

HABITAT SELECTION BY THE WESTERN KINGBIRD IN WESTERN NEBRASKA: A HIERARCHICAL ANALYSIS¹

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Abstract. This study examined the relationship between habitat structure and habitat use by the Western Kingbird (*Tyrannus verticalis*) in western Nebraska using hierarchical analysis. Multivariate statistics compared habitat used by Western Kingbirds with a null model of random, unused habitat at multiple scales: macrohabitat (habitat type and territory) and microhabitat (nest tree and nest site). Western Kingbirds exhibit different patterns of habitat use at different spatial scales. They are highly selective at the macrohabitat scale, using only a subset of the available habitat types. Used habitat types have large, widely spaced cottonwood trees with greater grass cover, while unused habitat types have smaller, more closely spaced trees with less grass cover. In contrast, Western Kingbirds are less selective within the macrohabitat scale. There are few significant differences between used and unused territories—only maximum canopy height was significantly different. Western Kingbirds are highly selective at the microhabitat scale, and nest in only a subset of the available trees—larger, taller trees with more available perches. This pattern of nest tree use is consistent between used study sites, even in the face of some inter-site differences in habitat structure. In addition, nest-site location is similar between used study sites and among nest trees. Habitat use by Western Kingbirds in western Nebraska is consistent with a hierarchical view of habitat selection in which Western Kingbirds use different sets of selection criteria at different scales, arriving within the habitat type and then selecting territories, nest trees and nest sites.

Key words: *Habitat selection; habitat use; hierarchical analysis; habitat structure; multivariate; spatial scale; Western Kingbird.*

INTRODUCTION

Habitat selection involves discrimination among alternative habitats that provide different sets of circumstances affecting survival and reproduction (Lack 1933, 1940; Hildén 1965; Fretwell and Lucas 1970; Parsons 1983; Willson 1974; Cody 1985). The choice of a particular habitat is affected by proximate cues from the environment such as habitat structure and floristics, and ultimate factors such as long-term food availability and phylogenetic constraints (Hildén 1965, Hutto 1985). Clearly, habitat selection has important ecological and evolutionary consequences for individual organisms and species; unfortunately, the mechanisms of the decision-making process are poorly understood (Hildén 1965, Cody 1985, Orians and Wittenberger 1991). Habitat use, on the other hand, does not connote a particular process but indicates the actual distribution of individuals (i.e., correlations with specific habitat features). This study will inves-

tigate the habitat use of Western Kingbirds to draw inferences about the process of habitat selection.

Environmental heterogeneity exhibits hierarchical spatio-temporal organization, forming the background against which individuals select habitats and communities are assembled (Allen and Star 1982, Maurer 1985, O'Neill et al. 1986, Wiens 1986, Kotliar and Wiens 1990, Kolasa and Pickett 1991). Biological components are sorted into different levels of spatial scale by abiotic and biotic processes nested within a hierarchy of habitat units or "patches" (Kolasa 1989, Kotliar and Wiens 1990). Because habitat selection involves responses to this hierarchical patch structure, hierarchical analysis can be useful in examining the multi-dimensional interactions between organisms and their environment (Wiens 1986, Kotliar and Wiens 1990). Descriptions of habitat selection are scale dependent; results at one scale cannot be extrapolated to other levels (Wiens 1986, Wiens et al. 1987, Kolasa 1989, Kotliar and Wiens 1990). It is important for ecologists to consider the hierarchical nature of environmental variation when studying processes such as habitat selection (Kotliar and Wiens 1990, Orians and Wittenberger 1991).

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One approach to this problem is to design ecological studies that are nested within a spatial hierarchy (Maurer 1985, Wiens 1986, Wiens et al. 1987, Legendre and Fortin 1989, Ver Hoef and Glenn-Lewin 1989, Orians and Wittenberger 1991). This study used hierarchical analysis to examine the relationship between habitat structure and habitat use by Western Kingbirds in western Nebraska, and addressed a series of inter-related questions: (1) Do Western Kingbirds use breeding habitat non-randomly; (2) If so, which parameters of habitat structure are correlated with habitat use; and (3) Can these important habitat parameters be used to discriminate between used and unused habitat in a predictable manner (i.e., cross-validation)? Each of these questions was evaluated for several spatial scales: macrohabitat (habitat type and territory) and microhabitat (nest tree and nest site). Hierarchical analysis can identify patterns of habitat use at different scales, illuminating ecological processes that affect habitat selection at different scales.

Other studies have evaluated habitat use of Western Kingbirds for multiple scales, but their descriptions of specific levels of a spatial hierarchy were not uniform (Hespenheide 1964, Smith 1966, Ohlendorf 1974, MacKenzie and Sealy 1981, Blancher and Robertson 1984). Several different descriptions were integrated into a spatial hierarchy relevant for Western Kingbirds: biogeographic; regional; macrohabitat and microhabitat (Eldredge 1985, Wiens et al. 1986, Morris 1987, Wiens et al. 1987, Blondel 1987, Kolasa 1989). The biogeographic scale (10^3 km²) is large enough that a species will encounter substantially different climates and assemblages of species at different sites (Wiens et al. 1986); populations of the same species at different sites may be genetically differentiated. The regional scale (10^2 km²) is often associated with specific biomes, such as grasslands, deserts or forests (Wiens 1986); regional comparisons usually involve different biomes. The macrohabitat scale (10 km²) includes the minimum area in which a population of individuals perform all of their biological functions during a typical activity cycle (Morris 1987). Within the macrohabitat scale, different habitat types (i.e., home range) are described by different suites of physical, chemical, and biological variables; within habitat type variation (i.e., territory) is described by similar suites of physical, chemical, and biological variables

(Morris 1987). Microhabitat can be quantified by physical, chemical, and biological variables that are associated with the allocation of time and energy by an individual within its nest tree and nest site (Morris 1987). This study focused on the analysis of macrohabitat and microhabitat use by Western Kingbirds.

METHODS

STUDY ORGANISM AND STUDY SITES

The Western Kingbird (*Tyrannus verticalis*), a migratory territorial insectivore, commonly inhabits open and partially open country, especially savanna, agricultural croplands, and areas with scattered trees (Bent 1942, Johnsgard 1979). Pairs mate monogamously, normally raising a single brood (Bent 1942, Johnsgard 1979). Its summer breeding range (Fig. 1) extends north to southern Canada from British Columbia to Manitoba, south to northern Mexico and southern Texas, west to the Pacific coast, and east to approximately the Mississippi River (AOU Checklist, 6th Ed. 1983). It arrives on summer breeding sites in western Nebraska during May and nests from late May to late July (Bent 1942, Johnsgard 1979). The winter range includes southern Mexico and central America south to Costa Rica.

Western Kingbirds in Keith County, Nebraska near Cedar Point Biological Station at Lake McConaughy (41°13'N; 101°40'W) have been studied since 1985. This study used data collected in 1986. The four study sites, two in which Western Kingbirds nested (i.e., used) and two in which they did not (i.e., unused), were east of the Kingsley Dam of Lake McConaughy. The first used site (site 1) was approximately 5 km east of Kingsley Dam on the north side of the North Platte River, just east of Keystone Lake, encompassing about 20 ha. The second used site (site 2) was adjacent to the east side of Kingsley Dam within the Lake Ogallala State Recreation Area, encompassing about 20 ha. The two unused sites (site 3 and 4) were directly across from site 1 on the south side of the North Platte River. Both unused sites encompassed approximately 15 ha. All study sites were of the same general habitat: floodplain riparian-grassland dominated by cottonwood trees (*Populus deltoides*). Shrubs included small cottonwood and cedar trees, and wild rose (*Rosa* sp.). Grass cover included downy brome (*Bromus tectorum*). Herbaceous vegetation included native forbs, poison ivy (*Rhus rad-*

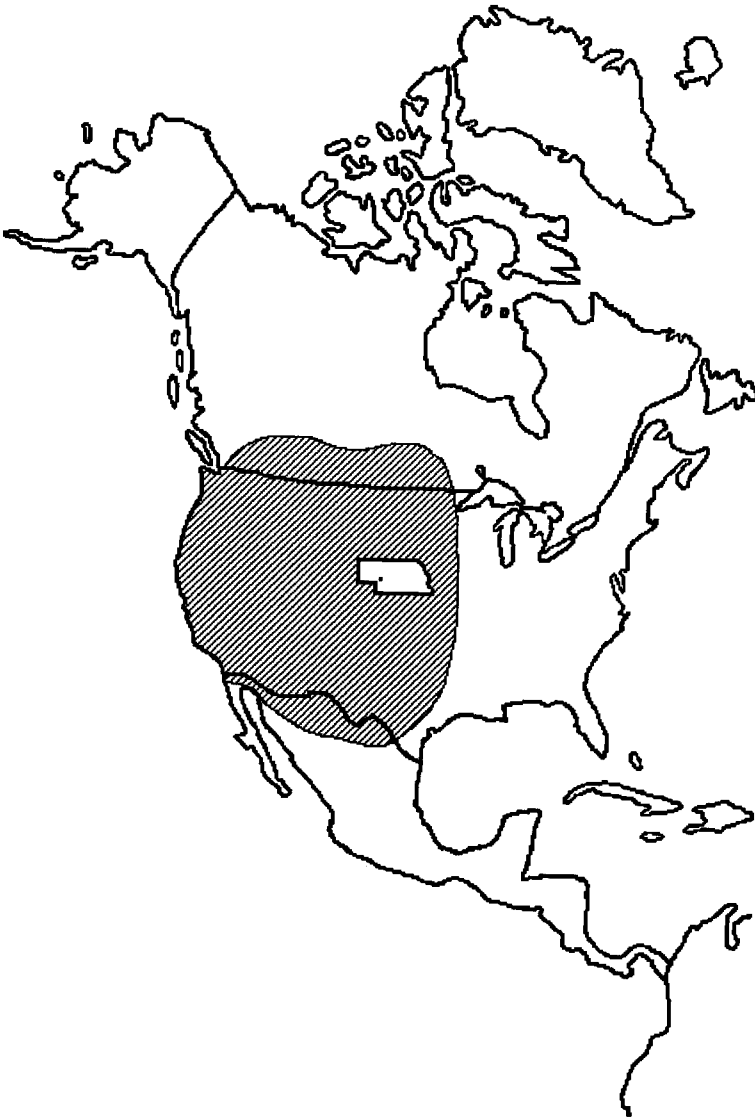


FIGURE 1. The breeding distribution of the Western Kingbird (*Tyrannus verticalis*). The state of Nebraska and the location of the study area (small black square) are indicated on the map.

icans) and prickly pear cactus (*Opuntia compressa*).

SAMPLING DESIGN AND ANALYSIS

Several different criteria were used when choosing study sites in 1986. Sites used by Western Kingbirds had to have a minimum of ten active nests. In contrast, unused sites needed potential nest sites, but could not have Western Kingbird nests; Western Kingbirds in western Nebraska nest almost entirely in trees (Johnsgard 1979).

Also, unused sites needed to be close enough to the used sites that Western Kingbirds could have considered them as possible alternatives. All study sites were surrounded by natural boundaries such as the Platte River, small lakes, roads or extended agricultural areas devoid of trees. Although Western Kingbirds were not restricted to foraging within used study sites, most foraging occurred there. The focus of this study was on nesting habitat use, but foraging habitat was also evaluated.

TABLE 1. Habitat variables measured at the macrohabitat (habitat type and territory) and microhabitat (nest tree and nest site) spatial scales.

Macrohabitat	Microhabitat
Habitat type and territory	Nest tree
Density of cottonwoods (number/plot)	Tree species (categorical)
Basal area of cottonwoods (cm ² /plot)	Tree height (m)
Density of red cedars (number/plot)	Diameter at breast height (cm)
Basal area of red cedars (cm ² /plot)	Number of main trunks per tree (number)
Total number of shrubs (number/plot)	Number of perches per tree (number)
Ground cover height (dm)	Nest site
Percent ground cover (%)	Nest height (m)
Maximum canopy height (m)	Relative nest height
Percent canopy cover (%)	Horizontal distance: nest to trunk (m)
	Horizontal distance: nest to perimeter of crown (m)
	Number of branches supporting the nest (number)

Macrohabitat variables described aspects of the trees, shrubs, ground vegetation and canopy (Table 1). A 0.75 km transect, consisting of five randomly spaced 0.04 ha circular plots (James and Shugart 1970), sampled habitat type within each study site ($n = 20$). Ten Western Kingbird nest trees were located within each used study site (site 1 and site 2) ($n = 20$). In addition, ten random unused trees were chosen within each used site using a random number table ($n = 20$). A 0.04 ha circular plot (James and Shugart 1970), centered on each used and unused tree, sampled territorial habitat. Within each 0.04 ha circular plot, the species of each tree was noted and size class determined with a modified Biltmore scale (Bergin 1987). The total number of shrubs was counted. Ground cover height was determined at 20 random points using a cover stick painted with alternating black and white decimeter segments. The highest segment touched by ground vegetation at each point was recorded. Points that had no ground vegetation were recorded as zero and used to determine percent ground cover within each circular plot ($\% = [20 - \# \text{ of zeros}] / 20$). Percent canopy cover was determined by sighting vertically through an ocular tube, and recording the presence or absence of leaves for twenty canopy sightings made on two randomly oriented, perpendicular transects across the circular plot. The maximum canopy height (CHGT) of each plot was calculated by determining the angle (ϕ) subtended between the ground and the top of the canopy from a point 15.25 m from the tree using a clinometer ($\text{CHGT } 15.25 \text{ m} [\tan \phi + 1.7 \text{ m}]$). The soil type and substrate, and any

special features of each plot such as roads or creeks were also noted.

Microhabitat variables described the physiognomic structure of used and unused trees, and used nest sites (Table 1). Each used and unused tree was identified to species. Tree and nest height was determined by the same procedure as maximum canopy height. The circumference was measured directly with flexible tape and converted into diameter at breast height (DBH). The number of main trunks and dead branches in the top of the canopy (i.e., watch perches) were counted. Relative nest height was calculated by dividing the nest height by the tree height. The horizontal distance from the nest to the main trunk and canopy periphery were determined by marking a point on the ground directly below the nest and measuring the distance with a tape. The number of branches supporting the nest were counted.

Multivariate analysis of variance (MANOVA) tested the null hypothesis of no difference between used and random, unused habitat (MacKenzie and Sealy 1981, Clark et al. 1983, Bekoff et al. 1987) by comparing linear vector combinations of habitat variables using Wilk's lambda (Johnson and Wichern 1982). A completely randomized design (CRD) was used for habitat type, and a randomized complete block (RCB) with used sites as blocking criteria was used for territories and nest trees (Zar 1984). Univariate ANOVA's tested each habitat variable separately, determining relative importance. The interaction error term was used to calculate the F -ratio in this mixed model design

of random effects (sites) and fixed effects (use) for both the MANOVA and ANOVA. If the interaction proved non-significant, then the mean square error was used to calculate the *F*-ratio (Zar 1984).

A posteriori discriminant function analysis (DFA) separated data sets into linear combinations of habitat variables that maximized the Mahalanobis distance between used and unused observations (Johnson and Wichern 1982). *A priori* DFA classification, which tested hypotheses of group membership, cross-validated habitat use of Western Kingbirds using the discriminant function generated from one study site to classify observations from the other study site (Efron 1983). Cross-validation provided an unbiased estimate of misclassification probabilities (Efron 1983, Williams 1983). *A priori* DFA classification contrasts with the most common use of DFA—*a posteriori* separation using posterior probabilities and resubstitution which is biased downward (MacKenzie and Sealy 1981, Clark et al. 1983, Bekoff et al. 1987, Solow 1990). The percent of misclassified observations gave an indication of the consistency of the discriminant function. Each *a priori* classification was tested against a null hypothesis of random assignment using Fisher's exact test. All statistical analyses were performed using the Statistical Analysis System (SAS Institute 1985).

RESULTS

MACROHABITAT (HABITAT TYPE AND TERRITORY)

The habitat types used by Western Kingbirds were significantly different from unused habitat types in several ways (Table 2; MANOVA). Used habitat types had fewer but larger trees, resulting in an open canopy with taller ground cover and more shrubs. Four out of nine variables were significantly different between used and unused study sites (Table 2; ANOVA). The *a posteriori* DFA of used vs. unused habitat type classified all observations correctly. The canonical structure of the discriminant function showed high correlations with (+) density of cottonwoods, (-) ground cover height, and (-) percent ground cover (Table 2). A test of homogeneity of covariance was significant; unpooled correlation matrices were used in the *a posteriori* DFAs. Much of this heterogeneity can be attributed to high variance in the number of shrubs on used

site 2, which contributed little to the canonical structure of the DFA (Table 2). Violation of this assumption does not appear to have significantly biased the *a posteriori* classification (Williams 1983). No *a priori* classification was performed at this scale.

There was no significant difference between used and unused territories; there was a significant site difference, but no significant selection \times site interaction (Table 3; MANOVA). The relative differences between used and unused variable means were similar among sites; the density of trees was less, and the basal area, percent ground cover and canopy height were greater on used vs. unused territories—only canopy height was significantly different (Table 3; ANOVA). The *a posteriori* DFA of both study sites classified correctly 90% of used and unused territories on site 1, and 90% used and 80% of unused territories on site 2. However, the *a priori* DFA classified correctly only 60% of used and 80% of unused territories, using the discriminant function of site 1 to cross-validate site 2 observations; this was not significantly different from random assignment. The canonical structure of the discriminant function was highly correlated with (+) maximum canopy height (Table 3). The covariance was homogeneous; pooled correlation matrices were used in the DFA.

MICROHABITAT (NEST TREE AND NEST SITE)

Used and unused trees were significantly different within study sites; there were significant site differences but no significant interaction (Table 4a; MANOVA). The mean value of each variable was greater for used trees than unused trees—only the number of main trunks was not significant (Table 4a; ANOVA). Used nest-site variables of Western Kingbird nests were not different between study sites (Table 4b; ANOVA). The *a posteriori* DFA, using tree height and diameter at breast height, classified correctly 80% of both used and unused trees on site 1, and 100% of used and 90% of unused trees on site 2. The *a priori* DFA classified correctly 90% of both used and unused trees, using the discriminant function of site 1 to cross-validate site 2 observations. This *a priori* classification was significantly different from random assignment. The covariance was homogeneous; pooled correlation matrices were used in the DFA.

TABLE 2. Macrohabitat (Habitat Type). The mean values, standard errors (SE), *F*-ratio (*F*), and the correlations with the discriminant function (DFA) for each habitat variable of both used and unused study sites (*n* = 20). The multivariate and univariate analysis of variance (MANOVA and ANOVA) compared the means of used and unused study sites using a completely randomized design.

Habitat Variable	Unused	Used	<i>F</i>	DFA
ANOVA				
Density of cottonwoods	10.5 (1.7)	1.8 (0.34)	24.32**	0.771
Basal area of cottonwoods	3.7 (0.73)	1.6 (0.68)	4.86*	0.469
Density of red cedars	1.6 (0.67)	1.2 (0.47)	0.24	0.117
Basal area of red cedars	0.1 (0.06)	0.04 (0.01)	1.78	0.305
Shrubs	5.7 (0.83)	16.3 (5.00)	3.96†	-0.432
Ground cover height	2.4 (0.21)	5.8 (0.52)	35.86**	-0.829
Percent ground cover	70.0 (2.0)	85.0 (3.00)	11.66**	-0.638
Max. canopy height	10.3 (0.93)	12.1 (1.93)	0.74	-0.203
Percent canopy cover	45.0 (6.00)	29.0 (6.00)	3.68†	0.419
MANOVA (Wilk's Lambda)				
Used vs. unused sites			32.43**	

** *P* < 0.01.
 * *P* < 0.05.
 † *P* < 0.10.

DISCUSSION

Western Kingbirds exhibited different patterns of habitat use at different spatial scales. They used only a subset of the available habitat types—large, widely spaced cottonwood trees with greater grass cover. In contrast, Western Kingbirds were less selective in use of territories within the habitat type—only maximum canopy height was important. Western Kingbirds were highly selective at the microhabitat scale using only a subset

of the available trees—larger, taller trees with more available perches. Western Kingbird nest sites were also similar between study sites and among nest trees.

What inferences about habitat selection of Western Kingbirds can be drawn from the patterns of habitat use? Even though suitable trees were available, Western Kingbirds did not nest in all sites, suggesting they use larger-scale information such as tree density, spatial distribution, canopy cover or ground cover when se-

TABLE 3. Macrohabitat (Territory). The mean values, standard errors (SE), *F*-ratio (*F*), and the correlation with the discriminant function (DFA) for each habitat variable of random and nest territories by used study site (*n* = 40). The multivariate and univariate analysis of variance compared the means of used and unused territories using a randomized complete block design with sites as blocking criteria.

Habitat Variables	Site 1		Site 2		<i>F</i>	DFA
	Unused	Used	Unused	Used		
ANOVA						
Density of cottonwoods	3.2 (0.88)	2.2 (0.36)	6.9 (0.86)	5.9 (1.40)	1.11	-0.235
Basal area of cottonwoods	5.5 (1.43)	6.3 (1.13)	7.2 (1.31)	9.1 (1.61)	0.92	0.246
Density of red cedars	2.0 (0.92)	2.2 (1.06)	1.1 (0.45)	0.8 (0.53)	0.001	-0.017
Basal area of red cedars	0.5 (0.22)	0.2 (0.12)	0.1 (0.04)	0.1 (0.04)	0.30	-0.140
Shrubs	2.4 (0.64)	2.4 (1.18)	15.1 (3.65)	18.0 (7.08)	0.13	0.083
Ground cover height	3.1 (0.26)	3.6 (0.21)	3.8 (0.93)	4.0 (1.01)	0.06	0.068
Percent ground cover	92.0 (2.00)	92.0 (3.27)	65.0 (3.72)	61.0 (5.25)	0.21	-0.077
Max. canopy height	12.6 (1.09)	15.2 (1.03)	13.9 (0.99)	18.1 (0.71)	12.45**	0.775
Percent canopy cover	46.0 (6.69)	56.0 (2.77)	69.5 (5.93)	62.5 (3.00)	0.09	0.071
MANOVA (Wilk's Lambda)						
Used vs. unused territories					2.25†	
Site					13.74**	
Interaction					1.18	

** *P* < 0.01.
 * *P* < 0.05.
 † *P* < 0.10.

TABLE 4. Microhabitat (Nest Tree and Nest-Site). The mean values, standard errors (SE), and *F*-ratio of each variable for random and nest trees ($n = 40$) by used study site. a) The multivariate and univariate analysis of variance compared means of used and unused trees using a randomized complete block design with sites as blocking criteria. b) The multivariate and univariate analysis of variance compared means of nest sites between used study sites ($n = 20$).

a) Nest tree					
Tree variables	Site 1		Site 2		<i>F</i>
	Unused	Used	Unused	Used	
ANOVA					
Tree height	12.6 (1.09)	15.8 (0.86)	12.9 (0.79)	17.9 (0.45)	24.65**
Diameter at breast height	51.3 (3.82)	73.5 (7.40)	35.1 (3.04)	74.0 (8.18)	25.60**
Number of main trunks	1.3 (0.15)	1.5 (0.31)	1.2 (0.13)	1.7 (0.30)	2.17
Number of perches	16.2 (2.55)	25.6 (4.70)	3.6 (0.85)	9.0 (1.56)	6.88*
MANOVA (Wilk's Lambda)					
Used vs. unused trees					8.93*
Site					9.27**
Interaction					0.70
b) Nest-site					
Nest-Site Variables	Site 1		Site 2		<i>F</i>
ANOVA					
Nest height	10.96 (0.91)		11.27 (0.80)		0.07
Relative nest height	0.73 (0.04)		0.66 (0.04)		1.89
Horizontal distance—trunk	3.55 (0.71)		4.60 (0.78)		0.90
Horizontal distance—perimeter	3.15 (0.69)		3.60 (0.57)		0.25
Supporting branches	3.00 (0.30)		3.00 (0.33)		0.00
MANOVA (Wilk's criteria)					
Site					1.13

** $P < 0.01$.

* $P < 0.05$.

lecting macrohabitat. Other environmental factors such as food availability, predation risk or presence of conspecifics, not simply the presence of suitable nest sites, must also influence selection of macrohabitat (Murphy 1983, Blancher and Robertson 1985a, 1987). In contrast, only characteristics of the nest tree appear to be important in determining territory quality. Although highly territorial Western Kingbirds do not defend foraging habitat (Hespenheide 1964, Smith 1966, Ohlendorf 1974, Blancher and Robertson 1984). Territorial defenses are usually initiated after intrusion into the nest tree canopy (Bergin 1987), suggesting that the canopy provides approximate spatial limits to the defended territory. Further, only maximum canopy height was important in distinguishing used from unused territories, and in each case measured the height of the central nest tree, suggesting that Western Kingbirds do not use macrohabitat characteristics to select territories.

The microhabitat use of Western Kingbirds is correlated with characteristics of the nest tree;

Western Kingbirds use only a small subset of the available trees within used habitat types. This pattern is consistent between sites and through time, suggesting that Western Kingbirds use a specific set of criteria such as tree size to discriminate between alternative trees. About half of all nest trees have been reused more than once, usually dependent on nest success the previous year (Bergin 1987, unpubl. data). Tree size may provide information about nest-site availability; larger trees provide more possible nest sites. The typical Western Kingbird nest is located high and toward the perimeter of the canopy (Murphy 1983), and several factors such as microclimate and nest predation are probably related to this specialization (Walsberg 1985, Martin 1988). The combination of large tree size and perimeter nest-site location increases the potential search area, decreasing the probability of detection by predators (Blancher and Robertson 1982, 1985a; Murphy 1983). Western Kingbirds exhibit directional preferences when selecting nest sites; few Western Kingbird nests are located on the

west side of trees (Bergin 1991). This may reduce the risk of thermal overload due to direct afternoon sunlight and catastrophic nest loss from prevailing westerly winds (Walsberg 1985).

Western Kingbirds are neotropical migrants, and larger scales are relevant. Neotropical migrants move between different biogeographic areas with different climates, vegetative formations and assemblages of species, encountering different natural selection regimes (Wiens 1986, Wiens et al. 1987). Western Kingbirds breed in several different biomes within North America including desert, grassland, shrub-steppe and forest (Bent 1942, Hespeneheide 1964, Smith 1966, Ohlendorf 1974, MacKenzie and Sealy 1981, Blancher and Robertson 1984). While habitat "decisions" at these larger scales are primarily historical, individual migrants still must make choices, even if innately. Many Western Kingbirds return to the same area year after year (Blancher and Robertson 1985b), but some will make mistakes or explore new areas, resulting in mortality or range expansion.

Hierarchical analysis of habitat use can reveal the hierarchical organization of habitat selection. The decision-making process of habitat selection is nested within a reference system of hierarchical habitat units (Kolasa 1989), and reflects the hierarchical structure of the environment (Kotliar and Wiens 1990). Organisms make a series of step-wise decisions based on different sets of selection criteria for each scale; first choosing a general place to live (habitat type), then making subsequent decisions about the use of different patches (territory), and finally selecting a place to build a nest (nest tree and nest site) (Hildén 1965, Hutto 1985, Klopfer and Ganzhorn 1985, Orians and Wittenberger 1991). The availability of patches and nest sites is dependent on the habitat type. Information from that scale may be necessary but insufficient; proximate cues of the nest site are closer to the ultimate factors determining reproductive success (Hutto 1985). Habitat use by Western Kingbirds in western Nebraska is consistent with this view of habitat selection. Western Kingbirds use different sets of selection criteria for different scales; first arriving within the habitat type and then selecting territories, nest trees and nest sites. Results of this study do not provide a test of such a hypothesis, but do point to the need for models of habitat selection to entail hierarchical organization.

Hierarchical analysis refines questions about

the ecological processes that affect habitat selection. Instead of focusing on a single scale, comparisons can be made at multiple scales, improving our understanding of species interactions and ecological processes. Focusing on a single scale reduces the ability of the observer to identify patterns only seen clearly at other scales (Maurer 1985). The spatial and temporal scales on which ecological systems are observed makes a difference in the patterns that are detected and the processes proposed to account for them (Wiens 1986). Explicit biological definitions of spatial and temporal scales are essential if we are to resolve the influence of space and time on patterns, structures, processes and functions in ecological systems (Morris 1987). We can no longer afford to ignore the implications of spatial and temporal variation for ecological research (Wiens 1986).

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LITERATURE CITED

- ALLEN, T., AND T. STARR. 1982. Hierarchy: perspectives for ecological complexity. Univ. of Chicago Press, Chicago and London.
- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds. 6th ed. American Ornithological Union, Lawrence, KS.
- BEKOFF, M., A. SCOTT, AND D. CONNER. 1987. Non-random nest-site selection in Evening Grosbeaks. *Condor* 89:819-829.
- BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows and their allies. U.S. Natl. Mus. Bull. 179.
- BERGIN, T. M. 1987. A multivariate hierarchical examination of habitat selection in *Tyrannus verticalis*. M.Sc. thesis, University of Nebraska-Lincoln, Lincoln, NE.
- BERGIN, T. M. 1991. A comparison of goodness-of-fit tests for analysis of nest orientation in Western Kingbirds (*Tyrannus verticalis*). *Condor* 93:164-171.
- BLANCHER, R., AND R. ROBERTSON. 1982. Kingbird aggression: does it deter predation? *Anim. Behav.* 30:929-930.

- BLANCHER, R., AND R. ROBERTSON. 1984. Resource use by sympatric kingbirds. *Condor* 86:305-313.
- BLANCHER, R., AND R. ROBERTSON. 1985a. Predation in relation to spacing of kingbird nests. *Auk* 102: 654-658.
- BLANCHER, R., AND R. ROBERTSON. 1985b. Site consistency in kingbird breeding performance: implications for site fidelity. *J. Anim. Ecol.* 54:1017-1027.
- BLANCHER, P., AND R. ROBERTSON. 1987. Effect of food supply on the breeding biology of Western Kingbirds. *Ecology* 68:723-732.
- BLONDEL, J. 1987. From biogeography to life history theory: a multithematic approach illustrated by the biogeography of vertebrates. *J. Biogeog.* 14: 405-422.
- CLARK, L., R. RICKLEFS, AND R. SCHREIBER. 1983. Nest-site selection by the Red-tailed Tropicbird. *Auk* 100:953-959.
- CODY, M. L. 1985. *Habitat selection in birds*. Academic Press, London.
- EFRON, B. 1983. Estimating the error rate of a prediction rule: improvement on cross-validation. *J. Am. Statis. Ass.* 74:777-785.
- ELDREDGE, N. 1985. *The unfinished synthesis*. Oxford Univ. Press, Oxford, England.
- FRETWELL, S., AND H. LUCAS. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-52.
- HESPEHIEDER, H. 1964. Competition and the genus *Tyrannus*. *Wilson Bull.* 75:265-281.
- HILDÉN, O. 1965. Habitat selection in birds: a review. *Ann. Zool. Fenn.* 2:12-34.
- HUTTO, R. 1985. Habitat selection by nonbreeding, migratory land birds, p. 455-476. *In* M. Cody [ed.], *Habitat selection in birds*. Academic Press, London.
- JAMES, F., AND H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JOHNSGARD, P. 1979. *Birds of the Great Plains*. Univ. of Nebraska Press, Lincoln, NE.
- JOHNSON, R., AND D. WICHERN. 1982. *Applied Multivariate Statistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- KLOPFER, P., AND J. GANZHORN. 1985. Habitat selection: behavioral aspects, p. 435-453. *In* M. Cody [ed.], *Habitat selection in birds*. Academic Press, London.
- KOLASA, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* 70:36-47.
- KOLASA, J., AND S. PICKETT. 1991. *Ecological heterogeneity*. Ecological studies. Vol. 86. Springer-Verlag, New York.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- LACK, D. 1933. Habitat selection in birds. *J. Anim. Ecol.* 2:239-262.
- LACK, D. 1940. Habitat selection and speciation in birds. *Brit. Birds* 34:80-84.
- LEGENDE, P., AND M. FORTIN. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107-138.
- MACKENZIE, D., AND S. SEALY. 1981. Nest site selection in Eastern and Western Kingbirds: a multivariate approach. *Condor* 83:310-321.
- MARTIN, T. M. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evol. Ecol.* 2:37-50.
- MAURER, B. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. *Ecol. Monog.* 55:295-312.
- MORRIS, D. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- MURPHY, M. 1983. Nest success and nesting habits of Eastern Kingbirds and other flycatchers. *Condor* 85:208-219.
- OHLENDORF, H. 1974. Competitive relationships among kingbirds (*Tyrannus*) in Trans-Pecos Texas. *Wilson Bull.* 86:357-373.
- O'NEILL, R. V., D. L. DE ANGELIS, J. B. WAIDE, AND T.F.H. ALLEN. 1986. *A hierarchical concept of ecosystems*. Princeton Univ. Press, Princeton, NJ.
- ORIAN, G., AND J. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137: 829-849.
- PARSONS, P. 1983. Ecobehavioral genetics: habitats and colonists. *Ann. Rev. Ecol. Syst.* 14:35-55.
- SAS INSTITUTE. 1985. *SAS user's guide: statistics*, version 5 ed. SAS Institute Inc., Cary, NC.
- SMITH, W. 1966. Communication and the relationships in the genus *Tyrannus*. *Publ. Nuttall Ornithol. Club* 6.
- SOLOW, A. R. 1990. A randomization test for misclassification probability in discriminant analysis. *Ecology* 71:2379-2382.
- VER HOEF, J., AND D. GLENN-LEWIN. 1989. Multiscale ordination: a method for detecting pattern at several scales. *Vegetatio* 82:59-67.
- WALSBERG, G. 1985. Physiological consequences of microhabitat selection, p. 389-413. *In* M. Cody [ed.], *Habitat selection in birds*. Academic Press, London.
- WIENS, J. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds, p. 154-172. *In* J. Diamond and T. Case [eds.], *Community ecology*. Harper and Row Publishers, New York.
- WIENS, J., J. F. ADDICOTT, T. J. CASE, AND J. DIAMOND. 1986. Overview: the importance of spatial and temporal scale in ecological investigations, p. 145-153. *In* J. Diamond and T. Case [eds.], *Community ecology*. Harper and Row Publishers, New York.
- WIENS, J. A., J. T. ROTENBERRY, AND B. A. VAN HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48:132-147.
- WILLIAMS, B. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* 64:1283-1291.
- WILLSON, M. 1974. Avian community organization and habitat structure. *Ecology* 55:1017-1029.
- ZAR, J. H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.