

MULTISCALE ASSOCIATIONS BETWEEN CAVITY-NESTING BIRDS AND FEATURES OF WYOMING STREAMSIDE WOODLANDS¹

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Abstract. From 1982 through 1984, we studied riparian habitat use by cavity-nesting birds on three spatial scales: (1) nest trees, (2) nest sites (vegetation surrounding nest trees), and (3) disjunct fragments (0.1 to 32.3 ha) of floodplain forest. Nest cavities and nest trees differed substantially among bird species in terms of tree diameter at breast and nest height, nest height, nest-entrance diameter, whether the nest was in a limb or bole, and whether the nest entrance pointed above horizontal, horizontally, or below horizontal. Nest trees also differed significantly from randomly selected trees with respect to tree species and whether they were snags or nonsnag trees. Nest-entrance bearing did not differ significantly among species or from random. Distances between nest trees and the nearest section of stream differed significantly among some species. Habitats at species' nest sites and at randomly selected sites were indistinguishable in terms of shrub cover, tree density, snag density, vertical space between upper and lower canopies, distance to edge, and distance to opening. The size, shape, degree of isolation, and vegetative structure of habitat fragments significantly influenced species richness and abundance.

Features of Wyoming streamside woodlands on all three spatial scales influence habitat use and are important in structuring communities of cavity-nesting birds. Some patterns of habitat use on the scales of nest trees and habitat fragments were not predictable from habitat associations observed elsewhere for the same species. Bird-habitat relations on one scale were (or were not) predictable from relations on other scales, depending on the species.

Key words: *Cavity-nesting birds; floodplain woodlands; forest fragments; habitat selection; multiscale associations; spatial scale; Wyoming.*

INTRODUCTION

Ornithologists have proposed that avian habitat use results in part from a sequence of selection responses to characteristics associated with decreasing spatial scales (e.g., Svårdson 1949, Hildén 1965, Hutto 1985). Studies describing varying associations by the same species on different scales (Wiens and Rotenberry 1981, Ambuel and Temple 1983, Haney 1986) and circumstantial evidence of stepwise feeding-site selection (Burger and Gochfeld 1982) support this hierarchical view (Klopfer and Ganzhorn 1985). Apparently, responses within a species to different habitat scales are elicited by separate stimuli. Further, proximate and ultimate habitat cues from broad-, intermediate-, and small-scale attributes seem necessary to ensure survival and reproduction (Hutto 1985). An important implication of this selection paradigm for ornithologists modeling the effects of habitat use on avian community

structure is that a more realistic description is likely to emerge if responses on several spatial scales are examined (Karr 1983).

Habitat use by cavity-nesting birds has been studied frequently (e.g., Crockett and Hadow 1975, Stauffer and Best 1982, Brush 1983, Raphael and White 1984, and many others), but no previous investigation has examined detailed responses on more than one or two spatial scales. Our study involved extensive analyses on three spatial scales. The smallest scale focused on physical and floristic characteristics of nest trees; an intermediate scale involved structural and spatial features of nest sites (habitats surrounding nest trees); and the broadest scale dealt with the size, shape, degree of isolation, and structural attributes of forest fragments. This three-scale approach is important because it provides community ecologists and conservationists with a more complete view of how habitat features influence cavity-nester richness and abundance. Our work is also valuable because it identifies habitat-use patterns that are not predictable from those observed elsewhere for the same species (cf. Collins 1983, Karr and Freemark 1983, Wiens 1985:248), and bird-habitat relations on one scale

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that are (or are not) predictable from relations on other scales (cf. Wiens 1983:368).

Our principal goals were to assess multiscale habitat associations within species of cavity-nesting birds and to determine whether there were differences in such relations among species. Secondly, we investigated the extent to which associations on one scale were related to those on other scales. We tested three null hypotheses: (1) there are no significant differences in characteristics of nest trees or nest sites among species; (2) no significant differences exist between nest trees and randomly selected trees or between nest sites and randomly selected sites; (3) species richness, mean number of nests for a species, and the probability of nesting by a species are not related significantly to the size, shape, degree of isolation, or structural diversity of riparian forest fragments.

STUDY AREA

This study was conducted along 24 km of the North Platte River and 12.1 km of the Laramie River between Guernsey and Fort Laramie in Platte and Goshen Counties, Wyoming (1,290 to 1,311 m elevation). Both rivers flow eastward and are bordered by widely spaced bluffs found principally on their south banks. Irrigated cropland, pastureland, and disjunct but homogeneous fragments of cottonwood-willow (*Populus-Salix*) timber cover both floodplains, which are each approximately 1.0 km wide. Floodplain soils belong to the Torrifuvents-Haplargids association; average annual precipitation is approximately 36 cm. Beyond both floodplains to the north and south are rolling, treeless grasslands used primarily for livestock grazing. Further descriptions of the area can be found in Young and Singleton (1977) and Gerhart and Olson (1982).

METHODS

NEST-TREE AND NEST-SITE COMPARISONS

Nest searching. During June 1982, we searched the entire study area for tree cavities occupied by diurnal, hole-nesting birds. We systematically examined riparian vegetation, regardless of successional stage. Searches were made from 08:00 to 18:00 and were restricted to periods without rain (except an occasional drizzle) and winds <20 km/hr (Robbins 1981). From mid-May to early July 1983 and 1984, nest searches

were restricted to 34 habitat fragments spaced along 22.2 km of the North Platte River between Guernsey and Fort Laramie.

Nest-tree and nest-site measurements. During August 1982 and July and August 1983 and 1984, we estimated structural, spatial, and directional habitat parameters for nest trees and nest sites (Table 1). We identified species of trees using keys by Dorn (1977) and Porter (1979). A square, 0.09-ha (30- × 30-m) plot for sampling vegetation was centered on each nest tree; from observations made during June 1982, this plot size corresponded roughly to the area around the nest defended by adults of various species. Based on estimates of shrub-cover variance at 65 active nest sites, we used two 30-m transects (Mueller-Dombois and Ellenberg 1974) at each site to ensure 10% precision and 90% reliability of shrub-cover estimates (computations based on Schemnitz 1980:312); large- and small-shrub cover were estimated with each transect. Four measurements of the vertical distance between upper and lower canopies were made 10 m apart along each 30-m shrub transect; initial sampling at 61 active nest sites indicated eight sample points per site were sufficient to give mean vertical-space values within 10% of the true mean 90% of the time (Schemnitz 1980:312).

Location of random trees and random sites. During August 1984, we randomly selected 30 sites in habitat fragments (no more than one site per fragment) along 22.2 km of the North Platte River in which birds had nested during 1983 and 1984. The tree (≥ 10.2 cm dbh and at least 1.8 m tall) closest to the intersection of two random coordinates defined the center of each randomly selected 0.09-ha sampling plot; this tree is referred to as the "center tree" hereafter. Center trees were considered randomly selected trees.

HABITAT-FRAGMENT USE

Nest searching. From mid-May to mid-July 1983 and 1984, we searched (at a rate of 15 min/ha) for active nests in 34 habitat fragments along 22.2 km of the North Platte River between Guernsey and Fort Laramie. We completed all searches between 06:45 and 17:30, well within the active period for adults with young, as indicated by our 1982 observations. We visited each habitat fragment biweekly (four times each breeding season). The 34 fragments were arranged into nine groups based on their proximity to each other. Each group took approximately

TABLE 1. Variables measured for trees, sites, and habitat fragments used by cavity-nesting birds in southeastern Wyoming.^a

Scale	Variable (Clarifying comments)	
Nest tree	Diameter at breast height	
	Diameter at nest height	
	Nest-entrance diameter	
	Nest height	
	Nest in limb or bole	
	Nest-entrance bearing	
	Nest-entrance angle (Indication of whether the entrance pointed above horizontal, horizontally, or below horizontal)	
	Nest in snag or nonsnag tree (Snags were trees with completely or partially dead boles ≥ 10.2 cm dbh and ≥ 1.8 m tall; usually had one or more completely or partially dead limbs [adapted from Thomas 1979]. Nonsnag trees were free of obvious bole decay, but may have had one or more dead limbs)	
	Nest site	Vertical space between upper and lower canopies (Upper canopy included limbs and foliage supported by large and small trees; lower canopy included limbs and foliage supported by large and small shrubs)
		Large-tree density (Large trees were > 2.5 m tall and > 15.2 cm dbh, excluding snags)
Small-tree density (Small trees were > 2.5 m tall and ≤ 15.2 cm dbh, excluding snags)		
Large-shrub cover (Large shrubs were > 0.5 m tall but ≤ 2.5 m tall, excluding snags)		
Small-shrub cover (Small shrubs were ≤ 0.5 m tall)		
Distance to edge (Edge was the point where streamside timber adjoined agricultural fields)		
Distance to opening (An opening was an area free of woody vegetation < 0.5 m tall)		
Distance to stream		
Habitat fragment		Amount of edge/hectare (Edge was the point where fragment vegetation met other vegetation)
		Diversity of plant strata
	Diversity of snag diameters	
	Frequency of plant-stratum class X ^b	
	Frequency of snag-diameter class X ^b	
	Mean plant-stratum diversity	
	Mean snag-diameter diversity	
	Area Distance to nearest streamside habitat fragment	
Size of nearest streamside habitat fragment		

^a Complete details of definitions and methods of measurement are in Gutzwiller (1985).^b X = 1, 2, 3, 4, 5, or 6, as defined in Table 2.

the same amount of time to search, and one group was searched each day. The order in which groups and individual fragments within each group were searched was randomized (and reversed in 1984) to avoid daily and seasonal biases related to the birds' activity levels. Doubling the nest-searching time did not appreciably change the number of nests found, and we therefore judged our search method to be adequate and time-efficient (Gutzwiller 1985).

Vegetation measurements. During July and August 1983, we estimated structural and spatial parameters of vegetation in habitat fragments (Table 1), and we recorded the presence or absence of six land-use types (herbaceous rangeland, irrigated cropland, mixed rangeland, palustrine wetland, riverine wetland, roads) adjacent to or within fragment boundaries. During June 1982, we found that only two of 90 active nests were about 25 m from mature timber, while the other 88 nests were in trees much closer to mature timber. Accordingly, we defined a habitat fragment to be a stand of trees (≥ 10.2 cm dbh) separated from all other such stands or individual trees by at least 30 m.

During July 1983, we sampled a 32.3-ha habitat patch, systematically and with a random start (Cochran 1977:205), in which six plant-stratum classes and six snag-diameter classes (Table 2) were represented. For the remaining fragments, we used estimates of means, variances, and proportions from this sample (163 3- × 20-m plots) to determine the number of sample plots necessary to estimate: (1) mean number of snag-diameter classes represented per 60-m² plot, (2) mean number of plant-stratum classes represented per 60-m² plot, and (3) the proportion (frequency) of 60-m² plots having individuals in the various plant-stratum and snag-diameter classes. For the means, precision and reliability levels were 25% and 80%, respectively; for the proportions, minimum precision and reliability values were 10% and 70%, respectively. We computed required sample sizes using formulas and adjustments from Cochran (1977:75-78) and Schemnitz (1980:312). For each of the 34 habitat fragments we averaged the required sample sizes for the means and proportions and used the resulting number of plots during July, August, and early October 1983 to sample all vegetation classes. From aerial photographs, we identified two canopy-coverage classes (strata) within habitat fragments: closed canopy (100% canopy cover, ground not visible), and open canopy ($< 100\%$

canopy cover, ground visible). This information was used to compute stratified (minimum-variance) estimates of the means and proportions described above (Cochran 1977:91, 107).

STATISTICAL ANALYSES

We used programs from Dixon (1981) and Nie et al. (1975) to obtain statistical information for control data (randomly selected trees and sites, $n = 30$) and data for 10 bird species: Downy Woodpecker (*Picoides pubescens*), $n = 29$; Hairy Woodpecker (*P. villosus*), $n = 4$; Northern Flicker (*Colaptes auratus*), $n = 28$; Red-headed Woodpecker (*Melanerpes erythrocephalus*), $n = 31$; American Kestrel (*Falco sparverius*), $n = 15$; Black-capped Chickadee (*Parus atricapillus*), $n = 7$; Common Grackle (*Quiscalus quiscula*), $n = 7$; European Starling (*Sturnus vulgaris*), $n = 31$; House Wren (*Troglodytes aedon*), $n = 32$; Tree Swallow (*Tachycineta bicolor*), $n = 4$. Nest-tree and nest-site comparisons involved control data and only those species for which we had located at least 15 nests. Most nest-tree and nest-site variables had severely skewed distributions, and transformations for normalizing such data (Zar 1974:182–188) were ineffective. We therefore used the Kruskal-Wallis test statistic (H), with Dunn's approximation for pairwise comparisons (experiment-wise error rate = 0.10 [Hollander and Wolfe 1973:124–129]), to test the null hypotheses of no significant differences in habitat variables among species' nest trees and random trees and among species' nest sites and random sites. We computed log-likelihood ratios (G statistics [Zar 1974:67]) to test null hypotheses concerning equal proportions. When hypotheses were rejected, we subdivided contingency tables to identify where the differences occurred (Zar 1974: 65). For 2×2 tables, we used Yates' (Zar 1974: 68) correction for continuity to compute corrected G statistics. Rayleigh's statistic (r) (Batschelet 1981:54–56) was used to test the null hypothesis that there was no mean nest-entrance bearing for each bird species. Extreme nonnormality and unequal covariance matrices precluded the valid use of multivariate analysis of variance and discriminant function analysis for inferential purposes (Morrison 1976:141; Johnson 1981:13; Williams 1981, 1983).

Combining 1983 and 1984 data for the 10 bird species, we used all possible subsets regression to assess relations between habitat-fragment variables and: mean number of nesting species,

TABLE 2. Definitions of plant-stratum classes and snag-diameter classes used to sample habitat fragments along the North Platte River.

Class	Definition
Plant-stratum	
1	woody stem ≤ 0.5 m in height
2	woody stem > 0.5 m and ≤ 2.5 m in height
3	woody stem > 2.5 m in height and ≤ 15.2 cm dbh
4	woody stem > 2.5 m in height and from 15.3–40 cm dbh
5	woody stem > 2.5 m in height and from 41–70 cm dbh
6	woody stem > 2.5 m in height and > 70 cm dbh
Snag-diameter ^a	
1	stems 10.2–25 cm dbh
2	stems 26–40 cm dbh
3	stems 41–55 cm dbh
4	stems 56–70 cm dbh
5	stems 71–85 cm dbh
6	stems > 85 cm dbh

^a Class boundaries determined by dividing distribution of 1982 nest-tree diameters ($n = 65$; distribution very uniform) into six equal parts.

total number of different nesting species, mean number of nests for a given species, and presence or absence of nests for a given species. Models with the highest R^2 values and the fewest number of variables were selected for further analysis (Neter and Wasserman 1974:376–378). To verify ordinary least squares models, we used the prediction error sums of squares to calculate an R^2 value for prediction (R^2_{pred}). This statistic describes a model's ability to predict each case correctly based on the model estimated from the remaining $n - 1$ observations and measures the percentage of variation the model would account for if tested with comparable new observations (Montgomery and Peck 1982:430–433).

We did not estimate individual regression models for species that nested in a total of six or fewer fragments during 1983 and 1984 (Common Grackle, Hairy Woodpecker, Black-capped Chickadee, Tree Swallow) because their use of fragments was consistently low and essentially invariable. Four species (Red-headed Woodpecker, Downy Woodpecker, American Kestrel, Northern Flicker) did not nest in a large proportion (53 to 71%) of the fragments. For each of these species, we first estimated a linear model with presence and absence data for 1983 and 1984 combined. But, because some predicted values were > 1.0 and < 0.0 , we fit logistic equa-

TABLE 3. Differences and similarities among bird species and control data for nest-tree and nest-site features.

Groups	Mean dimension \pm SE (<i>n</i>)				
	Nest-tree dbh (cm)	Nest height (m)	Tree diameter at nest height (cm)	Nest-entrance diameter (cm)	Distance to stream (m)
American Kestrel	67.9 \pm 8.8 AC ^a (15)	9.8 \pm 0.8 AB (15)	29.2 \pm 3.7 ^b (8)	7.65 \pm 0.71 ^c (6)	168 \pm 36 A (15)
Northern Flicker	46.3 \pm 4.1 AB (28)	7.3 \pm 0.6 AC (28)	27.1 \pm 2.0 A (19)	6.58 \pm 0.21 A (23)	89 \pm 22 AB (28)
Red-headed Woodpecker	59.2 \pm 4.3 AC (31)	10.0 \pm 0.7 BC (31)	21.2 \pm 1.7 AC (18)	5.87 \pm 0.24 AC (25)	137 \pm 23 AB (31)
Downy Woodpecker	40.9 \pm 4.5 B (29)	6.9 \pm 0.7 A (29)	14.4 \pm 1.2 B (20)	3.21 \pm 0.09 D (29)	65 \pm 10 B (29)
House Wren	53.9 \pm 5.1 AB (32)	6.9 \pm 0.6 A (32)	16.9 \pm 1.9 BC (19)	4.79 \pm 0.34 BC (24)	80 \pm 12 AB (32)
European Starling	82.7 \pm 6.7 C (31)	11.2 \pm 0.6 B (31)	34.4 \pm 4.9 A (22)	6.18 \pm 0.31 AB (18)	133 \pm 17 A (31)
Control data	44.2 \pm 4.6 AB (30)	—	—	—	177 \pm 33 A (30)

^a For each variable, means not marked with a common letter differ significantly (experiment-wise error rate = 0.10 for Dunn's pairwise comparisons).

^b American Kestrel not included in comparisons because *n* was only 8.

^c American Kestrel not included in comparisons because *n* was only 6.

tions using the same variables (Neter and Wasserman 1974:329–335).

Optimal least squares models were those with: the highest R^2 value, the fewest number of variables (with each contributing at least 3% to R^2), a significant ($P < 0.05$) F statistic, all significant ($P < 0.05$) t statistics, variance inflation factors < 10 for explanatory variables, and residual plots, normal-probability plots, and histograms consistent with regression assumptions (Neter and Wasserman 1974:97–112, Chatterjee and Price 1977:182–183). Optimal logistic models were those having significant improvement chi-square values for each explanatory variable (Dixon 1981: 336–337). Using t , F , and χ^2 (logistic models) statistics we tested the null hypothesis that there were no significant relations between habitat-fragment features and nesting activity. Additional details concerning bird and habitat sampling and statistical analyses are in Gutzwiller (1985).

RESULTS

NEST-TREE SELECTION

Structural data. Significant differences existed among species' nest trees and random trees (center trees) for tree dbh ($H = 41.05$, $P = 0.000$, $df = 6$ [Table 3]) and among species' nest heights ($H = 36.30$, $P = 0.000$, $df = 5$ [Table 3]). The patterns of differences among species for nest-tree diameter and nest height were almost iden-

tical. This was consistent with significant correlations (Pearson's r , $P < 0.03$) between these two variables for all species except the American Kestrel. Differences in tree diameter at nest height ($H = 41.82$, $P = 0.000$, $df = 4$ [Table 3]) reflect (roughly) differences in body size among species. Species with greater bill-to-tail lengths (Northern Flicker [27.9 cm], American Kestrel [21.6 cm], Red-headed Woodpecker [19.1 cm], European Starling [15.2 cm]) tended to nest in larger-diameter limbs and boles than the smaller species (Downy Woodpecker [14.6 cm], House Wren [10.8 cm]). The correlation between these live-body lengths (Robbins et al. 1966) and mean tree diameter at nest height among the six species was not, however, significant (Spearman's $\rho = 0.54$, $P = 0.266$). We expected tree diameter at nest height to be positively correlated with nest-tree dbh for each bird species, but the only significant correlation we found between these two variables was for Northern Flickers ($n = 17$, $r = 0.55$, $P = 0.022$). This is probably because most (64.7% of 17) Northern Flicker nests were in boles, which had diameters close to dbh, whereas the other species usually nested in limbs (see below), which were more variable in diameter relative to nest-tree dbh.

Nest-entrance diameters differed significantly among species ($H = 66.28$, $P = 0.000$, $df = 4$ [Table 3]), and these differences were consistent with a positive correlation (Spearman's $\rho = 0.83$, $P = 0.042$) between mean entrance diam-

TABLE 4. Frequencies of species' nest cavities in limbs and boles.^a

	Limbs	Boles
American Kestrel	10 (66.7)	5 (33.3)
Northern Flicker	8 ^b (28.6)	20 ^{b,c} (71.4)
Red-headed Woodpecker	25 (80.6)	6 ^d (19.4)
Downy Woodpecker	19 (65.5)	10 ^e (34.5)
House Wren	24 (75.0)	8 ^d (25.0)
European Starling	25 (80.6)	6 ^d (19.4)

^a Numbers in parentheses are percentages.
^b Proportion is significantly ($P < 0.001$) different from other proportions in the same column.
^c Proportion is significantly ($P = 0.004$) different from other proportion in same row.
^d Proportion is significantly ($P < 0.001$) different from other proportion in same row.
^e Proportion is significantly ($P = 0.037$) different from other proportion in same row.

eter and bill-to-tail length for the six species. We found no correlations among nest-height, tree diameter at nest height, and nest-entrance diameter for any of the six species. The frequency with which species nested in limbs and boles

TABLE 5. Frequencies of species' nest trees and random trees that were snags and nonsnag trees.^a

	Snags	Nonsnag trees
American Kestrel	6 (75.0)	2 (25.0)
Northern Flicker	14 ^{b,c} (73.7)	5 ^c (26.3)
Red-headed Woodpecker	13 ^d (72.2)	5 (27.8)
Downy Woodpecker	15 ^{e,f} (75.0)	5 ^f (25.0)
House Wren	9 (50.0)	9 (50.0)
European Starling	13 (61.9)	8 (38.1)
Random trees	12 (40.0)	18 (60.0)

^a Numbers in parentheses are percentages.
^b Proportion is significantly ($P = 0.009$) different from other proportion in same row.
^c Proportions are significantly ($P = 0.044$) different from those for random trees.
^d Proportion is significantly ($P = 0.020$) different from other proportion in same row.
^e Proportion is significantly ($P = 0.004$) different from other proportion in same row.
^f Proportions are significantly ($P = 0.035$) different from those for random trees.

TABLE 6. Frequencies of species' nest entrances pointing above horizontal, horizontally, and below horizontal.^a

	Above horizontal	Horizontal	Below horizontal
American Kestrel	11 ^{b,c} (73.3)	2 (13.3)	2 ^d (13.3)
Northern Flicker	7 (25.0)	7 (25.0)	14 (50.0)
Red-headed Woodpecker	7 (22.6)	6 (19.3)	18 ^b (58.1)
Downy Woodpecker	0 ^e (0.0)	3 (10.3)	26 ^{b,c} (89.7)
House Wren	11 (35.5)	1 ^b (3.2)	19 (61.3)
European Starling	18 ^f (58.1)	1 ^b (3.2)	12 (38.7)

^a Numbers in parentheses are percentages.
^b Proportion is significantly ($P < 0.001$) different from other proportions in the same row.
^c Proportion is significantly ($P < 0.001$) different from all other proportions in same column, except that for European Starling.
^d Proportion is significantly ($P = 0.008$) different from all other proportions in same column (except for Downy Woodpecker, $P < 0.001$).
^e Proportion is significantly ($P < 0.001$) different from all other proportions in same column.
^f Proportion is significantly ($P < 0.001$) different from all other proportions in the same column, except that for American Kestrel.

differed significantly (Table 4). Among and within American Kestrels, House Wrens, and European Starlings, snags and nonsnag trees were used in proportions that were not significantly different (Table 5). Red-headed Woodpeckers used snags and nonsnag trees in proportions that did not differ from the occurrence of these two tree types as center trees.

Directional data. Nest-entrance bearing was not significantly different from random for any of the species (Rayleigh tests, $P > 0.05$). American Kestrels and European Starlings used significantly more cavities with entrances that pointed above horizontal than the other species (Table 6). Most nest entrances for House Wrens and European Starlings pointed either above or below horizontal, agreeing with our observations that these species used both natural cavities (having upward-pointing entrances) and woodpecker holes (most of which had entrances pointing below horizontal).

Floristic data. Six tree species were nested in or occurred as center trees: green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), lanceleaf cottonwood (*Populus × acuminata*), narrowleaf cottonwood (*P. angustifolia*), plains cottonwood (*P. sargentii*), and peachleaf willow (*Salix amygdaloides*) (Table 7). Plains cottonwood was the only species that regularly attained

TABLE 7. Frequencies of tree species used by nesting birds and frequencies of tree species that occurred as randomly selected trees.^a

	Green ash	Boxelder	Plains cottonwood	Lanceleaf cottonwood	Narrowleaf cottonwood	Peachleaf willow
American Kestrel	0 (0.0)	1 (7.1)	13 ^{b,c} (92.9)	0 (0.0)	0 (0.0)	0 (0.0)
Northern Flicker	0 (0.0)	1 (4.0)	15 ^b (60.0)	0 (0.0)	2 (8.0)	7 ^{b,d} (28.0)
Red-headed Woodpecker	0 (0.0)	0 (0.0)	15 ^b (88.2)	1 (5.9)	0 (0.0)	1 (5.9)
Downy Woodpecker	0 (0.0)	0 (0.0)	10 ^b (55.6)	1 (5.6)	3 (16.6)	4 (22.2)
House Wren	0 (0.0)	1 (3.6)	17 ^b (60.7)	2 (7.1)	4 (14.3)	4 (14.3)
European Starling	0 (0.0)	0 (0.0)	26 ^{b,e} (96.3)	1 (3.7)	0 (0.0)	0 (0.0)
Random trees	4 ^f (13.3)	0 (0.0)	18 ^b (60.0)	2 (6.7)	4 (13.3)	2 (6.7)

^a Numbers in parentheses are percentages.

^b Proportion is significantly ($P < 0.001$) different from all other proportions in the same row.

^c Proportion is significantly ($P = 0.031$) different from all other proportions in the same column (except for European Starling, $P = 0.001$).

^d Proportion is significantly ($P = 0.023$) different from all other proportions in the same column.

^e Proportion is significantly ($P = 0.001$) different from all other proportions in the same column.

^f Proportion is significantly ($P = 0.003$) different from all other proportions in the same column.

the heights (and sufficient diameters) American Kestrels and European Starlings used, and it was the only species that grew in foraging areas for these species. These species nested primarily in plains cottonwood; the other species used plains cottonwood in proportion to its availability. To our knowledge, decadent green ash were essentially nonexistent in the study area. Peachleaf willows evidently provided height, diameter, and decay conditions that attracted more Northern Flickers than the other species.

NEST-SITE SELECTION

Structural and spatial traits. We found no significant differences among species' nest sites and random sites for large-shrub cover ($H = 3.16$, $P = 0.788$, $df = 6$), small-shrub cover ($H = 2.41$, $P = 0.879$, $df = 6$), large-tree density ($H = 10.22$, $P = 0.116$, $df = 6$), small-tree density ($H = 5.23$, $P = 0.515$, $df = 6$), snag density ($H = 10.03$, $P = 0.123$, $df = 6$), vertical space ($H = 5.57$, $P = 0.473$, $df = 6$), distance to edge ($H = 10.42$, $P = 0.108$, $df = 6$), or distance to opening ($H = 6.81$, $P = 0.338$, $df = 6$). Downy Woodpecker nests were closer to streams than either randomly selected trees, American Kestrel nests, or European Starling nests (Table 3). The latter two species nested in open habitats with herbaceous areas, which occurred near the point where streamside timber met agricultural fields; both species also

foraged in or near such areas. Vegetation bordering the North Platte and Laramie Rivers was dense and brushy, but habitats became progressively more open with distance from the streams. Compared to American Kestrels and European Starlings, Downy Woodpeckers fed and nested in the more dense vegetation closer to water. Further, means for small-shrub cover, large- and small-tree density, and snag density at Downy Woodpecker nest sites were greater (although not significantly) than those for American Kestrel and European Starling nest sites.

HABITAT-FRAGMENT SELECTION

Species richness vs. fragment features. Eighty-seven percent of the variation in the mean number (for 1983 and 1984) of nesting species was accounted for by five habitat-fragment characteristics: amount of edge/hectare, area, size of nearest streamside habitat fragment, frequency of class-6 snags, and the presence or absence of palustrine wetland (Table 8). The low standard deviation for the regression indicated observed numbers of species varied little from predicted numbers, and the R^2_{Pred} value of 76% affirms this model's validity.

The negative relation between species richness (mean number of nesting species) and amount of edge/hectare indicated fewer species nested in fragments that had irregular boundaries. High

TABLE 8. Optimal ordinary least-squares regression models relating numbers of cavity-nesting birds to habitat-fragment features ($n = 34$).

Dependent variable	Model ^a	R^{2b}	R^c	SD_{Est}^d	$R^2_{Pred}^e$
Mean number of nesting species	$2.701 - 0.002 (EPHA) + 0.173 (AREA) - 0.039 (SIZEH) + 31.104 (SNAG6) + 0.926 (PALUS)$	0.87	0.93	0.82	0.76
Total number of nesting species	$4.228 - 0.003 (EPHA) + 0.216 (AREA) - 0.056 (SIZEH) + 49.217 (SNAG6) + 1.416 (PALUS)$	0.86	0.93	1.20	0.73
Mean number of European Starling nests	$-1.183 + 0.541 (AREA) + 7.932 (PSC5)$	0.86	0.93	1.90	0.83
Mean number of House Wren nests	$0.040 + 0.140 (AREA)$	0.65	0.81	0.88	0.59

^a All regressions significant at $P < 0.000$; EPHA = amount of edge/hectare, AREA = area, SIZEH = size of nearest streamside habitat fragment, SNAG6 = frequency of snag-diameter class 6 (>85 cm dbh), PALUS = presence or absence of palustrine wetland, PSC5 = frequency of plant-stem class 5 (>2.5 m in height and 41–70 cm dbh).

^b Coefficient of multiple determination.

^c Coefficient of multiple correlation ($\sqrt{R^2}$).

^d Standard deviation of the observed values about the regression line.

^e Percentage of variation model would account for if tested with new, comparable data.

edge/hectare values (>834 m/ha) also characterized fragments that were long (>100 m) and narrow (<30 m), fragments that had an abundance of similar, narrow habitat extensions, and small fragments; such areas were used only occasionally by two species (European Starling, House Wren). The correlation between amount of edge/hectare and fragment area was -0.50 ($P < 0.002$), yet both variables contributed significantly ($t = -4.26$, $P = 0.000$ for edge/ha; $t = 8.92$, $P = 0.000$ for area) to the model.

Fragment area was correlated with the diversity of snag diameters ($r = 0.43$, $P < 0.01$) and the number of land-use types bordering islands ($r = 0.52$, $P < 0.002$). The diversity of snag diameters and the number of land-use types were also weakly correlated ($r = 0.48$, $P < 0.005$; $r = 0.49$, $P < 0.005$, respectively) with mean number of nesting species, but fragment area was a much better predictor ($r = 0.84$, $P < 0.001$) than either of these measures of fragment habitat diversity. The negative coefficient for size of nearest streamside habitat fragment indicated fewer species nested in fragments that were close to large streamside fragments.

Numbers of nesting species increased with higher frequencies (range = 0.0 – 0.09) of snags > 85 cm dbh. Snags of this size provided nest trees for several species (American Kestrel, Red-headed Woodpecker, European Starling) at once, and they attracted not only common nesters (House Wren, European Starling), but also species that did not nest in many of the fragments

(American Kestrel, Red-headed Woodpecker, Common Grackle) (Gutzwiller and Anderson 1986).

Fragments bounded by palustrine wetland had slightly higher frequencies ($r = 0.38$, $P < 0.05$) of class-2 snags (26 to 40 cm dbh) than fragments not adjoined by such wetlands. Eight of the 10 species (American Kestrel, Northern Flicker, Red-headed Woodpecker, Hairy Woodpecker, Downy Woodpecker, Black-capped Chickadee, House Wren, European Starling) nested in snags of this size; Northern Flickers and Downy Woodpeckers used this diameter class most often (eight of 14 snags and five of 15 snags, respectively). Thus, class-2 snags were useful to almost the entire community of cavity-nesting birds. Fragments bordered by palustrine wetland and having higher frequencies of snags in class 2 (presumably due to higher water tables and concomitantly higher decay rates) attracted a greater variety of these species than fragments without nearby wetland and lower frequencies of class-2 snags. In combination with the other four explanatory variables, the presence or absence of palustrine wetland was a better predictor of mean species richness than the frequency of class-2 snags.

As expected, the model for total species richness was almost identical to that for mean number of breeding species (Table 8). The same fragment characteristics accounted for 86% of the variation in total number of different species among fragments during the 2-year period, and,

TABLE 9. Optimal logistic regression models relating the probability of nesting by a given species to habitat-fragment characteristics ($n = 34$).

Dependent variable	Model*	Explanatory variable	Significance of improvement χ^2
Probability of Red-headed Woodpecker nesting	$\frac{e^{[-2.39+0.37(\text{AREA})-0.12(\text{SIZEH})]}}{1 + e^{[-2.39+0.37(\text{AREA})-0.12(\text{SIZEH})]}}$	AREA	0.000
		SIZEH	0.033
Probability of American Kestrel nesting	$\frac{e^{[-2.36+0.23(\text{AREA})]}}{1 + e^{[-2.36+0.23(\text{AREA})]}}$	AREA	0.000
Probability of Downy Woodpecker nesting	$\frac{e^{[-2.93+0.56(\text{AREA})]}}{1 + e^{[-2.93+0.56(\text{AREA})]}}$	AREA	0.000
Probability of Northern Flicker nesting	$e^{[9.65-0.01(\text{EPHA})-0.03(\text{DNEARH})-8.31(\text{PSC4})]}$	EPHA	0.000
	$1 + e^{[9.65-0.01(\text{EPHA})-0.03(\text{DNEARH})-8.31(\text{PSC4})]}$	DNEARH	0.017
		PSC4	0.011

* DNEARH = Distance to nearest streamside habitat fragment, PSC4 = frequency of plant-stratum class 4 (>2.5 m in height and 15.3–40 cm dbh); all other mnemonics defined under Table 8.

because $R^2_{\text{Pred}} = 0.73$, this model's validity is supported. The role each variable played in determining total richness was presumably the same as described above for mean species richness.

Primary cavity nesters vs. fragment features. Fragment area and size of the nearest streamside habitat fragment were the only variables that were significantly related to the presence and absence of nesting Red-headed Woodpeckers (Table 9). Only the larger fragments contained the nest trees (large-diameter snags) and feeding sites (clearings) these birds typically used. This species restricted its nesting activities to fragments >1.99 ha. The negative coefficient associated with the size of nearest streamside habitat indicates this species did not use small fragments (<1.99 ha) that were near large fragments.

Habitat size was the only fragment characteristic that was significantly correlated with the presence and absence of breeding Downy Woodpeckers (Table 9). Downy Woodpeckers only nested in fragments 2.90 ha in size and larger. Further, fragments bordered by riverine wetland were larger ($r = 0.65$, $P < 0.001$) than those without such habitat nearby. Downy Woodpeckers often selected densely vegetated sites close to streams (see above), and the larger fragments, which usually bordered streams, were the best sources for this type of habitat.

Three fragment characteristics were significantly correlated with the presence and absence of nesting Northern Flickers (Table 9). The negative coefficient for amount of edge/hectare indicates few individuals nested in fragments with

high edge/hectare values (>834 m/ha), which were fragments that were small and/or irregularly shaped. The probability of nesting by Northern Flickers decreased as distance to nearest streamside fragment increased. This agrees with our observations that individuals tended to avoid the smaller, isolated fragments that were disjunct (>124 m) from the streamside vegetation. Northern Flickers frequently nested in peachleaf willow (Table 7), which was concentrated near the river. Further, amount of edge/hectare and distance to nearest streamside habitat fragment were negatively correlated ($r = -0.57$, $P < 0.001$; $r = -0.53$, $P < 0.001$, respectively) with the presence of riverine wetland. So, fragments bordered by the river were not only larger, more regularly shaped, and closer to other such fragments, but they also supported more large peachleaf willows. Amount of edge/hectare and distance to nearest streamside fragment were the variables that entered the model, and evidently they were the best measures of these relations. The frequency of plant-stratum class 4 (15.3 to 40 cm dbh; range = 0.16–0.71 for fragments used by Northern Flickers) was inversely related to the frequency of class-5 ($r = -0.34$, $P < 0.05$) and class-6 ($r = -0.33$, $P < 0.05$) snags. Higher frequencies of class-4 nonsnag trees thus characterized fragments with fewer large, decayed trees. Northern Flickers primarily nested in snags belonging to classes 2, 3, and 4, but the larger classes (5 and 6) probably supplied feeding, perching, and roosting locations (Evans and Conner 1979). Habitat fragments with lower fre-

quencies of snags in classes 5 and 6 would tend to attract fewer breeding pairs. The best overall measure of this effect was the frequency of class-4 nonsnag trees, hence the negative coefficient relating the latter variable to the probability of nesting by Northern Flickers.

Secondary cavity nesters vs. fragment features. Fragment area and the frequency of plant-stratum class 5 (41 to 70 cm dbh) accounted for 86% of the variation in mean numbers of European Starling nests (Table 8); the R^2_{Pred} value of 83% suggests the model is reasonably accurate. The positive relation between number of nests and fragment area indicates larger fragments (>0.54 ha) had a greater abundance of suitable nest trees than smaller fragments. Further, fragment size was positively associated ($r = 0.34$, $P < 0.05$) with the presence of irrigated cropland, and pastureland (herbaceous rangeland) frequently bordered large fragments; adults and young foraged frequently in both habitat types. Thirteen of the 31 nest trees we analyzed for European Starlings belonged to plant-stratum class 5, explaining in part the significant positive relation between nest abundance and frequency of trees of this size. The range of frequencies of class-5 nonsnag trees for fragments used by European Starlings was 0.0 to 0.44.

Fragment area accounted for 65% of the variation in mean number of House Wren nests, and it was the only significant predictor (Table 8). R^2_{Pred} was 0.59, which indicates that in a test of this model with a different data set, this single variable would explain almost 60% of the variation.

The only fragment characteristic significantly correlated with the presence and absence of nesting American Kestrels was fragment area (Table 9). American Kestrels usually nested in large trees near edges of clearings, and only the larger fragments provided these conditions. The positive relation between probability of nesting and fragment area agrees with the relatively large (1.99 ha) minimum fragment size in which American Kestrels nested.

DISCUSSION

NEST-TREE SELECTION

For several reasons, actual cavity height (for secondary cavity nesters) and potential nest height (for primary cavity nesters), rather than nest-tree diameter may be the variables to which birds are

responding. First, most species' nest-tree diameters did not differ from those they would have used if they selected trees randomly. Nest-tree diameter may, therefore, have played little or no role in eliciting nest-tree selection in our area. Further, all of the species nested much higher than breast height (1.37 m) from the ground, so bole dbh per se could not confer direct advantages to adults or young. To the contrary, sufficient nest height could provide adult birds with enough time to detect and perhaps dislodge climbing nest predators (fox squirrels, *Sciurus niger*, and bullsnakes, *Pitouphis melanoleucus*, in the present study) and/or enough distance from the ground to avoid disturbance from man or terrestrial predators. In both cases, survival of young (and perhaps adults) may be directly enhanced (Nilsson 1984). The significant differences in nest-tree diameters among species may thus be the consequence of correlations (within species) between nest-tree diameter and nest height.

The significant correlation between body size and entrance diameter and the lack of a relation between body size and tree diameter at nest height indicates use or construction of specific nest-entrance diameters is tied more closely to these species' size. Yet, similarities in entrance diameter among several species of different size indicate considerable versatility among these birds, particularly the House Wren and European Starling. This latitude in the latter two species follows from their inability to excavate and their concomitant dependence on the Northern Flicker, Red-headed Woodpecker, Downy Woodpecker, and natural forces (wind, lighting, disease) for cavity formation. Ideally, one would expect species to select holes with entrances that preclude entry by larger, more competitively dominant species (Short 1979), and basically, this trend can be observed in our data (Table 3). But if secondary cavity nesters are to breed, they must use available cavities; thus, their versatility for this parameter (in addition to nest height and tree diameter at nest height) is expected.

The random nest-entrance orientation we observed contrasts with other studies in which nest-entrance orientation was significantly nonrandom. Researchers have attributed this to preference or avoidance of prevailing winds and solar radiation, as entrance orientation relative to these factors may affect adult and nestling energetics (e.g., Lawrence 1967, Ricklefs and Hainsworth

1968, Inouye et al. 1981). Conner (1975) believed nest-entrance orientation in woodpeckers was determined primarily by the direction of sloping tree trunks. He found most cavities excavated on the undersides of sloping boles and explained that entrances to such cavities permit less rain (and resulting stem flow) to enter the nest and that they are easier to defend against predators and competitors. Stauffer and Best (1982), working with many of the species involved in the present study, agreed with Conner (1975).

In the present study, all species' (primary and secondary cavity nesters) nest entrances were oriented randomly, but many (44.7% of all entrances) did not point below horizontal. These data are contrary to those of Stauffer and Best (1982), and they cast doubt on Conner's (1975) idea that cavities on the undersides of boles and limbs (i.e., those with entrances pointing below horizontal) should be preferred. Evidently, cavities with entrances pointing upward and horizontally were superior enough in other ways (e.g., appropriate dimensions, lack of parasites, proximity to food) that despite possible disadvantages relative to rain, predators, and competitors, they were still acceptable. We do not attribute random orientation of species' nest entrances to the direction in which sloping limbs or boles lean, but conclude instead that biotic (competitors, predators) and abiotic (rain, wind, insolation) factors had minimal (if any) influence on acceptability of nest-entrance bearing in our study area.

The variety of tree species used by these birds (see Conner et al. 1975, Conner 1976, Winternitz and Cahn 1983, Raphael and White 1984) indicates that no single tree species or group of species is vital for providing nesting habitat. Nest trees for each bird are, however, quite similar across each species' range in terms of physical dimensions and decay conditions (Lawrence 1967, Smith et al. 1972, Stauffer and Best 1982, Raphael and White 1984). This suggests that physical characteristics influence tree selection more than tree species per se.

Bird-habitat relations pertinent to entrance angle, nest-tree species, entrance bearing and whether the nest was in a limb or bole were completely or partially unpredictable from studies of the same species elsewhere (see references in three previous paragraphs). Further, positions of species along gradients of nest-tree dbh and tree

diameter at nest height for our study were not those observed by others (Stauffer and Best 1982, Raphael and White 1984). These data support the idea that habitat-selection responses may vary geographically within a species, presumably because biotic and abiotic stimuli that elicit responses vary geographically (Wiens 1985:248). The disparities we have identified may be due to the obvious differences among study areas in bird-community structure, plant-species composition, or precipitation and solar insolation levels. We do not believe variation in measuring technique accounts for these differences because these variables are accurately measured or recorded with standard methods.

Overall, our results demonstrate habitat associations within species on the scale of nest trees and differences in such associations among species.

NEST-SITE SELECTION

The lack of differences between species' nest sites and random sites in terms of structural and spatial characteristics suggests site selection was random with respect to these habitat parameters. All of these birds nest in open woodlands having scattered shrubbery with an otherwise open understory (e.g., Conner and Adkisson 1977, Scott et al. 1977, Harrison 1978, Evans and Conner 1979). In addition, Short (1979) explained that it is adaptive for hole-nesting birds to nest near snags and nonsnag trees (with cavities or the potential for cavities) because such trees can provide roosting sites (for adults and fledglings) and alternate nest sites. The six species involved in our comparisons use snag and nonsnag trees for roosting and nesting, and some of these species also perch and/or feed on such trees (Evans and Conner 1979). Further, all of these birds forage in mature, open stands interspersed with shrubs and herbaceous cover. The high overlap among species for these eight characteristics is thus expected from their similar habitat associations.

The use of dense habitat by Downy Woodpeckers agrees with data from Conner et al. (1975), Conner and Adkisson (1977), and Hardin and Evans (1977), who reported Downy Woodpeckers feeding and nesting in areas with high sapling density and low canopy height. The apparent preference for proximity to water shown by Downy Woodpeckers in the present study may simply reflect a tendency by this species to forage and nest in thicker habitats, which occurred close

to streams in our study area. Thus, on the scale of nest sites, there were no bird-habitat associations within species, except that involving Downy Woodpeckers and distance to stream. Differences among American Kestrels, European Starlings, and Downy Woodpeckers for this feature were consistent with feeding and nesting requirements.

HABITAT-FRAGMENT SELECTION

The positive relations (linear over the range of fragment sizes [0.1 to 32.3 ha, $\bar{x} = 7.17$ ha] we studied) between mean number of species, total number of different species, mean number of European Starling nests, mean number of House Wren nests, and fragment area are consistent with classical species-area trends and recent studies of species-area relations for birds (e.g., MacArthur and Wilson 1967, Galli et al. 1976, Morse 1977, Yahner 1983, Howe 1984). The logistic species-area relations we present for American Kestrels, Red-headed Woodpeckers, and Downy Woodpeckers are also in accord with expected positive trends. These relations are probably not simply the outcomes of a sampling effect, in which more species or individuals would occur solely because the area of consideration (the sampling frame) increases. Species-area relations in the present study hinge on nesting and feeding requirements associated with fragments, like adequate territory size, presence of nearby foraging areas, abundance of suitable nest trees, and diversity of habitat structure.

Larger fragments contained a greater diversity of nest-tree sizes and were associated with a larger number of habitat types useful to various species with different feeding strategies. Both of these features foster higher richness of cavity-nesting birds in habitat fragments (cf. MacArthur 1964). Fragment area was the best measure of the effects of the diversity of nest-tree diameters and adjacent land-use types on species richness; this agrees with reports by Simberloff (1976) and Morse (1977), who also found area to be a stronger predictor of species richness than habitat diversity.

The positive relations between mean and total number of species and fragment area suggest that minimal territory sizes required by a variety of species were accommodated more often by larger fragments than by smaller ones (cf. Forman et al. 1976, Morse 1977). The minimum areas we found acceptable to American Kestrels, North-

ern Flickers, Red-headed Woodpeckers, and Hairy Woodpeckers (1.99, 1.34, 1.99, 1.34 ha, respectively) are smaller than minimum estimates of their territory sizes (52, 11, 4.8, 2.4 ha, respectively) (Lawrence 1967, Call 1978, Samson 1979, Thomas 1979). When individuals of these species nested in fragments that were inadequate in size, they almost certainly used nearby agricultural land and other forest fragments as part of their territories. The smallest forest fragments used by European Starlings, House Wrens, Downy Woodpeckers, Black-capped Chickadees, Tree Swallows, and Common Grackles (0.54, 0.12, 2.90, 6.82, 15.05, 1.34 ha, respectively) were, however, larger than minimum estimates of their territory sizes (approximately 0.8 m² around the nest hole, and 0.1, 2, 3.4, 10.5, 1.2 ha, respectively) (Kendeigh 1941, Odum 1941, Kessel 1957, Lawrence 1967, Samson 1979). Thus, the latter six species could have typically used single fragments to meet their territory requirements. An alternative explanation that accounts for these latter data and the area-diversity correlations listed above is that fragment area was a combined measure of the diversity of snag sizes available, the variety of potential feeding areas, and the number of different species' minimal areas that could be accommodated.

MacArthur and Wilson (1967:8) noted that on oceanic islands "area seldom exerts a direct effect on a species' presence. More often area allows a large enough sample of habitats, which in turn control species occurrence." Evidence for this has been documented by Watson (1964). Habitat diversity would thus seem to be the controlling factor of species richness on true islands, rather than island area per se. The present study does not, however, support the idea that habitat diversity (instead of area) is the primary factor influencing species richness of cavity nesters in habitat fragments. Along with habitat diversity, fragment area itself, because it affects possible territory size, directly influences habitat selection by cavity-nesting birds, and hence species richness.

RELATIONS AMONG RESPONSES ON DIFFERENT SPATIAL SCALES

Wiens (1983:368) asserted that ornithologists "cannot extrapolate processes that operate at one level (e.g., competition among individuals in local populations) to explain patterns at another

level (e.g., regional distributions) or employ evidence derived from patterns at one scale (e.g., variations in γ -diversity) to test process explanations at some other scale (e.g., local competitive interactions)." Bird-habitat associations on one scale may, however, be related to those on other scales, despite differences in the causal mechanisms underlying such patterns. If habitat-selection responses on different scales are elicited by separate stimuli, as it appears they are, then the stimulus-response association would vary according to scale as well. But it is not axiomatic that the consequent habitat-use patterns on various scales should be unrelated. Actually, ornithologists should expect such patterns to be dependent if the paradigm of hierarchical habitat selection is realistic because responses on smaller scales are preceded by (and are therefore partially contingent upon) responses at broader scales. The question of whether there are related habitat-use patterns on different scales is important because the answer would indicate the extent to which patterns (but not stimulus-response events) on one scale are explicable by those on other scales.

On the scale of habitat fragments, the probability of nesting by Northern Flickers was negatively related to the amount of edge/hectare, the opposite of what one would predict from edge associations on a smaller scale (cf. Conner et al. 1975). Contrary to characterizations of House Wrens and European Starlings as edge species on a local scale (Robbins 1979), the average number of nests for these birds was not positively related to edge/hectare on the scale of forest fragments. The broad-scale, negative relation between the probability of Northern Flickers nesting and distance to nearest streamside habitat fragment is related in part to small-scale, nest-tree associations between Northern Flickers and peachleaf willow, which occurred primarily near the streams. The average number of European Starling nests was positively related to the frequency of nonsnag trees 41 to 70 cm dbh, a structural characteristic of woodland fragments. This association is related to nest-tree use in that 42% of the nest trees we analyzed for European Starlings were in this diameter class. Forest fragments bordering the streams were larger and had thicker habitats. The positive relation between the probability of nesting by Downy Woodpeckers and fragment area was dependent in part on the tendency of Downy Woodpeckers to use thicker vegetation on the scale of nest sites.

Based on our data and those of others, habitat-use patterns for a given species on one scale may or may not be predictable from those on other scales. Extrapolation of responses from one scale to another may therefore be senseless, unless there are interdependencies. Inappropriate extrapolations can lead to: (1) incorrect descriptions of how habitat scale influences bird-community structure, and (2) poor decisions about habitat management for avian conservation. A more complete and integrated view of how habitat features affect the structure of cavity-nester communities emerged than if we had restricted analyses to one or two spatial scales. The species-richness patterns we observed were influenced strongly by a combination of similar and dissimilar habitat associations among species on three spatial scales.

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