

TREE CHARACTERISTICS SELECTED BY WOODPECKERS
FOR FORAGING ON SNAGS AND DECLINING TREES IN
REGENERATING ACADIAN FOREST IN NEW BRUNSWICK

by

Jingyi Zhang

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Supervisor(s): Joe Nocera, PhD, Forestry and Environmental
Management

Examining Board: Meng Gong, PhD, Forestry and Environmental
Management, Chair
John A Kershaw, PhD, Forestry and Environmental
Management
Graham Forbes, PhD, Forestry and Environmental
Management

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ABSTRACT

The value of dead and decaying wood to woodpeckers as breeding substrates is well understood. Many authors have emphasized its positive influence on woodpecker population density. However, many forest management activities including clearcuts, shelterwood cuts and seed tree cuts that result in dense, old stands with reduced snag densities are thought to negatively impact woodpecker populations. Therefore, I conducted a study on the selection of tree-scale characteristics of snags and declining trees for foraging by woodpeckers in regenerating Acadian Forest in New Brunswick to improve knowledge of the foraging habitat requirements of local woodpeckers. I searched for signs of foraging (excavation holes) by woodpeckers on 129 snags and declining trees sampled in 10 linear transects across a section of the University of New Brunswick (UNB) Woodlot. I developed a negative binomial regression model based on the presence or absence of foraging signs. I tested several variables for their influence on the probability of tree choice by woodpeckers for foraging including tree species, diameter at breast height (dbh), fungus coverage, and decay stage. Results showed that woodpeckers selected significantly larger diameter trees for excavation foraging ($z = 3.197$, $p = 0.001$, $\beta = 0.085$). Therefore, retaining large-tree and old-growth forests on site after management operations is essential to the conservation of woodpeckers in New Brunswick.

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1.0 INTRODUCTION

Woodpeckers are an ecologically important avian Order (Piciformes) that occur in practically all types of forest and woodland ecosystems (Winkler and Christie 2010). As primary excavators, woodpeckers play a fundamental role in nest web communities because cavities they excavate may provide shelters and breeding sites to a broad range of avian and mammalian species (Martin and Eadie 1999, Martin et al. 2004). Given their disproportionate influence on the richness and abundance of other species requiring nest cavities to breed or roost through their cavity excavations, woodpeckers are regarded as keystone species and significant ecosystem engineers (Jones et al. 1994, Drapeau et al. 2009, Robles and Martin 2014). In addition, woodpeckers may be especially effective indicators of forest biodiversity and avian diversity because they are highly responsive to habitat changes and they share habitat preferences with many other forest birds (Mikusiński et al. 2001, van der Hoek et al. 2020). Woodpeckers also interact with a number of other organisms, such as wood-rotting fungi. Cavity excavation is time-consuming and laborious, so the presence of fungi and the decay they cause are important factors allowing woodpeckers to do so. Meanwhile, woodpeckers may also be vectors of decay-promoting fungi because the hyphae or spores of the fungi may adhere to their bill or feathers and thus infect the inside of the tree through their cavity excavation process (Jackson and Jackson 2004, Farris et al. 2004). Finally, woodpeckers may effectively control pests either directly by feeding on those insects and their larvae or indirectly by desiccating bark- and wood-boring larvae through flaking and puncturing bark (Hammond and Theimer 2020). Given the crucial roles that

woodpeckers play in forest ecosystems, a better understanding of their ecology, especially foraging ecology, is essential for successful conservation work in managed forest landscapes.

Most woodpecker species feed on insects and other invertebrates that live beneath tree bark and in the wood. However, woodpeckers show significant dietary flexibility, with many species being omnivorous. Their diet includes ants, termites, beetles and their larvae, caterpillars, spiders, other arthropods, bird eggs, nestlings, small rodents, lizards, fruit, nuts, and sap. Each species' diet varies with region and preference.

Woodpeckers forage by: (1) pecking: striking the bark with the bill and removing small pieces of bark; (2) scaling: systematically flaking off bark; (3) excavating: making repeated hard blows into the bark of a tree, resulting in a hole through the bark and often into the cambium or sapwood; and (4) licking: getting sap with the tongue (Villard 1994, Murphy and Lehnhausen 1998, Farris et al. 2004). Excavating is particularly important during winter due to food shortages (Conner 1979). Because woodpeckers excavate cavities for nesting, roosting, or foraging, it is important to discern between those different type of cavities. Nesting and roosting cavities lead into a large chamber and the characteristics and dimensions of these two types of cavities do not differ significantly. However, holes made by foraging woodpeckers differ significantly from nesting or roosting cavities. Foraging cavities are more irregular in shape and tend to appear lighter in color because they usually do not lead to hollow chambers.

Generally, live trees and large dead wood such as snags, stumps, and logs containing high levels of bark and wood boring insects are primary substrates selected by insectivorous woodpeckers for foraging (Flemming et al. 1999, Farris et al. 2002).

Woodpeckers do not only forage on these trees but also drill holes in these trees, creating nesting and roosting areas. Through foraging, nest construction, and roost construction, woodpeckers promote decomposition and nutrient cycling of live trees, decaying trees, and snags. These processes are expedited directly by breaking up sound and decomposed wood and indirectly by exposing the interior wood of trees and snags to insects and fungal infestation (Aubry and Raley 2002, Jackson and Jackson 2004).

Foraging site selection by birds is an important decision that impacts survival, growth, and reproductive success of foragers (Fox et al. 2001), and woodpeckers have evolved criteria for selecting their foraging sites. Many previous studies described the characteristics of foraging habitat for woodpeckers, most focus on the tree-scale, because that is the fundamental level at which woodpeckers obtain food and at which trees are managed. Those studies documented the relationships between woodpecker foraging and tree-scale characteristics in the context of tree structure, condition, location, physiology, and the tree's environment (Hammond and Theimer 2020). Woodpeckers tend to forage on the central part of tree trunks with a relatively moderate-large diameter, particularly if these trees show evidence of wood-boring beetles (Hammond and Theimer 2020).

Snags are standing, dead or dying trees, often missing a top or most of the smaller branches. These trees are important foraging substrates for insectivorous woodpeckers. However, forest practices such as shorter rotations, firewood removal, timber stand improvement, and insect and disease control efforts reduce the number of snags available for woodpeckers, negatively affecting foraging behavior of some woodpeckers and limit the habitat available. It is worth noting that the quality of snags may be more

important than the quantity on the landscape when determining the value of habitat for cavity-nesting wildlife (Bull et al. 1997, Conner et al. 2001, Jackson 1977, Jackson and Jackson 2004). Therefore, understanding the foraging ecology of woodpeckers and their relationships with tree characteristics on a narrower range of localities would improve our ability to develop strategies for sustainable forest management and ecological restoration aiming at improving the habitat supply for woodpeckers and associated species.

The objective of this study is to improve our understanding of the associations between woodpecker foraging excavations and characteristics of snags and declining trees in the Acadian Forest in New Brunswick. I focus this study on species that primarily prey on insects inhabiting bark surfaces and sub-surfaces because forest alterations affecting this insectivorous bark-foraging guild can have cascading effects on other forest wildlife. In New Brunswick, American three-toed woodpecker (*Picoides dorsalis*), Black-backed woodpecker (*P. arcticus*), Downy woodpecker (*Dryobates pubescens*), Hairy woodpecker (*D. villosus*), and Pileated woodpecker (*Dryocopus pileatus*) are the commonest species in that guild. I predicted that tree species, tree diameter, fungus coverage, and decay stage are important characteristics determining the selection of foraging substrates.

2.0 METHODS

2.1 Study Sites

I conducted this study in the University of New Brunswick (UNB) Woodlot, Fredericton, New Brunswick, Canada. The UNB Woodlot is over 1,500 ha of woods and wetlands, providing several forest habitats typical of the Acadian Forest region for a variety of wildlife species.

The Acadian Forest Region covers most of the Maritime provinces (Nova Scotia, New Brunswick, and Prince Edward Island) of Canada. It is where the northern Boreal Forest and the Southern Deciduous Forest meet and mix, resulting in a mix of hardwood and softwood tree species. Within this unique habitat, the productive soils and cool climate support a diversity of wildlife and unique plant communities. However, much of the Acadian Forest has been destroyed or altered by forest removal for agriculture, past forest management, and current clearcutting practices. Trees in the present Acadian Forest are much younger and smaller on average than they would have originally been. As well, the abundances of tree species have changed. Tree species such as balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*) and tamarack (*Larix laricina*) are more abundant, while red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), cedar (*Picea glauca*) and sugar maple (*Acer saccharum*) have decreased in abundance and distribution (Simpson 2008). The forest type at today's UNB Woodlot reflects these dynamics and has experienced intensive harvesting in recent years, as such it is better described as a *regenerating* Acadian Forest.

2.2 Foraging Tree Inventory

Fieldwork was carried out during the summer of 2020. I drew 10 linear transects across a section of the woodlot that represented a cross-section of the available habitat types (Figure 1) and conducted inventories of trees excavated by woodpeckers in search of prey (foraging trees). Foraging sign was indicated by a large, often rectangular excavation in the sapwood and/or the heartwood of snags. I inspected all snags and declining trees (129 in total) on the transects to quantify the amount of foraging sign (number of excavation holes) present and recorded tree species, diameter at breast height (dbh), fungus coverage, and decay class. Decay classes were determined according to Thomas et al.'s (1979) decay classification scheme, which recognizes nine classes for trees and snags (Figure 2). Because excavation is highly visible on trees, I am confident most foraging sign was detected within the surveyed areas.



Figure 1. Woodpecker foraging tree inventory study sites in UNB woodlot, Fredericton, New Brunswick, Canada.

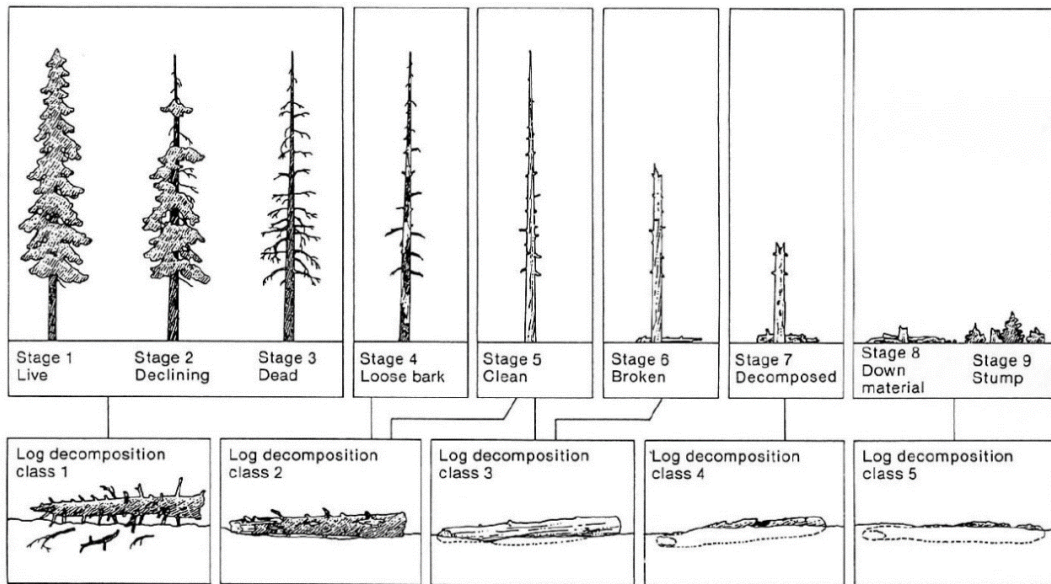


Figure 2. Visual representation of Thomas et al.'s (1979) decay classification system for snags and logs.

2.3 Statistical Analysis

Counts of individuals are one of the most common types of data used in ecological studies when temporal and/or spatial patterns of abundance are examined (Lindén and Mäntyniemi 2011). The distribution of counts is discrete, not continuous, and is limited to non-negative values. Count variables are usually positively skewed, with most values being low and relatively few values being high (Cameron and Trivedi 2013). The most common type of distribution for count variables is a Poisson distribution, assuming that the mean and variance of the variable are equal. However, count variables sometimes do not meet this assumption in practice, especially when there are more zeros or more high values than expected. This is called overdispersion and it occurs when a variable's variance is much larger than its mean. A good way of incorporating overdispersion is by using a negative binomial (NB) regression (Beaujean and Grant 2016). NB regression

can be considered a generalization of Poisson regression since it has the same mean structure as Poisson regression, and it has an extra parameter to model the over-dispersion. If the conditional distribution of the outcome variable is over-dispersed, the confidence intervals for the NB regression are likely to be wider than those from a Poisson regression model.

The data collected in this study were tree characteristics from 129 snags and declining trees. I retained all forest classifications and the nine decay classes in the analysis, rather than reducing them to collapsed categories, to avoid inflating the Type II error rate through sacrificial pseudoreplication (Hurlbert 1984). The response variable is the number of foraging holes excavated by woodpeckers on each tree (holes), from which I seek to define its relationship with 4 explanatory variables: tree species (`tree_species`), tree dbh (diameter at breast height), the percent fungi cover on a tree (`fungus_coverage`), and tree decay class (`decay_class`). As a first step, I examined the distribution of the response variable and determined that the mean is not equal to the variance. Therefore, I used a NB model to account for overdispersion in the count data and to reduce the effect of excess zeroes. I did not explicitly account for excess zeroes by including a zero-inflation term, as this would reduce model sensitivity to over-dispersion which is a greater risk in model interpretation. A comparison of NB and zero-inflated NB models can be made in future research. I therefore fitted a generalized linear model with a log link and negative binomial errors ($\alpha = 0.05$ for all analyses) using R v. 3.6.2 (R Development Core Team 2019) to analyze selection for different foraging substrates as a function of their characteristics (all R code used in these analyses is presented in Appendix A). To select the final model, I used a stepwise reverse selection

procedure. Non-significant (z-test; $P > 0.05$) parameter estimates were sequentially dropped.

3.0 RESULTS

Negative binomial regression analysis showed that tree diameter was the sole significant ($z = 3.197$, $p = 0.001$) predictor for the presence of woodpecker foraging excavations. The relationship was positive ($\beta = 0.085$); i.e., larger diameter trees were more likely to have excavations (Figure 3). For each one unit increase in diameter, the expected log count of the number of woodpecker foraging holes increases by 0.085, while holding the other variables in the model constant.

The remaining independent variables I assessed were not statistically significant. Fungus coverage showed the smallest parameter estimates ($z = 0.00$, $p = 1.00$) and was the first variable removed. Decay class, a categorical variable, was the second variable removed (worst parameter estimates: $z = -0.271$, $p = 0.787$ for decay class 4). The final variable removed was the categorical variable of tree species (worst parameter estimates: $z = 0.00$, $p = 1.00$ for white birch).

There were some indications of a potential negative relationship with white pine. In the penultimate model, the parameter estimates were significant ($z = -2.106$, $p = 0.035$). However, this relationship became insignificant in the final model ($z = -1.169$, $p = 0.243$).

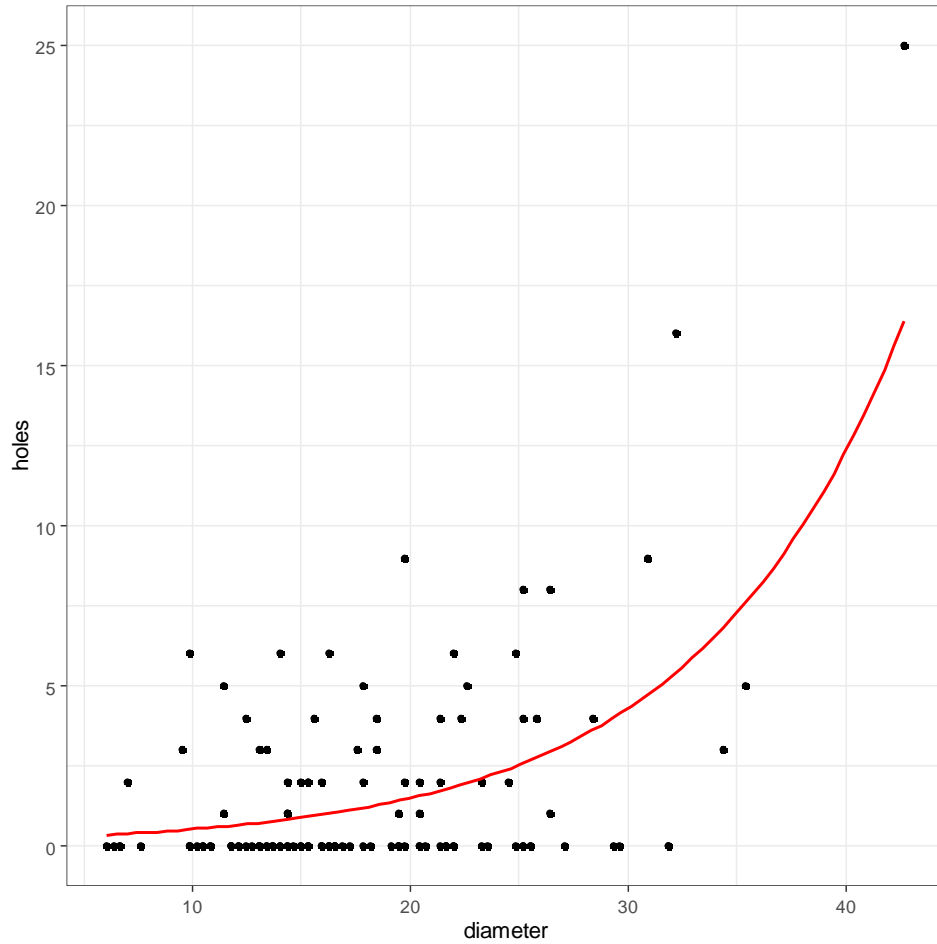


Figure 3. Relationship between abundance of woodpecker foraging holes and the diameter at breast height (dbh) of trees in which those holes were found. To present the response variable (holes) as continuous, and to illustrate the abundance of zeroes in the data, the geometric curvilinear trendline is fitted as Poisson (whereas analytical models were fitted as negative binomial).

4.0 DISCUSSION

I found that dbh was the most important factor influencing substrate selection by woodpeckers. Woodpeckers selected significantly larger diameter trees for excavation foraging in a second-growth forest (a regenerating Acadian Forest) in New Brunswick. This is consistent with results obtained in other studies. For example, Flemming et al. (1999) found that Pileated Woodpeckers commonly used larger, more decayed trees than were randomly available for excavation foraging in southern New Brunswick. In the boreal forest, Villard (1994) found that Black-backed Woodpeckers focused excavation activity at the base of large-diameter tree trunks. Such results were replicated in other studies and bioregions (e.g., Mannan et al. 1980, Brawn et al. 1982, Rosenberg et al. 1988, Jones and Hunt 1996, Doyon et al. 1999, Gunn and Hagan III 2000), even across stands that were altered by tree removal, wildfire, and prescribed burn (Hammond and Theimer 2020).

It is possible that woodpeckers focus more excavation on bigger trees because larger trees have greater structural diversity and surface area capable of supporting larger insect populations (i.e., larger trees host more arthropods). For example, Renken and Wiggers (1989) and Lemaître and Villard (2005) suggested larger trees are preferred for foraging by Pileated Woodpeckers because of the greater potential for high densities of carpenter ants (*Camponotus* spp.). Lemaître and Villard (2005) suggest that this pattern is a function of the ants choosing larger trees for greater nest stability. Nest stability for carpenter ants is greater in hardwood trees and lesser in softwood trees because most currently available coniferous substrates are too young for carpenter ants to invade their boles due to harvesting (Flemming et al. 1999, Lemaître and Villard

2005). Trees with large dbh are generally more mature, therefore they could provide enough space and conditions for insects and attract feeding woodpeckers.

The selection of snags and declining trees with larger dbh may be because these trees are more likely to be closer to death, and therefore more decayed and softer than smaller trees. A study of Pileated Woodpecker ecology in southern New Brunswick documented a strong preference for older forests for foraging (Flemming et al., 1999). Trees with softer wood may minimize the time and energy spent excavating for food, resulting in a woodpecker's tree selection. Two studies showed that woodpeckers foraged more at trees, or locations within trees, that were softer (Conner et al. 1994, Farris et al. 2004). In addition, decomposition may increase the suitability of wood substrates for colonizing fungi and epiphytes, thus enhancing the trunk as an environment for arthropods and woodpeckers. Indeed, previous studies have found that woodpeckers preferred snags with a larger diameter and a lower decay class (Imbeau 2002, Nappi et al. 2003, Raley and Aubry 2006, Gagné et al. 2007; *cf.* Swallow et al., 1988; Doyon et al., 1999; Flemming et al., 1999; Holloway et al., 2007).

Finally, larger diameter trees persist longer than smaller ones, and therefore would have had a longer time period for decay to occur and woodpeckers to forage on them, which could explain why I detected a relationship with tree size. However, it is worth noting that because the total number of foraging excavations on a tree should increase over time, excavation-generated estimates could reflect the amount of time trees were available as foraging substrates rather than greater use of trees due to their condition at the time of sampling (Hammond and Theimer 2020). Hence, measuring woodpecker tree

use through excavation counts should be done with caution, and perhaps avoided unless researchers can tell the difference between new and old signs.

Although my results are generally consistent with the literature, they should be interpreted with a modicum of caution. Firstly, the relatively small dbh of the trees recorded represents a skewness in the data that influenced results. I found that the average tree dbh was only 17.74 cm, which means that there were no really large trees to sample at the study site in UNB woodlot. The presence of large diameter trees would have provided a wider range of tree dbh and the results would have been more representative and probably different from the results obtained in this experiment. Secondly, the positive correlation between tree dbh and woodpecker foraging excavations should be described in a more rigorous way. Hammond and Theimer (2020) have mentioned that 38 of 44 papers they reviewed evaluating dbh suggested woodpeckers foraged on relatively moderate-large substrates. In those papers, when authors reported their evaluations of selection across the full range of available trees in well-defined, small categories (e.g., trees binned into 5–20 cm classes), they discovered that selection for foraging trees generally began at a diameter of 20–25 cm dbh, and that trees in the upper 10% of the diameter distribution were used disproportionate to their availability. Therefore, the conclusion that the number of excavation foraging holes increases as the diameter of the tree increases at breast height should be valid only within a certain range. Thirdly, the conclusion that woodpeckers focus more excavation on relatively large dbh trees may only be applied to several woodpecker species. Woodpecker foraging tree use was estimated based on counts of excavations on trees in this study. However, American three-toed woodpeckers, Black-backed woodpeckers and

Downy woodpeckers generally do not drill holes as they forage, instead they probe for insects by pecking or scaling off the bark. Excavating into wood in pursuit of insects is primarily a form of foraging behavior for Hairy woodpeckers and Pileated woodpeckers in New Brunswick. Therefore, most of the foraging signs recorded on the transects should have been left by Hairy woodpeckers and Pileated woodpeckers. In this way, the conclusions drawn in this experiment may only represent the foraging preference of these two woodpecker species rather than all insectivorous woodpeckers in New Brunswick.

It is somewhat surprising that the relationship between tree species and the presence of woodpecker foraging excavations was insignificant in my study. However, previous studies have reported that woodpeckers do have foraging preference for certain tree species, although both preferred and available species vary greatly among study regions. For example, Flemming et al. (1999) found that Pileated Woodpeckers in southern New Brunswick preferred red spruce and balsam fir for excavation foraging. Villard (1994) found that Black-backed and Three-toed Woodpeckers in the boreal forest of Manitoba foraged almost exclusively on coniferous tree species, primarily on spruce and less on tamarack (*Larix laricina*) and jack pine (*Pinus banksiana*). The preference for coniferous tree species could be explainable by the fact that the bark on those trees loosens relatively rapidly once the tree is dead (Lambert et al. 1980, Foster and Lang 1982) and the wood was softer than most hardwood species. Therefore, the wood of coniferous tree species may be easier and more efficient for both woodpeckers and their prey to excavate. Woodpeckers also used deciduous species as foraging substrate. For example, oaks (*Quercus* spp.) are preferred foraging sites by woodpeckers

across a wide range of timber types and geographical regions (Williams and Batzli 1979, Conner 1980, Nicolai 1986, Conner et al. 1994, Pasinelli and Hegelbach 1997). The possible reason is that the bark of oaks is deeply fissured and therefore likely to host a more abundant arthropod community.

Woodpeckers foraging on both live and dead trees may prefer tree species with rough bark texture and avoid tree species with smooth bark (Conner et al. 1994). An abundant supply of arthropods is the most probable reason for their preference (Southwood 1961, Nicolai 1986, Pasinelli and Hegelbach 1997). As it is more difficult for woodpeckers to cling to smooth bark, rough-barked trees probably facilitate locomotion due to the ladder-like function of the horizontal ridges (Jackson 1979), which could thus be an additional reason for preferring them.

In my observation, woodpecker foraging excavation tended to not occur in white pine, although the potential relationship was not statistically significant in the final model. The possible/slight aversion to white pine may be related to the oleoresin it produces. The pine tree's natural defense mechanism is its ability to "pitch out" invading pests by increasing its sap or oleoresin flow. One study found that woodpeckers used trees more when they produced little oleoresin, with the authors suggesting that birds may avoid oleoresin because it is a nuisance (Bergvinson and Borden, 1992). However, a formal analysis of the relationship was not conducted, and we need more research and data to support it.

No significant relationship was found between fungus coverage and the presence of woodpecker foraging excavations in this study. However, the interrelationships between woodpeckers and fungi are close and complex. Farris and Zack (2005) suggest that

woodpeckers may influence snag decomposition through their foraging behavior that can structurally degrade the wood and passively introduce the wood decaying fungi required for subsequent nest cavity excavation. Fungal fruit-bodies (also known as “bracket fungi”, “shelf fungi”, or “conks”) may not occur until the tree is substantially heart-rotted, so trees covered with fungus are generally of a high decay grade and the wood is already very soft. This provides invasion opportunities for arthropods and optimal excavation conditions for woodpeckers (Jackson and Jackson 2004). Additionally, many decay-inducing fungi can produce volatile organic compounds which can attract insects to inhabit that tree (Raffa and Smalley 1995), thus providing a food source for woodpeckers.

As mentioned, tree diameter is probably the most useful tree characteristic for effective management of forests used for foraging by woodpeckers across species and habitats. My findings highlight the potential importance of retaining relatively large and old-growth forests in supporting sustainable woodpecker populations, since woodpeckers are likely to require a constant supply of recently deceased snags as feeding substrates. Preserving moderate to large diameter trees would not only help create better quality foraging habitat for the insectivorous bark-foraging woodpeckers but would also provide good nesting and roosting conditions for many woodpecker species. Previous studies suggested that management recommendations on other aspects of tree-scale foraging ecology (e.g., tree species, tree condition) varied by woodpecker species and habitat, so managers should prioritize local knowledge of woodpecker foraging ecology and learn from the results of management in other areas with similar ecological conditions to the local area (Hammond and Theimer 2020). Therefore, I

suggest that conservation strategies for woodpeckers in New Brunswick should consider retaining large-treed and old-growth forests and creating more fresh dying trees and dead wood of different tree species to maintain a natural composition of tree species, which will not only benefit woodpeckers but many other wildlife also dependent on older forests.

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APPENDIX A

R Code

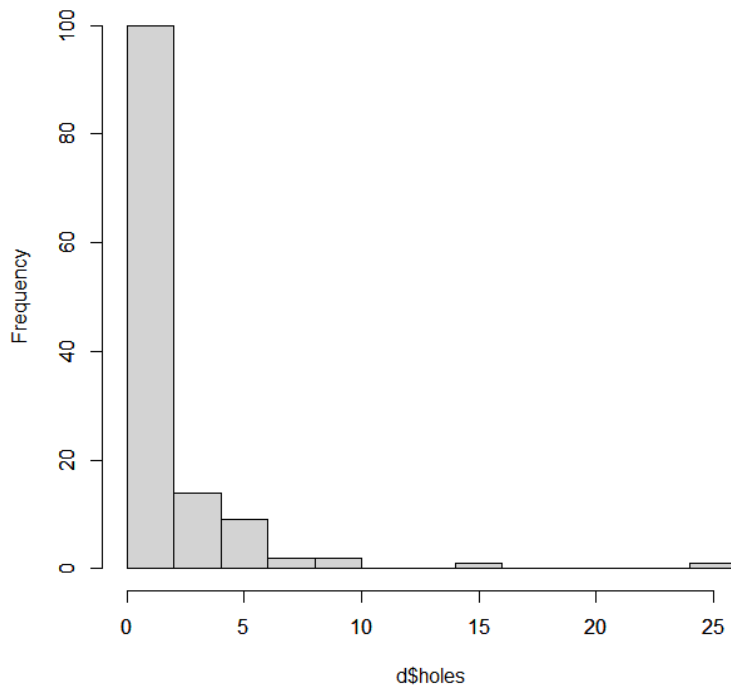
```
> d <- read.csv("Foraging trees.csv", stringsAsFactors = FALSE)
> d$tree_species <- as.factor(d$tree_species)
> d$decay_class <- as.factor(d$decay_class)
> summary(d)
```

holes	fungus_coverage	tree_species
Min. : 0.000	Min. :0.000000	BalsamFir :62
1st Qu.: 0.000	1st Qu.:0.000000	BlackAsh : 1
Median : 0.000	Median :0.000000	Cedar :26
Mean : 1.589	Mean :0.009767	RedMaple : 4
3rd Qu.: 2.000	3rd Qu.:0.000000	whiteBirch : 5
Max. :25.000	Max. :0.500000	whitePine :24
		whiteSpruce: 7

decay_class	diameter
2:16	Min. : 6.05
3:45	1st Qu.:13.06
4:40	Median :16.24
5: 5	Mean :17.74
6:17	3rd Qu.:21.66
7: 6	Max. :42.68

```
> hist(d$holes)
```

Histogram of d\$holes



```
> mean(d$holes);var(d$holes)
```

```
[1] 1.589147
```

```
[1] 10.63457
```

```
> var(d$holes)/mean(d$holes)
```

```
[1] 6.691997
```

Sample mean = 1.59, Sample variance = 10.63, the variance is almost 7 times bigger than the mean, which suggests that overdispersion is present and that a negative binomial model would be appropriate.

Below we use the glm.nb function from the MASS package to estimate a negative binomial regression.

```
> library(MASS)
```

```
> model.nb <- glm.nb(holes~fungus_coverage+tree_species+decay_class+diameter,data=d)
```

Warning message:

```
glm.fit: fitted rates numerically 0 occurred
```

```
> summary(model.nb)
```

```
Call:
```

```
glm.nb(formula = holes ~ fungus_coverage + tree_species + decay_class  
+
```

```
  diameter, data = d, init.theta = 0.4083456843, link = log)
```

```
Deviance Residuals:
```

```
      Min       1Q   Median       3Q      Max  
-1.4649 -1.0212 -0.8145  0.1280  1.6190
```

```
Coefficients:
```

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.328e+00	7.361e-01	-1.804	0.07127 .
fungus_coverage	-2.368e+03	2.034e+07	0.000	0.99991
tree_speciesBlackAsh	-2.623e-01	1.802e+00	-0.146	0.88428
tree_speciesCedar	-1.051e-01	4.619e-01	-0.228	0.82002
tree_speciesRedMaple	-7.300e-01	1.140e+00	-0.640	0.52191
tree_speciesWhiteBirch	-3.127e+01	3.098e+06	0.000	0.99999
tree_speciesWhitePine	-9.396e-01	4.941e-01	-1.902	0.05723 .
tree_speciesWhiteSpruce	1.418e-01	7.077e-01	0.200	0.84119
decay_class3	3.807e-01	5.607e-01	0.679	0.49711
decay_class4	-2.054e-01	6.116e-01	-0.336	0.73704
decay_class5	1.249e+00	9.489e-01	1.316	0.18821
decay_class6	4.755e-01	7.342e-01	0.648	0.51716
decay_class7	1.184e+00	8.847e-01	1.338	0.18074
diameter	8.471e-02	2.586e-02	3.276	0.00105 **

```
---
```

```
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
(Dispersion parameter for Negative Binomial(0.4083) family taken to be  
1)
```

```
Null deviance: 139.74  on 128  degrees of freedom
```

```
Residual deviance: 100.96  on 115  degrees of freedom
```

```
AIC: 395.74
```


Number of Fisher Scoring iterations: 1

Theta: 0.408

Std. Err.: 0.100

2 x log-likelihood: -365.743

The model above gave a warning message. That problem comes from the extremely poor fit of the fungus variable (z value is near zero). So I remove that variable and build again.

```
> model.nb <- glm.nb(holes~tree_species+decay_class+diameter,data=d)
```

```
> summary(model.nb)
```

Call:

```
glm.nb(formula = holes ~ tree_species + decay_class + diameter,  
       data = d, init.theta = 0.3817293547, link = log)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.4385	-1.0073	-0.8193	0.1792	1.6882

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.427e+00	7.554e-01	-1.889	0.05889 .
tree_speciesBlackAsh	-2.617e-01	1.849e+00	-0.142	0.88744
tree_speciesCedar	-6.180e-02	4.711e-01	-0.131	0.89562
tree_speciesRedMaple	-9.360e-01	1.078e+00	-0.868	0.38531
tree_speciesWhiteBirch	-3.687e+01	3.001e+07	0.000	1.00000
tree_speciesWhitePine	-1.046e+00	4.968e-01	-2.106	0.03519 *
tree_speciesWhiteSpruce	1.825e-01	7.254e-01	0.252	0.80133
decay_class3	3.439e-01	5.758e-01	0.597	0.55035
decay_class4	-1.701e-01	6.286e-01	-0.271	0.78670
decay_class5	1.405e+00	9.747e-01	1.441	0.14952
decay_class6	5.165e-01	7.432e-01	0.695	0.48707
decay_class7	1.327e+00	9.108e-01	1.457	0.14504
diameter	8.741e-02	2.658e-02	3.288	0.00101 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for Negative Binomial(0.3817) family taken to be 1)

Null deviance: 134.30 on 128 degrees of freedom
Residual deviance: 102.37 on 116 degrees of freedom
AIC: 398.91
Number of Fisher Scoring iterations: 1

Theta: 0.3817

Std. Err.: 0.0927

2 x log-likelihood: -370.9060

This time no warning, so it was fungus that created the warning.
However, in this model, the variable "decay class" is not helping the model at all, so I remove that and build again.

```
> model.nb <- glm.nb(holes~tree_species+diameter,data=d)
> summary(model.nb)
```

Call:

```
glm.nb(formula = holes ~ tree_species + diameter, data = d, init.theta
= 0.3469390151,
link = log)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.3242	-1.0076	-0.8778	0.1933	1.8654

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.139e+00	5.129e-01	-2.220	0.02642 *
tree_speciesBlackAsh	1.353e-02	1.859e+00	0.007	0.99419
tree_speciesCedar	-8.087e-02	4.580e-01	-0.177	0.85984
tree_speciesRedMaple	-7.657e-01	1.049e+00	-0.730	0.46537
tree_speciesWhiteBirch	-3.688e+01	2.970e+07	0.000	1.00000
tree_speciesWhitePine	-5.656e-01	4.839e-01	-1.169	0.24248
tree_speciesWhiteSpruce	-1.802e-02	7.519e-01	-0.024	0.98088

diameter 8.521e-02 2.665e-02 3.197 0.00139 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Negative Binomial(0.3469) family taken to be 1)

Null deviance: 126.84 on 128 degrees of freedom

Residual deviance: 102.34 on 121 degrees of freedom

AIC: 394.31

Number of Fisher Scoring iterations: 1

Theta: 0.3469

Std. Err.: 0.0829

2 x log-likelihood: -376.3070

In this model, only "diameter" variable is significant. The relationship with diameter is strongly positive (bigger trees = more holes)

CURRICULUM VITAE or CV

Candidate's full name: Jingyi Zhang

Universities attended (with dates and degrees obtained): Bachelor of Forestry, Nanjing Forestry University, 2019

Publications: None

Conference Presentations: None