

SNAG PREFERENCES OF WOODPECKERS FORAGING IN A NORTHEASTERN HARDWOOD FOREST

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ABSTRACT.—To assess the role of snags in cavity-nesting bird communities ornithologists need to identify the types of snags which foraging cavity-nesters select. Using data from a hardwood forest in central New York, this paper develops a logistic regression analysis of snags used for foraging by woodpeckers (Picidae) and compares these results to a companion study of snags used as nest-cavity sites. Snags used for foraging were in earlier stages of decay than snags used for nest cavities. Woodpeckers, however, exhibited less sensitivity to snag size and decay-stage when foraging than when excavating nest cavities. The importance of snags to cavity-nesters will depend both on the history of a particular forest and on the preferences which birds demonstrate for dead wood in various forms (such as snags, dead limbs, logs, etc.). *Received 17 June 1987, accepted 18 Nov. 1987.*

Many studies of cavity-nesting birds associate snag characteristics with the presence of nesting or roosting cavities to assess habitat quality. But basing descriptions of habitat quality on nesting or roosting sites alone may fail to consider other critical habitat components (Conner and Adkisson 1977; Mannan et al. 1980; Cline et al. 1980; Brawn et al. 1982; Carey 1983a, b; Davis et al. 1983; Raphael and White 1984; McComb et al. 1986; Sedgwick and Knopf 1986; Swallow et al. 1986). If sites used for nesting and roosting differ from those used for foraging, then habitat suitable for cavity sites may fail to include adequate feeding sites (see Conner 1980). This study addresses some habitat features important to the foraging requirements of cavity-nesting birds.

Some recent literature suggests that snags may not be essential to cavity-nesting birds. Several studies (Brawn et al. 1982, Carey 1983b, Sedgwick and Knopf 1986) suggest that live trees provide adequate supplies of dead wood (e.g., dead limbs) in many forests. However, snags remain as one potentially important and easily measured resource for cavity-nesters. Furthermore, while dead wood in the canopy may provide sufficient foraging or nesting substrate in some forests, forest manipulations to supply dead wood will likely prove most efficient when focused on snag (whole tree) management. In order to assess both the requirements of cavity-

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nesters for dead wood and to assess the role of snags in these bird communities, ornithologists need to identify those snags which foraging cavity-nesters select. While other sources of dead wood exist, this study concentrates on the snag resource.

Cavity-nesters, woodpeckers (Picidae) in particular, often leave identifiable foraging excavations on the tree boles. In this study, Hairy Woodpeckers (*Picoides villosus*) and Pileated Woodpeckers (*Dryocopus pileatus*) were the most common hewing species, while Red-bellied Woodpeckers (*Melanerpes carolinus*), Northern Flickers (*Colaptes auratus*), and Downy Woodpeckers (*P. pubescens*) were either less common or did less excavating. The first objective of the study was to differentiate between useful snags and snags not useful for foraging. The second objective was to compare factors which influence excavators' selection of snags for feeding or shelter. The study focused only on one major foraging method (excavation) used by cavity-nesters; foraging by other methods (e.g., gleaning and bark scaling, [Kilham 1965]) was eliminated.

METHODS

The data in the present study were collected at the Cornell Biological Field Station, Shackelton Point, Bridgeport, New York. In a 45-ha study area established during the summer of 1979, snags were sampled within 0.049-ha plots located by an unbiased procedure detailed by Swallow et al. (1986). The sample included snags in both mature sites (N = 10, age 90–110 years) and second growth forest sites (N = 51, age 25–45 years; total area of 0.49 ha and 2.5 ha, respectively) typical of central New York's maple (*Acer* spp.)-ash (*Fraxinus* spp.)-elm (*Ulmus* spp.) forest. The second growth forest sites developed on farmland abandoned in the mid-1930s, while adjacent mature forest sites were primarily old growth (post-Civil war) riparian sites. Second growth sites were in early aggradation, just becoming useful for cavity nesters, while mature sites were in middle to late aggradation, with greater supplies of dead wood. Carey (1983a) provides a brief introduction to forest development relative to dead wood supplies, while Swallow et al. (1986) quantify snag densities in the present study area. Snags were defined as any dead, standing woody stem ≥ 1.5 m tall and ≥ 10.1 cm in diameter at breast height (1.37 m).

Snag characteristics measured included dbh, total height, presence of external shelf fungi (*Fomes* spp.), number of limbs ≥ 7 cm in diameter at their origin and ≥ 1 m long, a subjective estimate of canopy closure above the snag (percent of a 3-m diameter circle occluded by canopy vegetation above the snag), percent of a snag's trunk covered by foliage (from nearby shrubs and trees) within 0.3 m of the trunk, wood density (g/cm dry weight of a 2.5–5 cm increment bore sample taken at breast height), snag species, forest type (second growth or mature), and percent (in quartiles) of the snag covered by bark. These variables measured snag size and/or served as indicators of the snag's stage of decay. Rather than using *a priori* definitions of decay stages (e.g., Cline et al. 1980), these methods allowed the data (i.e., the birds) to reveal those characteristics which best define the decay stage preferred for foraging.

Any snag with visible evidence of feeding by excavators (i.e., drilling or irregularly-shaped excavations) was classified as a "feeding snag." This bivariate classification separated snags not yet used for foraging by excavation from those which had been used and was compatible with logistic regression analysis (Hanusheck and Jackson 1977:179–245, Press and Wilson

Press and Wilson 1978). Qualitative observations during >500 man-hours of field work suggested that feeding snags continued to provide foraging substrate for hewing birds.

This study did not discriminate among excavating bird species. Qualitative observations and field station records (Severinghaus 1979; unpubl. data of R. A. Howard and C. Welsh [1982] and of R. A. Howard and C. Hibbard [1983]) provided substantial knowledge of the hewing species present in or near the study area at the time of and immediately following this study. Hairy and Pileated woodpeckers were the most common hewing species and Red-bellied Woodpeckers were occasionally reported. Northern Flickers and Downy Woodpeckers were also common, but they forage most often by means other than hewing (see Conner 1980, 1981). In addition, Bull (1974:349–363) listed the Three-Toed Woodpecker (*P. tridactylus*) and the Black-backed Woodpecker (*P. arcticus*) as very rare, irregular winter visitors in central New York, but these species have not been recorded at the field station.

Among the snag characteristics measured, logistic regression analysis (Hanusheck and Jackson 1977:179–245, Press and Wilson 1978, Harrell 1980) identified the set most strongly ($P < 0.05$) associated with the presence of foraging excavations. Chi-square analyses, with expected frequencies computed from the border totals (Snedecor and Cochran 1967:250–253), aided interpretation of multivariate results.

A preference index (Fig. 1) aided interpretation of results pertaining to dbh. The numerator of this index expressed the excess in the relative use of snags in a dbh class beyond the relative availability of snags in that class; this numerator was Strauss' L (Strauss 1979, Raphael and White 1984:37–38). The denominator of the present index (Fig. 1) weighted Strauss' L by relative availability. This set of L statistics was not independent; therefore, only the logistic regression and chi-square analyses were used for tests of significance.

For clarity in the remaining sections, the paper refers to both roost or nest cavities as "nest cavities" and refers to the associated snags as "nesting snags." One snag may be both a feeding snag and a nesting snag.

RESULTS

All analyses reported herein employed the full sample of 388 snags; 234 snags (60%) had some foraging excavations, and 220 (57%) were elm snags. Elm snags comprised 77% (89 of 116) of the snags in mature forest sites. Elm (89 of 220) and ash (18 of 27) snags were located more often than expected in mature forest sites, while all (64) poplars (*Populus* spp.), all (13) red maples (*A. rubrum*), and nearly all (41 of 42) willows (*Salix* spp.) were in second growth sites ($\chi^2 = 77.59$, $P < 0.005$, 5 df).

The results of chi-square tests of association between the presence of foraging excavations on a snag and various explanatory variables, considered singly, are summarized in Table 1. Foraging excavations probably were not independent of the presence of shelf fungi, dbh, percent of bark remaining, snag species, and the presence of nesting cavities (Table 1).

Based on logistic regression analysis, the probability that a snag had feeding excavations was higher for elm snags, increased with the proportion of bark lost, dbh, degree of canopy closure, and number of limbs, but decreased with snag height (Table 2). Only variables in this logistic regression model were significant ($P < 0.05$) in the multivariate context; however, wood density would have entered the model next (with a neg-

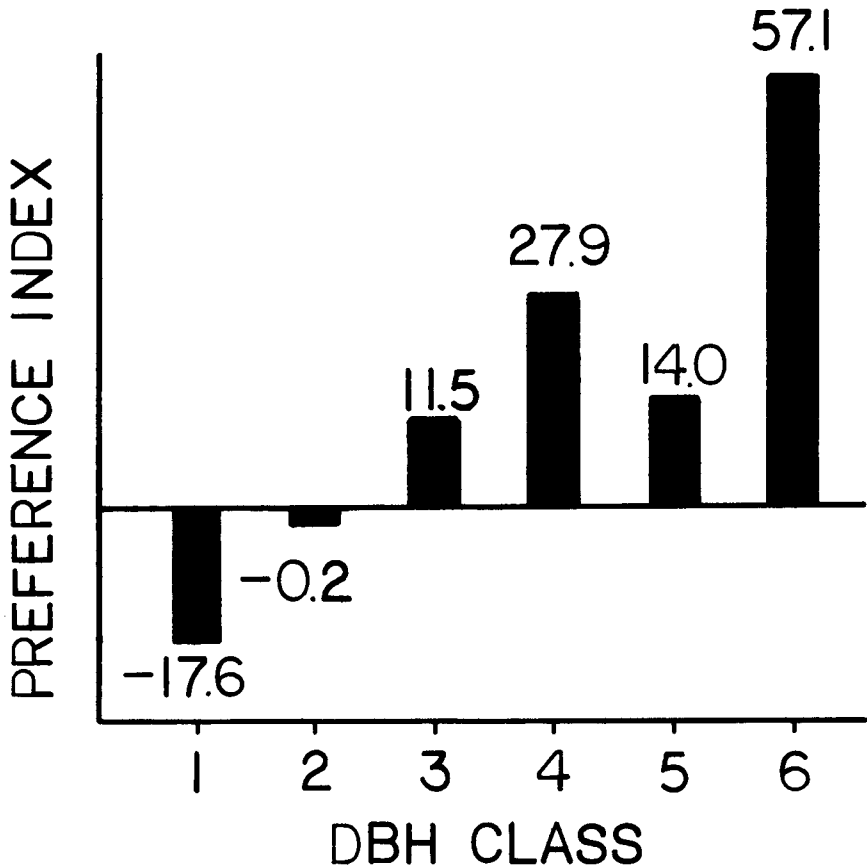


FIG. 1. Preference for snag dbh by foraging woodpeckers. Preference index = $(N \text{ feeding snags in dbh class} / N \text{ feeding snags}) / (N \text{ snags in dbh class} / N \text{ snags}) - 1$. Dbh classes in cm are: 1 = 10.1–15, 2 = 15.1–20, 3 = 20.1–25, 4 = 25.1–30, 5 = 30.1–35, 6 = >35. N for each dbh class is, respectively: 165, 98, 55, 35, 16, 19.

ative coefficient) under a less conservative significance criterion ($P < 0.10$). The logistic regression model (Table 2) correctly classified 74% of feeding snags and 70% of snags without feeding excavations.

Based on the same data set, Swallow et al. (1986:Table 1, Model 2) reported a logistic regression model for nesting snags. Only three variables entered the nesting snag model: dbh, bark cover, and snag height. In both the logistic regression model for feeding snags (Table 2) and the logistic regression model for nesting snags (Swallow et al. 1986:Table 1, Model 2), the coefficients for these variables (dbh, bark cover, and snag height)

TABLE 1
SIGNIFICANCE OF SNAG CHARACTERISTICS AS UNIVARIATE PREDICTORS OF THE
PRESENCE OF FORAGING EXCAVATION ON SNAGS IN CENTRAL NEW YORK

Variable name: levels	Feeding excavations present more often than expected ^a for:
Canopy cover: <25%, 25% to <50%, 50% to <75%, ≥75%	No pattern (2.48, >0.25, 3)
Total height (m): 1.5 m height classes between 1.5 m and 16.5 m (1.5 to 3 m, etc.)	No pattern (8.68, >0.25, 9)
Fungal conks ^b : present or absent	Snags with conks (11.68, <0.005, 1)
Dbh: 5 cm dbh classes between 10.0 cm and ≥35.0 cm ^c	Larger diameter snags ^c (22.90, <0.005, 5)
Dbh: ≤20 cm dbh, >20 cm dbh.	Snags >20 cm dbh (15.29, <0.005, 1)
Bark remaining: <25%, 25% to <50%, 50% to <75%, ≥75%	Snags with <75% of their bark intact (24.28, <0.005, 3)
Snag species: <i>Ulmus</i> spp., <i>Acer rubrum</i> , <i>Fraxinus</i> spp., <i>Populus</i> spp., <i>Salix</i> spp., all others ^d	<i>Ulmus</i> spp. and "other" snags, less than expected for <i>Fraxinus</i> spp. and <i>Populus</i> spp. (72.22, <0.005, 5)
Forest type: second growth or mature	No pattern (1.30, >0.25, 1)
Roosting/nesting cavities: present or absent	Snags with these cavities (5.26, <0.025, 1)

^a Result of chi-square test of variable levels versus presence or absence of foraging excavations. Expected frequency of foraging snags was 0.60 at each level. N = 388. Chi-square test statistic, P, and degrees of freedom in parentheses.

^b External shelf fungi (*Fomes* spp.).

^c See Fig. 1.

^d *Tilia americana*, *Alnus* spp., *Quercus* spp., *Pyrus* spp. were lumped in the "other" category due to small sample size (N < 5).

had the same sign. Notably, an indicator variable for the presence of foraging excavations did not improve ($P > 0.05$) the nesting snag model (after accounting for dbh, bark cover, and snag height); therefore, for the purposes of comparison, the two models were considered statistically independent.

The "logistic regression elasticity" measures the relative contribution of a dependent variable on the probability of bird use for a particular purpose (feeding or nesting). An elasticity measures the percentage change in the probability of bird use, given that a selected independent variable changes by 1%. For example, at the mean value of all independent variables, a 1% increase in dbh raises the probability that a snag contains foraging excavations by 0.19% and raises the probability that a snag contains a nest cavity by 1.3% (Table 3). An increase in snag height or bark coverage has a greater, adverse impact on a snag's probability of use for nesting than on its probability of use for feeding (Table 3).

TABLE 2
LOGISTIC REGRESSION MODEL^a FOR THE PROBABILITY THAT FORAGING EXCAVATIONS
WERE PRESENT ON A SNAG IN CENTRAL NEW YORK

Variable	Mean	Coefficient (SE)	
Intercept	—	0.566	(0.796)
Snag species ^b	0.567	1.01	(0.246)
Bark remaining ^c	3.34	-0.542	(0.150)
Dbh (cm)	19.15	0.0467	(0.0219)
Canopy cover ^c	2.76	0.327	(0.119)
Total height (m)	8.80	-0.00866	(0.00273)
Number of limbs	0.557	0.511	(0.197)

^a The probability that a snag contains feeding excavations = $1/[1 + \exp(-XB)]$ where XB is calculated by taking the product of each coefficient and the value of the corresponding variable, summing these products, and adding the intercept (Hanusheek and Jackson 1977:187-189, Harrell 1980). $P \leq 0.03$ for all variables; nonsignificant intercept retained for completeness; model $P < 0.01$.

^b Coded: *Ulmus* spp. = 1, other species = 0.

^c For the levels in Table 1, coded 1, 2, 3, 4, respectively.

DISCUSSION

The high proportion of snags with foraging excavations reported here (60%) and similar results in the west (Raphael and White 1984:44) indicate that snags can be important foraging sites for several excavating bird species. Relative to excavators, this study makes no attempt to determine whether the snag resource is an essential component of the available dead wood. Such a determination requires data measuring the proportion of foraging effort which birds invest on various sources of dead and live wood relative to the availability of these substrates.

Observations of foraging activity (Kilham 1965, 1976; Conner 1981;

TABLE 3
LOGISTIC REGRESSION ELASTICITIES FOR SNAG VARIABLES PRESENT IN THE FEEDING
SNAG MODEL (TABLE 2) AND IN THE NESTING SNAG MODEL (SWALLOW ET AL.
1986: TABLE 1, MODEL 2)

Variable	Elasticity ^a	
	Feeding model	Nesting model
Dbh (cm)	0.187	1.28
Total height (m)	-0.0159	-0.0882
Bark remaining	-0.378	-1.65

^a The logistic regression elasticity = $X_i(1 - P)B_i$, where P is the probability that a snag contains an excavation of the type corresponding to the model, X_i is the variable of interest, B_i is the corresponding coefficient and, by convention, the calculation employs the variable means (Table 2). In calculus notation, elasticity = $(X_i/P)(dP/dX_i)$ where "d" denotes partial differentiation.

Brawn et al. 1982; Raphael and White 1984:42–43) indicate that large cavity-nesters (e.g., Pileated and Hairy woodpeckers) forage on snags more often by excavation than by gleaning; this observation probably indicates that the present results are biased toward larger species. Furthermore, Kilham (1961, 1965, 1976) reports that Downy and Hairy woodpeckers remove only the outer bark while bark chipping, and that, after removing some bark, Pileated Woodpeckers almost always excavate in newly exposed wood. Thus, foraging behavior would not confound bark cover as an (imprecise) indicator of deterioration. Nevertheless, the present results suggest that, when foraging by excavation, birds select snags with less bark (older snags). Snags with most of their bark intact may still be selected by superficial foragers (Kilham 1965, Brawn et al. 1982, Raphael and White 1984:43–45).

The two broad characteristics considered most important in previous studies (e.g., Cline et al. 1980, Mannan et al. 1980) are snag size and decay-stage. Yet, few variables clearly measured either size or decay-stage. One important example is wood density. Wood density measured wood softness due either to decay or differences in tree species. However, after accounting for all other significant variables, wood density provided no significant ($P > 0.05$) new information; that is, the variables in the logistic regression (Table 2) jointly described wood softness/decay-stage and other critical features of foraging snags better than wood density. This result lends additional support to the discussions below.

Other studies (Mannan et al. 1980, Brawn et al. 1982, Raphael and White 1984) found no preference for foraging on particular snag species. Kilham (1961, 1965, 1970) did document preferences of Hairy and Downy woodpeckers for foraging on elms and paper birches (*Betula papyrifera*); however, Kilham's observations apply only to diseased or "defective" living trees (not snags) and only to superficial foraging methods (not excavation). Since elm snags constituted a high proportion of snags in mature forest sites in the present study, excavators' selection of elm snags may have indicated selection of mature forest sites. Alternatively, since ashes, which were also associated with mature forest sites, were generally young snags (usually with almost all their bark, few or no conks, more often with small branches and twigs intact) and elms were in a more advanced state of decay, the selection of elms may have represented a decay-stage preference. The latter interpretation was consistent with evidence discussed by Swallow et al. (1986) and with the moisture hypothesis discussed below relative to canopy closure.

At first, canopy closure appears unimportant (Table 1). However, after accounting for other characteristics of feeding snags, the results show that canopy closure significantly improves the logistic regression model for

feeding snags (Table 2). This result demonstrates the need to understand the relationship between snags and cavity-nesters in a multivariate context.

The positive association between feeding excavations and canopy closure (Table 2) conformed with several alternative interpretations. Canopy closure could have indicated a preference for snags with some overhead cover, for snags with more advanced decay, or for mature forest sites. Mannan *et al.* (1980) and Brawn *et al.* (1982) found a general tendency for cavity-nesters to feed in older forest plots. This study, however, found no clear evidence of a preference for their foraging in older forest sites (i.e., the forest type variable was insignificant, at $P > 0.05$, in the logistic regression analysis). The “canopy closure indicated decay” interpretation remained most persuasive for two reasons. First, the death of a large tree creates both a snag and a canopy opening; therefore, the degree of canopy closure indexed time since the tree died. Second, a closed canopy (typical of mature sites) possibly created moist conditions which promoted decay. This evidence suggested that canopy closure and the selection of elm snags partially defined a decay-stage preference.

Raphael and White (1984:43–45) reported a discriminant function analysis similar to the logistic regression reported here (Table 2). Their results showed a similar relationship between the presence of feeding excavations and dbh, total height, and deterioration of limbs.

The results in this paper show that as bark loss increases and total height decreases, the probability that a snag contains feeding excavations or nest cavities, or both, increases. These characteristics indicate deterioration of the snag. However, the number of limbs on a snag is inversely associated with decay stage (e.g., Cline *et al.* 1980) and is positively associated with feeding excavations (Table 2). These results support hypotheses (Mannan *et al.* 1980, Brawn *et al.* 1982) that, on average, snags become useful for feeding earlier in the decay process than when snags become useful for nest-cavity sites. Of course the relevant decay stages may differ across bird species.

The positive influence of snag dbh on feeding use (Table 2) indicates that foraging excavators may prefer large snags (especially snags > 20 cm dbh, Table 1 and Fig. 1). Two factors may account for this result: larger snags are likely to supply more prey for a given foraging effort (Raphael and White 1984:53) and both foraging excavators and their prey may encounter larger snags more often. This result underscores the importance of large snags for cavity-nesters (Brawn *et al.* 1982, Raphael and White 1984:53–54). However, future research should address the response of cavity-nesting birds to the distribution of dead wood among snags, dead portions of live trees, and fallen logs.

The dbh-bark-height similarities between feeding snags and nesting snags (i.e., signs on comparable coefficients agree) appeared as a significant univariate association between feeding excavations and nest cavities (Table 1). The presence of nest cavities was not significantly associated with the presence of feeding excavations in the multivariate context. Substantial differences between feeding snags and nesting snags were documented (i.e., relative influences of dbh, height, and bark cover quantified in Table 3 and the relative retention of limbs), yet these snag groups exhibited some similar characteristics.

A snag's suitability for both feeding and nesting depends on its size and decay-stage. Yet, while selecting snags as foraging substrate, woodpeckers appear more tolerant of size and decay-stage variation than they are while selecting snags as nest-cavity substrate; changes in key independent variables affect the probability of nesting use at a rate 4 to 7 times higher than similar changes affect the probability of feeding use (Table 3). This interpretation, however, remains sensitive to the assumption (supported by qualitative field observations) that excavations in a snag imply woodpeckers currently use that snag.

This study did not quantify any relationships between forest structure (e.g., species diversity, age structure) and foraging excavations. The occurrence of feeding excavations in 95% of the sample plots, however, provided some evidence that foraging woodpeckers accepted a broader range of forest structure/age characteristics than was accepted for nest-cavity sites (see Swallow et al. 1986; Conner 1980, 1981).

Although mature forest sites (in middle to late aggradation) may serve as a reservoir of suitable roosting/nesting snags (McComb et al. 1986, Swallow et al. 1986), the results reported here indicate that foraging on snags by woodpeckers extends proportionately into adjacent second growth forests (in early aggradation). Given that excavators may forage at long distances from nest sites (Kilham 1965, 1968, 1970, 1976), this observation is not surprising. Forests of both types supplied foraging substrate. In forest stands which produce suitable snags for both uses (primarily mature sites in this study), snags with similar characteristics may serve as feeding and nesting substrates. In particular, nesting snags may develop by normal decay from foraging snags. Research into snag dynamics and deterioration is clearly indicated, as is further research into forest development, from regenerative disturbances to steady state (see Carey 1983a), and the concomitant spatial and temporal distribution of dead wood.

Recent literature, particularly that which emphasizes nesting substrate, suggests that snags may serve only a minor role in support of cavity-nester populations (Carey 1983b, Carey and Gill 1983, Sedgwick and Knopf 1986). The role of snags may vary depending on a particular forest's

history and ecology, including not only the intensity of competition among snag-using birds, but also the management objectives of man. In some forests, whole, dead trees may prove the most easily managed and most useful form for a given volume of dead wood.

Rather than arbitrarily concentrating on single factors (e.g., habitat for nest cavities), an evaluation of the role of snags should consider the spectrum of services which a snag may supply. An integrated multivariate approach is beneficial in assessing preferences for feeding sites just as in assessing nest-site preferences. Logistic regression appears well suited for this purpose as it captures important ecological complexities but may be applied with relative ease (Brennan et al. 1986, Swallow et al. 1986).

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