selection would appear to be a combination of habitat and nest tree variables. Western Kingbird nest sites were characterized by fewer but larger trees than Eastern Kingbird sites, and Western Kingbird nest trees were larger and their nests were higher than those of Eastern Kingbirds.

In such a widely distributed species as the Eastern Kingbird, exposed to a wide variation in habitats throughout its range, sufficient intrapopulational variation may exist that some individuals may, in fact, demonstrate a preference for north-zone type sites and others for south-zone type sites, totally independently of the presence of a congener. Alternatively, strong intraspecific competition may force some individuals from their preferred sites. In either case, this plasticity may well explain the much greater density of Eastern Kingbirds at Delta Marsh. The stenotypic response of the Western Kingbird, on the other hand, may prevent individuals from selecting south-zone type sites, or even a greater range of north-zone type sites, in spite of their availability and suitability, and thereby may limit the density well below that of the Eastern Kingbird. Alternatively, because the Western Kingbird is at the periphery of its range at Delta Marsh, the population may never reach a density sufficient to force individuals into sites perceived to be less acceptable.

ACKNOWLEDGMENTS

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RECENT PUBLICATIONS

Search for the Spiny Babbler/A Naturalist's Adven-ture in Nepal.—S. Dillon Ripley. 1978. Ratna Pustak Bhandar, Kathmandu, Nepal. 301 p. $12.50. Source: Smithsonian Institution Press, P.O. Box 1579, Wash-ington, DC 20013. This is a reprint edition of a work first published in 1952, the story of Ripley's 1948 ex-pedition in Nepal. It is a colorful and engrossing nar-rative of exotic places and animals, with many anec-dotes about the operation of the expedition itself. The account gains historical interest as a record of a now-past setting and a manner of ornithological field work. The book is illustrated with the original map and pho-tographs, as well as a new color plate of the quarry, *Turdoides nipalensis.* Bibliography, index.

Birds of Africa.—John Karmali. 1980. Viking Press, New York. 191 p. $25.00. This oversize book is pri-marily a showcase for the author's outstanding photo-graphs of birds, in color and monochrome. Karmali lives in Nairobi, and his pictures bespeak long ac-quaintance with his subjects, as well as patience and technical excellence. These are not the shots of a vis-itor on safari. Supplementing them is an accurately in-formative nontechnical text that characterizes each family and describes the species shown. Contrary to the book's title, coverage is limited to *some* of the species in East Africa. In closing, the author gives notes on the color plates, explaining the circumstances in which the picture was taken and his photographic technique. In both text and illustrations, this book sur-passes the usual coffee table volumes on birds. Ref-erences, index.

Winter Population Trends of Raptors in Washing-ton from Christmas Bird Counts.—Dwight G. Smith and Richard L. Knight. 1981. Washington Dept. of Game, Olympia. 76 p. Paper cover. Source: Washing-ton Dept. of Game, 600 N. Capitol Way, Olympia, WA 98504. Data from Christmas Bird Counts (CBC) are in-creasingly being used for population studies because they are often the only long-term, wide-coverage fig-ures available. Such is the case here. Counts spanning 33 years were analyzed for 16 species of hawks and eagles and 10 species of owls in Washington. Temporal and geographic trends are summarized for each species, supplemented by many graphs. Overall trends, cautions to be observed in using CBC data, and questions for future study are discussed. A useful com-pilation for raptor-watchers in the Pacific Northwest and for those who would like to analyze CBC data else-where. References.

Proceedings of the Washington Bald Eagle Sym-posium.—Edited by R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen. Date and publisher not given. 254 p. Paper cover. Presumed source: as above. A symposium to assemble the results of research on the ecology of the Bald Eagle in Washington and ad-jacent states was held at the Seattle Aquarium in June 1980. Its papers are published here, grouped according to theme: overviews, management, nesting studies and winter studies. The opening address, by Gordon Ori-ans, is a stimulating examination of plumage patterns in eagles and their possible roles in social interactions. The volume offers much information of interest to ea-gle biologists, chiefly within its region of coverage and Alaska. Illustrated, references.