

## HABITAT AND NESTING SUCCESS OF BLUE JAYS (*CYANOCITTA CRISTATA*): IMPORTANCE OF SCALE

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**ABSTRACT.**—Nesting success of birds often is influenced by habitat features surrounding nests. However, few studies have investigated habitat influences at multiple levels and spatial scales. We examined the relationship between Blue Jay (*Cyanocitta cristata*) nesting success and habitat at three levels (macrohabitat, microhabitat, and nest site) and at three different scales within the microhabitat level (3.1, 0.3, and 0.07 ha circular plots surrounding nests) in central Florida. We defined successful nests as those fledging at least one offspring. An eight-fold difference in probability of nesting success existed among seven distinct macrohabitats, with Mayfield success estimates ranging from 8 to 63%. However, no difference in number of fledglings per nest existed among macrohabitats when unsuccessful nests were excluded from the analysis. Macrohabitats in which nests were more often successful had more extensive slash pine (*Pinus elliottii*) forest. Logistic regression analyses indicated that slash pine canopy cover was significantly related to nesting success at all three microhabitat scales, although the tree species in which a nest was placed was unimportant to nesting success. Other microhabitat and nest-site features were unrelated to nesting success. Strong circumstantial evidence indicates predation was the major cause of nest failure, but relative abundance of one potential predator, the gray squirrel (*Sciurus carolinensis*), was not related to nesting success in macrohabitats or slash pine canopy cover within microhabitats. In this study, logistic regression models using habitat features measured at higher levels and larger scales had better predictive power, indicating that habitat may have influenced predation at scales larger than that of a typical nest patch. Received 21 August 2001, accepted 8 June 2002.

**RESUMEN.**—El éxito de nidificación en las aves es a menudo influenciado por las características del hábitat que circunda a los nidos. Sin embargo, pocos estudios han investigado las influencias del hábitat a múltiples niveles y escalas espaciales. Examinamos la relación entre el éxito reproductivo de *Cyanocitta cristata* y el hábitat a tres niveles (macrohábitat, microhábitat y sitio del nido) y a tres niveles diferentes dentro del microhábitat (parcelas circulares alrededor de los nidos de 3.1, 0.3 y 0.07 ha) en Florida central. Definimos como nidos exitosos a aquellos en que por lo menos una cría llegó a la etapa de emplumamiento. Encontramos una diferencia de ocho veces en la probabilidad de anidar exitosamente entre siete macrohábitats distintos, con valores de la estimación del éxito de Mayfield entre un 8 a un 63%. Sin embargo, no se encontró diferencia en el número de volantones por nido entre macrohábitats cuando se excluyeron los nidos no exitosos del análisis. Los macrohábitats en que los nidos fueron exitosos más a menudo, presentaban una mayor extensión de bosques de pino (*Pinus elliottii*). Los análisis de regresión logística indicaron que la cubierta del dosel de *P. elliottii* se relacionó significativamente con el éxito de nidificación a los tres niveles de microhábitat, aunque la especie del árbol en que se encontraba un nido no fue importante para el éxito de nidificación. Otras características del microhábitat y rasgos del sitio del nido no se relacionaron con éxito de nidificación. Fuerte evidencia circunstancial indica que la depredación fue la mayor causa de fracaso de los nidos, pero la abundancia relativa de un de predator potencial, la ardilla gris (*Sciurus carolinensis*), no se relacionó con el éxito de nidificación en los macrohábitats ni con la cubierta del dosel de *P. elliottii* dentro de los microhábitats. En este estudio, los modelos de regresión logística que utilizan características del hábitat medidas a niveles más altos y a mayores escalas tuvieron un mejor poder de

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predicción, indicando que el hábitat puede influenciar a los patrones de depredación a una escala mayor que a la de un parche típico de un nido.

SUCCESS OF OPEN passerine nests may be influenced by habitat surrounding them (e.g. Martin and Roper 1988, Kelly 1993, Tarvin and Smith 1995). For example, at a coarse-grained level based on community composition (here defined as "macrohabitat"), the abundance or distribution of food or predator species may be greatly influenced by characteristics such as abiotic factors, relative abundance of prey species, community structure, etc. At a finer-grained, local level ("microhabitat"), structural complexity (e.g. plant architecture, stem density) of surrounding features may influence the ability of predators to find nests by interfering with visual or olfactory cues (Martin and Roper 1988), impeding predator movement through an area (Bowman and Harris 1980), or influencing reward rates when predators must search many similar potential nest sites to find dispersed nests (Martin 1988, Martin and Roper 1988, Tarvin and Smith 1995). A third level at which habitat features may influence nesting success is that of the nest site, which comprises the substrate in or on which the nest is placed and its qualities (e.g. height, concealment, stability, etc.). Features of nest sites may preclude predators from accessing nests (Cullen 1957, Lawton and Lawton 1980), affect the deterrent or vigilant behaviors of parent birds (Belles-Isles and Picman 1986), or simply hide nests from predators (Kelly 1993). Nesting habitat also can influence the probability of nest failure through factors other than nest predation. For instance, structural characteristics of nest sites may affect the probability of nest safety during strong winds, or provide shelter from climatic factors such as rain, snow, insolation, or thermal variation (Walsberg 1981, Marzluff 1988).

Within the level of microhabitat, the scale at which habitat influences nesting success may vary, depending on the local suite of predators, distribution of food, or other factors (Martin and Roper 1988, Martin 1992). For example, influence of structural complexity on predator olfactory search efficiency may be important within a certain distance from the nest, but may have little effect at greater distances. Determining the appropriate spatial scale at which to study the relationship between habitat and nesting success often is difficult, and

any chosen scale is to some degree arbitrary. Because processes influencing nesting success are likely to be scale dependent, the ability of studies to detect relationships between habitat and nesting success is in part dependent on the scale chosen for measurements.

In this study, fate of Blue Jay (*Cyanocitta cristata*) nests in central Florida was determined and tested for relationships between nesting success and habitat features at the levels of macrohabitat, microhabitat, and nest site. For a subset of nests, we further tested for relationships between nesting success and microhabitat features measured at three different spatial scales. Some published studies have used the term "nest patch" instead of microhabitat (Martin and Roper 1988, Martin 1992, Tarvin and Smith 1995); however, we use the latter term because our study focuses on habitat occurring within arbitrary plot boundaries rather than distinct clumps of vegetation (see Burhans and Thompson 1999).

Blue Jays serve as a good species for studies of this kind because they exhibit extreme variation in use of nesting habitat. Blue Jays nest in deciduous, mixed coniferous-deciduous, and coniferous forest, as well as suburban, agricultural, and other human-disturbed landscapes (Tarvin and Woolfenden 1999). Nests range from ~2 m above ground in shrubs or saplings to the uppermost branches of the tallest trees available, and may be placed in virtually any tree species present (Tarvin and Woolfenden 1999). Furthermore, Blue Jays nest in all parts of trees, including crotches in the main trunk, large horizontal limbs, and near the tips of terminal branches. Thus, they nest in a wide array of macrohabitats, as well as a wide range of microhabitats and nest sites within those macrohabitats. If the influence of habitat on Blue Jay nesting success is strong, such relationships should be detectable if an appropriate scale of habitat measurement is used.

#### METHODS

*Study site.*—We conducted our study at and near Archbold Biological Station, Highlands County, Florida. Archbold Biological Station (Archbold) is a 2,025 ha preserve of primarily pristine upland scrub and related vegetation communities (Abrahamson et al.

1984). To the east are expansive citrus groves and to the west lies expansive improved pasture. Areas disturbed by human habitation, including lawns and roadsides, lie between Archbold and the citrus groves and comprise a few small areas within Archbold property. Our study site included all of Archbold, and portions of the surrounding area.

*Nesting success.*—Nests were found via extensive searches in all macrohabitats and throughout the study area in 1994, 1995, and 1996. Once discovered, nests were monitored until termination (i.e. either fledging or failure) and checked approximately once every three or four days, depending on the phase of the nesting cycle. As nestlings approached fledging age, or in cases in which we were unsure of the age of the nest contents, nests were checked daily or on alternate days. Nest checks were rarely invasive, and almost always consisted of observing nests through binoculars to determine whether the breeding female was incubating or brooding. If she was not, the observation continued until the female returned to sit or until adults provisioned the nestlings. If neither event occurred after a reasonable time (15 to 60 min, depending on the phase of the nesting cycle), the nest was considered terminated. In such cases, if the nest was in the late nestling phase, we searched its surroundings for fledglings. A similar confirmation check was repeated on one or more subsequent days. We determined number of young surviving to fledging by observing nests during feedings of older nestlings. During those feedings, nestlings raised their heads well above the nest rim, allowing us to easily count the number of offspring in the nest by observing with binoculars. We repeated nestling head counts at each nest over a period of several days to confirm the number of young in the nest. Because we infrequently monitored multiple nests by the same breeding pair (most individuals were marked with color bands), either within or between seasons, we treated all nests in the three-year sample as independent.

*Habitat assessment.*—We related nesting success to habitat features measured at three levels, and at three different scales within one of those levels (Fig. 1). The macrohabitat level comprised qualitative categories based on composite habitat features summed across many nest and non-nest plots, and were defined independently of individual nests (although habitat features surrounding nests were in part used to define macrohabitats—see below). The microhabitat level comprised quantitative assessments of habitat characteristics surrounding each individual nest. We measured microhabitat characteristics at three different spatial scales. The nest-site level was defined as characteristics describing features of the nest site per se. Because some of the data used to determine macrohabitat categories also were used in assessments of microhabitat at the large scale, our analyses of the effects of macrohabitat and large-scale

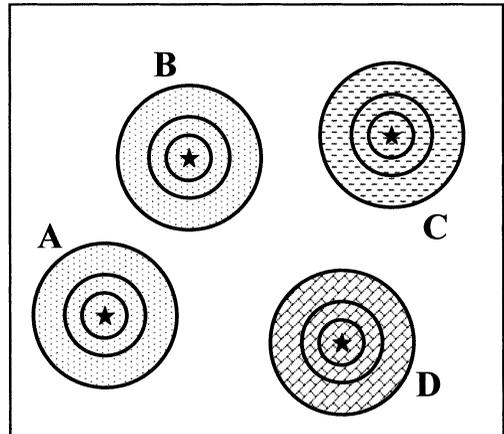


FIG. 1. A schematic diagram illustrating levels and scales of habitat analysis used in this study. Shown are four nest sites (A, B, C, and D, depicted by stars). Microhabitat features surrounding these nest sites were measured at three different scales (small, medium, and large concentric circles surrounding nest sites). A cluster analysis of features measured at the largest microhabitat scale (both for nests and for an additional 134 non-nest plots) was used to identify seven macrohabitats occurring on the study site. Each nest was assigned to one of those seven macrohabitats on the basis of habitat features measured at the large microhabitat scale (different macrohabitats are depicted by different background patterns in the figure; thus, nests A and B occur within the same macrohabitat type). Although assignment of nests to macrohabitats is dependent on the microhabitat features surrounding those nests, analyses of macrohabitat and microhabitat at the large scale are not completely redundant for a variety of reasons (see text). Thus, quantitative assessments of microhabitat features in plots A and B could differ substantially. Moreover, methods of analysis of data at the macrohabitat and microhabitat levels are necessarily different, and potentially could yield different results. Scale in this figure is not representative of actual plots.

microhabitat features on nesting success are not entirely independent. Although we realize that is a potential statistical problem, we present analyses at both levels because they reflect dramatically different ways of assessing effects of habitat features on nesting success, a point that is addressed in this paper.

Understorey vegetation communities (Abrahamson et al. 1984) and forest canopy distribution across the entire study site were mapped onto 1:2,400 aerial photographs and digitized in a geographic information system (GIS) at a resolution of 2 m. Locations of nests known to be active during the study period

TABLE 1. Habitat variables measured using GIS in 3.1 ha circular plots in this study. See text and Abrahamson et al. (1984) for description of understory types.

Feature class	Feature
Understory features	Proportion of plot covered by: Bayhead Citrus Flatwoods Human-modified landscape Oak shrubs Seasonal pond Simpson (1949) index of understory diversity
Forest canopy features	Proportion of plot covered by: Slash pine canopy Sand pine ( <i>Pinus clausa</i> ) canopy Forest of any type
Disturbance features	Time since disturbance (fire, grazing, mowing)

TABLE 2. Macrohabitats designated by hierarchical cluster analysis of habitat variables.

Macrohabitat	Description
Dry forest	Oak-dominated understory dense, xeric, homogeneous, and long undisturbed. Dense sand pine canopy (~90%), occasionally with slash pine.
Moist forest	Understory relatively diverse, but primarily long undisturbed flatwoods and bayhead communities. Dense (~80%) slash pine canopy.
Shrubby flatwoods	Diverse understory a mix of flatwoods, oak, and seasonal pond communities with varying times since disturbance. Slash pine canopy sparse to moderate.
Open flatwoods	Understory dominated by cut-throat grass ( <i>Panicum abscissum</i> ) or other native grasses resulting from abundance of seasonal ponds. Scattered patches of oak and flatwoods shrubs. Slash pine canopy moderate to dense. Disturbance rarely recent.
Shrubby park	Understory consists of xeric, low diversity, oak communities with occasional to moderate human-modified patches. Sparse to moderate slash pine canopy cover. Varying time since disturbance.
Open park	Understory greatly modified by humans and recently disturbed. Scarce patches of oak-dominated shrubs. Sparse to moderate slash pine canopy.
Citrus	Citrus grove. Other elements occasional when plot is near edge of grove.

also were digitized. Habitat features (Table 1) were quantified within 3.1 ha plots (radius = 100 m) centered on nests using GIS. Those features consisted of the proportion of total plot area covered by each of six understory types and three forest canopy types, and time since major disturbance (i.e. fire or mowing). Because fires often are patchy, time since disturbance may not be uniform across the plot. Therefore, we assessed time since disturbance on the basis of the status of the majority of the plot area (i.e. at least 50% of the area of each plot). Time since disturbance was categorized as (1) <1 year, (2) 1–5 years, (3) 6–20 years, and (4) >20 years post-disturbance (Tarvin 1998). Diversity of understory types within each plot was indexed using Simpson's (1949) formula.

Seven macrohabitats (Table 2) were defined using a hierarchical cluster analysis based on habitat features (Table 1) of 169 nest plots and 136 non-nest plots (all plots = 3.1 ha). The non-nest plots were used for point counts in concurrent studies (Tarvin 1998, Tarvin et al. 1998). Because the majority of them were placed at random throughout the study site, their inclusion provided a more representative sample of the study site than would have occurred if only nest plots were used to define macrohabitats. Distinctiveness of macrohabitats derived from the cluster analysis was confirmed with stepwise polytomous logistic regression. Logistic regression was used instead of discriminant function analysis to test for true differences among clusters because logistic regression analysis does not require assumptions of multivariate normality or equal covariance matrices (Press and Wilson 1978, Hosmer and Lemeshow 1989). We used polytomous, rather than dichotomous, logistic regression because the cluster analysis indicated seven macrohabitat categories existed. Although macrohabitat categories identified in the cluster analysis were nominal (i.e. unordered), we were unable to devise a stepwise polytomous logistic

regression that did not order the response variable with the available statistical software. Results of the polytomous logistic regression technique we used are dependent to some degree on the order of the levels of the response variable, which in this case are the macrohabitat types. To determine whether the ordering of macrohabitats affected the ability of the procedure to distinguish them, we performed several stepwise logistic regression analyses that differed only in the order of macrohabitats. Each of those logistic regression models significantly fit the data, indicating that macrohabitats were distinct (Tarvin 1998). Additionally, we tested a series of logistic regression models in which each plot was randomly assigned to one of the macrohabitat categories. That was done to confirm that the earlier models were not overfitting the data. None of the models incorporating these "dummy" macrohabitat categories significantly fit the data. We therefore concluded that the seven macrohabitats were indeed distinct. The clustering procedure assigned each nest to one of the seven macrohabitats.

Probability of nesting success was calculated for each macrohabitat on the basis of daily mortality rates (Mayfield 1961, 1975). Differences in nest survival rates for the entire nesting period ( $= 1 - \text{nest mortality rate}$ ) among macrohabitats were identified with program CONTRAST (Hines and Sauer 1989), using a Bonferroni correction to account for multiple comparisons. Program CONTRAST compares rates based on a general chi-square statistic that addresses an unambiguous null hypothesis of homogeneity among several survival rates (Sauer and Williams 1989). Variation in number of young fledged per successful nest across macrohabitats was tested using a Kruskal-Wallis one-way ANOVA.

Preliminary analyses indicated that the week the first egg was laid influenced nesting success in some years. We analyzed week of the first egg instead of date of the first egg because we were unsure of the exact laying date for some nests. For most of those nests, we were able to estimate the week in which the first egg was laid with confidence. We tested for variation in week of the first egg among macrohabitats using the Kruskal-Wallis one-way ANOVA.

We assessed microhabitat features surrounding nests at three spatial scales, namely in circular plots of 3.1 (radius = 100 m), 0.3 (radius = 30 m), and 0.07 ha (radius = 15 m) (hereafter, "large", "medium", and "small" microhabitat plots, respectively). At each plot size, we used stepwise logistic regression to identify variables that were related to nesting success. Each nest was categorized as successful if at least one jay fledged from it, and as failed if not. Stepwise logistic regression was used to identify habitat variables and variable interactions that were good at predicting nesting success and failure for each microhabitat plot size separately. In initial logistic regression analyses of microhabitat and nest-

site features, macrohabitat was included as a factor in a manner analogous to analysis of covariance (ANCOVA) to determine whether the ability of habitat variables to predict nesting success was influenced by macrohabitat. All models in which macrohabitat was selected as an important variable were highly unstable. Subsequent models were run in which macrohabitat was unavailable in the variable pool (see below). The model based on large microhabitat plots was built by allowing it to select from among year, week of first egg, the habitat variables presented in Table 1, and terms reflecting interactions among certain variables that we suspected might affect one another. Although our choice of interactions for analysis was somewhat arbitrary, it was based on an attempt to avoid overloading the models by testing all possible interactions among variables.

Models based on the medium and small microhabitat plots were built by allowing selection from a pool of variables pertinent to those plot sizes (described below). Microhabitat features within medium and small plots surrounding nests were measured for a subset of 52 nests monitored during 1995 using ground surveys (i.e. not with GIS). Within each of those plots, we estimated proportion of canopy cover (modified from James and Shugart 1970), proportion of shrub cover, and proportion of grass cover, and each tree >4 cm diameter at breast height (DBH) was counted, identified to species, and its DBH measured. From those raw data, the following 15 variables were generated and included in our analyses: proportion of canopy cover, shrub cover, and grass cover in each plot; number of slash pines, sand pines, pines of any species, oaks of any species (*Quercus myrtifolia*, *Q. chapmanii*, *Q. laevis*, *Q. virginiana*, *Q. geminata*), bay trees (*Gordonia lasianthus*, *Persia borbonia*, *Magnolia virginiana*), other hardwood species, all hardwood species, dead trees, "large trees" (those for which DBH was greater than the median DBH of all nest trees in the entire data set [32 cm]), "small trees" (those for which DBH was less than or equal to the median DBH), and all trees. Two variables found to be related to nesting success in other studies (Martin and Roper 1988, Tarvin and Smith 1995) also were generated from the woody plant count data for use in statistical analyses at the medium and small microhabitat scales. Those consisted of a variable representing for each plot all trees >4 cm DBH that were the same species as the nest tree, and a second variable representing all trees that were the same species and in the same size class as the nest tree. Because several of these variables were correlated, we used a forward stepwise procedure to reduce the number of variables entered into each logistic regression model, and to thereby avoid overloading the models.

Although our macrohabitat variables reflect to a great degree the underlying microhabitat features as

measured at the large plot scale, we view our analysis of large plot variables as a microhabitat-level (as opposed to a macrohabitat-level) analysis for a variety of reasons. First, although macrohabitat categories are based on data obtained in 3.1 ha plots, many non-nest plots were included in the cluster analysis; therefore, although the two data sets are related, they are not necessarily redundant. Second, the point at which the increase in radius of a plot shifts the plot from microhabitat to macrohabitat is arbitrary. Third, macrohabitat distinctions generally were dependent far more upon presence or absence of understory features than on quantitative variation in any single feature such as canopy cover or shrub cover. Fourth, even though variables in large microhabitat plots were measured using techniques that differed from those used to measure variables in medium and small microhabitat plots, the variables were correlated across the different scales. Finally, a *post-hoc* analysis revealed that many habitat features contributed to the distinctiveness of macrohabitats, whereas only slash pine canopy cover was important at the level of microhabitat (see below).

To assess nest-site characteristics, we identified nest tree species and measured nest tree DBH and height, nest height, and distance from nest tree to nearest shrub and adjacent tree; recorded the relative position of the nest in the nest tree; and categorized each nest according to a concealment index (estimated from the ground, but with an effort to consider concealment in the horizontal plane) ranging from 0 (not concealed) to 4 (completely concealed). We also recorded whether the nest was in a clump of vines or Spanish moss (*Tillandsia usneoides*), and whether vines or Spanish moss were present elsewhere in the nest tree. Nest tree species was categorized as slash pine, sand pine, scrub oak (*Q. geminata*, *Q. myrtifolia*, *Q. virginiana*), or other species (*Citrus* spp., *Ilex* spp., laurel oak [*Q. laurifolia*], long-leaf pine [*Pinus palustris*]). As before, we used stepwise logistic regression analysis to identify nest-site variables that were related to nesting success. Again, we included macrohabitat as a covariate in initial analyses of nest-site variables.

In 1995, the number of gray squirrels (*Sciurus carolinensis*) detected on 30 non-nest 3.1 ha plots during 1 h surveys was tallied to assess relative abundance of this potential nest predator across macrohabitats (Montague and Montague 1985). Plots were assigned to macrohabitat following the procedures used to assign nest plots, and a Kruskal-Wallis one-way ANOVA was used to test for differences in squirrel abundance across macrohabitats. Open flatwoods and citrus were not sampled, but squirrels were not observed in those macrohabitats. We tested for a correlation between Mayfield estimates of nesting success and squirrel abundance across macrohabitats. In this case, data from plots in similar macrohabitats were pooled because Mayfield estimates can not be calculated for in-

dividual nests. We also tested for correlations between squirrel abundance and microhabitat variables within 3.1 ha plots. In this case, squirrel abundance was calculated as mean number of squirrels detected per survey from March to May in plots within each of five macrohabitats.

## RESULTS

One hundred seventy-four nests were appropriate for Mayfield analysis of nesting success among macrohabitats. We did not know whether young fledged in all 174 nests in this sample, but each of the nests was observed over a sufficient duration for inclusion in the Mayfield analyses (Mayfield 1961, 1975). We were able to determine fate of 169 nests, and those nests were appropriate for logistic regression analyses. Forty-seven of those nests were monitored in 1994, 82 were monitored in 1995, and 40 were monitored in 1996. We were able to determine the week of laying of the first egg for 129 of those nests. We measured microhabitat features at the medium and small plot scales and nest-site features for 52 of the nests monitored in 1995.

Fifty-two of the 169 nests for which we knew fate produced at least one fledgling. Sixteen of 52 nests for which habitat features were measured in medium and small microhabitat plots and at nest sites produced at least one fledgling.

*Nesting success and fledgling production among macrohabitats.*—Nesting success varied significantly among the seven macrohabitats (Table 3; Fig. 2). However, number of fledglings per nest did not differ among macrohabitats when only successful nests were considered and effects of nest predation were thereby removed (Kruskal-Wallis one-way ANOVA,  $\chi^2 = 7.08$ ,  $df = 5$ ,  $P = 0.21$ ,  $n = 6$  macrohabitats because only one successful nest was observed in open flatwoods). Relative abundance of gray squirrels varied among macrohabitats (Kruskal-Wallis one-way ANOVA,  $\chi^2 = 20.60$ ,  $df = 4$ ,  $P < 0.001$ ), with dry forest having more squirrels than other macrohabitats (Bonferroni *post-hoc* test). Squirrel abundance was not correlated with probability of nesting success across macrohabitats ( $r = -0.39$ ,  $n = 5$ ,  $P = 0.51$ ); however, power of the test was low because of the small number of macrohabitats. Week of the laying of the first egg did not differ among the six macrohabitats for which data were available (Kruskal-Wallis one-way ANOVA,  $\chi^2 = 6.58$ ,  $df = 5$ ,  $P = 0.25$ ).

TABLE 3. Chi-square scores reflecting differences in Mayfield estimates of probability of nesting success among macrohabitats as detected using program CONTRAST (Hines and Sauer 1989). Because 21 comparisons were made, a Bonferroni correction was employed, and two-tailed *P* values  $\leq 0.0024$  were considered significant. Chi-square scores (*df* = 1 for each) are shown in the cells of the matrix. Scores  $\geq 9.2$  meet the significance criterion. Thus, all but three of the comparisons are significant (significant scores in boldface). Macrohabitats are ordered by success rate from highest (moist forest) to lowest (citrus). Sample sizes and nesting success rates among the macrohabitats are depicted in Figure 2.

Macrohabitat (number of nests)	Moist forest	Shrubby park	Open flatwoods	Open park	Shrubby flatwoods	Dry forest	Citrus
Moist forest (13)	—	<b>87.5</b>	<b>16.0</b>	<b>226.5</b>	<b>267.7</b>	<b>331.0</b>	<b>340.4</b>
Shrubby park (30)		—	0.1	<b>388.2</b>	<b>533.0</b>	<b>890.3</b>	<b>504.6</b>
Open flatwoods (3)			—	4.1	6.8	<b>11.4</b>	<b>14.9</b>
Open park (68)				—	<b>83.4</b>	<b>512.7</b>	<b>153.4</b>
Shrubby flatwoods (32)					—	<b>102.4</b>	<b>65.7</b>
Dry forest (21)						—	<b>11.0</b>
Citrus (7)							—

*Nesting success, microhabitat, and nest site.*—Interactions between macrohabitat category and certain microhabitat variables were selected by logistic regression as predictors of nesting suc-

cess at all three microhabitat plot sizes and in analysis of nest-site variables. However, in each case, the slopes of the interaction terms were not significant and their associated standard errors were extremely high. Such results indicate that those models were overfit and dependent on the data, and were therefore unstable (Hosmer and Lemeshow 1989). Therefore, analyses including interactions between macrohabitat and other variables are not presented below.

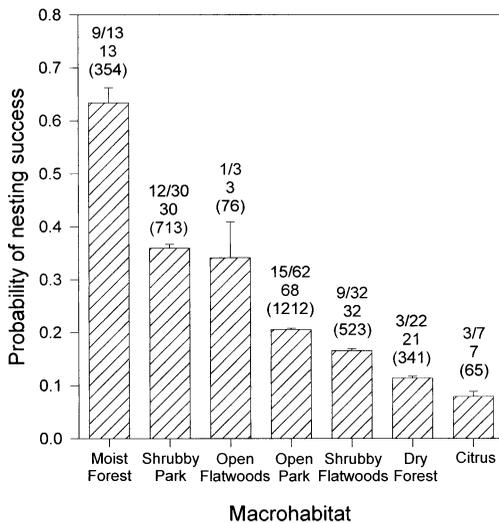


FIG. 2. Mayfield estimates of nesting success (probability of nest survival from first egg to fledging) across macrohabitats. Error bars represent variance of nest survival estimates. Numbers presented above bars represent proportion of successful nests and number of nests (days of exposure) used in Mayfield analyses. Sample sizes differ for traditional and Mayfield analyses in some instances because we were unsure whether a few nests failed or fledged young. Such nests still were appropriate for Mayfield analysis because the number of days of exposure without failure could be determined. Likewise, in fewer cases, a nest failed within a day of its discovery by us, and therefore was not observed over a period sufficient for Mayfield analysis (Mayfield 1961, 1975).

Stepwise logistic regression analysis identified week of first egg and proportion of slash pine canopy cover as predictors of nesting success at the large microhabitat plot scale (Table 4; Fig. 3A). Week of first egg was the most important predictor of nesting success and failure, but the addition of proportion of slash pine canopy cover significantly improved the model ( $-2 \log$ -likelihood ratio = 151.38, improvement  $\chi^2 = 9.89, P = 0.002$ ). The model correctly classified 82% of 78 failed nests and 57% of 51 successful nests, correctly classifying 72% of nests overall.

Squirrel abundance was related to proportion of plot covered by sand pine canopy ( $n = 30$  plots,  $r_s = 0.81, P < 0.001$ ) and proportion of the plot covered by total forest canopy ( $n = 30$  plots,  $r_s = 0.77, P < 0.001$ ), but not to proportion of the plot covered by slash pine canopy ( $n = 30$  plots,  $r_s = 0.03, P > 0.89$ ).

Because data from medium and small microhabitat plots were collected only in 1995, we tested for an effect of week of first egg on nesting success using only nests monitored in 1995. Week of first egg was not related to nesting success in this sample (logistic regression,  $\chi^2 =$

TABLE 4. Variables selected by stepwise logistic regression as good predictors of nesting success based on large (3.1 ha) microhabitat plots ( $n = 129$ ).

Variable	Variables in the model					Effect on model if variable removed				
	$\beta$	SE	Wald statistic	df	$P$	Partial correlation	exp ( $\beta$ )	$-2 \log LR$	df	$P$
Week of first egg	-0.27	0.087	9.70	1	0.0018	-0.211	0.76	12.24	1	0.0005
Proportion covered by slash pine canopy	0.03	0.009	8.95	1	0.0028	0.200	1.03	9.89	1	0.0017
Constant	0.23	0.505	0.20	1	0.6550					

0.87,  $P = 0.35$ ,  $n = 63$  nests). Therefore, week of first egg was not considered in analyses of data from medium and small microhabitat plots, or of nest sites. Omitting week of the first

egg from those analyses allowed us to include 11 nests for which we were unable to determine the laying date.

At the medium microhabitat scale, number of slash pines in the plot was significantly related to nesting success (Table 5). A logistic regression model including the variable was significantly better than a model including only the constant ( $-2 \log$ -likelihood ratio = 54.25, improvement  $\chi^2 = 9.95$ ,  $df = 1$ ,  $P = 0.002$ ,  $n = 52$  nests). The model correctly classified 94% of 36 failed nests and 31% of 16 successful nests, correctly classifying 75% of nests overall. Successful nests were in plots having more slash pines (Fig. 3B).

At the small microhabitat scale, both number of slash pines and number of dead trees in the plot were selected as predictor variables by the stepwise logistic regression procedure. However, the slope associated with number of dead trees was not significant ( $P = 0.52$ ), and the contribution of number of dead trees to the model was marginal ( $P = 0.06$ ). A model including only number of slash pines remained significantly better than a model containing only a constant ( $-2 \log$ -likelihood ratio = 57.14, improvement  $\chi^2 = 7.05$ ,  $df = 1$ ,  $P = 0.008$ ,  $n = 52$  nests; Table 6). The model correctly classified 94% of 36 failed nests and 38% of 16 successful nests, correctly classifying 77% of nests overall. In this case, number of slash pines did not differ between successful and unsuccessful nest plots in a univariate analysis (Fig. 3C). Substitutions of correlated variables for number of slash pines in the plot did not improve the logistic regression model for either the medium or small microhabitat plot sizes.

Nest-site characteristics were unrelated to nesting success (i.e. all  $P > 0.05$ ). Nest height and nest-tree height each had probability values  $< 0.1$ , but models into which those variables were forced performed poorly ( $P > 0.08$ , per-

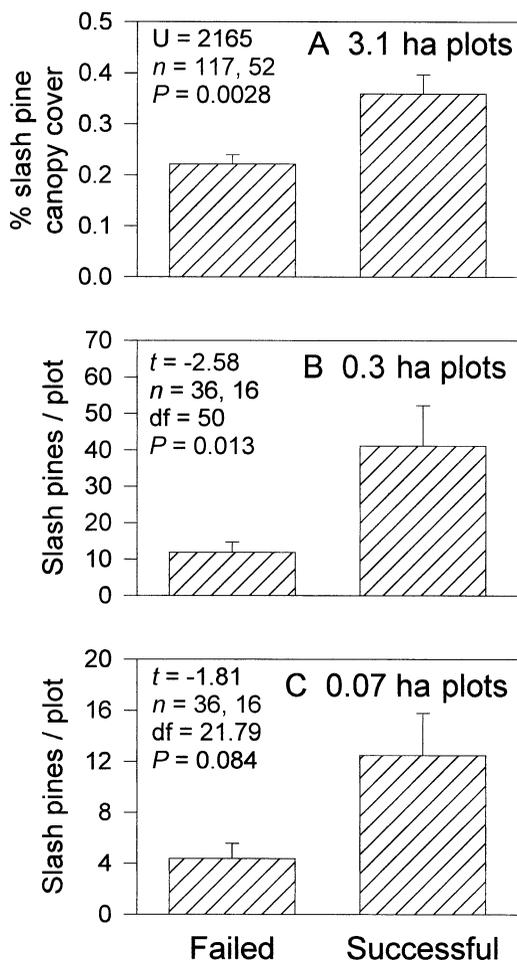


FIG. 3. Univariate tests for difference in (A) slash pine canopy cover and (B, C) number of slash pines per plot between failed and successful nests at three microhabitat scales.

TABLE 5. Stepwise logistic regression analysis of the relationship between nesting success and microhabitat features based on medium (0.3 ha) microhabitat plots ( $n = 52$ ).

Variable	Variables in the model						Effect on model if variable removed			
	$\beta$	SE	Wald statistic	df	$P$	Partial correlation	exp ( $\beta$ )	-2 log LR	df	$P$
Number of slash pines	0.35	0.014	6.60	1	0.0100	0.268	1.04	9.95	1	0.0016
Constant	-1.58	0.434	13.32	1	0.0003					

centage of successful nests correctly classified <19% for each model). Thirty-five (67.3%) of the 52 nests for which nest-site features were measured were in slash pines. Nest tree species was unrelated to nesting success when tree species were lumped into slash pine, sand pine, scrub oak, or other species categories and included in the logistic regression analysis of nest-site features ( $P > 0.05$ ), and when a univariate comparison was made between nests in slash pine versus all other tree species using a  $G$  test ( $G = 2.2$ ,  $df = 1$ ,  $P = 0.14$ ).

DISCUSSION

*Congruency among habitat levels and scales.*—One habitat feature—abundance of slash pines surrounding nests—was consistently related to nesting success in both the macrohabitat and microhabitat levels of habitat analysis, and at all three scales within the microhabitat level. Although the way it was measured differed among habitat levels and scales, slash pine canopy cover was more extensive in macrohabitats with high nesting success ( $r_s = 0.89$ ,  $n = 7$ ,  $P < 0.001$ ), and it or number of slash pines was the most important habitat variable at all three microhabitat scales. Although slash pines appeared to be important components of the habitat surrounding nests, nests in slash pines were no more successful than nests in other tree species. Because most nest plots contained at least one slash pine (e.g. 80.2% of medium microhabitat scale plots contained at least one

slash pine), we did not have sufficient data to contrast success of nests in slash pines versus those in other tree species as a function of whether the nest tree was surrounded by slash pines.

Perhaps we should not be surprised at the degree of congruency among the analyses presented in our study. Our analyses were effectively nested, and it is therefore no surprise that the same feature appeared important at each level and scale of analysis. The interesting pattern in our study is that, in general, our ability to detect habitat influences on nesting success increased as the spatial scale of analysis increased. Other studies that have considered multiple levels of habitat features often found both nest site and higher level features were important (e.g. Martin and Roper 1988, Kelly 1993, Norment 1993, Tarvin and Smith 1995, Matsuoka et al. 1997). However, they rarely measured variables at different scales within a single habitat level. Although it is difficult to know how general our results are, they indicate that the scale of analysis may influence the conclusions of a study.

*Causes of nest failure.*—Before further consideration of level and scale of habitat analysis, we need to address the causes of nest failure in our study. Although slash pine abundance was clearly related to nesting success, we do not have direct evidence revealing the basis of that relationship. We observed only two cases of nest predation, one by a Swallow-tailed Kite (*Elanoides forficatus*) and another by a pair of

TABLE 6. Stepwise logistic regression analysis of the relationship between nesting success and microhabitat features based on small (0.07 ha) microhabitat plots ( $n = 52$ ).

Variable	Variables in the model						Effect on model if variable removed			
	$\beta$	SE	Wald statistic	df	$P$	Partial correlation	exp ( $\beta$ )	-2 log LR	df	$P$
Number of slash pines	0.08	0.033	5.92	1	0.0150	0.247	1.09	7.05	1	0.008
Constant	-1.43	0.411	12.10	1	0.0005					

Fish Crows (*Corvus ossifragus*). A breeding female was found dead and maimed on a third nest. At a fourth nest, we observed a raccoon (*Procyon lotor*) sleeping on a limb supporting a depredated nest which had been active on our previous check. Although several other nests were found damaged at termination, indicating predation, we could not be certain of the cause of failure of most unsuccessful nests because they were situated in parts of trees that were inaccessible to us. Even so, there was strong circumstantial evidence that predation was the primary cause of nest failure in our study.

The fact that nesting success was unrelated to features of the nest site excludes the influence of weather as major factor leading to differential success among macrohabitats. Structural susceptibility of nest substrate to wind or thermal flux should be related to at least some of the nest site variables we measured, yet position of the nest within the nest tree (i.e. on distal branches vs. near the trunk), size of the nest tree, and nest height were unrelated to nesting success.

Food limitation apparently was not an important cause of nest failure in our study. We would expect effects of food limitation to be manifested as a decrease in the number of fledglings per successful nest (i.e. effects of nest predation removed, because arboreal predators typically remove all nest contents) in poorer macrohabitats (Martin 1987, 1992). However, significant variation in number of fledglings per successful nest across macrohabitats did not exist. Alternatively, differences in nest predation rate should lead to differences in the proportion of failed nests among macrohabitats, but are less likely to lead to differences in number of fledglings per successful nest (but see Larivière 1999). We observed the latter pattern in our study. Although we did not assess factors directly responsible for nest failure (because access to most nests was limited), nest predation is the greatest source of nest mortality in temperate open-nesting passerines (Ricklefs 1969, Martin 1992), and has been shown to be the most important cause of Blue Jay nest failure in studies for which causes of failure were identified (Best and Stauffer 1980, Tarvin and Smith 1995). Likewise, nest predation accounts for virtually all nest mortality in the sympatric, closely related Florida Scrub-Jay (*Aphelocoma coerulescens*) on the same study site

(Woolfenden and Fitzpatrick 1984, 1990; Schaub et al. 1992).

*What do scale-dependent patterns tell us about nest predation?*—Effect of habitat on nesting success of Blue Jays was most dramatic when examined at the level of macrohabitat. Indeed, nests in moist forest were 8× more likely to produce a fledgling than were nests in citrus groves. Probabilities of nesting success in each of the seven macrohabitats were distinct from those in virtually all other macrohabitats (we detected significant differences in 18 of 21 possible pairwise comparisons), indicating that the strong effect was not an artifact resulting from one particularly good or poor macrohabitat. Within the level of microhabitat, abundance of slash pines was consistently related to nesting success, regardless of the spatial scale at which it was measured. The relationship between slash pine abundance and probability of nesting success appeared much stronger in the analysis conducted at the largest spatial scale, suggesting that features immediately surrounding the nest exert less influence on predation than do features summed across a greater area. Although, that pattern may be simply an artifact of the greater number of large microhabitat plots ( $n = 169$ ) than medium and small plots ( $n = 52$  for each), the effects detected at the medium plot scale were stronger than those at the small plot scale, and sample sizes (and indeed the sample of nests) at those two scales were identical. The dramatic effect of level of habitat on which the analysis is based is further illustrated by the complete lack of influence of nest-site features on nesting success. Probability of success appeared independent of where a nest was placed within a macrohabitat: nesting success was unrelated to nest tree species, nest height, nest placement within the nest tree, or concealment. Admittedly, our measurements of concealment may have been poor, but we were unable to detect even slight trends in effect of concealment.

The patterns we observed in our study indicate that habitat characteristics do not influence nest predation by influencing predator access to nests or by simply concealing nests from predators. Instead, our analyses indicate that the relationship between habitat and nesting success results either from the influence of habitat on predator abundance or distribution, or from more complex interactions between hab-

itat and predator search efficiency (Bowman and Harris 1980, Martin and Roper 1988, Martin 1992, Tarvin and Smith 1995, Filliater et al. 1994). A possible explanation is that nesting success may be higher in some macrohabitats because fewer nest predators occur in them. Our analysis of squirrel abundance across macrohabitats (and in relation to large-scale microhabitat features) did not support this explanation, because squirrel abundance was neither correlated with nesting success across macrohabitats, nor with microhabitat features that were related to nesting success. However, squirrels are not the only potential nest predators on our study site, and we did not attempt to measure abundance of other predator species. Perhaps a more reasonable explanation is that predator diversity varies among macrohabitats. In habitats having greater predator species richness, birds are unable to choose nest sites that allow them to thwart the efforts of all potential predators simultaneously, whereas in simpler communities having only one or two potential predators, nesting birds may be able to choose nest sites that are unlikely to be found or accessed by those predators (Filliater et al. 1994).

An alternative explanation is that predator movement or search efficiency within an area may be impeded by microhabitat features (Bowman and Harris 1980, Martin 1992). Martin and Roper (1988) and Tarvin and Smith (1995) found that the similarity of the nest tree to other trees in the nest patch was an important predictor of nesting success for Hermit Thrushes (*Catharus guttatus*) and Blue Jays. That has been termed the "needle in a haystack hypothesis" (Filliater et al. 1994), and predicts that reward rates of predators focusing on a limited number of types of nest sites are reduced when they must search many similar sites. Our data do not fit that explanation in the present study, although increasing abundance of slash pines (i.e. increasing patch size) could similarly lead to inefficient searching by predators (Bowman and Harris 1980). For example, Swallow-tailed Kites may have greater difficulty detecting or accessing nests in expansive pine forests, whereas nests in smaller patches are more easily found and preyed upon.

Influences of habitat on nest predation may be indirect. For example, certain habitats may be higher in quality for reasons other than nest

predation. If higher quality or older individuals occupy the higher quality habitats and are better able to defend their nests against predators than are younger individuals or those of lower quality, then average probability of nesting success may be greater in some habitats than others (e.g. Curio 1983, Dhondt et al. 1992, Ferrer and Donazar 1996, Holmes et al. 1996). However, patterns of age structure and other indices of individual quality do not support that scenario on our study site (Tarvin 1998). Likewise, if nesting begins earlier in higher quality habitats because of greater food availability early in the breeding season, those habitats may exhibit greater overall nesting success. Nonetheless, although week of first egg influenced nesting success in our study, it did not vary among macrohabitats, and cannot explain the patterns of nesting success we observed. Similarly, because Blue Jays may prey upon other Blue Jay nests, variation in jay density across macrohabitats could lead to corresponding variation in nest predation rate. Although density of adult Blue Jays varied tremendously among macrohabitats on our study site, it was not correlated with nesting success ( $r_s = 0.29$ ,  $P = 0.53$ ; Tarvin 1998).

Regardless of the causes of nest failure and the mechanisms by which habitat influences its likelihood, we find it interesting that Blue Jays choose to nest in such a wide variety of macrohabitats, given the clear and predictable differences in probability of nesting success among them. The patterns we observed in our study raise questions about the ways in which predator species richness and competition among and survival of Blue Jays vary with habitat. A clearer understanding of habitat-specific demographic profiles of Blue Jays may shed light on the relationship between habitat and nesting success.

#### ACKNOWLEDGMENTS

We thank J. Jawor and K. Dayer for slogging through many hours of hot, humid, buggy vegetation sampling. We also thank B. Remley, K. Dayer, J. Jawor, and S. Lindemann for excellent help with finding and monitoring nests, R. Pickert for help with GIS work, K. Main for providing Archbold fire history data, L. Petit, F. Moore, O. Olsson, S. Pruettt-Jones, G. Woolfenden, J. Fitzpatrick, H. Mushinsky, E. McCoy, M. and R. Lawton, C. Handel, and J. Lawrence for critically reading earlier versions of the manuscript, J. Witmer for statistical advice, and the

directors and staff of Archbold Biological Station for providing logistical support. Financial support from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, Archbold Biological Station, the Florida Ornithological Society, and kind relatives was integral to the study, and was much appreciated. C. and R. Crews, G. Reynolds, R. and L. Brown, M. J. McJunkin, and K. and W. F. Thompson, Jr., kindly allowed us to work on their properties, and to them we are grateful.

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Associate Editor: F. Moore