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DOES NONRANDOM NEST PLACEMENT IMPLY NONRANDOM NEST PREDATION?—A REPLY¹

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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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port branch, where leaves are clustered, so there are few suitable woody forks in these two species.

Bottomland hardwood forests are characterized by periodic inundation that is highly unpredictable both spatially and temporally. Slight differences in elevation often result in establishment and growth of very different tree species (Messina and Conner 1998). Consequently, bottomland hardwood forests are among the most diverse communities in temperate North America. Many organisms in these systems tend to be most influenced by extremes in hydroperiod rather than central values. Thus, from year to year and even within years, a different set of nest sites is likely to be available because smaller trees may be inundated and leaf expansion in larger trees may be delayed. Nesting birds, their food, and their predators are all likely to be affected. An analysis that pools years, always a questionable practice (Fowler 1990), is especially suspect here.

ANALYSES INVOLVING SELECTIVITY

Many different tree species provide suitable nest sites for Acadian Flycatchers, as evidenced by our data and those of other researchers from other locations. We believe our data show that, whereas certain tree species were selected proportionally more than others, this selectivity was not related to the probability of nest survival. A possible exception to this conclusion is Nuttall oak (*Quercus nuttallii*). Acadian Flycatchers selected this species in proportions that significantly exceeded availability in both years, and nests built in it had a higher than average probability of nest success (Table 3 and Fig. 1 of Wilson and Cooper 1998a). However, the relationship was not consistent when we included other tree species in the analysis.

The principal criticisms of our analyses by Schmidt and Whelan (1999) are that we: (1) included tree species represented by only 1 or 2 nests, (2) employed % use – % available as our metric for selection, and (3) analyzed years separately instead of pooling them. Using only tree species with ≥ 4 observations, a different metric for selectivity, and years pooled, Schmidt and Whelan found a significant relationship between nest tree selection and nest survival.

In the first criticism they are correct. We elected to use all data because we could not detect a significant relationship even when we eliminated tree species represented by only a few nests. Furthermore, small sample sizes are a reality if one is to test the “rare site hypothesis” proposed by Filiater et al. (1994). Therefore, we decided to show all of the data. The problem with using central points to depict nest success is that small numbers of nests lead to large variances associated with those points. Many of the samples in Figure 1 and Table 1 of Schmidt and Whelan (1999) also suffer from this problem.

Regarding the second criticism, we employed % use – % available because it is part of the Friedman (1937) test, which is commonly used for resource selection analyses (Allredge and Ratti 1986). This metric was deemed inappropriate by Schmidt and Whelan (1999) because of its bias in favor of common categories. On the other hand, Chesson’s (1983) selectivity index places all categories on “equal footing.” But as

a result, rare categories tend to dominate this metric; this is exactly why we chose not to use this measure of selectivity. Consider a field effort in which 100 nests of a bird species are located and monitored. Suppose tree species A comprises 50% of the trees available for nesting, and 75 of the 100 nests are located there. Suppose tree species B comprises only 1% of the trees available, and 3 nests are located there. Clearly species A is strongly selected by this bird, whereas species B was used so seldom that this result could be due to chance, and could vary considerably from year to year. Yet Chesson’s index indicates that species B has a selectivity coefficient twice that of species A. Although emphasizing rare categories might be advantageous in some settings such as foraging or diet analysis, where rare items might be energetically important and therefore eaten frequently, this is clearly a misleading result in a nest placement setting because an individual of a rare tree species can only be used by one pair of territorial birds at a time.

The above scenario is more or less what is depicted by Schmidt and Whelan’s (1999) reanalysis of our data. Again, if there is a tree species that is consistently selected, it is clearly Nuttall oak. Yet in Figure 1 of Schmidt and Whelan, it has the fifth highest selectivity (out of eight) and is located in the central cloud of points. If the two species with very small sample sizes, willow oak (*Q. phellos*) and sweetgum (*Liquidambar styraciflua*), are eliminated from the analysis, then the relationship is no longer significant. Furthermore, we question the conferring of significance onto a relationship where the individual points have such a large associated variance. The relationship disappears entirely when only the four species with adequate sample sizes of nests (Hensler and Nichols 1981) are used. Schmidt and Whelan suggest that this was expected because “predators should be more focused on the common species.” Yet those four species alone provide a vast number of nest locations, consistent with the potential prey-site hypothesis (Martin 1988, 1993). As is often the case with small sample sizes, there was tremendous variability in selectivity for these species between years. The best example is bitter pecan, which had the lowest probability of nest success of these species when both years were pooled but had the highest success rate in 1994. Whereas Schmidt and Whelan acknowledge other inconsistencies among years, we add that the high selectivity values (means) for sweetgum and willow oak, coupled with the low value for bitter pecan, are largely responsible for the significant relationship depicted in their Figure 1.

Schmidt and Whelan (1999) apparently do not believe that a % use – % available index is meaningless, because they used it for their second analysis (see their Table 1). They refer to it as the “magnitude of disproportionate use,” which is identical to selectivity in our original analysis. Unlike the results of their first analysis, a completely different species, Nuttall oak, was chosen here as being selected, which was obvious from Figure 1 in Wilson and Cooper (1998a) and is the observation that began this section of the discussion. Also, because of the large variances resulting from the small number of exposure days, there is only one significant difference in nest survival among these tree

species (Nuttall oak had higher nest success than possumhaw [*Ilex decidua*], $\chi^2_1 = 5.6$, $P = 0.02$, Program CONTRAST; Hines and Sauer 1989). Even this result is negated when the alpha level is appropriately adjusted for the number of comparisons being made. Thus, the biological advantages of nesting nonrandomly inferred by Schmidt and Whelan may just be the result of sampling error.

The third criticism was that we analyzed years separately, and this masked patterns evident when years were pooled. However, pooling two years of data is in no way the same as pooling over the time span necessary to achieve the "long-term expectation of survival rates" suggested by Schmidt and Whelan (1999). An attempt to average data for only 2 years in a system of such high annual variability, especially when dealing with small sample sizes, reminds one of the person who, standing with one foot in hot coals and the other in ice water, is on average comfortable.

There are literally dozens of ways to analyze these data, and the results depend on the quantitative analyses chosen, which species are included, and whether or not years are pooled. One such combination results in a significant relationship between selectivity and nest success, others do not. Thus it is up to the investigator to choose the most appropriate analysis, taking into consideration the data, hypotheses to be tested, and other key factors (Alldredge and Ratti 1986).

SHOULD PREDATION BE VIEWED AS RANDOM IN TIME AND SPACE?

First, it is important to state the question specifically. In the context of Wilson and Cooper (1998a) and this paper, we should ask "Is predation of Acadian Flycatcher nests at the White River National Wildlife Refuge (WRNWR) a function of largely random events in space and time?" To provide an answer, there are several spatial scales to consider. Foraging theory predicts that predators minimize energy expenditure when foraging; they do not aimlessly wander through their environment in search of food. On a broad scale, then, their search is directed to particular locations and is nonrandom. Raccoons (*Procyon lotor*) in our study area, for example, tend to follow watercourses, locating principally aquatic prey. However, at a finer scale within this search area, their foraging behavior takes on a random component. That is, they are opportunistic foragers, and when they encounter a novel but relatively rare prey item like a nest, they often take advantage of it. This is what we mean by "random."

Snakes follow a similar pattern. Our radio telemetry work has shown that gray rat snakes (*Elaphe obsoleta spiloides*) often forage in a particular, restricted location (ground, low canopy) (S. J. Mullin, unpubl. data). They search opportunistically for multiple prey types within that area (Mullin et al. 1998). Because many predators, including snakes, have home ranges that are not likely to include more than a few nests of any one bird species, it is unlikely that they would develop a search image for a particular species. For example, Eichholz and Koenig (1992) found that gopher snakes (*Pituophis catenifer*) captured and marked at nests of Western Bluebirds (*Sialia mexicana*) were never found at >1 nest. Even if snakes in our system do develop a search image for nests, that image is likely based on

visual cues, like provisioning activity of adult birds (Neal et al. 1993, Mullin and Cooper 1998), or scent (Eichholz and Koenig 1992), rather than a cue based on tree species.

Nest predation models based on foraging theory predict that alternative food for predators would decrease nest predation rates (Schmidt 1999). For at least one species at WRNWR, the Prothonotary Warbler (*Protonotaria citrea*), we do believe that nests are predated more when primary prey are unavailable. In years of low water, when aquatic prey are scarce, raccoons apparently predate nests of this cavity-nesting species more frequently, resulting in low nest success (R. J. Cooper, unpubl. data). It is unclear, however, whether raccoons actively search for nests, or if they just encounter them more because Prothonotary Warblers nest over water, which is much reduced during dry periods. Interestingly, an assumption of these and similar models developed by Schmidt and Whelan (1998) was that "predators encounter nests randomly." Apparently, what we are calling random predation is the same as what Schmidt (1998) refers to as opportunism while foraging for preferred prey.

The behavioral game between predators and prey suggested by Schmidt and Whelan (1999) presupposes that predators actively search specifically for Acadian Flycatcher nests. In some systems where nesting birds specialize on one or a few tree species (Martin and Roper 1988), or on cavities, predators may develop search images for nests of particular species. Based on our knowledge of this system, we think this is highly unlikely for Acadian Flycatchers. Each of the predators in question principally forage for other prey. Furthermore, Acadian Flycatchers are just one of about 50 bird species nesting at this time, each with its own set of microhabitat characteristics used for nesting. To develop a search strategy for any one species seems maladaptive, in that the biomass of their nest contents is a tiny fraction of other available prey.

We therefore maintain that, although not the case for all bird species and systems, predation on Acadian Flycatcher nests in our system is largely the result of random processes.

ON CONSERVATION AND MANAGEMENT

At several points in their critique, Schmidt and Whelan (1999) make reference to the importance of the issue of random vs. nonrandom nest predation in conservation and management. Yet the exact message to land managers is unclear. Should certain tree species be favored over others in silvicultural decisions based on their analyses? Clearly not, because there are many other species of concern, avian and otherwise, that might be harmed by those decisions. Furthermore, the different analyses they used provide conflicting answers to this question.

Just because we conclude that Acadian Flycatcher nests are predated in a random fashion does not lead to a futile management scenario. The density of predators, alternate food for predators, forest structure and composition, ecosystem processes, and landscapes are all important and can be managed. Whether or not nest predation is random may not enter into the daily decision processes of most land managers. However, the

land managers we know are very concerned about the consequences of their management activities on the system they are charged with managing. Questions involving those consequences should be paramount among research topics in avian conservation.

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