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ACADIAN FLYCATCHER NEST PLACEMENT: DOES PLACEMENT INFLUENCE REPRODUCTIVE SUCCESS?[1]

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Abstract. We located 511 Acadian Flycatcher (*Empidonax virescens*) nests in bottomland hardwood forest of eastern Arkansas. Microhabitat characteristics were measured and their relationship with nest success evaluated. Fifty-two percent of all nesting attempts resulted in predation. Attributes of nest placement were similar between successful and unsuccessful nests, although successful nests were placed higher. Similarly, nonparasitized nests were typically higher than parasitized nests. Nests initiated late in the breeding season were placed in larger trees with higher canopy bases resulting in increased vegetation around the nest. Fifteen different tree species were used for nesting. Acadian Flycatchers chose nest trees in a nonrandom fashion, selecting Nuttall oak (*Quercus nuttallii*) and possumhaw (*Ilex decidua*) in greater proportions than their availability. However, there was no relationship between tree species used for nesting and nest success. Nest height was positively correlated with concealment at the nest site, supporting the predator-avoidance theory. No other attribute of nest placement differentiated successful nest sites, suggesting that nest predation is likely a function of random events in space and time.

Key words: Acadian Flycatcher, Empidonax virescens, *habitat selection, nest placement, nest success.*

INTRODUCTION

Nest placement affects the probability of nest success in a variety of species (Caccamise 1977, Martin and Roper 1988, Kelly 1993). Therefore, selection of specific nest sites may decrease the probability of nest predation, the leading cause of nest failure for many avian species (Ricklefs 1969, Martin 1992), through increased concealment around the nest (Martin and Roper 1988, Martin 1993). However, Howlett and Stutchbury (1996) found no relationship between the probability of nest success and the amount of concealment around the nest in a manipulative study.

If a high density of suitable nest sites makes it difficult for a predator to locate a single nest, then the availability of suitable nest sites within a habitat would be expected to influence the probability of nest predation (Martin 1993). Some have even suggested that availability of suitable nest sites is the most important determinant of habitat selection (Steele 1993, Petit and Petit 1996). Therefore, knowledge of what constitutes a suitable nest site and how nest placement affects reproductive success is an important step towards understanding the proximate cues birds use in habitat selection.

Here, we evaluate nest placement attributes of Acadian Flycatchers (*Empidonax virescens*) in an insular but unfragmented bottomland hardwood forest in eastern Arkansas. Specifically, we examined attributes of nest placement at the microhabitat scale (characteristics of the nest tree and nest placement within the tree). Microhabitat characteristics were compared between (1) successful and depredated nests, (2) parasitized and nonparasitized nests, and (3) nests initiated early and late in the breeding season. In addition, to examine preferences for nest trees, we tested the hypothesis that Acadian Flycatchers used nest trees in accordance to their availability.

METHODS

STUDY AREA

The White River National Wildlife Refuge (WRNWR) is located in eastern Arkansas and consists of 60,000 ha of mostly bottomland hardwood forest that ranges from 4.8 to 16 km wide and extends approximately 104 km along the White River (see Wilson 1997 for detailed description). This study was conducted in a sin-

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gle 1,376-ha management compartment of contiguous homogeneous habitat. Six, 50-ha study plots were established within the compartment. The dominant overstory tree species were sugarberry (*Celtis laevigata*), overcup oak (*Quercus lyrata*), Nuttall oak (*Q. nuttallii*), green ash (*Fraxinus pennsylvanica*), and bitter pecan (*Carya aquatica*). Codominant canopy trees consisted of water locust (*Gleditsia aquatica*), persimmon (*Diospyros virginiana*), American elm (*Ulmus americana*), cedar elm (*U. crassifolia*), bald cypress (*Taxodium distichum*), sweetgum (*Liquidambar styraciflua*), tupelo (*Nyssa aquatica*), willow oak (*Q. phellos*), and sweet pecan (*Carya illinoensis*). Understory vegetation was primarily seedlings and saplings of canopy trees plus possumhaw (*Ilex decidua*), swamp privet (*Forestiera acuminata*), hawthorns (*Crataegus* spp.), and water elm (*Planera aquatica*).

FIELD METHODS

Nest searches were conducted throughout the breeding seasons of 1994 and 1995. Estimates of daily nest success were calculated following the methods of Mayfield (1975, also see Wilson and Cooper 1998). For comparison of successful and depredated nest sites, only nests lost to predators are considered; losses to abiotic factors such as inundation, weather, etc., were excluded from analyses. Initial egg laying dates showed a bimodal distribution with a second peak in nest initiation occurring circa 14 June (Wilson and Cooper 1998). Thus, we classified nests initiated ≤ 14 June as early nests and those > 14 June as late nests.

Microhabitat characteristics were recorded at each nest site based upon Breeding Biology Research and Monitoring Database (BBIRD) protocol (Martin et al. 1996). At each nest, plant height, nest height, and canopy base (defined as the lowest part of the nest tree's canopy) were measured using a clinometer. Diameter at breast height (dbh) was measured using a dbh-tape, and percentage canopy cover was measured using a spherical densiometer. Relative nest height was derived as the ratio of nest height from the ground over nest tree height. Other measurements of nest placement included tree species, distance from the tree crown, and distance from the bole.

In 1995, we estimated the percentage of vegetation surrounding each nest from 1 m away at each of the four cardinal compass directions on the horizontal plane as well as directly above and below the nest. Vegetation estimates were scored on a scale of 0–4 (i.e., 0 = 0% vegetation, 1 = 25% vegetation, 2 = 50% vegetation, etc.) and scores for each of the six directions were then summed and used in analyses following the methods of Holway (1991). Percentage vegetation was selected over the more common approach of percentage visible in an attempt to reduce estimation problems associated with the parallax of observing high nests.

To quantify availability of nest trees, trees ≥ 10-cm dbh were sampled in 0.04-ha circular plots following a modification of the methods described by James and Shugart (1970). In each of the six study plots, 27 points were selected using a systematic sampling scheme with random origin. For all analyses, possumhaw and swamp privet were pooled, hereafter referred to as possumhaw. Although taxonomically distinct, they were structurally similar enough to initially cause identification problems. Tree species comprising less than 1% of the total frequency were pooled for use versus availability analysis.

STATISTICAL ANALYSIS

Comparison of nest survival estimates was conducted using the software CONTRAST (Hines and Sauer 1989). Habitat data were judged to be normally distributed using graphical procedures (PROC UNIVARIATE, SAS Institute 1992). Percentage data were arcsine transformed. Student's t-test was used to test for univariate differences in group means. When variances were heteroscedastic, an approximate t-test based on unequal variances was used to test for differences in group means (Sokal and Rohlf 1981). A Bonferroni procedure was used to calculate the table-wide significance level to control for Type-I errors in multiple comparisons of independent variables (Rice 1989). The Friedman (1937) test, a nonparametric method of analyzing a randomized complete block design, was used to test for differences in use and availability (number of stems per species/total number of stems) of nest trees among the six study plots. We used Fisher's least significant difference (LSD) procedure to make *a posteriori* multiple comparisons, in order to determine which tree species were significantly different in usage (Alldredge and Ratti 1986, 1992). Pearson's product-moment correlation analysis was used to test linear relationships between habitat vari-

TABLE 1. Mean ± SE of microhabitat characteristics at early and late Acadian Flycatcher nest sites on White River NWR, Arkansas, 1994–1995. Asterisks placed between values represent significant differences (t-test, *** $P \leq 0.003$).

	1994				1995			
	Early[a] $n = 103$		Late $n = 27$	Overall[b] $n = 172$	Early $n = 211$		Late $n = 96$	Overall $n = 339$
Nest substrate height (m)	11.8 ± 0.6	***	17.5 ± 1.5	13.4 ± 0.5	12.1 ± 0.4		13.4 ± 0.7	12.8 ± 0.3
Nest substrate dbh (cm)	19.0 ± 1.7	***	34.1 ± 4.4	22.6 ± 1.4	20.5 ± 1.1		25.9 ± 2.0	22.9 ± 1.0
Nest height (m)	5.5 ± 0.2	***	7.3 ± 0.4	6.3 ± 0.2	6.1 ± 0.1		6.8 ± 0.2	6.6 ± 0.1
Canopy base (m)	3.6 ± 0.1	***	4.8 ± 0.3	4.1 ± 0.1	4.3 ± 0.1		5.0 ± 0.2	4.7 ± 0.1
Distance crown edge (m)	0.5 ± 0.1		0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1		0.5 ± 0.2	0.5 ± 0.1
Distance from bole (m)	3.6 ± 0.1		4.3 ± 0.3	3.8 ± 0.1	3.0 ± 0.1	***	3.8 ± 0.1	3.3 ± 0.1
Canopy cover (%)	95.2 ± 0.7		94.6 ± 1.1	95.6 ± 0.4	94.2 ± 0.3		94.7 ± 0.6	94.4 ± 0.3
Relative nest height (%)	56.3 ± 2.1		51.0 ± 4.6	54.6 ± 1.5	58.9 ± 1.4		59.2 ± 2.1	59.1 ± 1.1
Total concealment	—		—	—	7.6 ± 0.3	***	9.5 ± 0.5	8.5 ± 0.2

[a] Early = nests initiated on or before 14 June; late = nest initiated after 14 June.

[b] Includes nests whose initiation dates were undeterminable.

ables and rates of nest survival. All tests were two-tailed and judged significant at $\alpha = 0.05$ unless otherwise noted. Means ± SE are reported for summary statistics.

RESULTS

We collected data from 511 Acadian Flycatcher nests (172 in 1994 and 339 in 1995). Predation was the leading cause of nest failure in both years, resulting in 57% (73/129) and 51% (155/306) failure of all nesting attempts in 1994 and 1995, respectively (see Wilson and Cooper 1998). Brood-parasitism by Brown-headed Cowbirds (*Molothrus ater*) was 20% (26/129) in 1994 and 23% (68/300) in 1995. However, brood-parasitism only accounted for 8% (33/429) of nest failures because parasitized nests were often depredated.

Over all years of the study, nests were generally located in subcanopy trees 13.0 ± 0.3 m tall (Table 1). Nests were 6.5 ± 0.1 m above the ground and placed 0.57 ± 0.01 m from the crown edge, often located over sloughs and shaded trails. Canopy base, distance from bole, and canopy cover at nest sites differed between years ($P < 0.002$; Table 1). We therefore analyzed microhabitat separately by year.

Microhabitat of successful and depredated nests was generally similar in both years ($t < 2.8$, $P \geq 0.02$, Bonferroni adjusted $\alpha = 0.005$), although successful nests were significantly higher (6.7 ± 0.3 m) than depredated nests (5.4 ± 0.2 m) in 1994 ($t_{104} = -2.89$, $P = 0.004$; Table 2). Nonparasitized nest sites were significantly higher (6.2 ± 0.2 m) than parasitized nests (4.5 ± 0.2 m, $t_{54.8} = 4.38$, $P = 0.001$) and had higher canopy bases (parasitized: 3.1 ± 0.2, nonparasitized: 4.1 ± 0.1, $t_{57.9} = 3.89$, $P = 0.001$) in 1994 (Table 2). We found no habitat differences between parasitized and nonparasitized nest sites in 1995 ($P > 0.2$). Late season nests had higher nest heights and were located in taller and larger diameter trees with higher canopy bases compared to early season nests in 1994 (ts > 3.5, Ps ≤ 0.001; Table 1). In 1995, distance from the bole and percentage vegetation at the nest were significantly higher in late compared to early nests (ts ≥ 2.9, $P \leq 0.003$; Table 1). Percentage vegetation at the nest site also was significantly correlated with nest height ($r = 0.15$, $P = 0.01$).

We found nests in 15 tree species, with most (91%) in sugarberry, possumhaw, Nuttall oak, or overcup oak (Table 3). However, Acadian Flycatchers did not use trees in proportion to their availability in 1994 ($\chi^2_9 = 37.0$, $P < 0.001$) or 1995 ($\chi^2_9 = 24.8$, $P = 0.003$; Fig. 1). Acadian Flycatchers consistently chose Nuttall oak and possumhaw in 1994 (Fisher's LSD: $t_{50} = 2.0$, $\alpha = 0.05$) and Nuttall oak in 1995 ($t_{50} = 2.0$, $\alpha = 0.05$) at a significantly higher percentage relative to their availability. Likewise, they consistently avoided green ash and bitter pecan in 1994 ($t_{50} = 2.0$, $\alpha = 0.05$) and green ash in 1995 ($t_{50} = 2.0$, $\alpha = 0.05$) in relation to their availability. However, there was no correlation between the probability of nest survival and nest tree use (% use–% available) in 1994 ($P > 0.3$) or in 1995 ($P > 0.2$; Fig. 1). We also found no relationship between percentage vegetation at the nest site and nest substrate in 1995 ($\chi^2_{11} = 14.1$, $P > 0.2$).

TABLE 2. Mean ± SE of microhabitat characteristics at successful, depredated, parasitized, and nonparasitized Acadian Flycatcher nests on White River NWR, Arkansas, 1994–1995. Asterisks between values represent significant differences (*t*-test; *** $P \leq 0.002$; $\alpha = 0.005$).

	1994						1995			
	Successful $n = 38$		Depredated $n = 73$	Parasitized $n = 24$		Nonparasitized $n = 102$	Successful $n = 38$	Depredated $n = 73$	Parasitized $n = 64$	Nonparasitized $n = 223$
Nest substrate height (m)	14.8 ± 1.1		11.5 ± 0.8	10.2 ± 1.3		13.3 ± 0.7	13.0 ± 0.6	12.1 ± 0.5	12.3 ± 0.9	12.0 ± 0.4
Nest substrate dbh (cm)	26.1 ± 3.4		18.9 ± 2.1	17.6 ± 3.2		22.5 ± 2.0	22.9 ± 2.0	21.4 ± 1.3	22.2 ± 2.6	20.9 ± 1.1
Nest height (m)	6.7 ± 0.3	***	5.4 ± 0.2	4.5 ± 0.2	***	6.1 ± 0.2	6.6 ± 0.2	6.3 ± 0.1	5.9 ± 0.2	6.2 ± 0.1
Canopy base (m)	4.4 ± 0.2		3.7 ± 0.1	3.1 ± 0.1	***	4.1 ± 0.1	4.7 ± 0.2	4.5 ± 0.1	4.4 ± 0.2	4.4 ± 0.1
Distance crown edge (m)	0.5 ± 0.1		0.5 ± 0.1	0.6 ± 0.1		0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1
Distance from bole (m)	3.5 ± 0.2		3.9 ± 0.2	3.5 ± 0.3		3.8 ± 0.2	3.3 ± 0.2	3.2 ± 0.1	3.1 ± 0.2	3.2 ± 0.1
Canopy cover (%)	93.8 ± 1.2		95.3 ± 0.8	93.2 ± 2.3		95.4 ± 0.5	94.9 ± 0.4	94.0 ± 0.4	94.8 ± 0.7	94.6 ± 0.3
Relative nest height (%)	51.8 ± 3.7		56.7 ± 2.4	56.1 ± 4.4		55.6 ± 2.2	58.0 ± 2.1	60.4 ± 1.6	56.6 ± 2.6	60.3 ± 1.3
Total concealment	—		—	—		—	9.2 ± 0.6	7.9 ± 0.3	7.6 ± 0.5	8.3 ± 0.3

DISCUSSION

Martin (1993) suggested that specialized attributes of nest placement within a species evolved to allow interspecific coexistence and to reduce losses to nest predation. As such, aggressive nest defense and nest placement attributes are likely coevolved traits in tyrant flycatchers (Murphy 1983). That is, placement of nests on the periphery of the tree crown over an opening may allow air space for aggressive nest defense by species with powerful flight abilities (Ricklefs 1977). Indeed, Acadian Flycatchers exhibited aggressive nest defense behavior during our concurrent study (Wilson and Cooper 1998). For example, during nest monitoring activities, it was not uncommon for the female to hover near the nest attacking the mirror pole.

Nest placement in tyrant flycatchers may represent a compromise that balances risk from predation and extreme weather (Murphy 1983). Nests are typically located on the periphery of the tree crown, thus making them inaccessible to some predators, while increasing the chance of damage or loss to high winds. Although this population of Acadian Flycatchers endures high rates of nest predation, our results are consistent with this compromise. Nests were located far from the bole on weak branches presumably inaccessible to large predators such as raccoons (*Procyon lotor*), but a small percentage of nests were lost to high winds (Wilson and Cooper 1998).

The nest placement attributes reported here are similar to previous reports in the literature for Acadian Flycatchers. Walkinshaw (1966) reported an average nest height of 4.1 m for Acadian Flycatchers in Michigan, with nests located 3.3 m from the bole and 0.8 m from the end of the branch, often over trails, shaded roads, or shaded streams. Likewise, Bent (1943) reported nest heights for Acadian Flycatchers of 3.0–7.6 m with a mean of 3.3 m in the vicinity of Raleigh, North Carolina, and Li (1994) reported a mean nest height of 4.6 m for Acadian Flycatchers in northwestern Arkansas. We initially suspected that the increased nest height in this study reflected nesting over water during flooded conditions as floodwaters annually inundated the study area to a depth of 2–3 m. However, inundation occurred in late May to early June when nest heights averaged 6.1 ± 0.1 m, compared to 7.4 ± 0.2 m late in the season when

TABLE 3. Tree species composition, frequency of species used as nest substrates, and daily nest survival rates for Acadian Flycatchers on White River NWR, Arkansas, 1994–1995.

Tree species	% Composition[a]	Nest substrate		Daily survival rate
		%	n	$\bar{x}$ ± SE
Sugarberry (CELA)	0.284	0.301	153	0.951 ± 0.005
Nuttall oak (QUNU)	0.178	0.273	139	0.959 ± 0.004
Overcup oak (QULY)	0.164	0.143	73	0.950 ± 0.007
Possumhaw[b] (ILDE)	0.114	0.194	99	0.942 ± 0.006
Green ash (FRPE)	0.110	0.002	1	1.000 ± 0.000
Bitter pecan (CAAQ)	0.058	0.026	13	0.923 ± 0.026
Water locust (GLAQ)	0.028	0.006	3	
Water elm (PLAQ)	0.014	0.002	1	0.818 ± 0.164
Persimmon (DIVI)	0.011	0.000	0	
American elm (ULAM)	0.009	0.004	2	
Cedar elm (ULCR)	0.008	0.022	11	0.952 ± 0.023
Hawthorn spp. (CRSP)	0.006	0.004	2	0.939 ± 0.041
Bald cypress (TADI)	0.006	0.004	2	1.000 ± 0.000
Sweetgum (LIST)	0.004	0.008	4	0.980 ± 0.019
Tupelo (NYAQ)	0.002	0.000	0	
Willow oak (QUPH)	0.002	0.010	5	0.971 ± 0.020
Sweet Pecan (CAIL)	0.001	0.002	1	0.818 ± 0.164

[a] Number of stems (≥ 10 cm)/total number of stems (≥ 10 cm).

[b] Represents both possumhaw and swamp privet (FOAC).

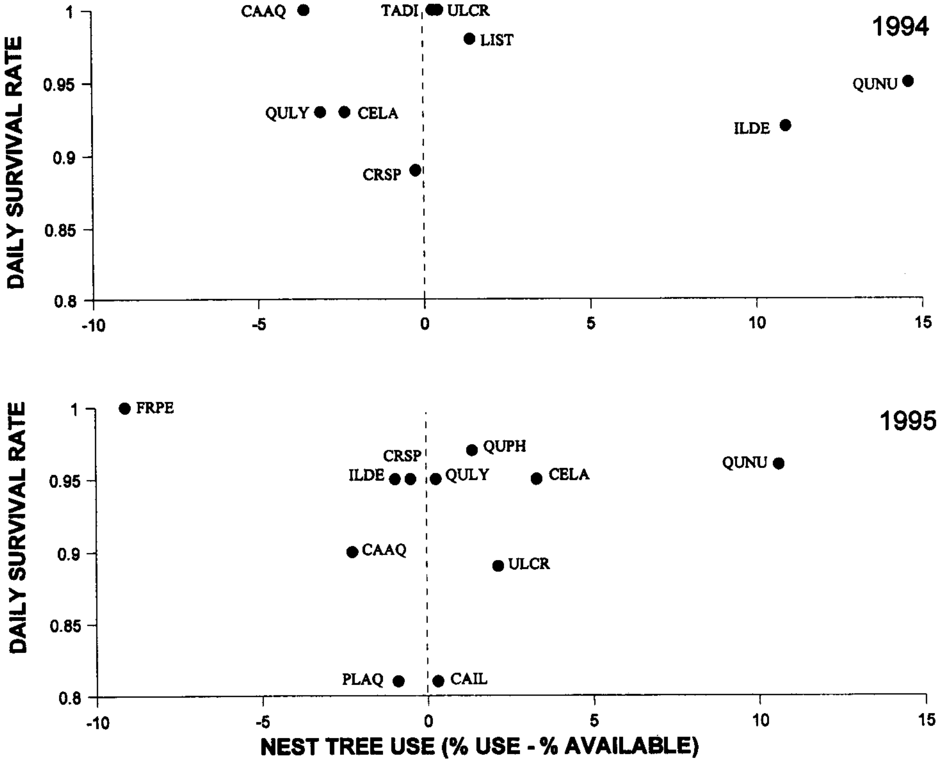

FIGURE 1. Tree use vs. availability for Acadian Flycatchers, illustrating no relationship between Mayfield estimates of daily nest success and nest substrate use (% use–% available) in 1994 (r = 0.09, $P \geq 0.3$) or in 1995 (r = 0.07, $P \geq 0.2$) on White River NWR, Arkansas (See Table 3 for tree codes and $\bar{x}$ ± SE of daily nest success estimates).

the area was dry. Therefore, we suggest that differences in nest heights among studies probably represent structural differences within forests or other site-specific factors.

One such factor that could have influenced nest placement was nest predation, the leading cause of nest failure for this population. Successful nests were generally located in taller trees with high canopy bases and greater nest heights above the ground. This same trend became more apparent as the breeding season progressed. Acadian Flycatchers nested higher by selecting larger nest trees with taller canopy bases, resulting in an increase in vegetation around the nest. Late season nests also were more successful than early season nests (Wilson and Cooper 1998). Comparison of nest placement attributes at successful and depredated and parasitized and nonparasitized nest sites revealed significant differences in nest height. The increased nest height in 1994, along with the increased nest height late in the breeding season, is presumably related to an increase in concealment. It has been suggested that flycatchers counteract high rates of nest predation by making nests less accessible to ground predators through increased nest height (Murphy 1983). This supports the predator-avoidance theory in that it allows a means of compensating for high rates of predation through increased concealment over long periods of nest occupancy. However, we believe that the major nest predators of Acadian Flycatchers on WRNWR are birds and snakes (Wilson and Cooper 1998). Therefore, increased nest height may increase the vulnerability of a nest to avian predators in predator rich communities, compensating for increased protection from ground predators.

Analysis of nest tree selection revealed that Acadian Flycatchers selected some tree species (Nuttall oak, possumhaw) significantly more than the percentage available, and others (green ash, bitter pecan) less than predicted, based on availability. Nest tree selection did not influence nest success, thus, there was little apparent benefit to using any specific tree species with regard to protection from nest predators as suggested by Filliater et al. (1994). However, bottomland hardwood forests are among the most diverse ecosystems in North America, with many different tree species associated with different flooding frequencies and duration in a single forest (Mitsch and Gosselink 1986).

Not surprisingly, other investigators have found different tree species to be regularly used as nest substrates in other parts of the Acadian Flycatchers' range. Of 140 Michigan nests, 63 were in American beech (*Fagus grandifolia*), 34 in eastern hemlock (*Tsuga canadensis*), and 25 in maple (*Acer* spp.; Walkinshaw 1966). In a west Tennessee bottomland forest, nests were commonly found in red maple (*Acer rubrum*), boxelder (*A. negundo*), and sugarberry (R. J. Cooper, unpubl. data). However, in South Carolina nests were "invariably built in the forks of small dogwoods" (*Cornus florida*; Bent 1943) and in Virginia, 18 of 21 nests were placed in eastern hemlock (G. A. Gale, unpubl. data). Although Acadian Flycatchers are not consistent in selection of nest trees throughout their range, it appears that they consistently choose certain tree species within a geographical region or habitat type. In this study, Acadian Flycatchers also selected nest trees in a nonrandom fashion, presumably based on some geometric configuration of the nest tree and the surrounding nest patch, which provides air space for nest defense. For example, Wilson (1997) found that nests were often placed in more open places when compared with random sites. It is likely that these tree species provide structurally similar open sites.

In conclusion, higher nest heights apparently provide an increase in concealment around the nest, thus decreasing the probability of depredation. Other than nest height, no attribute of nest placement statistically differentiated between successful and depredated or parasitized and nonparasitized nests, suggesting that predators do not have a specific search image for Acadian Flycatcher nests. Alternatively, we may have measured the wrong habitat characteristics, or many predators may find nests the same way researchers do, by detecting adult behavior at or near the nest. Birds are visually-oriented predators, and at least some snakes have demonstrated the ability to use visual cues in pursuit of nest contents (Mullin 1998). Likewise, Brown-headed Cowbirds probably also focus on adult behavior rather than structural attributes of nest placement to locate nests. Accordingly, in diverse, predator-rich systems like bottomland forests, nest predation and brood-parasitism on some species of passerine birds may best be thought of as a function of largely random events in space and time.

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