FOREST INVENTORY ATTRIBUTES PREDICT THE PRESENCE OF CAVITIES SUITABLE FOR NESTING BY WOOD DUCKS

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SUMMARY OF FINDINGS

Secondary cavity-nesting birds such as waterfowl and raptors rely on tree cavities developed principally through decay and damage processes or excavation by woodpeckers. Forest and wildlife managers are tasked with maintaining and producing these essential habitat components through forest management practices. Generating predictions about where cavities have developed based on commonly collected forest-inventory data would aid in the conservation of important bird species. Wood ducks (*Aix sponsa*) are a common and well-studied example, though until recently, population-management efforts have primarily focused on artificial nesting structures as opposed to influencing forest-management decisions. We measured and inspected 7,869 trees and 1,186 potential cavities to determine their suitability for use by nesting wood ducks in forests of north-central Minnesota during 2016-2018. Fifteen logistic regression models using tree- and stand-level forest attributes were compared and tested for their utility in predicting whether trees had developed suitable cavities. Our top model was additive and included 3 tree-level predictors: diameter at breast height (DBH), health status, and species. We also found some support for including an interaction between DBH and health status, but it was not in our top model. The top model predicted whether trees had suitable cavities well, with an average area under the receiver-operating-characteristic curve of 0.85. For every 1cm increase in DBH, the odds that a given tree would have a suitable cavity increased by 7.3% (95% CI; 6.0-8.7%). Dead and declining trees were more likely to have suitable cavities than live-healthy trees, with 834% (483-1420%) and 477% (276-807%) higher odds, respectively. When comparing 7 common deciduous species with cavities, sugar maple (*Acer saccharum*) and American basswood (*Tilia americana*) were most likely to have developed cavities. These results can be applied to existing forest-inventory datasets to predict the availability of cavities in the landscape and to maximize conservation benefits for wood ducks and other large-bodied secondary cavity-nesting species.

INTRODUCTION

Conservation of cavity-nesting bird populations depends on diverse cavity excavator communities, but also knowledge of the decay and damage processes associated with both excavated and non-excavated cavities (Wesołowski 2012, van der Hoek et al. 2017, Edworthy et al. 2018). Forest attributes such as tree size and decay class are often linked to these processes (Fan et al. 2003*b*, Gutzat and Dormann 2018). Identifying the forest characteristics associated with cavity formation is particularly important for the conservation of large secondary cavity-nesting species (e.g., waterfowl, raptors), which rely on previously formed cavities that only develop through tree decay and damage or excavation by 1 or 2 woodpecker species (Martin et al. 2004, Cockle et al. 2011).

Wood ducks (*Aix sponsa*) are among the most studied large secondary cavity-nesting species (Bellrose and Holm 1994, Hepp and Bellrose 1995). Although much research and management has focused on artificial nesting structures for this species, recognition that natural cavities are used by most of the population (Bellrose 1990) has led to increased research on use (Robb and Bookhout 1995, Ryan et al. 1998, Yetter et al. 1999, Roy Nielsen and Gates 2007) and availability of natural cavities (Zwicker 1999; Nielsen et al. 2007; Denton et al. 2012*a*, *b*). Most studies have been conducted in east-central USA, often in bottomlands and floodplain forests. However, northern portions of the western Great Lakes states, northern Wisconsin and most of Minnesota, have received relatively little research on natural cavities, despite including portions of the most productive wood duck breeding habitat (Soulliere et al. 2007, Sauer et al. 2017; *but see* Nagel 1969, Gilmer et al. 1978).

Forest attributes associated with the formation of suitable nesting cavities for wood ducks have primarily included tree species and diameter at breast height (DBH) (Bellrose and Holm 1994, Nielsen et al. 2007, Denton et al. 2012*a*). However, broader studies of cavities have also identified tree health status, stand-level variables such as stand age and site productivity, as well as potential interactions between these variables as being important predictors of the occurrence of cavities (Carey 1983; Fan et al. 2003*a*, *b*; Larrieu and Cabanettes 2012). Data on these characteristics are collected during most routine forest inventories and hence can be used to predict the presence or abundance of cavities and provide information to guide forest-management decisions at both stand and regional scales (Fan et al. 2003*b*, Denton et al. 2012*b*, Gutzat and Dormann 2018).

Cavities and associated forest-structural elements like snags are increasingly being considered during forest-management activities. For example, some agencies provide timber-harvest regulations or guidelines specifically targeted at retaining cavities or promoting conditions associated with cavity development (e.g., Minnesota Forest Resources Council 2012). However, specific quantitative measures of forest attributes related to cavity formation are lacking for most secondary cavity-nesting species, including wood ducks. Models that predict cavity occurrence with these standard forest metrics would help managers determine the effects of forest management and target management activities for these species.

In this study, we assessed the utility of selected forest attributes for predicting the occurrence of suitable wood duck nesting cavities in north-central Minnesota. Our primary objectives were to 1) describe the physical characteristics of cavities available for use by wood ducks in this region and 2) compare and validate statistical models based on commonly collected tree and stand-level forest attributes for predicting whether trees have suitable cavities. This information will be useful for forest and wildlife managers tasked with conserving wood ducks and other large-bodied cavity-nesting birds.

METHODS

Study Area

The study was conducted on a 254,000 ha site in northeastern Cass County, Minnesota, USA (47˚N 94˚W; Figure 1) during 2016-2018. The landscape is dominated by forest, with interspersed wetlands, lakes, and small municipalities. Forest types are diverse due to the proximity of the boreal forest to the north and east and the prairie-forest boundary to the south and west (Aaseng et al. 2011). Portions of 3 ecological units occur within the study area: Chippewa Plains, Pine Moraines-Outwash Plains, and St. Louis Moraines (Hanson and Hargrave 1996). The most common forest cover-types are aspen (*Populus* spp), upland pine, northern hardwoods, lowland conifer, lowland hardwoods, and oak (*Quercus* spp). Ownership is largely public, covering 82% of the study area.

Forest Stand and Plot Selection

We focused sampling efforts on publically owned lands with geo-referenced forest-inventory databases. Data from Cass County, State of Minnesota, and United States Department of

Agriculture (USDA) Forest Service were combined by categorizing similar cover types into 6 basic forest-types: aspen-birch, lowland hardwoods, upland conifer, northern hardwoods, oak, and other. 'Other' largely consisted of non-forest lands (e.g., brush, grassland, and wetland) and lowland-conifer forests, which likely has few or no cavities that can be used by wood ducks (Soulliere 1990, Clugston 1999, Vaillancourt et al. 2009).

Within the 5 general forest types, we used estimates of stand age to further eliminate stands unlikely to have trees large enough to produce cavities suitable for use by wood ducks. In a nearby study site, Gilmer et al. (1978) indicated that aspen forests >60 years old and northern hardwoods stands >100 years old were most likely to produce cavities used by wood ducks. To ensure we captured the breadth of stands producing trees with potential cavities, we eliminated aspen-birch stands <50 years old and stands of all other types <80 years old. Nearly 7,000 stands met these criteria (22% of public lands). We then randomly selected 60 stands of each forest type for possible cavity sampling.

We randomly placed 1 or 2 0.126-ha (20-m radius) plots in each stand with the stipulation that plots were >50 m apart and >30 m from the nearest stand boundary. Small stands or those with narrow and irregular shapes could often only accommodate 1 plot. Where appropriate, we used ground reconnaissance to adjust the location of plots to be more representative of forest structure (e.g., plots located near ecotones that were not identified in available GIS layers were moved into the stand interior). We attempted to visit all stands and plots, but some were dropped due to accessibility issues, cultural heritage sites, timber harvesting, or improper cover types (e.g., after ground reconnaissance). In addition, we sampled fewer upland conifer and lowland hardwoods stands when compared to other types due to limited numbers of cavities. The random points were placed using 'genstratrandompnts' in Geospatial Modelling Environment (Beyer 2012).

Forest Plot Sampling

Tree surveys

Plots were surveyed in leaf-off conditions during late-fall through early spring to ensure adequate detection of cavities in the tree canopy (Denton et al. 2012*a*). At each plot we classified the general forest type based on dominant and codominant trees. In addition, we measured all trees large enough to potentially develop cavities used by nesting wood ducks (≥22cm DBH; Haramis 1975) and tall enough for DBH to be measured (≥1.37 m). For each tree, we recorded species, DBH (0.1cm increments) and health status. Health status codes included 7 categories along a continuum from live-healthy to dead-decomposing trees (Thomas et al. 1979): 1) Healthy live trees with no defects that will threaten its long-term health, 2) live trees with defects that suggest a decline in health (defects include dead limbs, decay on the bole, and the presence of fungi), 3) recently dead trees with bark, limbs, and twigs largely intact, 4) dead trees that have lost some limbs and almost all twigs, 5) dead trees that have lost most limbs and all twigs, 6) dead trees with broken tops and bole wood that is hard, and 7) dead trees with broken tops and bole wood that is soft. Trees with their center beyond the edge of the 20-m radius plots were not measured (e.g., 41-cm DBH tree 19.8 m from plot center). We followed established Forest Inventory and Analysis (FIA) protocols for determining when to delineate an individual stem as a tree to be sampled (e.g., forking trees) and where to measure DBH (e.g., leaning trees; U.S. Department of Agriculture Forest Service 2014).

Cavity surveys

At each tree, 2 to 4 observers used binoculars to conduct a preliminary ground-search for cavities that were potentially suitable for nesting by wood ducks. Depending on the size and height of a given tree, observers circled the tree, stopping frequently to look for cavity entrances and ensuring that all portions of the tree had been examined. During this initial search, we used the minimum entrance dimensions used by a nesting wood duck (6 X 6 cm; Zwicker 1999, Denton et al. 2012*a*) and minimum height of cavity entrance (0.6 m; Strom 1969) to identify all potential cavities to further assess with a camera system. Since observers could not explicitly measure the entrance dimensions at this point in the survey, they were conservative and documented any cavity entrance or similar situation that could potentially meet minimum dimensions and lead to a suitable cavity, including blind spots on tree branches and splits that could not be adequately observed from the ground. We did not formally estimate cavity detectability; with similar minimum entrance dimensions and leaf-off conditions Denton et al. (2012*a*) reported a 98-100% detection rate with ground surveys under similar conditions.

At each potentially suitable cavity, we used a Pyle Model PLCM22IR camera attached via braided wire to a 15.2 m Crain CMR Series telescoping pole (*sensu* Waldstein 2012) to perform a more thorough examination of the entrance and interior of the cavity. We used a handheld tablet to view the camera feed from the ground. We first determined whether cavity-entrance dimensions met minimum criteria by attempting to pass a circular 6 X 6 cm disc attached to the camera through the cavity opening. We then examined cavity interiors with the camera to ascertain whether it was suitable for use by nesting wood ducks using the following criteria: 1) Horizontal depth (from inner edge of the entrance opening toward the back of the cavity) that appeared deep enough for hens to move from the entrance to the interior of the cavity, 2) vertical depth (from the bottom of the cavity to the bottom of the entrance) of ≥10 cm and ≤4.5 m and not hollow to the ground (Bellrose and Holm 1994), 3) nest-platform dimensions of ≥14 x 15 cm (Boyer 1974, Haramis 1975, Denton et al. 2012*a*), and 4) lack of standing water or excess debris in the cavity (Sousa and Farmer 1983).

We classified the suitability of each examined cavity as suitable, marginal, unsuitable, or unknown. We considered a cavity to be ‘suitable’ if all of the above conditions were met. Since we were not able to definitively measure each dimension, a cavity was classified as ‘marginal’ if it was unclear whether all dimensional requirements were met (i.e., ≥1 dimensional measurement appeared to be close to some minimum or maximum value). Cavities were classified as ‘unknown’ if we were unable to completely observe the cavity, either because the location of the cavity or some structural attribute did not permit observation with the camera system. We considered a cavity to be ‘unsuitable’ if any of the dimensional criteria were not met or if there was standing water or excess debris in the cavity. Reasons cavities were unsuitable were recorded and based on the order that structural restrictions would have been encountered as a wood duck entered a cavity (i.e., entrance dimensions, followed by horizontal depth, vertical depth, and finally, dimensions and other characteristics of the platform).

In addition to suitability, we recorded cavity height (0.1-m increments), entrance type (3 classes: opening on the top of the tree, side, or a combination of top and side openings that are joined on the exterior of the tree), the primary source of cavity formation (11 classes: split, broken limb, broken top, woodpecker, fire, lightning, insect, logging wound, decay/rot, other, unknown), and any recent evidence of animal use.

Statistical Analyses

Predictor variables

We identified 3 tree- and 2 stand-level predictor variables expected to influence whether a given tree would develop a cavity suitable for nesting by wood ducks. Tree-level variables were collected as described above and included tree species, health status, and DBH. Stand-level variables included stand age and site index, which were acquired from publically available forest-inventory datasets used in the stand- selection process. Each metric has been shown to influence cavity availability in previous studies (e.g., Carey 1983; Brawn et al. 1984; Allen and

Corn 1990; Fan et al. 2003*a*, *b*; Gutzat and Dormann, 2018) and are collected as part of most standard forest inventories, including FIA.

Health status and species were categorical variables, whereas stand age, site index and DBH were continuous variables. Data were sparse for health status codes 3-5; thus, we collapsed categories into: 1) live-healthy tree, 2) live tree with signs of declining health (e.g., dead limbs, decay), and 3) dead trees (all dead types 3-7). Twenty-seven tree species were sampled (Appendix A), but only 7 species with >500 observations were used in statistical analyses: American basswood (*Tilia americana*), bigtooth aspen (*Populus grandidentata*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), red maple (*Acer rubrum*), red oak (*Quercus rubra*), and sugar maple (*Acer saccharum*).

We defined stand age as the number of years between when a stand originated and when it was sampled for cavities. Site index was recorded as the number of feet a tree would grow in 50 years in a given stand. Site index data were not available for 11 stands on the Chippewa National Forest, so we imputed values from adjacent stands within the same Terrestrial Ecological Unit and of the same cover type (USDA Chippewa National Forest, unpublished data). Trees with at least 1 unknown cavity and no other suitable cavity were removed prior to analysis (n=61) because suitability could not be determined. None of the numeric predictors were highly correlated (r <0.45) and all variance inflation factors (Zuur et al. 2010) were smaller than 2, thus we included all numeric predictors in our analysis.

Model development

We developed 15 candidate logistic regression models to explain the relationship between tree- and stand-level characteristics and the probability that a tree would develop a cavity suitable for nesting by wood ducks (Table 1). Our response metric was the presence-absence of a suitable cavity. DBH was included in each model due to the clear relationship it has with cavity development (Jensen et al. 2002, Fan et al. 2003b). We predicted that stand-level variables were more likely to influence cavity dynamics either in conjunction with or in addition to tree-level factors, thus there were no models with just stand-level predictors (*but see* Fan et al. 2003*a*). We also evaluated potential interactions, primarily between DBH and tree health status or species, as suggested by Fan et al. (2003*b*). Finally, we considered a random effect to account for the clustering of tree data within plots.

We used the ‘glm’ function in R version 3.4.3 (R Core Team 2017) with a logit link function and binomial distribution in all models. Each tree was classified as either having a suitable cavity or not. There was limited support for including plot as a random effect in exploratory models ran using ‘glmer’ (Bates et al. 2014), so all models included fixed effects only. We used odds ratios to compare the relative contribution of each predictor on the outcome that a tree had suitable cavity.

During preliminary modelling, we found a strong, positive, effect of DBH on cavity presence, but confidence intervals were wide at high DBH values. Thus, we collected additional field data targeting only large DBH trees during spring, 2018. Plot selection was similar to the description above, but included aspen-birch stands ≥65 years old and northern hardwoods or oak stands ≥100 years old. In addition to randomly selecting older stands, we also targeted larger trees by only measuring early-successional species >40cm DBH (bigtooth aspen, paper birch, quaking aspen, red maple) and late-successional species >50cm DBH (American basswood, red oak, sugar maple). Up to 5 plots were placed in each stand, using the same criteria as the original plot selection. Other aspects of data collection were unchanged.

Model selection and predictability

We compared the value of candidate models in 2 ways, AIC-based model-selection (Burnham and Anderson 2002) and an evaluation of model predictability using the area under the receiver operating characteristic curve (AUC; Fawcett 2006). We compared AICc values for each model and considered all models within ∆2AICc of the top model as competing models (Arnold 2010). Ultimately, we selected the most parsimonious model (i.e., fewest parameters) from within this group to be the top model for interpretation and recommended application to forest-inventory data (Burnham and Anderson 2002).

Model predictability was measured using 10-fold cross-validation. Tree data were divided into 10 equal subsets; 90% of data were used to train a given model with the remaining 10% used to test the model. The subsets were shuffled 10 times, so each unique set containing 10% of data was used as a test set once. We then bootstrapped this process 1,000 times, averaging the AUC scores of test data calculated in the R package modEVA (Barbosa et al. 2016). In our case, AUC values assessed the combination of the true-positive and false-positive rates when predicting whether a given tree had a suitable cavity. We interpreted the model with highest mean AUC as having the best predictability and compared this to the top model selected based on AICc.

RESULTS

We surveyed 213 forest plots during 2016-2017 (trees ≥22 cm) and an additional 110 plots in 2018 (trees ≥40 cm). Plots were classified as northern-hardwoods (36%), aspen-birch (27%), oak (24%), lowland hardwoods (7%), and upland conifer (6%). A total of 7,869 trees of 27 species were measured and inspected for cavities (Appendix A). We examined 1,186 potential cavities in 880 of these trees with the camera-system (i.e., some trees had multiple cavities). Of these, 223 were suitable for nesting by wood ducks. Eleven tree species had at least 1 suitable cavity.

Cavity Characteristics

Most cavities were classified as unsuitable for nesting by wood ducks (768; 65%), and the remainder were classified as suitable (223; 19%), marginally suitable (111; 9%), or of unknown suitability (84; 7%). The reasons cavities were considered unsuitable were: insufficient vertical depth (44%), entrance dimensions too small (21%), insufficient horizontal depth (18%), insufficient platform dimensions (14%), excessive debris (2%), and too deep or hollow to the ground (1%). For the cavities considered suitable, the primary sources of development included broken limb (38%), split (21%), broken top (18%), woodpecker excavation (16%), decay or rot (2%), other (4%), and unknown (1%). Entrances were primarily on the side of trees (74%), though top (19%) and combination (7%) entrances were also common. Suitable cavities averaged 7.8 m off the ground (0.9-15.2 m).

Thirty-six percent of suitable cavities had evidence of recent animal use. Most signs of use included nesting materials or food caches perceived to be from squirrels (eastern gray squirrel (*Sciurus carolinensis*), northern flying squirrel (*Glaucomys sabrinus*), or American red squirrel (*Tamiasciurus hudsonicus*)) and other small mammals. However, we also found an active wood duck nest, northern saw-whet owl (*Aegolius acadi*cus) nest, 5 additional bird nests containing unknown eggs or eggshell fragments, 2 raccoon (*Procyon lotor*) den sites and a wasp (*Hymenoptera* spp.) nest.

Statistical Model

Our final analysis dataset contained 5,976 trees from 7 species: American basswood, bigtooth aspen, paper birch, quaking aspen, red maple, red oak, and sugar maple. We identified 2 competing models (ΔAICc <2) for predicting the probability that a tree would have a suitable cavity; 1) an additive model with DBH, health status and tree species (Mod4), and 2) a similar model but with an interaction between DBH and health status (Mod9; Table 2).

Cross-validation identified a similar subset of models as having the highest predictability (Table 2). The model with highest AUC (0.85) was Mod4, although an additional 6 models had AUC ≥0.83 and all models had relatively good predictability with the univariate DBH model having AUC=0.79. Therefore, our set of competing models was limited to Mod4 and Mod9, where the only difference between the 2 models was an interaction between DBH and health status. Though it has marginally lower AICc, the model with the interaction term included more parameters and had lower overall AUC. Thus, the more parsimonious model (Mod4) was the top model and is what we used for inference. However, we examined the implications of the interaction between DBH and health status (i.e., Mod9).

Mod4 showed a strong positive effect of DBH on the probability that a tree had developed a suitable cavity (Table 3; Figure 2). Holding other predictors at fixed values, for every 1cm increase in DBH the odds that a given tree would have a suitable cavity increased by 7.3% (95% CI; 6.0-8.7%). Dead and declining trees were much more likely to develop suitable cavities than live-healthy trees, with 834% (483-1420%) and 477% (276-807%) higher odds, respectively. Including an interaction between DBH and status (Mod9) resulted in similar conclusions with respect to health status and DBH (Figure 3), although the predicted rates of cavity development were slightly different.

Sugar maple had the highest probability of having a suitable cavity (Figure 2). The odds of finding a suitable cavity in a sugar maple were 26% (95% CI;-21-103%), 79% (-3-246%), 86% (14-211%), 192% (66-439%), 310% (157-566%), and 455%% (149-1381%) higher than in American basswood, red maple, red oak, bigtooth aspen, quaking aspen, and paper birch, respectively.

DISCUSSION

Our results suggest that tree-level attributes collected during most forest inventories can be used to accurately predict the presence of cavities suitable for use by large, secondary cavity-nesting birds like wood ducks. DBH, tree health status, and tree species were good predictors of whether a tree had developed a suitable cavity. Several other studies have found a similar combination of variables when studying cavities and tree-microhabitats available for a broader range of taxa (Fan et al. 2003*b*, Larrieu and Cabanettes 2012, Gutzat and Dormann 2018). We also found support for an interaction between tree health status and DBH. Fan et al. (2003*b*) proposed a similar association, though to our knowledge no studies have explicitly tested for this relationship. With widely available forest-survey data (e.g., FIA) and, increasingly, modelled forest attributes (e.g., via LiDAR; Dubayah and Drake 2000), management agencies can apply these results from local to regional scales for conservation purposes.

Cavity Characteristics

Most cavities that appeared potentially suitable from the ground were not suitable for use by nesting wood ducks when the interior dimensions were inspected. For large species with restrictive dimensional requirements like wood ducks, other studies have found similarly low proportions of suitable cavities (15-33%; Soulliere 1990, Robb and Bookhout 1995, Yetter et al. 1999, Zwicker 1999). However, when a wider range of dimensions were considered suitable, studies have found around 70% of cavities were useable by secondary cavity-nesters (Jensen et al. 2002, Remm and Lõhmus 2011). Studies that do not inspect cavity interiors are likely overestimating cavity availability (Allen and Corn 1990, Fan et al. 2003*b*), especially for species requiring large entrances and interior dimensions.

Similar to other regions, broken tree limbs provided most of the suitable cavities in north-central Minnesota (Soulliere 1990, Denton et al. 2012*a*). Likewise, less than 20% of cavities were excavated by woodpeckers (Soulliere 1990, Yetter et al. 1999, Zwicker 1999, Denton et al. 2012*a*). When assessing cavities available for a broader spectrum of secondary users, woodpeckers appear to excavate higher proportions (Cockle et al. 2011). The relatively low proportion of available wood duck cavities produced by woodpeckers is likely associated with their large dimensional requirements, whereby only pileated woodpeckers (*Dryocopus pileatus*), or, occasionally, enlarged northern flicker (*Colaptes auratus*) cavities can be used (Martin et al. 2004). Yet, several studies have found that wood ducks might actively select woodpecker cavities (Gilmer et al. 1978, Robb and Bookhout 1995, Yetter et al. 1999), indicating that many of the non-excavated cavities in our region, though suitable for nesting, might not be used when abandoned woodpecker cavities exist.

Our cavity-source results differed from more southerly studies of wood duck cavities, with a higher proportion of cavities developed from splits. Frost cracks, which we believe contributed to the majority of the splits we observed, are much more common in trees near their northern range limits (Burton et al. 2008). Most of the cavity-producing trees in our study are in the far northern portions of their ranges in northern Minnesota: sugar maple, American Basswood, red maple, and red oak (Little 1971).

Cavity entrance types were generally similar to those observed in other wood duck studies, with a predominance of side entrances (Soulliere 1990, Denton et al. 2012*a*). Though, broken tree tops and associated bucket-style entrances were somewhat more common [18% in this study vs. 4% in Denton et al. (2012*a*) and 10% in (Zwicker 1999)] and potentially receive proportionally more use by nesting wood ducks in Minnesota (Gilmer et al. 1978). Relatively high density of aspen (*Populus* spp.) in the northern USA might explain this difference. Aspen is commonly infected with heartrot (*Phellinus tremulae*) and other fungal diseases that make the trees more susceptible to windthrow (Hinds 1985), often leaving standing boles with broken tops that can develop useable cavities from the top down (E.Z. and J.B., personal observation).

Our assessment of animal use of cavities was conservative, given sampling only occurred once in fall, winter, or early spring. Many bird species that utilize cavities in our region either had migrated or were not using cavities during sampling. In addition, most evidence of nesting by birds, even large species like wood ducks, deteriorate or are removed after nesting and might not be accurately identified in winter or early spring (Utsey and Hepp 1997). This might explain why we found relatively low use by wood ducks and other secondary cavity-nesting species when compared to studies that actively searched cavities during the primary spring nesting season (<3% this study, 5-13% in Nagel 1969, Robb and Bookhout 1995, Yetter et al. 1999, Zwicker 1999). Yet, results appear to indicate that many suitable cavities are unused and support the finding that a surplus might be available for large-bodied secondary cavity nesting species across much of the Midwestern USA (Denton et al. 2012*b*). Results also provide further evidence that, across the wood duck range, squirrels are likely the primary competitors and users of potential cavities (Bellrose and Holm 1994).

Low use of suitable cavities by wood ducks suggests that cavity-availability is not a major limiting factor of populations in north-central Minnesota and other portions of wood duck range (Zwicker 1999, Denton et al. 2012*b*). However, it might also suggest that the dimensional requirements deemed suitable in these studies are somewhat broad and could include cavities that portions of the nesting population do not select for use. Proposed ideal cavity dimensions and characteristics include entrance dimensions close to minimum requirements, woodpecker cavities, and cavities that are higher above ground level, oriented towards forest openings and close to brood-rearing wetlands (Soulliere 1990, Hepp and Bellrose 1995). However, little is known about nest-site selection by wood ducks and how it relates to cavity dimensions and site-level characteristics (Hepp and Bellrose 1995). Future research should characterize the process whereby cavities are inspected and either rejected or selected for nesting and how this relates to optimum cavity dimensions.

Forest Attributes

We recommend using the more parsimonious additive model that had DBH, health status, and species as predictors (Mod4; Table 3) for application to forest inventory datasets. A strong, positive effect of DBH on the presence of cavities has been repeatedly shown in other studies and our data revealed no exceptions (e.g., Jensen et al. 2002, Fan et al. 2003*b*). The proportion of trees with suitable cavities was generally low for trees <30-cm DBH, but as trees increased beyond 40-cm DBH, the proportion of trees with suitable cavities tended to increased exponentially. Tree size is directly related to the potential size of cavity entrances and interior dimensions and thus is particularly important for large-bodied species like wood ducks (Soulliere 1990). Our data indicate that a reasonable model for predicting the presence of suitable wood duck cavities could be developed solely with DBH. However, the inclusion of tree health status and species significantly improved predictability and model fit. When relating tree-level attributes to cavities, studies have often used live/dead tree status (e.g., live vs. snags; Larrieu and Cabanettes 2012), but our results indicate that including at least 1 additional level distinguishing live-healthy from live-declining trees is important (Fan et al. 2003b, Gutzat and Dormann 2018). Tree health status is acknowledged as an important factor in cavity development for wood ducks (Soulliere 1990), though it has not previously been used to model cavity trees (Nielsen et al. 2007, Denton et al. 2012*b*).

We found declining trees, showing signs of decay through features like fungal growths and dying branches, to be highly associated with the development of cavities. Indeed, decay and related fungal infections of trees are likely the ultimate causes of nearly all cavities, whether they be from woodpecker excavation (Jackson and Jackson 2004, Lorenz et al. 2015) or cavities formed through sources like broken limbs and splits (Wesołowski 2012). With high rates of cavity formation, snags are appropriately thought of as the prototypical cavity tree (e.g., Thomas et al. 1979), though trees in decline are their precursor and likely provide cavities over longer periods of time, resulting in a greater diversity of use by secondary cavity-nesters (Wesołowski 2012, Edworthy et al. 2018).

Results from our competing statistical model (Mod9) support the idea that an interaction between DBH and health status could be important for predicting cavities (Fan et al. 2003*b*). When compared to dead and declining trees, large (>60 cm DBH), live-healthy trees had higher rates of increase in the probability of having suitable cavities. Though in smaller trees, both competing statistical models predicted lower rates of increase for live-healthy trees. The potential synergy between DBH and health status provides further evidence for the utility of using health-impacted or dead trees as a predictor of cavity development, especially in smaller DBH classes.

The propensity of different tree species to produce cavities generally agreed with other studies of wood ducks (Soulliere 1990), as well as more broad taxa (Fan et al. 2003*b*), with sugar maple being a dominant cavity producer. Similar to our study, Denton et al. (2012*a*) found sugar maple and American basswood to be most important on a per tree basis in central Wisconsin. Hard and soft maples (sugar maple, red maple, silver maple; *Acer saccharinum*) were the most important cavity producers in more northern studies of wood ducks and other cavity-nesting waterfowl (McGilvrey 1968, Prince 1968, Gilmer et al. 1978). Conversely, these species were not as important in the southern portions of their ranges (Zwicker 1999), indicating the importance of spatial differences in intraspecific tree damage and disease that eventually lead to cavity formation (Morin et al. 2016).

Though they have a lower number of suitable cavities on a per tree basis, aspen species (*Populus* spp.) are also important cavity sources, given the large number of stems in the region (Minnesota Forest Resource Council 2017). Quaking aspen were the most important species for nesting wood ducks in north-central Minnesota (Gilmer et al. 1978). Many studies in northern temperate and boreal forests have also identified aspen as the dominant producer of wildlife cavities (Martin et al. 2004, Weir et al. 2012) due to their predominance in these regions, but also their attractiveness to woodpeckers for excavation (Jackson and Jackson 2004, Witt 2010). With the exception of yellow birch (*Betula alleghaniensis*), species not included in the analysis appeared to have low rates of suitable cavities, e.g., pines (*Pinus* spp.), ashes (*Fraxinus* spp.), and bur oak (*Quercus macrocarpa*).

Stand-level predictors were not useful in predicting whether trees had developed suitable cavities in our study area. Across the continuum of age classes, stand-age is related to cavity formation (Fan et al. 2003*a*), but in the restricted window of relatively old stands that we selected for sampling, it did not improve model fit. We predicted that site index would be related to cavity formation, as site quality inherently affects growth patterns of trees and associated development of decay processes, with better sites generally growing larger, healthier trees (Carey 1983). However, it is possible that site index was a poor predictor as variations in these processes e.g., tree size and health, were accounted for by tree-level variables, DBH and health status. Additionally, site quality could have more confounding effects than we anticipated, for example, the overall positive effects of DBH in a high quality site might be competing with the negative effects of improved tree health on cavity development.

Forest and Wildlife Management Recommendations

When considering the impacts of forest management decisions on cavity availability for large secondary cavity-nesting species like wood ducks, we recommend retaining large DBH, declining or dead, deciduous trees. In the forests of north-central Minnesota, the most suitable tree species are maples (*Acer* spp.) and American basswood in hardwood forests, northern red oak in oak forests, and quaking or bigtooth aspen in aspen and birch forests. Retention of dead-standing trees is commonly recommended in regards to wildlife and cavity considerations (e.g., Thomas 2002). However, forest and wildlife managers might have the most impact on these resources by identifying declining trees, as most cavities are in live trees and their potential for future and diverse use by secondary cavity-nesters is greater (Fan et al. 2003*b*, Edworthy et al. 2018).

Forest management and harvest techniques including leave trees, selection harvests, and extended rotation forestry could all be used to address these recommendations. For example, Gilmer et al. (1978) found that many of the cavities used by wood ducks were in trees retained after harvest either as leave trees or in uncut patches. Similarly, the tree-level characteristics we found most associated with cavities likely only develop when at least some trees are allowed to grow beyond standard harvest rotations used in temperate deciduous forests.

These characteristics, widely collected as part of forest inventories, are useful for developing practical models of cavities and other habitat components (Fan et al. 2003*a*, *b*; Denton et al. 2012*b*). Managers can use the cavity model and associated quantitative data to predict how harvest and other management decisions might affect cavity availability. Depending on the grain and scale of forest-inventory datasets and intended application, predictions can be made for site-level prescriptions to broader regional strategies. Linking conservation strategies for wood ducks and other secondary cavity-nesting species to forest attributes and forest management decisions will help to consistently provide suitable nesting habitat.

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LITERATURE CITED

Aaseng, N. E., J. C. Almendinger, R. P. Dana, D. S. Hanson, M. D. Lee, E. R. Rowe, K. A. Rusterholz, and D. S. Wovcha. 2011. Minnesota’s native plant community classification: A statewide classification of terrestrial and wetland vegetation based on numerical analysis of plot data. Biological Report.

Allen, A. W., and J. G. Corn. 1990. Relationships between live tree diameter and cavity abundance in a Missouri oak-hickory forest. Northern Journal of Applied Forestry 7:179–183.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike’s Information Criterion. Journal of Wildlife Management 74:1175–1178.

Barbosa, A. M., J. Brown, A. Jiménez-Valverde, and R. Real. 2016. modEvA: model evaluation and analysis. R package version 1.3.2 <https://cran.r-project.org/web/packages/modEvA/index.html>

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting Linear Mixed-Effects Models using lme4. arXiv:1406.5823 [stat]. <http://arxiv.org/abs/1406.5823>. Accessed 3 Oct 2018.

Bellrose, F. C. 1990. The history of wood duck management. Pages 13–20 *in* Proceedings of the 1988 North American Wood Duck Symposium. G.V. Burger technical editor. St. Louis, Missouri, USA.

Bellrose, F. C., and D. J. Holm. 1994. Ecology and management of the wood duck. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Beyer, H. L. 2012. Geospatial Modelling Environment (Version 0.7. 2.1). Spatial Ecology, LLC.

Boyer, R. L. 1974. A survey of wood duck nest sites and brood rearing habitat on the Shiawassee National Wildlife Refuge. Thesis. Mount Pleasant: Central Michigan University, USA.

Brawn, J. D., B. Tannenbaum, and K. E. Evans. 1984. Nest site characteristics of cavity nesting birds in central Missouri. USDA Forest Service Research Note NC-314.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.

Burton, J. I., E. K. Zenner, and L. E. Frelich. 2008. Frost crack incidence in northern hardwood forests of the southern boreal–north temperate transition zone. Northern Journal of Applied Forestry 25:133–138.

Carey, A. B. 1983. Cavities in trees in hardwood forests. Pages 167–184 in. Snag habitat management symposium.

Clugston, D. A. 1999. Availability of nest cavity trees for wood ducks (*Aix sponsa*) at Sunkhaze Meadows National Wildlife Refuge, Maine. Northeastern Naturalist 6:133–138.

Cockle, K. L., K. Martin, and T. Wesołowski. 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9:377–382.

Denton, J. C., C. L. Roy, G. J. Soulliere, and B. A. Potter. 2012a. Change in Density of Duck Nest Cavities at Forests in the North Central United States. Journal of Fish and Wildlife Management 3:76–88.

Denton, J. C., C. L. Roy, G. J. Soulliere, and B. A. Potter. 2012b. Current and projected abundance of potential nest sites for cavity-nesting ducks in hardwoods of the north central United States. The Journal of Wildlife Management 76:422–432.

Dubayah, R. O., and J. B. Drake. 2000. Lidar remote sensing for forestry. Journal of Forestry 98:44–46.

Edworthy, A. B., M. K. Trzcinski, K. L. Cockle, K. L. Wiebe, and K. Martin. 2018. Tree cavity occupancy by nesting vertebrates across cavity age. The Journal of Wildlife Management 82:639–648.

Fan, Z., D. R. Larsen, S. R. Shifley, and F. R. Thompson. 2003a. Estimating cavity tree abundance by stand age and basal area, Missouri, USA. Forest Ecology and Management 179:231–242.

Fan, Z., S. R. Shifley, M. A. Spetich, F. R. Thompson III, and D. R. Larsen. 2003b. Distribution of cavity trees in midwestern old-growth and second-growth forests. Canadian Journal of Forest Research 33:1481–1494.

Fawcett, T. 2006. An introduction to ROC analysis. Pattern recognition letters 27:861–874.

Gilmer, D. S., I. J. Ball, L. M. Cowardin, J. E. Mathisen, and J. H. Riechmann. 1978. Natural Cavities Used by Wood Ducks in North-Central Minnesota. The Journal of Wildlife Management 42:288.

Gutzat, F., and C. F. Dormann. 2018. Decaying trees improve nesting opportunities for cavity-nesting birds in temperate and boreal forests: A meta-analysis and implications for retention forestry. Ecology and Evolution 00:1-11.

Hanson, D. S., and B. Hargrave. 1996. Development of a multilevel ecological classification system for the state of Minnesota. Environmental monitoring and assessment 39:75–84.

Haramis, G. M. 1975. Wood duck (*Aix sponsa*) ecology and management within the green-timber impoundments at Montezuma National Wildlife Refuge. Thesis. Cornell University, Ithaca NY, USA.

Hepp, G. R., and F. C. Bellrose. 1995. Wood Duck (*Aix sponsa*). A. Poole and F. Gill, editors. The Birds of North America Online. <https://birdsna.org/Species-Account/bna/species/wooduc/introduction>. Accessed 26 Mar 2019.

Hinds, T. E. 1985. Diseases in Aspen: Ecology and Management in the Western United States. General Technical Report RM-119. N.V. DeByle and R.P. Winokur editors. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA.

Jackson, J. A., and B. J. S. Jackson. 2004. Ecological relationships between fungi and woodpecker cavity sites. The Condor 106:37.

Jensen, R. G., J. M. Kabrick, and E. K. Zenner. 2002. Tree cavity estimation and verification in the Missouri Ozarks. Pages 114-129 *in* Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium: Post-treatment Results of the Landscape Experiment. S.R. Shifley and J.M. Kabrick editors. General Technical Report NC-227. St. Paul, MN, USA: US Dept. of Agriculture, Forest Service, North Central Forest Experiment Station.

Larrieu, L., and A. Cabanettes. 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. Canadian Journal of Forest Research 42:1433–1445.

Little, E. L. 1971. Atlas of United States trees Volume 1. Conifers and important hardwoods US Dept of Agriculture USA.

Lorenz, T. J., K. T. Vierling, T. R. Johnson, and P. C. Fischer. 2015. The role of wood hardness in limiting nest site selection in avian cavity excavators. Ecological Applications 25:1016–1033.

Lüdecke, D. 2018. sjPlot: Data Visualization for Statistics in Social Science, R package version 2.6.2. <https://CRAN.R-project.org/package=sjPlot>.

Martin, K., K. E. H. Aitken, and K. L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior british columbia, canada: nest characteristics and niche partitioning. The Condor 106:5-19.

McGilvrey, F. B. 1968. A guide to wood duck production habitat requirements. US Fish and Wildlife Service.

Minnesota Forest Resource Council. 2017. North Central Landscape Forest Resources Plan. Minnesota Forest Resource Council, St. Paul, Minnesota. <http://mn.gov/frc>.

Minnesota Forest Resources Council. 2012. Sustaining Minnesota forest resources: Voluntary site-level forest management guidelines for landowners, loggers and resource managers. Minnesota Forest Resources Council.

Morin, R. S., S. A. Pugh, and J. Steinman. 2016. Mapping the occurrence of tree damage in the forests of the northern United States. Gen. Tech. Rep. NRS-GTR-162. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station.

Nagel, R. E. 1969. Predation on eggs in simulated nests and tree cavity abundance in wood duck nesting habitat. Thesis. Iowa State University, Ames, IA, USA.

Nielsen, C. L. R., R. J. Gates, and E. H. Zwicker. 2007. Projected Availability of Natural Cavities for Wood Ducks in Southern Illinois. Journal of Wildlife Management 71:875–883.

Prince, H. H. 1968. Nest Sites Used by Wood Ducks and Common Goldeneyes in New Brunswick. The Journal of Wildlife Management 32:489-500.

R Core Team. 2017. R: A language and environment for statistical computing.

Remm, J., and A. Lõhmus. 2011. Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. Forest Ecology and Management 262:579–585.

Robb, J. R., and T. A. Bookhout. 1995. Factors Influencing Wood Duck Use of Natural Cavities. The Journal of Wildlife Management 59:372-383.

Roy Nielsen, C. L., and R. J. Gates. 2007. Reduced nest predation of cavity-nesting wood ducks during flooding in a bottomland hardwood forest. The Condor 109:210-215.

Ryan, D. C., R. J. Kawula, and R. J. Gates. 1998. Breeding Biology of Wood Ducks Using Natural Cavities in Southern Illinois. The Journal of Wildlife Management 62:112-123.

Sauer, J., D. Niven, J. Hines, D. Ziolkowski Jr, K. L. Pardieck, J. E. Fallon, and W. Link. 2017. The North American breeding bird survey, results and analysis 1966-2015.

Soulliere, G. J. 1990. Review of wood duck nest-cavity characteristics. Pages 153–162 *in* Proceedings of the 1988 North American Wood Duck Symposium. G.V. Burger technical editor. St. Louis, Missouri, USA.

Soulliere, G. J., B. A. Potter, J. M. Coluccy, R. C. Gatti, C. L. Roy, D. R. Luukkonen, P. W. Brown, and M. W. Eichholz. 2007. Upper Mississippi River and Great Lakes region joint venture waterfowl habitat conservation strategy. US Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

Sousa, P. J., and A. H. Farmer. 1983. Habitat suitability index models: wood duck. US Fish and Wildlife Service.

Strom. 1969. A determination and evaluation of what constitutes wood duck habitat in the Nelson-Trevino Bottoms of the Upper Mississippi Refuge. US Fish and Wildlife Service, Division of Wildlife Refuges.

Thomas, J. W. 2002. Dead wood: from forester’s bane to environmental boon. F. William and Jr. Laudenslayer, technical editors. Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests. US Forest Service Proceedings GTR-181, Pacific Southwest Research Station, Albany, California, USA.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags, p. 60–77. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook.

U.S. Department of Agriculture Forest Service. 2014. Forest inventory and analysis national core field guide, Volume 1: field data collection procedures for Phase 2 plots. Version 6.1. <http://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/2014/Core%20FIA%20field%20guide_6-1.pdf>. Accessed 1 Nov 2016.

Utsey, F. M., and G. R. Hepp. 1997. Frequency of Nest Box Maintenance: Effects on Wood Duck Nesting in South Carolina. The Journal of Wildlife Management 61:801–807.

Vaillancourt, M.-A., P. Drapeau, M. Robert, and S. Gauthier. 2009. Origin and Availability of Large Cavities for Barrow's Goldeneye (Bucephala islandica), a Species at Risk Inhabiting the Eastern Canadian Boreal Forest. Avian Conservation and Ecology <http://www.ace-eco.org/vol4/iss1/art6/>

Van der Hoek, Y., G. V. Gaona, and K. Martin. 2017. The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. Diversity and Distributions 23:1120–1131.

Waldstein, A. L. 2012. An inexpensive camera system for monitoring cavity nests. Journal of Field Ornithology 83:302–305.

Weir, R. D., M. Phinney, and E. C. Lofroth. 2012. Big, sick, and rotting: Why tree size, damage, and decay are important to fisher reproductive habitat. Forest Ecology and Management 265:230–240.

Wesołowski, T. 2012. "Lifespan" of non-excavated holes in a primeval temperate forest: A 30year study. Biological Conservation 153:118–126.

Witt, C. 2010. Characteristics of aspen infected with heartrot: Implications for cavity-nesting birds. Forest Ecology and Management 260:1010–1016.

Yetter, A. P., S. P. Havera, and C. S. Hine. 1999. Natural-Cavity Use by Nesting Wood Ducks in Illinois. The Journal of Wildlife Management 63:630-638.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in ecology and evolution 1:3–14.

Zwicker, E. 1999. Availability and use of tree cavities by wood ducks in southern Illinois. Thesis. Southern Illinois University Carbondale, Carbondale, IL, USA.

Table 1 Candidate models for explaining the relationship between tree and stand-level characteristics and the probability that a tree would develop a cavity suitable for nesting by wood ducks in Cass County, MN, 2016-2018. For each model, the predicted effects of covariates are indicated. Models were given an abbreviation for reference between the text and tables.

Model	Abbreviation	Prediction
P(suitable cavity) = DBH	Mod1	Positive effect of DBH
P(suitable cavity) = DBH + Status	Mod2	Positive effect of DBH and differential effects of tree health status levels
P(suitable cavity) = DBH + Species	Mod3	Positive effect of DBH and differential effects of tree species
P(suitable cavity) = DBH + Status + Species	Mod4	Positive effect of DBH and differential effects of levels of tree health status and species
P(suitable cavity) = DBH + Status + Species + StandAge	Mod5	Positive effects of DBH and stand age and differential effects of levels of tree health status and species
P(suitable cavity) = DBH + Status + Species + StandAge + SiteIndex	Mod6	Positive effects of DBH, stand age and site index and differential effects of tree health status levels and species
P(suitable cavity) = DBH * Status	Mod7	Overall positive effect of DBH which varies by levels of tree health status
P(suitable cavity) = DBH * Species	Mod8	Overall positive effect of DBH which varies by tree species
P(suitable cavity) = DBH * Status + Species	Mod9	Overall positive effect of DBH which varies by levels of tree health status and differential effects of tree species
P(suitable cavity) = DBH * Species + Status	Mod10	Overall positive effect of DBH which varies by tree species and differential effects of tree health status levels
P(suitable cavity) = DBH + Status * Species	Mod11	Positive effect of DBH and effect of tree health status that depends on tree species
P(suitable cavity) = DBH * Species * Status	Mod12	Overall positive effect of DBH which varies by both tree species and health status
P(suitable cavity) = DBH + StandAge + SiteIndex	Mod13	Positive effects of DBH, stand age and site index
P(suitable cavity) = DBH + SiteIndex * Species	Mod14	Positive effect of DBH and overall positive effect of site index that varies by tree species
P(suitable cavity) = DBH + StandAge * Species	Mod15	Positive effect of DBH and overall positive effect of stand age that varies by tree species

Table 2 Comparison of candidate statistical models for predicting whether trees have developed suitable cavities for wood ducks in Cass County, MN, 2016-2018. Models were compared based on overall predictability (AUC) and information-theoretic approaches (AICc). The top selected model based on parsimony and predictability is indicated in bold, while the competing model is italicized. Refer to Table 1 for model descriptions.

Model	k	AICc	∆AICc	AICcWt	LL	AUC
Mod9	12	1359.28	0	0.45	-667.62	0.84
Mod4	10	1360.17	0.89	0.29	-670.07	0.85
Mod5	11	1361.85	2.56	0.12	-669.9	0.84
Mod6	12	1362.58	3.3	0.09	-669.26	0.84
Mod11	22	1364.3	5.01	0.04	-660.06	0.83
Mod10	16	1365.34	6.05	0.02	-666.62	0.84
Mod12	42	1384.71	25.42	0	-650.05	0.81
Mod7	6	1397.54	38.26	0	-692.76	0.83
Mod2	4	1397.76	38.47	0	-694.88	0.84
Mod14	15	1450.42	91.14	0	-710.17	0.79
Mod15	15	1462.42	103.14	0	-716.17	0.79
Mod3	8	1463.81	104.53	0	-723.89	0.79
Mod8	14	1469.63	110.35	0	-720.78	0.79
Mod1	2	1483.65	124.37	0	-739.83	0.79
Mod13	4	1484.51	125.23	0	-738.25	0.79

Table 3 Model summary of the top-supported model (Mod4) for predicting suitable cavities for nesting wood ducks in Cass County, MN, 2016-2018. The reference group reflects health status live-healthy and species sugar maple.

Mod4	β	SE
Intercept	-6.72	0.35
DBH	0.07	0.01
Health status		
Declining	1.75	0.22
Dead	2.23	0.24
Species		
American basswood	-0.23	0.24
Red maple	-0.57	0.32
Red oak	-0.62	0.26
Bigtooth aspen	-1.07	0.30
Quaking aspen	-1.41	0.24
Paper birch	-1.71	0.45

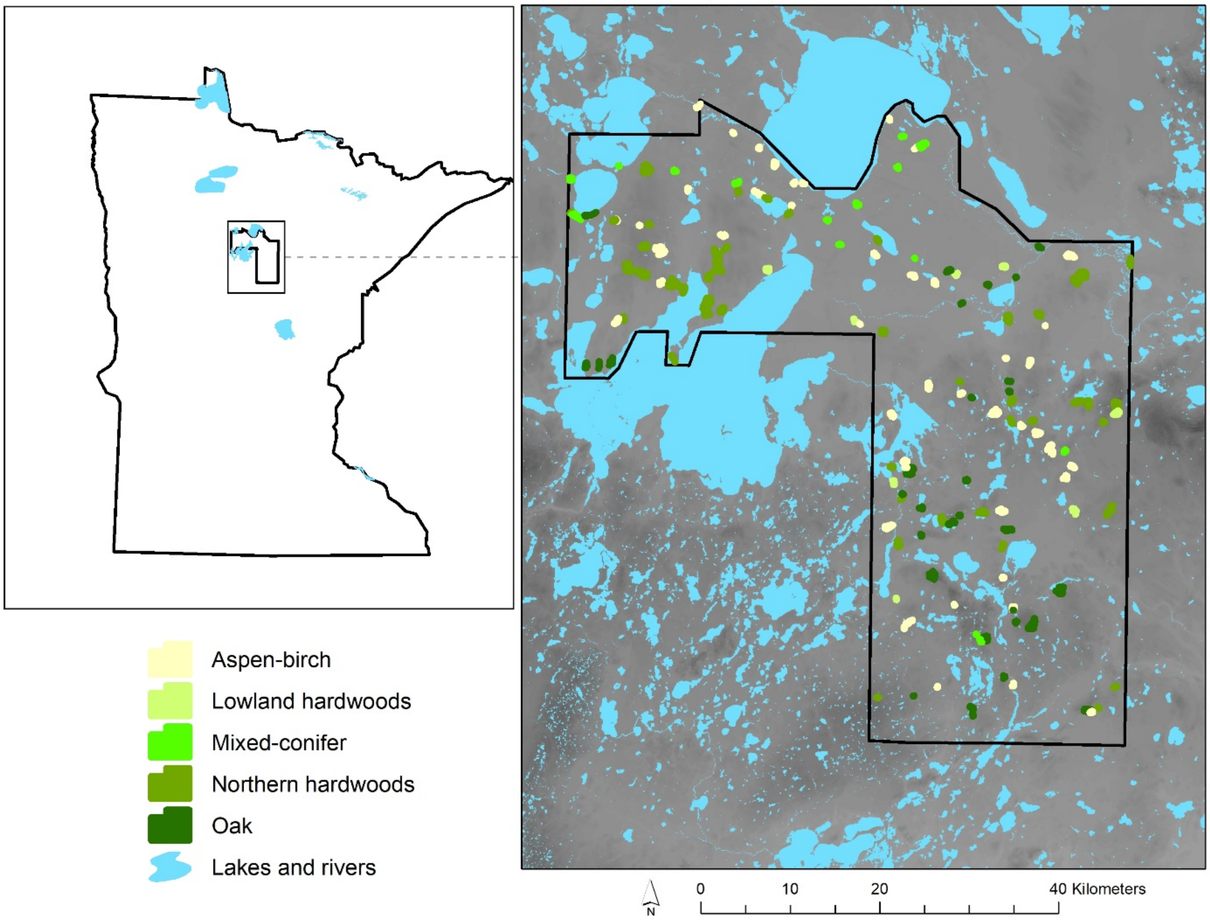

Figure 1. Forest stands sampled for cavities that were suitable for use by nesting wood ducks in Cass County, MN, 2016-2018. Stands were on public lands in county, state, and federal ownerships and were classified into 5 general cover types. Between 1 and 5 20-m radius plots were sampled for cavities in each stand.

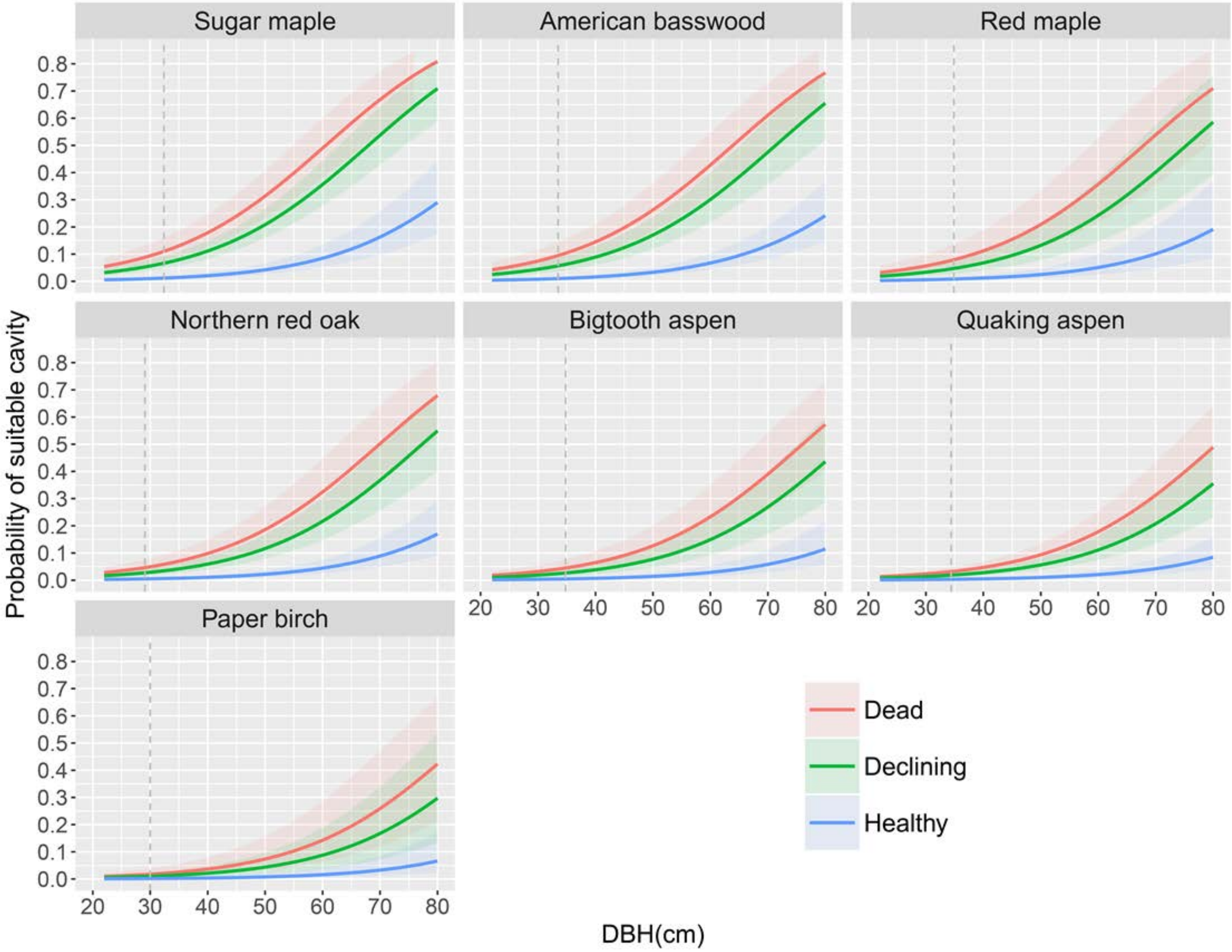

Figure 2. Effect of DBH, health status, and tree species on the probability that trees will have a suitable cavity for nesting by wood ducks in Cass County, MN, 2016-2018. 95% confidence limits are indicated. Dashed lines indicate the mean DBH for a given species.

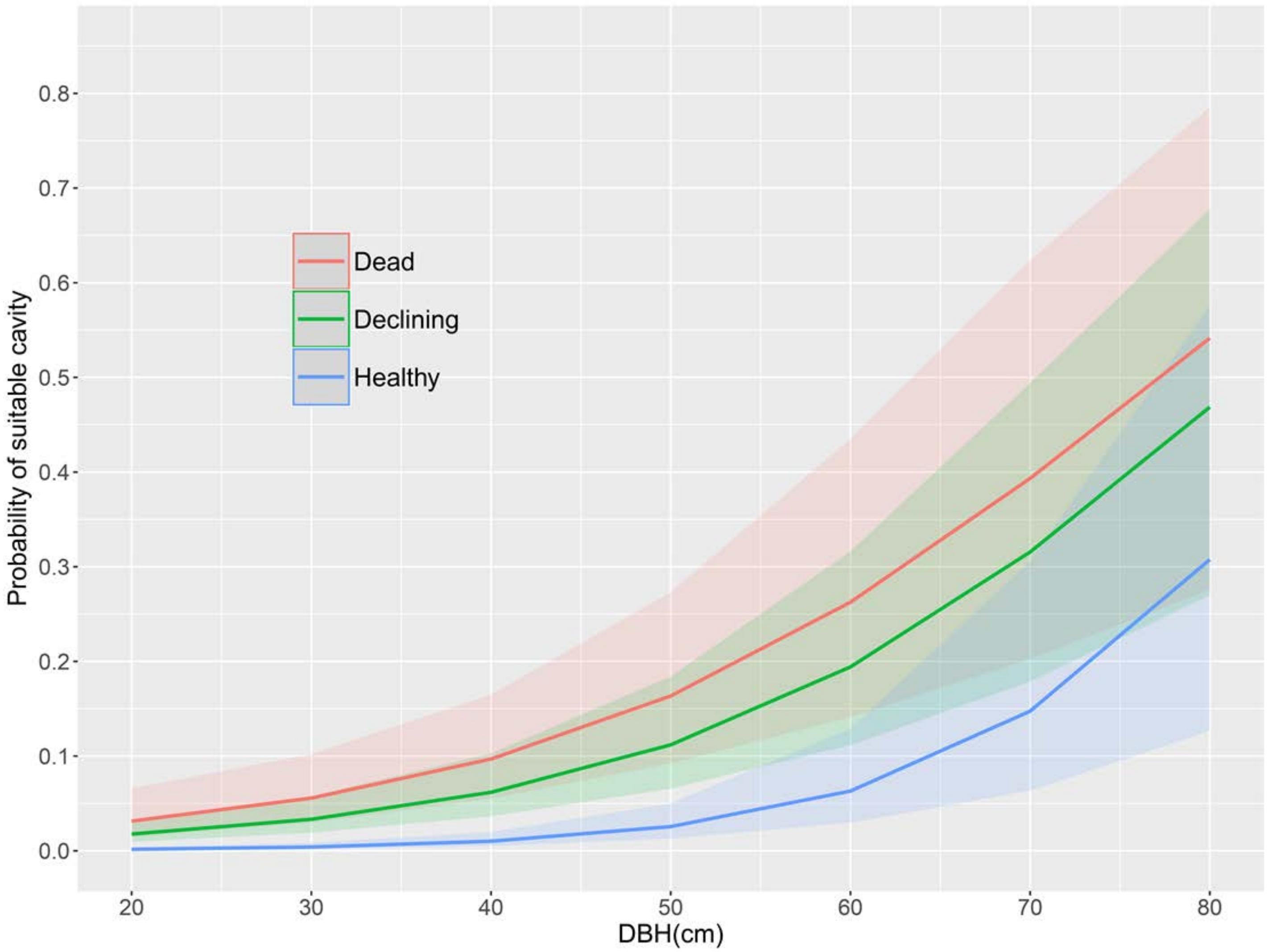

Figure 3. Predicted probability of a suitable wood duck cavity as a function of DBH for dead, declining, and healthy trees in Cass County, MN, 2016-2018. Tree species, the confounding factor, was integrated out to provide a population-level relationship between DBH and health status. Marginal effects were calculated and plotted using package sjPlot in program R (Lüdecke 2018).

Appendix A Total number of trees and suitable cavities counted for each tree species sampled in Cass County, Minnesota, 2016–2018. The proportion of each species within tree health status levels (healthy, declining and dead) is summarized. Some trees had more than 1 suitable cavity, so the number of trees with suitable cavities is also indicated in parentheses. The number of trees sampled in 6 DBH by species bins is also indicated. The proportion of trees with suitable cavities and the associated standard error (calculated from a binomial distribution) are in parentheses. Dashed lines indicate that no trees were sampled or standard errors were not estimable for a tree species-DBH class.

Species	Trees (% total)	Health status	Suitable cavities	22-29cm	30-39cm	40-49cm	50-59cm	60-69cm	70-79cm	≥80cm
Balsam fir (*Abies balsamea*)	126 (1.6)	0.56, 0.17, 0.27	–	105 (0,–)	18 (0,–)	3 (0,–)	–	–	–	–
Box elder (*Acer negundo*)	5 (0.06)	0.4, 0.6, 0	–	3 (0,–)	1 (0,–)	1 (0,–)	–	–	–	–
Red maple (*Acer rubrum*)	569 (7.23)	0.5, 0.4, 0.1	16 (14)	353 (0.008,0.005)	167 (0.024,0.012)	41 (0.146,0.055)	5 (0.2,0.179)	3 (0.667,0.272)	–	–
Sugar maple (*Acer saccharum*)	840 (10.67)	0.57, 0.35, 0.08	61 (57)	393 (0.01,0.005)	218 (0.055,0.015)	103 (0.204,0.04)	93 (0.14,0.036)	26 (0.308,0.091)	5 (0.2,0.179)	2 (1,0)
Yellow birch (*Betula alleghaniensis*)	63 (0.8)	0.52, 0.37, 0.11	5 (5)	20 (0.05,0.049)	12 (0.083,0.08)	18 (0.056,0.054)	11 (0.091,0.087)	–	1 (0,–)	1 (1,0)
Paper birch (*Betula papyrifera*)	809 (10.28)	0.61, 0.2, 0.19	6 (6)	444 (0.005,0.003)	288 (0.01,0.006)	72 (0,–)	4 (0.25,0.217)	1 (0,–)	–	–
Hackberry (*Celtis occidentalis*)	4 (0.05)	1, 0, 0	–	3 (0,–)	1 (0,–)	–	–	–	–	–
Black ash (*Fraxinus nigra*)	291 (3.7)	0.85, 0.12, 0.03	–	214 (0,–)	55 (0,–)	14 (0,–)	5 (0,–)	3 (0,–)	–	–
Green ash (*Fraxinus pennsylvanica*)	231 (2.94)	0.81, 0.15, 0.04	1 (1)	129 (0.008,0.008)	63 (0,–)	27 (0,–)	11 (0,–)	1 (0,–)	–	–
Ash spp (*Fraxinus spp*)	6 (0.08)	0.83, 0.17, 0	–	5 (0,–)	–	1 (0,–)	–	–	–	–
Eastern larch (*Larix laricina*)	2 (0.03)	0.5, 0, 0.5	–	–	1 (0,–)	1 (0,–)	–	–	–	–
Eastern hophornbeam (*Ostrya virginiana*)	1 (0.01)	0, 1, 0	–	1 (0,–)	–	–	–	–	–	–
White spruce (*Picea glauca*)	23 (0.29)	0.83, 0.04, 0.13	–	12 (0,–)	9 (0,–)	2 (0,–)	–	–	–	–

Species	Trees (% total)	Health status	Suitable cavities	22-29cm	30-39cm	40-49cm	50-59cm	60-69cm	70-79cm	≥80cm
Black spruce (*Picea mariana*)	1 (0.01)	0, 1, 0	–	1 (0,–)	–	–	–	–	–	–
Jack pine (*Pinus banksiana*)	25 (0.32)	0.16, 0.04, 0.8	–	12 (0,–)	10 (0,–)	3 (0,–)	–	–	–	–
Red pine (*Pinus resinosa*)	449 (5.71)	0.93, 0.03, 0.04	–	90 (0,–)	181 (0,–)	106 (0,–)	51 (0,–)	16 (0,–)	4 (0,–)	1 (0,–)
Pine spp (*Pinus spp*)	4 (0.05)	0, 0, 1	1 (1)	1 (0,–)	3 (0.333,0.272)	–	–	–	–	–
Eastern white pine (*Pinus strobus*)	133 (1.69)	0.65, 0.17, 0.19	2 (2)	18 (0,–)	31 (0,–)	34 (0,–)	22 (0.045,0.044)	15 (0,–)	6 (0.167,0.152)	7 (0,–)
Balsam poplar (*Populus balsamifera*)	31 (0.39)	0.42, 0.23, 0.35	–	7 (0,–)	17 (0,–)	6 (0,–)	1 (0,–)	–	–	–
Eastern cottonwood (*Populus deltoides*)	1 (0.01)	0, 0, 1	–	1 (0,–)	–	–	–	–	–	–
Bigtooth aspen (*Populus grandidentata*)	511 (6.49)	0.54, 0.28, 0.18	17 (17)	182 (0,–)	154 (0.013,0.009)	109 (0.073,0.025)	49 (0.102,0.043)	14 (0.143,0.094)	3 (0,–)	–
Poplar spp (*Populus spp*)	37 (0.47)	0.05, 0, 0.95	2 (2)	7 (0,–)	16 (0.125,0.083)	10 (0,–)	4 (0,–)	–	–	–
Quaking aspen (*Populus tremuloides*)	1261 (16.02)	0.31, 0.38, 0.3	36 (32)	371 (0,–)	447 (0.018,0.006)	361 (0.05,0.011)	70 (0.129,0.04)	10 (0.1,0.095)	1 (0,–)	1 (0,–)
Black cherry (*Prunus serotina*)	1 (0.01)	0, 0, 1	–	1 (0,–)	–	–	–	–	–	–
Northern pin oak (*Quercus ellipsoidalis*)	13 (0.17)	0.23, 0.77, 0	–	6 (0,–)	7 (0,–)	–	–	–	–	–
Bur oak (*Quercus macrocarpa*)	317 (4.03)	0.83, 0.15, 0.02	5 (4)	163 (0.012,0.009)	90 (0,–)	25 (0,–)	23 (0,–)	15 (0.133,0.088)	–	1 (1,0)
Northern red oak (*Quercus rubra*)	834 (10.6)	0.65, 0.25, 0.1	29 (27)	278 (0.007,0.005)	315 (0.041,0.011)	153 (0.039,0.016)	65 (0.077,0.033)	20 (0.1,0.067)	1 (0,–)	2 (0.5,0.354)

Species	Trees (% total)	Health status	Suitable cavities	22-29cm	30-39cm	40-49cm	50-59cm	60-69cm	70-79cm	≥80cm
Northern white-cedar (*Thuja occidentalis*)	36 (0.46)	0.78, 0.22, 0	−	14 (0,−)	15 (0,−)	4 (0,−)	3 (0,−)	−	−	−
American basswood (*Tilia americana*)	1213 (15.41)	0.84, 0.11, 0.05	40 (39)	522 (0.006,0.003)	381 (0.016,0.006)	168 (0.054,0.017)	95 (0.137,0.035)	37 (0.135,0.056)	5 (0.4,0.219)	5 (0.4,0.219)
American elm (*Ulmus americana*)	19 (0.24)	0.58, 0.26, 0.16	−	16 (0,−)	2 (0,−)	1 (0,−)	−	−	−	−
Unknown spp	13 (0.17)	0.38, 0, 0.62	2 (1)	9 (0,−)	2 (0,−)	−	−	2 (1,0)	−	−