

## COMMENTARY

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### NEST PLACEMENT AND MORTALITY: IS NEST PREDATION A RANDOM EVENT IN SPACE AND TIME?<sup>1</sup>

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**Abstract.** In their recent article, Wilson and Cooper (1998) reported that Acadian Flycatchers (*Empidonax virescens*) selected nest trees nonrandomly, but that their choice of nest tree did not influence nest success. They concluded that nest predation appears random in time and space. However, we show their metric for nest tree use (% use - % available) is a poor indicator of nest tree selection. We reanalyzed their data using an appropriate selectivity index (from Chesson 1983), and found that nest tree selectivity was greater for nest tree species with higher daily nest survival rates. In general, nest predation, while it may appear unpredictable, may often be related to nest site characteristics.

**Key words:** *Acadian Flycatcher, behavioral games, Empidonax virescens, nest mortality, nest tree selection.*

There is confusion in the literature over whether nest mortality is influenced by nest site characteristics and placement or vice versa. Nest-site selection strategies are probably considerably more complicated. For instance, some nests may have better success than others based on site-specific attributes that influence such factors as the physiological costs of rearing a brood (Martin and Ghalambor 1999) or ability of parents to defend the nest (Wilson and Cooper 1998). From a traditional perspective, these sites might be expected to be used disproportionately relative to their abundance.

From the perspective of behavioral games, in contrast, the nest site selection strategy of any given species will depend on the nest site strategies of co-occurring species (Hoi and Winkler 1994, Schmidt and Whelan 1998) and the search strategies of the available predators (Schmidt 1996, 1999). From this perspective, nest site selection will depend on frequencies with which sites are used. Furthermore, a predator's search strategy should reflect its information on nest locations. In the absence of any information, predators may simply check all possible nesting sites, leading to no relationship between selectivity for a site and nest predation (Murphy et al. 1997). If prey select some sites

disproportionately to site abundance (use > availability), predators should concentrate their search to those sites and avoid those used infrequently. In this case, predation rates should be greater for selected sites (Wilson and Cooper 1998). However, prey may avoid sites where the expected predation rate is higher than average and select those sites where the expected predation rate is lower than average. In this case, selectivity should be higher for sites with low predation rates (Bekoff et al. 1987). Whether a pattern is discernible may depend upon whether the predator or prey has the upper hand. Prey are most likely to have the upper hand for sites that are rarely used because predators, as a consequence of infrequent encounters, have the least and poorest quality of information about the usage of such sites and there is a low penalty, in terms of missed meals, for under-exploiting rare sites relative to under-exploiting common sites.

Despite these complications, recent studies have attempted to address the relationship between nest placement and predation by looking for a simple association. When this has been absent, nest predation has been interpreted as a random (Wilson and Cooper 1998) or nearly random (Filliater et al. 1994) process. In this note, we reanalyze the data of Wilson and Cooper (1998) to show that a positive relationship between nest tree selection and nest survival is an equally likely interpretation of their data, and we argue against the view of random predation (Filliater et al. 1994, Wilson and Cooper 1998).

Wilson and Cooper (1998) reported that Acadian Flycatchers (*Empidonax virescens*) inhabiting a bottomland hardwood forest in Arkansas selected nest trees nonrandomly, but that their choice of nest tree did not influence nest success. They concluded that nest predation is random in time and space. They based their interpretation on the results of regressing daily survival rate (DSR) against nest tree use (% use - % available), implying they favor the hypothesis that selectivity drives predation rates. They tested two years of nesting data separately with similar results; the regressions were not significant ( $P > 0.20$ ) and fit the data poorly ( $r^2 < 0.10$ ).

However, we believe this interpretation may be unjustified. The linear regression analysis of Wilson and Cooper (1998) seems inappropriate because both daily survival and nest tree selection are random (as opposed to fixed) variables in the regression analysis, and their exact functional relationship is unknown. Second, as their independent variable, they calculated nest tree use as: (% use - % available). This metric is a poor indicator of nest tree selection. For example, assume that birds within a population select two tree species twice as often as their availability in the environment. For tree species that have availability of 30% and 3%, respectively, nest tree use as calculated by Wilson and Cooper would equal 30% in the first case and 3% in the second. If, on the other hand, the birds select two tree species half as often as their availability, nest tree use would equal -15% and -1.5%, respectively. In

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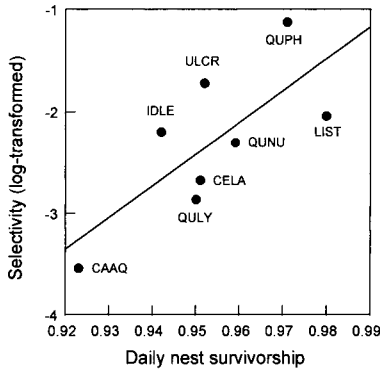


FIGURE 1. Nest tree selectivity (log-transformed) vs. daily survival rate. Tree selectivity is positively correlated to survival rate (data from Table 3 in Wilson and Cooper 1998). See our Table 1 for tree species codes.

each example, the two tree species are selected identically relative to their abundance, but in the first case, the more common tree species has a much higher nest tree use value relative to the less common species, whereas in the second case, the more common species has a much lower nest tree use value relative to the less common species. For this reason, we believe that the metric (% use - % available) is a poor indicator of nest tree selection. Finally, for five tree species, estimates of daily survival rate were calculated from as few as one or two nest attempts (see Table 3 in Wilson and Cooper 1998).

We reanalyzed the data of Wilson and Cooper (1998) after making the following changes. First, we used Chesson's (1983) measure of selectivity calculated as:

$$\alpha_i = (R_i/N_i) / \sum_{i=1}^m (R_i/N_i)$$

where  $R_i$  = percent use of the  $i$ th ( $i = 1, 2, \dots, m$ ) tree species, and  $N_i$  = percent available of the  $i$ th tree species. This is an appropriate measure of selectivity when resources, in this case nest trees, are non-depletable (Chesson 1983; we assume that appropriate nest trees far outnumber nests and can thus be considered non-depletable). Selectivity was logarithmically transformed to remove variance problems associated with creating a ratio of two random variables. In addition, we pooled data between the two years (as reported in Table 3 in Wilson and Cooper 1998), but we did not include tree species when daily survival was estimated from one or two nesting attempts. In all, we used the eight most commonly chosen nest tree species (representing > 97% of nest attempts) for analysis. We used Pearson's correlation to examine the relationship between nest site selection and DSR, and linear regression analysis to compare our analysis with that of Wilson and Cooper (1998). Analyzed this way, nest tree selectivity was greater for nest tree species with higher daily nest survival ( $r = 0.74$ ,  $P < 0.05$ , two-tailed probability; Fig. 1). For comparison to Wilson

TABLE 1. The benefit of nonrandom nest-tree selection in terms of increased daily nest survivorship over the strategy of randomly chosen nest trees. The second column calculates the disproportionate tree use for each of the eight most commonly used trees from Wilson and Cooper (1998). The third column calculates the difference in daily survivorship between each tree species ( $DS_i$ ) and the mean survivorship for all nest attempts ( $DS_x = 0.951$ ). The last column calculates the product of these two columns and gives the realized benefit in terms of daily nest survivorship.

Species (codes)	% use - % avail- able	$DS_i$ - $DS_x$	Product
Sugarberry (CELA)	0.017	0	0
Nuttall oak (QUNU)	0.095	0.008	0.0008
Overcup oak (QULY)	-0.021	-0.001	0.00002
Possumhaw (ILDE)	0.080	-0.009	-0.0007
Bitter pecan (CAAQ)	-0.032	-0.028	0.0009
Cedar elm (ULCR)	0.014	0.001	0.00001
Sweetgum (LIST)	0.004	0.029	0.00012
Willow oak (QUPH)	0.008	0.020	0.00016

and Cooper (1998), the fit of the regression to the data was substantially improved ( $r^2 = 0.54$ ;  $P = 0.04$ ).

If nest predation is a random event in time and space (Filliater et al 1994, Wilson and Cooper 1998), there should be no benefit (reduced predation) of nesting nonrandomly. Unfortunately, with the data of Wilson and Cooper (1998), it is impossible to calculate the true benefit of nesting nonrandomly because some tree species represent a substantial portion of the trees available, yet are rarely used for nesting (e.g., green ash, *Fraxinus pennsylvanica*, is a canopy dominant but was used once in 511 nest attempts). Thus it is unknown what nest success would be if these species were used. However, we can estimate the benefit of nonrandom nesting based on the tree species that are used, which should underestimate the true benefit if trees with the lowest success are strongly avoided. We calculated for the eight most commonly used trees (Table 1): (1) the difference in percent use of tree species and percent available, (2) the difference in the nest survivorship when nesting in each tree species vs. mean nest survivorship, and (3) the product of these two variables. The first variable calculates the magnitude of disproportionate use, whereas the second calculates the cost or benefit (in terms of nest survivorship) of nesting in a particular species in comparison to the mean success. The product of the two variables calculates the realized effect (in terms of increased nest survivorship) per nest attempt through nonrandom nesting.

This analysis reveals two principal points. First, in seven of the eight tree species, flycatchers benefited from nonrandom nest site selection. Tree species with nest survivorship below the mean were used less frequently than their availability, while those with nest survivorship above the mean were used more frequently than their availability. The single exception is possumhaw (*Ilex decidua*). This is an interesting case be-

cause possumhaw and swamp privet (*Forestiera acuminata*) were pooled together in the original analyses, and it is unknown to what extent this negative effect might reflect that.

Second, the benefit to an individual nest attempt ranged from little benefit (0.0001 increase in DSR) in the case of cedar elm (*Ulmus crassifolia*), to a larger benefit for bitter pecan (*Carya aquatica*; 0.0009 increase in DSR) and for nuttall oak (*Quercus nuttalli*; 0.0008 increase in DSR). Because overall predation is very high in this system (> 75%), these benefits represent small increases in nest survivorship over a 28-day nest cycle (approximately 0.55–0.65% increase in survivorship per nest attempt). At somewhat lower nest predation (55%), this difference would increase to 1.5% per brood, or about a 1.5% increase in annual reproductive output per female for species like Acadian Flycatchers that are double brooded (Ehrlich et al. 1988). This magnitude may appear small, but it is similar to estimates of annual percent decline for many North American passerines (Sauer et al. 1996). Evolutionarily, a 1–3% increase in reproductive output represents a modest selection differential (Endler 1986). If these results also apply to other avian species, then the management considerations that address habitat and nest site features (Martin 1992) can be of great value to conservationists.

Our two analyses indicate that different tree species influence nest success, but this is not unexpected. Tree species used rarely contribute to the significance of the correlation analysis, and in fact, removal of all but the four common species produces a nonsignificant, negative correlation ( $r = -0.12$ ,  $P > 0.5$ ). This is interesting, because predators should be more focused on the common species for at least two reasons. First, as indicated above, under-exploiting common nest sites has much larger consequences than under-exploiting rare nest sites. Second, if the quantity and quality of information is based on nest encounters, common species should provide the predator with the best information. Thus, we should expect no relationship between the variables for commonly used sites. In the second analysis, nuttall oak and bitter pecan contribute the most to the benefits of nonrandom nesting, the former through selection of a site more successful on average, the latter through avoidance of a site less successful on average. Possumhaw contributes negatively and may be considered an ecological trap (Gates and Gysel 1978) in the sense that it is over-selected (use > availability) but has lower than average nest success.

The results of these analyses (as those for Wilson and Cooper 1998) should be interpreted cautiously for several reasons. First, daily survival rates for sweetgum (*Liquidambar styraciflua*) and willow oak (*Q. phellos*) were estimated from 4 and 5 nests, respectively, whereas Hensler and Nichols (1981) caution against estimates based on fewer than 20 nests. This simply reflects a limitation of the data set and a potential source of error also present in the original analysis by Wilson and Cooper (1998). In fact, their analysis used estimates of nest survival based on single nest attempts. Second, we pooled the data between years when yearly differences existed. For example, sweetgum had the highest selectivity coefficient, but it was

not used in 1995. Possumhaw was used disproportionately more than its availability in 1995, but not in 1994 (Fig. 1 of Wilson and Cooper 1998). However, nest tree selection will likely be based on the expected nest survival rates across many years (Clark and Shuter 1999), and thus pooling between years should be quite reasonable.

There are several circumstances which may obscure or reverse a positive relationship between nest tree selectivity and nest success. First, there may be novel (through introduction or invasion) tree species present in the environment. For example, Filliater et al. (1994) found no relationships between the tree species used for nesting and nest outcome for Northern Cardinals (*Cardinalis cardinalis*). However, they did not measure tree availability, and thus they have no measures of nest site selectivity. Even so, 65% of their nests were built in two exotic species, multiflora rose (*Rosa multiflora*) and honeysuckle (*Lonicera* spp.). Similarly, Schmidt and Whelan (in press) found that American Robins (*Turdus migratorius*) and Wood Thrushes (*Hyllocichla mustelina*) use exotic shrubs (*Lonicera maackii*, *Rhamnus cathartica*) extensively despite decreased DSRs relative to native trees. Novel predator species or unnaturally high predator abundance, say through mesopredator release (Soulé et al. 1988, Rogers and Caro 1998), should have similar consequences. Finally, the search mode of some predator species may not result in different encounter rates with nests placed in different tree species, for example, if avian predators cue in on the movements of parental birds.

We suggest that the data in Wilson and Cooper (1998) can be interpreted as evidence for a relationship between nest site selection and nest predation. However, this interpretation is tentative because of the limitations of the data set. Furthermore, neither analysis has considered whether birds are responding to other habitat features to which nest tree distribution is itself correlated, or whether birds switch nest trees between nest attempts, particularly if an earlier attempt was depredated. In the face of such alternatives and caveats, the ultimate conclusion may be that we can conclude nothing. As defeatist as this may appear, we nonetheless believe that this is more appropriate than concluding that nest predation represents random events in time and space.

#### SHOULD NEST PREDATION BE VIEWED AS RANDOM IN TIME AND SPACE?

We can ask whether, in the presence of a behavioral game between predators and prey, we expect to see relationships between nest site selectivity and nest predation? There is no simple answer to this question because it depends on explicit assumptions concerning, e.g., predator searching behavior (see above). This question highlights a critical underlying issue, namely, what is the standard of proof necessary to confirm whether a process like nest predation is random in time and space? The answer depends on the types of questions we are asking and the types of conclusions we are drawing. For example, if a population is distributed in an ideal free fashion across habitat types such that the fitness of individuals is constant across habitats, are we justified in saying that fitness is random with respect to habitat choice? No, because in the ab-

sence of a mechanistic understanding, this would imply that any other distribution of individuals across habitats would result in, on average, equal fitness. But in reality it would not. In fact, both behavioral and evolutionary adjustments should result in patterns that appear superficially to be random, because if any non-randomness associated with survivorship or reproduction can be detected and exploited, individuals should further exploit the process that resulted in the nonrandom survivorship, at least until feedback mechanisms kick in. Similarly, are we anymore justified in saying that patterns of nest predation that are unrelated to nest site selectivity represent random predation events? Not if we have ignored the mechanisms that may simultaneously cause and obscure the relationship, that is, if we have attempted to infer a process from an analysis of pattern without regard to mechanism.

In a similar vein, Filliater et al. (1994) concluded that predation on Northern Cardinal nests was a nearly random predation because "[A] rich guild of nest predators precludes the existence of predictable safe nest sites. . ." (p. 761). However, they also state that each predator has its own search strategy, indicating that they do not consider each predator species to forage randomly. We emphasize that unpredictable does not imply random, and we suggest it may be more enlightening to view this particular situation as one in which there are tradeoffs between avoidance strategies when there are multiple predators (Sih et al. 1998, Turner et al. 1999), but that each predator type has a predictable bias or association between predation risk and nest site feature(s). This distinction is not trivial. By understanding the mechanisms of predation, we can understand how different assemblages of nest predators (in either time or space) will likely impact communities of nesting birds. Furthermore, we can predict the outcome of managing or controlling particular species of predator. If nest predation is viewed as random in time and space, managers may simply resign from any action, because any management, except removing predators, would be considered futile.

In conclusion, the interpretations of Wilson and Cooper (1998) and Filliater et al. (1994) that nest predation may be thought of as largely random events in time and space may be incorrect regarding nest tree species, or at least is currently unsubstantiated by their analyses. Particular tree species (or other habitat features associated with nest sites) may have predictably better success than others. When this occurs, we expect to see selection of those habitat features that promote higher nest success. Identifying and promoting these habitat features is critical to properly manage landscapes for avian conservation.

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## DOES NONRANDOM NEST PLACEMENT IMPLY NONRANDOM NEST PREDATION?—A REPLY<sup>1</sup>

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**Abstract.** In response to the critique by Schmidt and Whelan (1999), we find that the relationship between nest success and tree selectivity is dependent upon inclusion or exclusion of particular tree species, whether or not years are pooled, and the selectivity index used. We question their use of point estimates of nest success with extremely high variances, defend

our index, question the application of the Chesson (1983) index to our data, and explain the need to analyze years separately. Bottomland hardwood forest systems are extremely variable; hydroperiods alter the suitability of nesting substrates, availability of alternative food, and behavior of predators and their prey. Given these features, actively searching for Acadian Flycatcher (*Empidonax vireescens*) nests is seldom an efficient predator foraging strategy. Therefore, these predation events are best described as random; nests are principally encountered opportunistically by generalist predators while searching for other prey.

**Key words:** *Acadian Flycatcher, bottomland hardwood forest, Empidonax vireescens, forest management, nest mortality, nest tree selection.*

The critique by Schmidt and Whelan (1999) focuses on two concerns regarding our initial assessment (Wilson and Cooper 1998a) of the relationship between nest substrate selection and reproductive success. First, they question our analyses that resulted in a nonsignificant relationship between the selectivity of particular tree species and fitness. Second, they question our conclusion, based on our analyses and knowledge of the system, that "... in diverse, predator-rich systems like bottomland forests, nest predation ... on some species of passerine birds may best be thought of as a function of largely random events in space and time." After a brief summary of Acadian Flycatcher (*Empidonax vireescens*) nest site selection and our particular system, we will respond to these criticisms in turn.

### FOCAL SPECIES AND SYSTEM

Acadian Flycatchers almost invariably nest over open airspace for a variety of reasons most likely related to ease of access, departure, and defense. Unlike most birds, we can actually observe the manner in which Acadian Flycatchers apparently choose branches for their nest sites. They fly from branch to branch within a patch of several trees, choosing a fork where they squat down, seemingly to assess if a nest will fit there. Some trees do not provide suitable forks or open airspace below the nest. Other nest sites may be too exposed to the elements (Wilson and Cooper 1998a, 1998b). Hence, nest site selection is likely a result of many proximate and ultimate factors (Hilden 1965) acting in concert. The supposition by Schmidt and Whelan (1999) that random nest predation does not confer any benefits for nesting nonrandomly is therefore negated if factors other than predation influence nest placement. For example, the two common tree species that were most avoided by Acadian Flycatchers as nest sites in our study area were green ash (*Fraxinus pennsylvanica*) and bitter pecan (*Carya aquatica*). Although it is possible that the reason for this avoidance was increased likelihood of nest predation, our data do not support that hypothesis. The most parsimonious explanation is that the fork and foliage structure required by this species for nest placement does not occur very often in trees with compound leaves, probably because: (1) leaflets are attached to a nonwoody rachis 30–40 cm in length instead of a woody twig, so there are fewer secure sites to place a nest, and (2) Acadian Flycatchers usually nest in the outer 0.5 m of the sup-

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