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Microhabitat factors influencing predation and success of suburban Blue Jay *Cyanocitta cristata* nests

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We examined how microhabitat features surrounding nest-sites influence probability of nest predation by testing unique predictions generated from the "distance to human activity," the "habitat complexity," and the "multiple nest-site" hypotheses. During spring and summer 1990, we quantified nine features of nest-sites and 11 features of 0.1 ha nest-patches surrounding 42 nests of suburban Blue Jays *Cyanocitta cristata* in Fayetteville, Arkansas, to determine differences associated with depredated and successful nests. Overall nesting success was 52% and mean daily survival rate of nests was 0.983 (± 0.004 SE). Twenty-four nests fledged at least one young, and 18 failed as a result of nest predation. Features of the nest-site, including nest height, size of the nest tree, and nest concealment, were not related to nest predation, although distance from a nest to the nearest building was inversely related to duration of nest survival. The latter relationship suggests human activity may decrease nest predation in suburban areas. Density of vegetation surrounding nests did not influence nest fate, thus providing no support for the habitat complexity hypothesis. Instead, failed nests occurred in patches containing fewer trees of the same species, size class and vine cover as the nest tree. Because this pattern was not an effect of size or species of either the nest tree or neighboring trees, nor an effect of vines in the nest tree or neighboring trees, it provides support for the multiple nest-site hypothesis.

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Because nest predation is a major factor limiting breeding success in open nesting passerine birds (e.g., Ricklefs 1969, Martin 1988, 1992), natural selection should favor birds that behave in ways that reduce the probability of nest predation. If quality of nesting microhabitats differs among potential nest-sites, such that nests differ in the likelihood of being found by a predator, and if such differences are identifiable, selection should favor birds that choose nesting microhabitats associated with a low probability of nest predation (Martin 1992).

A number of hypotheses have been proposed to explain how nesting microhabitat may influence nest predation (Filliater et al. 1994). Here we examine two hypotheses that address the manner in which structure of the habitat surrounding nests may affect predator search efficiency, and a third that addresses the way in which the suburban landscape may influence nest predation. The "habitat complexity" hypothesis (Bowman and Harris 1980) suggests increasing spatial habitat complexity reduces predator search efficiency by impeding travel or by inhibiting transmission of visual, auditory, or chemical cues that predators use to find nests. The "multiple nest-site" hypothesis (Martin and Roper 1988) suggests that increasing numbers of potential nest-sites surrounding an actual nest may reduce predator efficiency because predators are more likely to encounter empty nest-sites, and, being rewarded less frequently, are more likely to move to a different area. The "distance to human activity" hypothesis (Collias and Collias 1984) states that nests closer to human activity suffer lower predation rates because human activity deters predators from using such areas.

In this study we quantified microhabitat features surrounding nests of suburban Blue Jays *Cyanocitta cristata* to determine differences associated with failed and successful nests. We also tested unique predictions generated from the habitat complexity, multiple nest-site, and distance to human activity hypotheses to examine how microhabitat features may influence the probability of nest predation. A unique prediction of the habitat complexity hypothesis is that the probability of nest predation should decrease as vegetation density increases. The multiple nest-site hypothesis uniquely predicts that the probability of nest predation should decrease as the number of potential, but unoccupied, nest-sites within an area increases. Because potential nest-sites are difficult to identify for species that nest in a variety of nest substrates, we tested the corollary prediction that variables that reflect similarities between the actual nest-sites and the surrounding vegetation are good predictors of nest fate. Finally, we tested a prediction generated from the distance to human activity hypothesis, that probability of nest predation increases with distance from nest to nearest building.

Methods

Study species

Blue Jays nest in deciduous and mixed coniferous/deciduous forest habitats across the eastern United States and southern Canada. In modern times, Blue Jays have become numerous in suburban habitats, where they build nests in a wide array of tree species. Nests may be as low as 1 m above the ground or near the top of the nest tree, although typical nest height is between 3 and 8 m (Taylor 1965, Woolfenden and Rohwer 1968). Nests consist of a rather bulky outer shell made of sticks surrounding a compact cup. They may be placed near the end or at the base of a branch, directly on a large horizontal limb, or in a fork in the trunk of the nest tree. Nests may or may not be concealed by vegetation, and adults usually vigorously defend their nests from potential nest predators. Females incubate eggs and brood nestlings, and food for incubating females and young nestlings is provided by males. Regardless of whether nests are well concealed by vegetation, provisioning males approach the nest indirectly, usually moving to several perches in the vicinity of the nest before delivering food to the sitting female or nestlings. Hardy (1961) concluded that Blue Jays build "false" nests, small platforms of sticks that are abandoned prior to completion. We know of no published studies addressing the effects of false nests, tendency of adults to defend the nest, or approach patterns of provisioning males on probability of nest predation, nor did we attempt to quantify them in the present study.

Study area

Our study was conducted within the city limits of Fayetteville, Washington Co., Arkansas during spring and summer, 1990, in neighborhoods containing park-like stands of oaks *Quercus* spp., elms *Ulmus* spp., and sugar maples *Acer saccharum* that formed patchy canopies over lawns, scattered shrubs, and copses. Lawns often were bordered by overgrown brush along property lines, small streams, or vacant lots. Several dense woodlots, ranging in area from a few to tens of hectares, were interspersed throughout the city.

Common potential nest predators on our study site included gray squirrels *Sciurus carolinensis*, house cats *Felis domesticus*, American Crows *Corvus brachyrhyncos*, and other Blue Jays. Less common predators included black rat snakes *Elaphe obsoleta*, House Wrens *Troglodytes aedon*, raccoons *Procyon lotor*, and Virginia opossums *Didelphis virginiana*. We did not attempt to assess relative impact of each predator species on our study site; however, Blue Jays usually responded vigorously to the presence of American Crows and gray squirrels near nest-sites, indicating jays view those species as threatening. We observed American Crows taking eggs from one jay nest, and an unmarked Blue Jay flying from another nest with an egg in its beak. Eggs of a third jay nest contained puncture holes characteristic of egg destruction by House Wrens (Belles-Isles and Picman 1986). We observed no other predation events.

Nesting success

Upon discovery, nests were checked for activity every 1 to 6 days; usually every 2–3 days depending on number of active nests on any given day. We used Student's t test to determine whether frequency of nest checks influenced probability of nest predation by comparing the ratio of number of nest checks per nest observation period (in days) between successful and depredated nests for all nests that were checked more than once. If a nest appeared inactive during a nest check, contents were checked with a mirror mounted on a pole. Nests were considered active if at least one egg or nestling was seen in a nest, or if an adult was observed brooding on the nest over a span of at least three days.

Nests were considered successful if they survived at least 34 days beyond the laying of the penultimate egg. Throughout the geographic range of the Blue Jay, the time between laying of the penultimate egg and successful fledging of young jays is about 34 days (e.g., Tyler 1946, Woolfenden and Rohwer 1968, this study). When we could not determine the age of a nest, success was assumed if (1) fledglings were found in the area surrounding a nest after it was empty; (2) adults became extremely agitated as we searched for fledglings, but no fledglings were found; or (3) nestlings were seen perched on the nest rim.

Active nests were assumed to have failed due to predation if contents disappeared before young were expected to fledge or if punctured or broken eggs were found. If a predator removed only a portion of the nest contents and the nest continued to survive, it was considered active until the remaining contents later disappeared. When dead nestlings were found below a failed nest and showed signs of predation (such as puncture holes), the nest was assumed to have been preyed on. If no signs of predation were found on fallen young, the nest was assumed to have failed as a result of unknown causes. Active nests were considered abandoned when adults were not seen tending them for several consecutive nest checks, even though they still contained eggs. Only successful nests and nests known to have been depredated were included in nest predation analyses. Nests that were abandoned before completion were not included in analyses of nest success because Blue Jays may build "false" nests (Hardy 1961).

We estimated the week that the first egg of each nest was laid to determine if temporal variability existed in nest failure, and hence whether the Mayfield (Mayfield 1961, 1975) method was appropriate for estimating overall nest success for the entire nesting period (Johnson and Shaffer 1990). We were unable to calculate survival rates for the egg and nestling periods separately because many nests were not readily accessible due to their height or position within the nest tree, and we feared frequent checking of nest contents would cause abandonment (personal observation). Nests that likely failed due to observer disturbance were excluded from analyses.

The minimum duration of survival of each nest was calculated to provide an index of susceptibility to nest predation. Duration of nest survival was determined by assuming that for successful nests, the post-laying incubation and nestling periods each lasted 17 days (Tyler 1946). Unsuccessful nests found after clutch completion were assumed to have survived one day for each egg in the clutch plus the number of days the nest was under observation after it was discovered.

Habitat sampling

We measured nest-site and nest-patch microhabitat features (MacKenzie et al. 1982, Martin and Roper 1988, Kelly 1993) between 20 June and 5 September 1990. Nest-site features reflected qualities of the nest substrate. A "nest-patch" was defined as a 0.1 ha circle (radius = 17.8 m) centered around the nest. Nest-patch features were features we felt potentially could influence predator occurrence, or predator foraging or search efficiency within the area (Bowman and Harris 1980, MacKenzie et al. 1982, Martin and Roper 1988).

Table 1. Size class categories of woody stems used for statistical analyses.

Size class	Growth form	Diameter at breast height (cm)
Shrub	clumped[a]	< 2.5
Tiny	single	< 2.5
Small	single	2.5 – 7.4
Medium[b]	single	7.5 – 30.5
Large[b]	single	> 30.5

[a] Clumps of stems were assumed to comprise single shrubs only when the stems appeared to be ramets of the same genet.

[b] Stems in these size classes were large enough to support a Blue Jay nest.

Nine nest-site variables reflected nest-substrate characteristics and nest concealment. For each nest, we determined nest-tree species, height, and diameter at breast height (dbh); height of the nest and whether it was situated in a clump of vines; distance from the nest to the center of the nest tree; distance from nest to the top of the nest tree; compass orientation of the nest relative to the center of the nest tree; distance from nest to nearest building; and degree of nest concealment.

Nest concealment was determined by visually estimating percent of the nest that would be concealed by foliage or branches if viewed from 1 m away in both vertical (above/below) and horizontal (cardinal directions) planes relative to the nest (Martin and Roper 1988, Kelly 1993). Because of the subjectivity involved in these measurements, especially when nests were too high to be examined from 1 m away, we performed three independent manipulations on concealment data to create three types of concealment index. Concealment indices represented the sum of concealment values in a given plane, the mean concealment across all measured directions of a given plane, and the direction exhibiting the lowest percent concealment in the horizontal plane (Martin and Roper 1988). The "lowest value" concealment index was created for the horizontal planes only. The "summed" and "mean" concealment indices were created for both the horizontal and vertical plane. Because of their relative subjectivity, the above nest concealment indices were not included in any multivariate analyses.

Eight measurements were used to provide descriptions of the nest-patch. We counted and measured dbh of all woody stems in the patch, and noted the presence or absence of vines on them (hereafter referred to as "vine status"). Clumps of stems less than 2.5 cm dbh that were obviously ramets of the same genet were considered as a single shrub and tallied separately. Woody stems were grouped into size classes for most statistical analyses (Table 1). Percent of the ground surface in the nest-patch covered by buildings and shrubs was estimated visually, as was the percent of the ground surface that was not covered by buildings, shrubs or trees (hereafter referred to as "open ground"). Percent canopy was estimated at 40 points as described by James and Shugart (1970). All percentage values were arcsine transformed.

To test the multiple nest-site hypothesis, we had to identify potential nest-sites within each nest-patch. We defined a potential nest-site as any tree large enough to support a Blue Jay nest (> 7.5 cm dbh based on observed nest trees), regardless of tree species. Two indices of the number of potential nest trees that were similar to the actual nest tree in the nest-patch were obtained from the stem frequency data. The first index was the number of trees in the nest-patch that were of the same species and in the same size class as the nest tree. The second index was the number of trees in the nest-patch that were of the same species, in the same size class, and of the same vine status as the nest tree. Although the two indices were similar, the latter was a more refined estimate of the similarity of the other trees to the actual nest tree.

Statistical analysis

Statistical analyses were conducted using SAS (SAS Institute, Inc. 1985). Because we tested for differences in 20 microhabitat features associated with successful and depredated nests (continuous nest-site and nest-patch variables combined), we should expect at least one significant, yet perhaps spurious, relationship at an α level of 0.05. We corrected for this problem by using a "protected ANOVA" technique (Scheiner 1993). We first conducted a MANOVA, which allowed us to examine for an overall difference in microhabitat with a single test, thereby reducing the chance of committing a type I error (Scheiner 1993). We then proceeded with univariate tests, using the Wilcoxon Rank Sums test to determine which continuous microhabitat variables differed between successful and depredated nests. Linear regression was used to examine the relationship of all continuous variables with duration of nest survival to determine relative ability of single variables to predict nest fate.

Categorical nest-site variables were not included in the MANOVA. Rayleigh's test and the Watson-Williams test (Zar 1974) were used to test effects of nest orientation on fate of nests having distinct directional orientation relative to the center of the nest tree. Fisher's exact test was used to compare predation frequency of nests having distinct orientation with those for which directional orientation relative to the center of the nest tree was not distinct. Chi-square contingency analysis and Fisher's exact test were used to determine if nests were preyed upon more or less often than expected by chance in a particular nest substrate, nest tree size class, or in commonly used nest tree species.

A stepwise logistic regression procedure (Harrell 1986) was used to identify interacting variables that were good predictors of nest fate and that discriminated between depredated and successful nests. Stepwise logistic regression was chosen over discriminant function analysis because the former does not assume multivariate normality or equal covariance matrices between groups (Press and Wilson 1979). After creating a model with stepwise logistic regression, we used non-stepwise logistic regression to examine the contribution of particular variables to the original logistic regression model. Cohen's kappa statistic (Titus et al. 1984) was used to determine whether classification produced by logistic regression was significantly better than expected by chance.

Results

Nesting success

Sixty-seven Blue Jay nests were found between 22 March and 24 July 1990. Forty nests were found before egg laying began; five were found during laying; two were found after completion of the clutch, but before hatching; and six were found after hatching, but before fledging. One nest was found the day the young fledged. We found 12 other nests with eggs, but could not determine if they were found before the clutch was completed because their contents could not be checked (due to the presence of an adult on the nest) until several days after discovery. We were unable to determine the contents of one other active nest. Of the 67 nests, only 58 were known to have contained eggs; of the 58 nests, we were able to determine success or failure for 47. Twenty-one of 47 nests whose fate was known failed to produce a fledgling. Predation accounted for 18 (90.0%) of the 20 failed nests for which cause of failure could be determined. Virtually complete habitat data sets were obtained on 42 nests, 24 of which were successful and 18 of which failed as a result of predation. Because most of our habitat analyses concerned only successful and depredated nests, sample sizes range from 38 to 42 nests, depending on the number of nests for which the appropriate habitat characteristics were measured.

Frequency of nest checks did not differ between successful and depredated nests (all nests checked at least twice: $N = 23$ successful nests, 15 depredated nests; Student's $t = -1.635$; $df = 30.4$; $P > 0.11$). Mean week of nest initiation did not differ between depredated and successful nests (Wilcoxon Rank Sums: $Z = 0.678$, $P > 0.40$), nor did it explain significant variation in duration of nest survival ($r^2 = 0.025$, $P > 0.30$), suggesting the Mayfield method was appropriate for calculating nesting success (Johnson and Shaffer 1990). Of the 47 nests for which we determined fate, 45 were observed over a period of at least 24 hours and thus were appropriate for Mayfield analysis (Mayfield 1961, 1975). Based on those 45 nests, population nesting success was 52% (1099 nest-days) and mean daily survival rate of nests after the first egg was laid was 0.983 (S.E. = 0.004).

Nest-site characteristics

We found Blue Jay nests in 18 tree species, and on two houses (Table 2). No differences in probability of predation were detected in common nest tree species (i.e., those in which at least five nests were found; Table 2) vs other species ($N = 40$, $\chi^2 = 0.009$, $df = 1$, $P = 0.923$), nest trees with vines vs trees without vines ($N = 37$, $\chi^2 = 0.035$, $df = 1$, $P = 0.852$), or in large vs medium nest trees (Table 1; $N = 39$, $\chi^2 = 0.010$, $df = 1$, $P = 0.921$). Blue Jay nests were uniformly distributed around the centers of nest trees (Rayliegh's $Z = 0.842$, $0.20 < P <$

Table 2. Tree species used as nest-sites by Blue Jays in Fayetteville, Arkansas during spring and summer, 1990, and number of nest-patches in which at least one individual of the species was present.

Common name	Scientific name	Number used as nest-sites	Number of patches in which species was present
Sugar Maple	*Acer saccharum*	7	19
Post Oak	*Quercus stellata*	5	14
Winged Elm	*Ulmus alata*	5	14
Red Elm	*Ulmus rubra*	3	17
Red Mulberry	*Morus rubra*	3	13
Black Jack Oak	*Quercus marilandica*	3	9
Shortleaf Pine	*Pinus echinata*	2	4
Redbud	*Cercis canadensis*	2	17
Hackberry/Sugarberry	*Celtis* sp.	2	18
Flowering Magnolia	*Magnolia grandiflora*	1	3
Tree of Heaven	*Ailanthus altissima*	1	6
Honeysuckle[a]	*Lonicera maackii*	1	2
Osage-orange	*Maclura pomifera*	1	4
Pecan	*Carya illinoensis*	1	6
Plum	*Prunus* sp.	1	1
Cherrybark Oak	*Quercus falcata* var. *pagodaefolia*	1	4
Chestnut	*Castanea* sp.	1	2
Boxelder	*Acer negundo*	1	5
Dead snag	*Pinus* sp.	1	2
House	–	2	31

[a] *Lonicera maackii* is abundant as a shrub on our study site. However, we found individuals having stems large enough to support a nest in only 2 nest-patches.

0.50) and no differences were found between depredated and successful nests in orientation (depredated nests, $Z = 0.356$, $P > 0.50$; successful nests, $Z = 1.529$, $0.20 < P < 0.50$) or mean angle (Watson-Williams test, $F = 1.27$, $P > 0.25$). Nine nests were considered to have no distinct orientation; they were depredated at the same rate as those positioned peripherally to the main trunk or center of the nest tree (Fisher's exact test, $N = 42$, $P > 0.20$).

MANOVA indicated overall microhabitat differed between successful and depredated nests ($N = 42$, $F = 2.43$, $df = 20, 16$, $P = 0.04$). Continuous (i.e., non-categorical) nest-site variables, however, did not differ significantly between depredated and successful nests when considered individually (Table 3). Distance from nest to nearest building was inversely related to duration of nest survival ($r^2 = 0.124$, $P = 0.04$). No other nest-site variables were significantly related to duration of nest survival (linear regression for all other nest-site variables, $r^2 < 0.025$, $P > 0.35$).

Distance from nest to nearest building may reflect effects of proximity of nests to buildings (a characteristic of the nest-site) or of relative openness of understory near buildings (a characteristic of the nest-patch; see below). To determine whether vegetation density varied with increasing distance from buildings, density of vegetation in each size class (Table 1) was regressed against distance from nest to nearest building. In no size class of vegetation was density linearly related to distance from buildings ($r^2 < 0.009$, $P > 0.50$).

Nest-patch characteristics

Univariate tests revealed depredated nests were in patches associated with fewer trees of the same species, size class, and vine status as the nest tree; however, no other nest-patch variables differed between depredated and successful nests (Table 4). When considered univari-

Table 3. Relationship of continuous nest-site variables to fate of suburban Blue Jay nests (Wilcoxon Rank Sums test).

Variable	n	Successful $\bar{x}$ (S. E.)	Depredated $\bar{x}$ (S. E.)	P
Nest tree height (m)	40	11.8 (1.1)	11.6 (1.1)	0.74
Nest tree diameter (cm)	40	36.3 (5.3)	41.3 (6.8)	0.72
Nest height (m)	42	4.8 (0.4)	4.1 (0.5)	0.24
Distance from nest to center of nest tree (m)	42	1.4 (0.4)	1.5 (0.5)	0.69
Distance from nest to nearest building (m)	42	9.6 (1.2)	15.9 (2.7)	0.14
"Summed" concealment index[a] (horizontal)	42	13.7 (0.79)	13.8 (0.64)	0.84
"Summed" concealment index[a] (vertical)	41	7.2 (0.36)	7.9 (0.41)	0.41
"Mean" concealment index[a] (horizontal)	42	58.6 (4.10)	61.1 (3.24)	0.85
"Mean" concealment index[a] (vertical)	41	62.8 (3.60)	69.4 (4.28)	0.57
"Lowest value" concealment index[a] (horizontal only)	42	28.7 (5.60)	28.7 (4.83)	0.56
Distance from nest to top of nest tree (m)	42	6.97 (0.90)	7.52 (0.82)	0.77

[a] See text for explanation of these indices.

Table 4. Relationship of nest-patch variables to fate of suburban Blue Jay nests (Wilcoxon Rank Sums test). Stem size classes are defined in Table 1.

Variable	n	Successful $\bar{x}$ (S. E.)	Depredated $\bar{x}$ (S. E.)	P
Number of shrubs in the patch	41	14.3 (3.4)	16.0 (4.7)	0.68
Number of tiny stems	41	20.1 (5.1)	20.1 (6.0)	0.82
Number of small stems	41	17.5 (3.8)	16.8 (6.0)	0.63
Number of medium stems	41	20.1 (4.8)	12.9 (3.1)	0.33
Number of large stems	41	4.1 (0.4)	4.4 (0.3)	0.35
Total number of trees > 7.4 cm dbh	41	24.2 (4.70)	17.3 (3.03)	0.35
Total number of stems	41	74.9 (14.8)	70.3 (17.7)	0.84
Number of trees of the same species and size class as the nest tree	39	9.1 (3.4)	1.8 (0.4)	0.07
Number of trees of the same species, size class, and vine status as the nest tree	39	8.1 (2.9)	1.4 (0.3)	0.03
Number of trees with vines	41	8.0 (2.4)	6.2 (2.1)	0.85
% open ground	42	79.4 (2.9)	74.3 (5.1)	0.52
% ground covered by buildings	42	14.7 (2.8)	14.4 (4.5)	0.30
% ground covered by shrubs	42	4.5 (0.9)	10.4 (3.7)	0.32
% canopy cover	42	66.8 (3.3)	69.7 (3.2)	0.74

ately, no nest-patch variables accounted for significant variation in duration of nest survival (all variables, $r^2 < 0.086$, $P > 0.088$).

Multivariate analyses

Four variables were selected by the initial stepwise logistic regression as good predictors of nest fate (Table 5). The model predicted nest success (non-predation) better than nest predation: 76.5% of depredated nests and 86.4% of successful nests were correctly classified. This classification is 63% better than expected by chance (Cohen's test for chance correctness, $P_c = 0.511$, $P_o = 0.821$, Kappa = 0.633 ± 0.252, P = 0.0001).

The stepwise logistic regression procedure selected as an important predictor of nest fate a variable describing number of trees in the patch that were of the same species, in the same size class, and of similar vine status as the nest tree (Table 5). To examine the importance of the similarity of other trees to the nest tree, logistic regression models were run again, but with variables that were less refined in their estimates of the similarity of other trees to the nest tree. Those logistic regression models were not as good at predicting nest fate (i.e., they had lower multiple correlation coefficients) as were the initial models, although the overall ability of the models to classify successful and depredated nests varied little (Table 6).

Distance from nest to center of the nest tree also was selected by the original stepwise logistic regression procedure. However, its effects may have reflected the influence of other variables. Distance from nest to center of the nest tree was positively correlated with nest tree dbh, nest tree height, and nest height (for each variable,

Table 5. Initial stepwise logistic regression analysis of the relationship of fate of suburban Blue Jay nests with continuous nest-site and nest-patch variables (n = 39 nests). (a) Parameters of variables selected by the forward stepwise procedure. (b) Overall model parameters.

(a) Parameters of individual variables

Variables	Beta	S. E.	χ^2	r	P
Intercept	–9.96	4.68	4.52		0.03
Distance from nest to nearest building	–0.02	0.01	4.58	–0.22	0.03
Percent of open ground in patch	13.85	6.46	4.60	0.22	0.03
Number of trees of the same species, size class, and vine status as the nest tree[a]	1.19				
Distance from nest to center of nest tree	0.02	0.01	3.87	0.19	0.05

(b) Overall model parameters

Model			Residual				
χ^2	d.f.	P	χ^2	d.f.	P	–2 Log L	r
31.33	4	0.00	17.40	15	0.30	22.09	0.66

[a] Beta was assumed to be infinite during at least one iteration and parameter estimation was consequently suppressed (Harrell 1986).

Table 6. Comparison of the ability of three logistic regression models to predict fate of suburban Blue Jay nests. Four variables were forced into each model: distance from nest to nearest building, percent of open ground in the nest-patch, distance from nest to center of the nest tree, and one of the variables below. Each of the variables below represents an estimate of the number of potential nest-sites within the nest-patch. They differ in the degree of similarity of the potential nest-sites to the actual nest-site.

			Overall model parameters			
Variable	Similarity	N	χ^2	r	P	% correct classification
Number of trees of the same species, size class, and vine status as the nest tree.	greatest	39	31.3	0.661	< 0.01	82.1
Number of trees of the same species and size class as the nest tree	intermediate	39	28.3	0.617	< 0.01	84.6
Number of trees large enough to support a Blue Jay nest, regardless of species	least	41	22.4	0.510	< 0.01	82.9

$r > 0.51$, $P < 0.0007$), and was negatively correlated with number of medium trees in the nest-patch ($r = -0.355$, $P < 0.025$). Because distance from the nest to the center of the nest tree was not significant in univariate tests, we are unsure of its importance.

Discussion

In this study, we tested unique predictions generated from the "habitat complexity" (Bowman and Harris 1980), the "multiple nest-site" (Martin and Roper 1988), and the "distance to human activity" (Collias and Collias 1984) hypotheses. Each hypothesis is designed to explain how microhabitat surrounding nests may influence nest predation, although they are not necessarily mutually exclusive. The distance to human activity hypothesis (Collias and Collias 1984) was supported by our results. Blue Jay nests near buildings suffered less predation than those further away from buildings (Table 5). Proximity to buildings probably can be equated with proximity to human activity, which may deter predators from approaching nest-sites and prey items (Baeyens 1981, Collias and Collias 1984, Doncaster 1994). An alternative explanation is that, because suburban buildings are usually associated with lawns, the relationship between probability of nest predation and proximity to buildings may in fact reflect the effects of the "openness" of vegetation on predation; i.e., predators may avoid areas with little cover because they have a greater chance of being detected by prey, or because predators themselves may be subjected to greater predation pressures in such areas. However, no linear relationship existed between density of vegetation and distance from nest to nearest building ($r^2 < 0.009$, $P > 0.50$), suggesting the presence of buildings did not affect the openness of the surrounding vegetation.

Our results do not support the habitat complexity hypothesis. The total number of stems within a nest patch, a good indicator of the complexity of the vegetation structure (Bowman and Harris 1980), had no effect on probability of nest predation on our study site, nor did number of stems within particular size classes (Table 4). Bowman and Harris (1980) found support for the habitat complexity hypothesis using artificial ground nests and a mammalian predator (raccoon). Perhaps the important predators on our study site (most likely American Crows, gray squirrels, and Blue Jays) find nests by cuing on particular kinds of vegetation or on movements of breeding adults, rather than by randomly moving through vegetation in search of nests.

Our results provide some support for the multiple nest-site hypothesis. Number of trees in the nest-patch that were similar to the nest tree was the most important predictor of nest fate. Furthermore, logistic regression models that included variables representing more refined estimates of the similarity of other trees to the nest tree consistently were better at predicting nest fate than were models using variables that represented a wider array of potential nest trees.

The patterns we found supporting the multiple nest-site hypothesis may reflect effects of variables related to those describing the similarity of other trees to the nest tree. However, we found that importance of number of trees of the same species, size class, and vine status as the nest tree did not reflect an influence of tree size because nest-tree size did not differ between successful and depredated nests. Likewise, this variable included only large trees or only medium trees, depending on a particular nest tree. Thus, it did not reflect effects of absolute numbers of medium or large trees in the patch. Neither number of medium trees, nor of large trees, differed between patches surrounding successful and depredated nests, nor did the total number of trees in the patch (Table 4).

Similarly, number of trees of the same species, size class, and vine status did not reflect an effect of vines around a nest or on other trees because presence of vines around nests had no effect on nest fate. Likewise, number of vine-clad trees did not differ among patches containing successful and depredated nests (Table 4). Nest concealment also appeared to have no influence on the likelihood of nest success (Table 3). Finally, the variable probably did not reflect an effect of nest tree species on nest fate, as we detected no patterns of association between nest tree species and probability of nest predation.

Few studies have examined the effect of potential nest-sites on nest predation rates. Martin and Roper (1988) found nests of Hermit Thrushes *Catharus guttatus* were surrounded by more small white firs *Abies concolor*, the nest substrate used almost exclusively by the thrush, than were randomly selected non-use sites. Furthermore, nests surrounded by a lower density of white firs had a higher probability of predation than those surrounded by a greater density of firs. However, nests associated with a low probability of predation also were better concealed than were high predation-risk nests, making evaluation of the importance of multiple nest-sites difficult. Kelly (1993), on the other hand, found no support for the multiple nest-site hypothesis in a population of Dusky Flycatchers *Empidonax oberholseri*, but found vegetation density was positively correlated with nest success. Mountain junipers *Juniperus scopulorum*, the most common nest substrate of the flycatchers, were less dense around successful than unsuccessful nests, and other, structurally different, tree species were more dense around successful nests. Neither of the latter two trends was statistically significant, however.

The Hermit Thrushes studied by Martin and Roper nested exclusively in white firs, potentially allowing predators searching explicitly for thrush nests to cue on a particular nest substrate. Blue Jays, however, typically place nests in a variety of substrates, even within a local population (Tyler 1946, Woolfenden and Rohwer 1968; Table 2). The wide array of nest-sites chosen by Blue Jays in our study may reflect a strategy by which Blue Jays preclude predators from cuing on potential nest-sites, thus reducing the probability of nest predation. If so, perhaps we should not expect a strong relationship between incidence of nest predation and similarity of potential nest-sites and actual nest-sites.

Inferences from studies of this nature, including the present one, should be made with caution, as foraging method of potential predators will influence the importance of spatial complexity on foraging efficiency. To understand how differing microhabitats affect probability of nest predation, we must better understand the cues that specific predators use to locate bird nests (Martin 1988). Indeed, a diverse array of potential nest predators may impede the ability of birds to choose a particular strategy that allows them to avoid nest predation (Filliater et al. 1994). The findings in the present study are important because they demonstrate that microhabitat may influence patterns of nest predation in multiple ways, and that human activity may actually decrease the probability of nest predation in suburban habitats.

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