

VARIATION IN GRAY CATBIRD NEST MORPHOLOGY

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Abstract.—Dimensions of nests of the Gray Catbird (*Dumetella carolinensis*) were measured in 1986–1987 and examined for variation among years and habitats, and for relationships to measures of individual reproductive success. Nest cup depth was greater in 1987 than in 1986. Nest cup diameter varied spatially on the 80-ha study site, and covaried with several microhabitat (vegetation structure) variables measured around nests. Total nest depth did not vary significantly, and there were no associations between nest morphology and several measures of catbird reproductive success. Variation in nest morphology was most likely related to concurrent variation in nesting substrates and availability of building materials. Nest variation could also have resulted from catbirds adaptively modifying their nest structure to suit local microhabitat conditions.

VARIACIÓN EN LA MORFOLOGÍA DE LOS NIDOS DE *DUMETELLA CAROLINENSIS*

Sinopsis.—Durante 1986–1987 se midieron las dimensiones de nidos de zorzal gato (*Dumetella carolinensis*). Se estudiaron variaciones entre años y en diferentes habitats, y se relacionaron las medidas tomadas al éxito reproductivo de los individuos. La profundidad de la copa fue mayor en 1987 que el 1986. En los 80 ha de estudio, el diámetro de la copa varió. Se encontró covarianza a tono con variables en el microhabitat (estructura de la vegetación) alrededor del nido. La profundidad total del nido varió significativamente y no se encontró asociación, entre la morfología de los nidos y varias medidas, al éxito reproductivo del ave. Las variaciones en la morfología de los nidos pudieron relacionarse a variaciones concurrentes en los sustratos de anidamiento y la disponibilidad de materiales de construcción. Las variaciones en los nidos pueden ser el resultado de la adaptabilidad del zorzal gato a modificar la estructura de su nido en armonía con particularidades del microhabitat.

Intraspecific variation in the size and shape of bird nests may be of interest for several reasons. Thermal properties of nests may vary geographically, with nest morphology and with the nest microsite, with concurrent variation in the nest's ability to insulate eggs and young (e.g., Collias and Collias 1984, Schaefer 1980, Skowron and Kern 1980). Searching predators may respond to the overall size of a nest as well as its degree of concealment by vegetation (e.g., Jones and Hungerford 1972, Snow 1978). Differential predation may also result according to the materials used in nest construction (Møller 1987). Nest characteristics can also indicate whether or not the breeding attempt was successful (e.g., Watt and Dimberio 1990). Furthermore, nests can be viewed as being extensions of the phenotypes of their builders (Dawkins 1982), so that

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nest morphology may exhibit important variation among the individuals of a population, with possible fitness implications.

As part of a 5-yr study (R. A. Howard, unpubl. data; Lent 1990) of the breeding ecology of a population of Gray Catbirds (*Dumetella carolinensis*) on Long Island, New York, I collected two seasons (1986 and 1987) of data on the habitat characteristics and dimensions of 67 nests. Here I use those data to analyze patterns of variation in catbird nest morphology and its association with individual reproductive success.

METHODS

The study site, Seatuck National Wildlife Refuge, is an 80-ha preserve in Islip, Long Island, New York. The regional vegetation was described by Clark (1986). Upland oak (*Quercus*) woods, fields and landscaped areas in the northern end of Seatuck grade to the south into moist woodlands, then into a shrubland transitional zone, eventually becoming salt marsh bordering a large bay. The entire refuge was surveyed in a 50-m grid system (Fig. 1).

Catbird nests were found by systematically searching all suitable habitats. Nest dimensions, measured with a plastic or metal ruler, included a single inside diameter and depth of the nest cup and depth of the entire nest from the rim to the lowest extent of nest material. All nests were measured *in situ* from several days to approximately 2 wk after termination (either by the young fledging or by nest failure). Nests that were obviously deformed were not measured. Locations of all nests were known exactly.

Nest locations were plotted on a vegetation map of Seatuck (Fig. 1) and associated with a vegetation covertype, or macrohabitat. Catbirds nested in three broadly defined covertypes: woods, shrub and edge. These covertypes differed significantly in vegetation structure (discriminant analysis, $P < 0.001$; see Lent 1990) and were broad-scale, macrohabitat indices of nest site selection. In addition to these macrohabitat categories, microhabitat (vegetation structure) was quantified in a 0.04-ha circular plot centered on each nest, following the methods of Noon (1981). Seven variables (abbreviations used in Results are capitalized) measured the total basal area (TOTBASAL, m^2/ha), number (NUMTREES, stem count/ha), and species diversity (TREESPEC, species count/plot) of trees ≥ 7.6 cm diameter, percent canopy closure and ground cover, shrub stem density (SHRUBS, stem count/ha), and mean vegetation height (m). Catbird habitat selection was thus measured at two simultaneous scales, macrohabitat and microhabitat. The height of each nest above the ground in m, measured from the nest rim, was also recorded.

I used multiple regression, with a mixture of categorical and continuous predictor variables, to describe patterns of temporal and spatial variation in the three nest dimensions (Pedhazur 1982). As the nest dimensions were not significantly intercorrelated ($r = 0.087, 0.117$ and 0.115 , all $P > 0.4$, $n = 47-48$), each was used separately as the dependent variable in a multiple regression analysis. Predictors were the year (YEAR), macrohabitat category (MACROHAB), the interaction of year and mac-

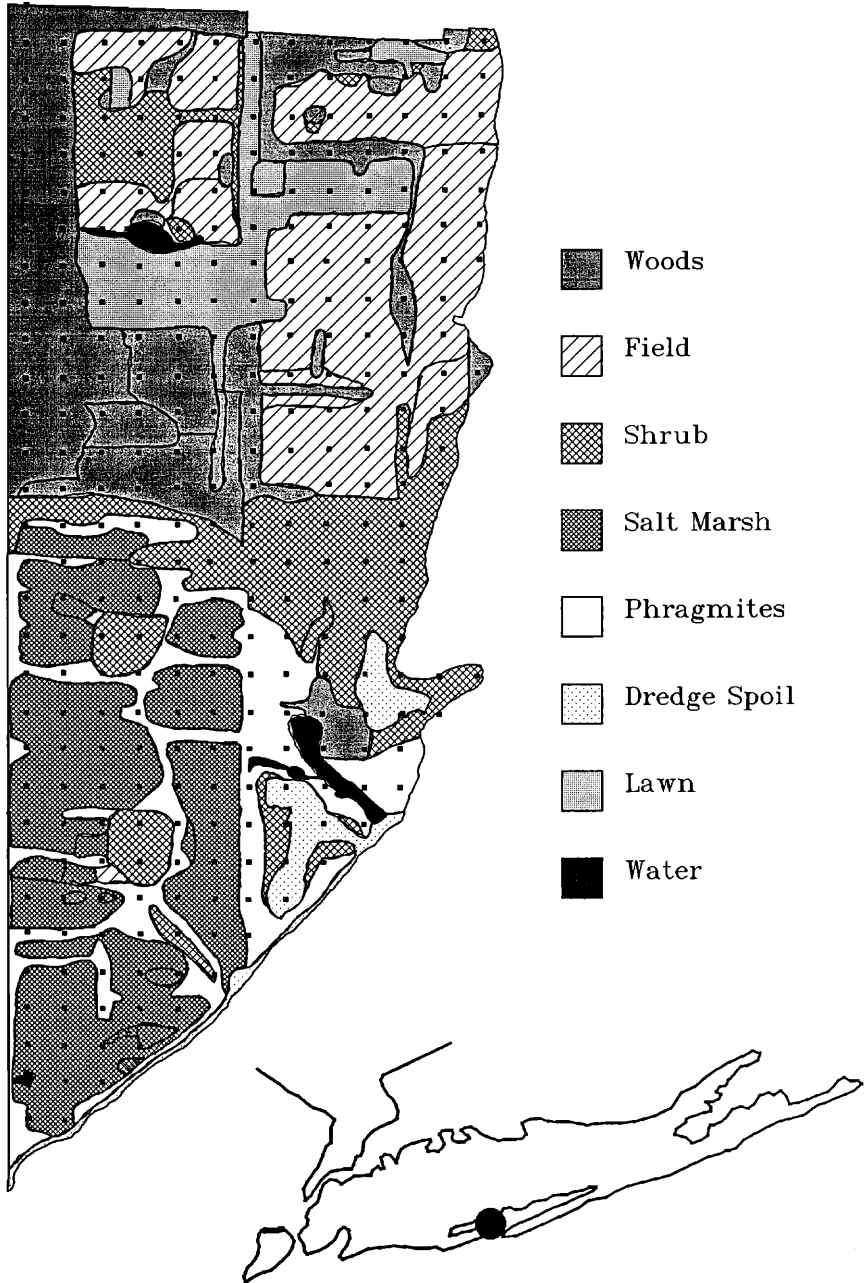


FIGURE 1. Vegetation and location maps of the 80-ha Seatuck National Wildlife Refuge, Long Island, New York. This map is a simplified version of a map published in Norton et al. (1984). Refuge is gridded at 50-m intervals.



FIGURE 2. Maps of catbird nests found at Seatuck National Wildlife Refuge, 1986 and 1987. Nest locations are shown by circles, the diameter of which is proportional to the magnitude of each of three nest dimensions. A. Total nest depth. B. Nest cup depth. C. Nest cup diameter. Vegetation covertypes have been deleted from these maps for clarity; see Figure 1.

rohabitat, the seven microhabitat variables, nest height above ground, and the spatial location of the nest, indexed by its x- and y-coordinates (X, Y) in m. (The x- and y-coordinates are the left-to-right [west-east] and bottom-to-top [south-north] directions, respectively, in Fig. 1.)

Spatial variation in measures of nest morphology was also examined using Moran's *I*, a coefficient of spatial autocorrelation (SA). SA analysis detects clumps, clines, and other patterns in mapped quantitative variables (see Legendre and Fortin 1989 and references therein). Moran's *I* was calculated from nest maps using each of the three nest dimensions as the mapped variable of interest (Fig. 2). Values of Moran's *I* can range between approximately +1 (meaning that morphology of nests paired at a particular distance apart is perfectly positively correlated) and -1 (perfect negative spatial autocorrelation). An *I* of 0 corresponds to the null hypothesis of complete spatial randomness. Moran's *I* was computed for nest pairs falling into 18 50-m distance classes. Separate spatial analyses were done for each of the three nest dimensions. A computer program kindly provided by J. S. Heywood was used for computations (see Dewey and Heywood 1988).

Several measures of individual reproductive success were obtained for each nest (Lent 1990). These were (1) nest failed or successful (success being the fledging of at least one chick), (2) clutch size, (3) number of

TABLE 1. Means of catbird nest dimensions by year and macrohabitat. Significance of differences in means among years and macrohabitats is indicated by the significance of those terms in Table 2.

Year	Macrohabitat	Nest dimension in cm: mean (range, <i>n</i>)		
		Total depth	Cup depth	Cup diameter
1986	Woods	8.4 (6.6, 8)	4.3 (2.1, 6)	8.0 (1.7, 6)
	Shrub	8.1 (7.1, 12)	4.3 (1.1, 6)	7.9 (1.3, 5)
	Edge	8.3 (4.1, 11)	4.2 (2.0, 9)	8.3 (2.9, 9)
	Annual mean	8.2 (7.1, 31)	4.3 (2.4, 21)	8.1 (2.9, 20)
1987	Woods	9.0 (3.0, 11)	5.1 (3.0, 10)	8.2 (2.0, 10)
	Shrub	11.6 ^a (16.0, 14)	4.9 (2.2, 14)	8.1 (3.5, 14)
	Edge	8.7 (1.0, 3)	5.0 (1.0, 3)	8.2 (0.5, 3)
	Annual mean	10.3 (16.0, 28)	5.0 (3.2, 27)	8.1 (3.5, 27)
Grand mean		9.2 (18.4, 59)	4.7 (4.0, 48)	8.1 (4.0, 47)

^a Includes the single tallest nest, total depth = 23.5 cm.

young fledged, (4) mean nestling weight and (5) the standard deviation of brood weight (for broods of two or more). Relationships of the three nest dimensions to each of these fitness components were examined using multiple linear regression, logistic regression or discriminant analysis, depending on the nature of the response variable.

Measurements of catbird morphology were used to check for association between female body size and nest morphology. Adult catbirds were captured in mist nets and given a unique combination of colored leg bands. Birds were sexed by presence of a brood patch (females), cloacal protuberance (males), or by subsequent observation of behavior (e.g., singing for males). Length of unflattened wing chord, tarsus length and body weight were measured on adults and used as indices of overall body size. Weight was measured to the nearest 0.1 g using a hand-held spring scale. Wing length was measured to the nearest mm with a ruler. Tarsus length was measured to the nearest 0.1 mm with calipers. Pearson correlations between female morphology and nest morphology were tested for significance by one-tailed *t*-tests, the alternative hypothesis being that female body size would be positively correlated with the nest dimensions.

RESULTS

Variation in nest morphology.—Nest dimensions are summarized by year and macrohabitat in Table 1. Total nest depth decreased ($b = -0.009$) with increasing values of the x-coordinate of the nest (Table 2). This result, however, depended largely on a single tall nest (total depth, 23.5 cm). When the outlier was deleted from the analysis, the x-coordinate became nonsignificant ($P = 0.09$) and the significance of the entire regression model became marginal ($F = 1.93$, $P = 0.048$). None of the SA coefficients for the map of total nest depth (Fig. 2A) were significantly different from zero.

Nest cup depth was significantly ($P < 0.001$) greater in 1987 than in

TABLE 2. Summary of regression analyses of variation in Gray Catbird nest morphology.

Dependent variable	<i>n</i>	Significant predictors ^a	<i>R</i> ²	<i>P</i> ^b
Total nest depth	59	X*	0.44	0.019
Nest cup depth	48	YEAR***	0.40	0.184 ^c
Nest cup diameter	47	X***, Y***, MACROHAB*, TOTBASAL**, NUMTREES*, TREESPEC**, SHRUBS***	0.65	0.0009

^a Asterisks indicate significance of individual regression terms: *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$. See text for variable abbreviations.

^b Probability associated with significance of overall regression equation.

^c Although the overall cup depth regression was non-significant, the YEAR term remained highly significant ($P = 0.0004$) when the model was re-fitted with non-significant predictors deleted (a simple one-way analysis of variance). This increased the degrees of freedom from 32 to 46.

1986 (Tables 1 and 2). None of the SA coefficients for this map (Fig. 2B) were significantly different from zero.

Nest cup diameter showed significant microgeographic variation in both the x- and y-directions ($b = 0.004$ and 0.002 , respectively; Table 2). The smallest diameters occurred in the southern half of the refuge, while there were more wider-cupped nests to the east (Fig. 2C). SA analysis confirmed that this pattern was nonrandom. Nest pairs in the 800–850-m distance class ($n = 17$) were strongly negatively autocorrelated at a global level of significance ($I = -0.76$, $P = 0.0016$). Cup diameter also varied with macrohabitat; edge nests tended to have wider cups than nests in woods or shrub habitats (Tables 1 and 2). At the microhabitat scale, cup diameter decreased with total basal area and number of trees ($b = -0.042$ and -0.001 , respectively), and increased with tree species diversity and shrub stem density ($b = 0.238$ and 0.005).

Nest morphology and reproductive success.—Failed ($n = 13$) and successful ($n = 33$) nests did not differ in morphology (discriminant analysis, $P = 0.7$; logistic regression, $P = 0.6$). Nest morphology also did not vary with clutch size (discriminant analysis, $P = 0.8$; logistic regression, $P = 0.7$). Multiple linear regressions of the nest dimensions on number of young fledged, mean nestling weight and variability of brood weight (measured by the standard deviation of brood weight) were all nonsignificant ($P = 0.3$, 0.1 and 0.1 , respectively).

Nest morphology and body size.—None of the correlations between measures of female body size and nest morphology was significantly greater than zero (experimentwise $P > 0.05$, one-tailed t -tests, $n = 16$ – 22); in fact, seven of the nine correlations were negative. Correlations ranged from -0.44 ($n = 17$) for body weight versus cup diameter to 0.38 ($n = 16$) for tarsus length versus cup depth.

DISCUSSION

The structure of nests of the Northern Oriole (*Icterus galbula*) was shown by Schaefer (1976) to vary geographically, and Kern (1984) found significant differences in nest characteristics among races of White-crowned

Sparrows (*Zonotrichia leucophrys*). Watt and Dimberio (1990) measured 14 features of American Goldfinch (*Carduelis tristis*) nests at a site in Indiana, and found that eight features differed significantly between 19 successful and 8 unsuccessful nests. I found significant temporal and microgeographic variation in catbird nest morphology, but no relationships between nest morphology and measures of reproductive success.

One explanation for the lack of a relationship between nest morphology and fitness in my data, in contrast to the results of Watt and Dimberio (1990) for goldfinches, is that the two species use very different materials in their nests. Goldfinch nests expand as the nestlings grow due to nest construction with spider webs and flexible plant fibers (D. Watt, pers. comm.). In contrast, catbird nests are more rigidly constructed of twigs, bark strips, leaves, grass, weed stems, and even paper or plastic (Harrison 1975, Nickell 1965). Hence, catbird nests have little ability to expand as the nestlings grow.

Nest size among species of small, open-nesting birds may be related to clutch size, with larger nests being required to hold larger clutches. Selection pressure for smaller, inconspicuous nests probably results in the smallest nest size consistent with the average clutch size for a given species (Collias and Collias 1984, Snow 1978). While nest morphology did not vary with clutch size at Seatuck in 1986 and 1987, mean clutch size was greater in 1985 and 1986, years of reduced catbird population density, than in 1983 and 1984 (3.24 and 3.60 eggs for high and low density years, respectively; see Lent 1990). Thus the deeper-cupped nests in 1987 may have been partly a result of density-dependent variation in clutch size (Fretwell 1972), in the latter years of the study, a relationship that would not be detectable in the 1986 and 1987 data only.

Spatial and habitat-related variation in nest morphology at Seatuck may have been caused by variation in the structure of the particular species of understory plants in which nests were built. Nest variation may have also been related to differential availability of materials with which to build the nest. Nest cup diameters were smaller in the southern part of the refuge, a region of moist soils and dense thickets of *Viburnum*, *Clethra* and *Vaccinium*. In contrast, nest cups were wider to the east, an area of drier edge habitats consisting of mixed fields, lawns, forest and shrubs (Figs. 1 and 2). Another possibility is that catbirds modified their nest structure (e.g., Kern and van Riper 1984) in edge habitats, building wider cups that could retain the eggs and young better during buffeting by wind in the more open habitats. The microhabitat associations of narrow-cupped nests with forested areas (variables TOTBASAL and NUMTREES, Table 2), and of wider-cupped nests with the dense thickets found in edge habitats (TREESPEC and SHRUBS, Table 2), is consistent with this interpretation.

My results and those of Watt and Dimberio (1990) suggest that the relationships of bird nest structure to individual fitness may vary with species and with temporal and spatial variation in the environment. More data are needed to elucidate these relationships. Measurements of bird nests found in forest understory or in low vegetation are easy to obtain

in the field. Such data would be of interest for other catbird populations and for other bird species, particularly if combined with data on genetic and environmental variability. Bird nest morphology should be viewed as a phenotypic trait subject to variation and, possibly, natural selection.

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