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Research Paper

Prothonotary Warbler demography and nest site selection in natural and artificial cavities in bottomland forests of Arkansas, USA

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ABSTRACT. Anthropogenic alterations to bottomland forests in the United States that occurred post-European settlement likely negatively affected many avian species. The Prothonotary Warbler (*Protonotaria citrea*), a secondary cavity nester that breeds predominantly in these forests, has steadily declined over the past 60 years, and our ability to mitigate this trend is partially limited by a lack of basic biological data. Although much research has been devoted to Prothonotary Warblers, most studies have focused on local breeding populations that use nest boxes; we lack information about habitat selection behavior and demographic parameters of individuals that use natural cavities, which includes the vast majority of the global population. We studied warblers nesting both in boxes and natural cavities in central Arkansas, USA. We aimed to evaluate: (1) microhabitat features important for nest site selection, (2) relationships between these features and nest survival, and (3) demographic parameters of individuals breeding in natural cavities versus nest boxes. We hypothesized (1) selected nest site characteristics are associated with nest survival, and (2) natural cavities and nest boxes provide similar nest features related to clutch size and number fledged, but that predation protection differs. We found that warblers preferred nesting in dead trees with cavities that were higher and shallower than available random cavities, and that canopy cover within 5 m of nests was inversely related to nest survival. Demographic parameters did not differ between natural cavities and nest boxes; however, when excluding flooded nests, boxes experienced lower rates of nest depredation. We believe that forest management strategies that increase the number of suitable dead nest trees and restore the natural hydrology of these ecosystems would create and improve habitat for this iconic species. We advocate multiscale experimental canopy cover manipulation to explore the causal mechanism (s) of the relationship we found between canopy cover and nest survival.

Démographie et sélection du site de nidification de la Paruline orangée dans des cavités naturelles et artificielles en forêts sur terres basses de l'Arkansas, É.-U.

RÉSUMÉ. Les changements d'origine anthropique apportés aux forêts des terres basses aux États-Unis suivant la colonisation européenne ont vraisemblablement affecté négativement de nombreuses espèces d'oiseaux. Les effectifs de la Paruline orangée (*Protonotaria citrea*), oiseau utilisateur secondaire de cavités qui niche surtout dans ces forêts, ont fortement diminué depuis les 60 dernières années, et notre capacité à freiner cette tendance est en partie limitée par un manque de données biologiques fondamentales. Bien que cette espèce ait fait l'objet de nombreuses recherches, la plupart de celles-ci se sont concentrées sur les populations nicheuses locales utilisant des nichoirs; nous n'avons pas de données sur le comportement de sélection d'habitat ni sur les paramètres démographiques des individus qui utilisent les cavités naturelles, soit la grande majorité de la population mondiale. Nous avons étudié des parulines qui nichent dans des nichoirs et des cavités naturelles en Arkansas, É.-U. Nous avons cherché à évaluer : 1) les caractéristiques des microhabitats importantes dans la sélection du site de nidification; 2) les liens entre ces caractéristiques et le taux de survie des nids; et 3) les paramètres démographiques des individus nichant dans des cavités naturelles c. ceux nichant dans des nichoirs. Nous avons émis les hypothèses selon lesquelles : 1) les caractéristiques des sites de nidification choisis sont associées à la survie au nid; et 2) les cavités naturelles et les nichoirs présentent des caractéristiques de nid similaires quant à la taille de la ponte et au nombre de jeunes prenant leur envol, mais leur protection contre la prédation diffère. Nous avons trouvé que les parulines préfèrent nicher dans des arbres morts avec cavités qui étaient plus hautes et plus profondes que les cavités disponibles en général, et que le couvert forestier dans les 5 m des nids était inversement lié à la survie au nid. Les paramètres démographiques des cavités naturelles et des nichoirs étaient les mêmes; toutefois, lorsqu'on excluait les nids inondés, les nichoirs avaient un taux de prédation de nids plus faible. Nous pensons que les stratégies d'aménagement forestier qui augmentent le nombre d'arbres morts à cavités propices et rétablissent l'hydrologie naturelle de ces écosystèmes créeraient de l'habitat ou l'amélioreraient pour cette espèce emblématique. Nous privilégions la manipulation expérimentale multiéchelle du couvert forestier afin d'explorer le ou les mécanismes causaux de la relation que nous avons établies entre le couvert et la survie au nid.

Key Words: *bottomland forests; forest management; habitat selection; Lower Mississippi Alluvial Valley; Protonotaria citrea; secondary cavity nester*

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INTRODUCTION

Understanding the process of habitat selection, and the subsequent effect of these decisions on fitness, has long been a research goal for ornithologists (Grinnell 1917, Kendeigh 1945, MacArthur et al. 1962). Recently, interest in understanding habitat selection has taken on greater practical importance because of the implications these behaviors may have on the conservation of species of concern. Because habitat destruction and degradation continue to be the strongest drivers of population decline for animal species worldwide (Brooks et al. 2002, Fahrig 2003), understanding which habitat features that animals prefer, and which features are associated with greater fitness, is crucial for successfully managing the remaining habitat for these species and restoring important degraded habitat features.

One region where natural ecosystems have been greatly altered is the Lower Mississippi Alluvial Valley (hereafter LMAV; Fig. 1). Bottomland forests, the predominant land cover in this region prior to European settlement, decreased by > 70% from pre-European settlement to present (Twedt and Loesch 1999, Fredrickson 2005), largely as a result of agricultural conversion in the early 20th century (Twedt and Loesch 1999). Although the decline of these bottomland forests has slowed since the 1970s (Twedt and Loesch 1999), the remaining forests differ from their historical conditions. Almost exclusively, current forests in the region are relatively young second-growth stands (Twedt and Henne-Kerr 2001) that differ in their historical plant species composition, partially related to changes in hydrology and flood regimes (Interagency Floodplain Management Review Committee 1994, Gee et al. 2014).

Fig. 1. Prothonotary Warbler (*Protonotaria citrea*) breeding range (yellow), Lower Mississippi Alluvial Valley (red), and the study site in White River National Wildlife Refuge (black dot).

The extensive loss of these forests, and alteration of the remaining bottomland forests, likely contributed to the extinction of several avian species over the past century (Bachman's Warbler, *Vermivora bachmanii*; Carolina Parakeet, *Conuropsis carolinensis*; Ivory-billed Woodpecker, *Campephilus principalis*; Brawn et al. 2001, Hedeen 2013), and has had negative impacts on many avian populations in the region (Twedt and Henne-Kerr 2001, Heltzel and Leberg 2006). In general, bird species that are typically associated with older and larger trees, as well as habitats with consistent and predictable flooding events, have been negatively affected by these habitat alterations (Heitmeyer 2006, Cockle et al. 2010). Both primary and secondary cavity nesters are impacted because damaged or dying trees, in which primary cavity-nesting species can more easily excavate nest cavities (Lõhmus 2016), are typically more abundant in bottomland forests that consist of trees in older age classes and undergo regular flood events. Accordingly, older forests can have up to 12 times as many cavities and 6 times as many cavity nests as younger forests (Robles et al. 2011) and support greater species diversities and population densities of secondary cavity-nesting birds than younger forests (Twedt and Henne-Kerr 2001, Robles et al. 2011). The close association between cavity nesters and older, bottomland forests makes the preservation and maintenance of this habitat type crucial for the management of cavity-nesting species.

One secondary cavity-nesting species impacted by the loss of quantity and quality of bottomland forests in the LMAV is the Prothonotary Warbler (*Protonotaria citrea*). This warbler is a Nearctic-Neotropical migrant that breeds predominantly in bottomland forests of the southeastern United States (Petit 1999). Despite the recent stabilization of bottomland hardwood forest loss in the LMAV, Prothonotary Warblers have declined by ~1% range-wide per year from 1966 to 2014 (Pardieck et al. 2018). The cause of this decline is likely varied (Petit 1999), but it is potentially at least partially related to the current state of the remaining bottomland forests: younger (and structurally less complex) stands with less decaying wood, altered hydrology, and greater fragmentation of surrounding habitat. In the last few decades, mangrove forests on the species' wintering grounds have also experienced severe degradation and destruction (Sandilyan and Kathiresan 2012), which may contribute to the Prothonotary Warbler population decline, encouraging mangrove conservation efforts (Petit 1999). Because of continued population declines and a relatively low population size (estimated at 1.6 million; PIFSC 2013), the Prothonotary Warbler is considered a Bird of Conservation Concern in the United States (USFWS 2008), is an Audubon Yellow WatchList species (Butcher et al. 2007), and is Endangered in Canada (COSEWIC 2012).

Although many studies have explored various aspects of Prothonotary Warbler breeding ecology (e.g., Petit 1991*a,b*, 1999, Hoover 2003, Cooper et al. 2009, Bulluck et al. 2013, McKim-Louder et al. 2013), they have almost exclusively focused on individuals using artificial nest boxes (but see Hoover 2006 and Cooper et al. 2009). This reliance on nest box studies has left a number of knowledge gaps currently limiting our ability to manage and conserve this species and to help mitigate this decline. First, it is not clear which microhabitat, e.g., nest site, characteristics breeding Prothonotary Warblers prefer or how these various features are related to reproductive success. Until we understand which characteristics Prothonotary Warblers select for when using natural cavities, we will lack critical information needed to provide appropriate habitat conditions for the majority of individuals in the population. Understanding how these habitat features relate to reproductive success may also be critical to directing management strategies. Reproductive

Table 1. Summary of a priori, nonmutually exclusive hypotheses that may explain the relationship between microhabitat characteristics and (a) habitat selection and (b) nest survival of Prothonotary Warbler (*Protonotaria citrea*) nests in White River National Wildlife Refuge, Arkansas, USA in 2014–2015.

Variable	Hypothesized mechanism	Predictions	Pertinent references
Water	Deep water acts as protection from predators and provides appropriate foraging habitat.	Used cavities will be located over deeper water than random cavities. There will be a positive relationship between water depth and nest survival.	Petit and Petit (1996)†, Petit (1999)†, Hoover (2006)†, Cooper et al. (2009)†
Vegetation	More vegetation conceals nests from predators.	Used cavities will have more live vegetation immediately surrounding the nest than random cavities. There will be a positive relationship between vegetation density and nest survival.	Martin (1992), Rangen et al. (1999), Fisher and Wiebe (2006), Cooper et al. (2009)†
Canopy cover	Nests located under dense canopy cover are more concealed from predators.	Used cavities will be located under greater canopy cover than random cavities. There will be a negative relationship between canopy cover and nest predation.	Martin and Roper (1988)
Nest height	Higher nests experience reduced flooding and predation risk.	Used cavities will be located higher above the ground than random cavities. There will be a positive relationship between nest height and nest survival.	Gutzwiller and Anderson (1987), Albano (1992), Fisher and Wiebe (2006), Cooper et al. (2009)†, Miller (2014)
Cavity size	A smaller diameter opening guards against predation, brood parasitism, and larger, more competitive species, e.g., swallow species.	Used cavities will have a smaller entrance diameter than random cavities. There will be a positive relationship between cavity opening size and depredation.	Gutzwiller and Anderson (1987), Cockle et al. (2015), Louder et al. (2015)†
Tree vitality	Dead trees are more likely to hold available cavities.	Used cavities will be located in more dead trees than live trees. Nest survival will be higher for nests in dead trees.	Petit (1999)†, Lõhmus (2016)

†Studies of Prothonotary Warblers; all others are pertinent studies of other cavity-nesting birds.

performance may relate to nest site characteristics directly, by affecting the nest microclimate (Demeyrier et al. 2016), or indirectly by influencing predation, which can be related to nest concealment, nest height, or habitat structure around the nest (Martin 1995) or food resources adjacent to the nest site (Petit and Petit 1996, Foth et al. 2014, Demeyrier et al. 2016). However, the relationship between habitat selection and reproduction is not always positive (Schlaepfer et al. 2002, Demeyrier et al. 2016), and it is important to ensure that a mismatch does not exist, e.g., possibly resulting in a habitat sink population. This information will allow for improved management of the remaining bottomland forests for Prothonotary Warbler habitat and, potentially, also guide the restoration process that is occurring in much of the LMAV (Twedt and Henne-Kerr 2001; D. J. Twedt, *personal communication*).

Another concern associated with the preponderance of studies using nest boxes is that they may provide biased demographic information because nest boxes can be designed with many features that improve the quality of a nesting site. For example, installing boxes on metal poles, placing them over water, and designing boxes with narrow openings and deep cavities that exclude many predators and brood parasites, would be expected to decrease likelihood of nest collapse, improve nest survival, and increase productivity (e.g., Purcell et al. 1997). Accurate estimates of demographic parameters, e.g., clutch size, number fledged, and nest success, for Prothonotary Warblers and other species of concern are needed as critical inputs into full-annual-cycle (FAC) models. FAC models, which are developed to help determine the geographic regions and annual stages that should be targeted for the greatest conservation benefits, are rapidly growing in popularity among many avian ecologists and conservationists (Sheehy et al. 2010, Hostetler et al. 2015) as well as conservation organizations (e.g., Partners in Flight) and the Prothonotary Warbler Working Group. In addition, reproductive parameters from individuals using natural cavities have yet to be compared with those using nest boxes at the same breeding site.

In this study, we (1) assessed nest site microhabitat characteristics selected by Prothonotary Warblers using natural cavities (and nest boxes), (2) explained variation in warbler nest survival as a function of microhabitat characteristics, as well as other potentially important temporal and biological factors, and (3) estimated and compared warbler breeding demographic parameters for individuals using natural cavities and nest boxes. With respect to the first two objectives, we hypothesized that Prothonotary Warblers select nest cavities based on nest site characteristics that are (or historically were) associated with nest survival or productivity (see Table 1 for a list of hypotheses, mechanisms, and predictions related to the habitat selection process and associated nest survival). With respect to the final objective, we hypothesized that nests located in nest boxes and natural cavities provide some similar features related to nest microclimate but differ with respect to predation protection. Therefore, we predicted that they will not differ with respect to clutch size and fledglings produced from successful nests, but nest boxes will have increased nest survival. Our results from this study will improve our ability to manage the limited remaining bottomland forest habitat in the southeastern United States and help us conserve an iconic species of this region.

METHODS

Study area

We conducted our research on a ~96-ha study area in the Dale Bumpers White River National Wildlife Refuge (White River NWR) in eastern Arkansas County, east-central Arkansas (34.24° N, 91.11°W). The refuge is relatively long (~70 km from north to south) and narrow (<10 km in most areas), consisting of 65,000 ha of mostly bottomland hardwood forest.

Across our study area, we installed 65 nest boxes ~1.5 m over the ground in a grid pattern spaced 50–100 m apart over or near (≤ 50 m from) water. We constructed boxes from 1.9-L cardboard milk cartons and painted them greenish-brown (Fleming and Petit 1986). We attached 80% of the boxes (52) to metal conduit poles (3.05 m by 1.27 cm) and placed the other 20% (13) on trees. We cut circular cavity openings of one of three sizes: 32, 35, or 38 mm (and distributed these equally); most cavity openings faced south.

Study species: nest selection process

Male Prothonotary Warblers arrive at White River NWR during the first two weeks of April, followed by females 1–2 weeks later (M. C. Slevin, *personal observation*). Soon after arriving on the breeding grounds, males establish a ~1 to 3-ha territory, inspect many nest cavities, and use moss to pad often multiple cavities in trees, boxes, or other substrates (Petit 1989, 1999). During the subsequent courtship period, females will follow the male and inspect the cavities he visits and ultimately will select one of the cavities for nesting (Petit 1999). The female, exclusively, then builds the nest cup on top of the moss (Petit 1999). The nest selection process can last several days (M. C. Slevin, *personal observation*), and building occurs over a period of 3–8 d (Petit 1999).

Field methods

Habitat selection and reproduction

To address our hypothesis regarding nest site selection behavior and the relationship between habitat features and nest survival (hereafter Hypothesis 1), we located and monitored Prothonotary Warbler nests in both natural cavities and nest boxes during the breeding seasons of 2014 and 2015 (mid-April to mid-July). We located nests in natural cavities by following behavioral cues of males and females, such as carrying nesting material or food to a cavity; we also checked all nest boxes for activity weekly. We monitored all potential nests daily until active, i.e., ≥ 1 egg, and then every 1–3 d, using a digital inspection camera mounted at the end of a flexible fiber optic cord (Explorer Premium Wireless Inspection Camera with Recordable Monitor). To estimate demographic parameters and address our hypothesis regarding the comparison of these parameters between natural cavities and nest boxes (hereafter Hypothesis 2), each time we checked a nest, we recorded number and species of eggs (Prothonotary Warbler or the brood parasite Brown-headed Cowbird; *Molothrus ater*), as well as number and species of nestlings. Once nestlings reached ~7 d in age, we monitored nests every day until fledging (or failure) to ascertain nest fate and estimate the number of fledglings produced (of each species). We also inferred the cause of failure (predation, flooding, or parasitism) from evidence at each nest that did not successfully fledge warbler young. We considered all nests that fledged ≥ 1 Prothonotary Warbler nestling to be successful.

Within a week after each nest failed or fledged young, we measured microhabitat variables, which we chose a priori based on previous literature (Table 1) and our own experience with Prothonotary Warblers. To best reflect the spatially hierarchical process of habitat selection, i.e., birds assess large-scale features first, then nested smaller-scale features (Johnson 1980), we separated these variables into three suites associated with the presumed scales of Prothonotary Warbler nest site selection. First, we evaluated variables related to surrounding water characteristics. We included water depth and cavity height over water surface (or ground if no water present; measured at the start [for habitat selection] and end [for nest survival] of nest attempt), which we measured at the base of the nest tree or poles. Second, we evaluated variables related to surrounding vegetation, including mean leaf density within a 1-m and 5-m buffer centered on the nest tree (visually estimated as a relative index of 0–3), vegetation vitality within 1 m and 5 m of the nest tree (alive or dead), percent forest canopy cover (visually estimated vegetation blocking visible sky; average of five measurements: one at nest, and four at four points 5 m in each cardinal direction from nest), and absolute nest height (as opposed to height-above-water measurement above, this was absolute nest height from the bottom of the cavity opening to the ground, regardless of water depth). Finally, we evaluated variables related to the cavity itself, including cavity opening diameter (because some cavities had multiple openings, we used the smallest dimension of the largest hole; Cockle et al. 2011), nest tree vitality as alive (≥ 1 green leaf on the tree) or dead (no green leaves), nest tree diameter at breast height (DBH), and cavity opening direction (transformed from azimuth degrees to aspect code for analysis; Beers et al. 1966). We included absolute nest height in the vegetation suite because we assumed the bird assessed this prior to individual cavity inspection. We also measured distance from entrance to cup (distance from bottom of cavity opening to top of cup), but we did not include this in habitat selection analysis because we could not obtain an accurate comparative measurement from random cavities (see below).

For each natural cavity, we randomly selected another cavity to use as a paired available nest site. To eliminate overlap of microhabitat features between used and available cavities, but to ensure that the available cavity was likely within the male's territory, we selected available cavities located 25–100 m from the used cavity by walking a transect in a random direction from the nest, carefully inspecting all trees along the transect, and selecting the first cavity that was characterized by microhabitat features that made it available for Prothonotary Warbler use (based on personal observations and literature). We considered cavities available if they were in trees with DBH < 35 cm (M. C. Slevin, *personal observation*), ≤ 100 m from water (Petit 1991*b*), and 0.5–4 m above the ground (Cooper et al. 2009). We also constrained our random sample by excluding cavities with openings too small to allow entry (< 20 mm in diameter), or too shallow or narrow to hold moss, a nest cup, and the minimum observed clutch size of three eggs (< 40 mm deep; M. C. Slevin, *personal observation*). We measured the same microhabitat variables (as described above) at all random cavities. At nest boxes, we measured the same microhabitat variables but excluded distance to cup (all boxes were 117 mm deep), nest tree vitality (we only mounted boxes on live trees or poles), and DBH; we added the feature of mounting substrate (pole or tree) into the third variable suite (cavity characteristics). After the breeding season, we categorized each box as "used" (all boxes that had active nests) or "unused" (never held an active nest).

Relative abundance estimate

To estimate relative Prothonotary Warbler abundance across our study site (for later use as a covariate in nest survival modeling), we divided the study site into 12, 8-ha plots and conducted point counts across each plot. Each plot contained eight point count locations spaced 100 m apart. Although individuals may fly > 100 m away from a territory, thus leading to double counting, we expect this to be such a rare occurrence that its effect on our results was inconsequential. At each location, we conducted three 50-m fixed-radius point counts and recorded all male Prothonotary Warblers that we detected visually or aurally. We averaged the number of males detected across the three visits for each location as an estimate of the number of males at each location. We then averaged abundance estimates from all point counts within 150 m of each nest (a large enough radius to include most adjacent Prothonotary Warbler territories) and assigned that value to each nest as its relative abundance estimate.

Data analyses

We analyzed our data by considering six model selection sets: two describing habitat selection of used natural cavities versus random natural cavities (for two different subsets of data), one describing habitat selection of used boxes versus unused boxes, two describing nest survival (for natural nests and boxes), and one comparing demographic variables in natural cavities versus boxes.

Habitat selection: natural cavities

Prior to analysis, we tested for collinearity among all habitat variables ($r \geq 0.5$); we removed vegetation vitality at both radii because these variables were highly correlated with leaf densities. We did not measure all habitat variables in both years because of the addition of several habitat variables in the second breeding season, so we split our sample of natural cavity nests into two subsets. Subset "A" included nests from both years (2014–2015) where we measured seven microhabitat variables. Subset "B" only included nests from 2015 when we measured those same seven variables plus an additional four (water depth, height over water or ground, nest tree vitality, and DBH). To limit the number of models built and to best reflect the process of habitat selection, we hierarchically built, and compared, generalized linear mixed models (GLMMs) with a binomial distribution and logit link. The dependent variable was cavity type, either "used" or "random," and we modeled this variable with respect to three suites of habitat variables: water, vegetation, and cavity characteristics (for Subset A we could only model the second two suites of variables because we did not measure water variables in 2014). At each hierarchical step, we evaluated all models based on Akaike's Information Criterion corrected for small sample size (AIC_c) and considered all models with $\Delta AIC_c \leq 2$ to be of equivalent model fit (Burnham and Anderson 2002). We also examined model weight (w_i) to assess relative model likelihood. After evaluating the first suite of variables (related to water), we carried all equivalent top models over to the next suite of variables and built both univariate and bivariate models. All models included territory ID as a random effect (to pair each nest cavity to the random cavity in the same territory). We evaluated the potential for relationships to differ by year by including year and an interaction effect between year and each variable included in the model. Finally, once we had assembled our final list of equivalent top models, we assessed the directionality and strength of selection for variables included in the model(s) by examining the sign of the β coefficient (slope) and the associated 85% (as suggested appropriate by Arnold 2010) and 95% confidence intervals (CIs) for each covariate included. We considered variables to be strong predictors of nest site selection when the 95% CI of the β estimate did not include 0, or to be suggestive of a biologically significant relationship when the 85% CI did not include 0. For subset B, we did not evaluate interactions with year because this subset only included nests from 2015. We performed all habitat selection analyses in the lme4 package in Program R (Bates et al. 2015, R Core Team 2016).

Habitat selection: nest boxes

To evaluate features of nest boxes that Prothonotary Warblers selected for, we followed the same process as described above, with a few minor adjustments. The dependent variable was again binomial, but the two possible responses were "used" and "unused," and because used and unused boxes were independent from one another, we did not employ a random effect to pair used and unused boxes. Therefore, we built generalized linear models (GLMs) with a binomial distribution. However, unlike the natural cavity habitat selection analysis, the nest box microhabitat variables were measured for each box, and not for the nests in each box. Therefore, we did not record highly dynamic metrics such as water, because those varied between nest attempts. See Table A1.1 and A1.2 (Appendices 1 and 2) for a complete list of models built for natural cavities and nest box habitat selection analysis.

Nest survival

We modeled relationships between daily nest survival rate (DSR) and microhabitat features by building logistic exposure models in Program MARK (White and Burnham 1999). To limit the number of models we compared, we built univariate and bivariate models from three hierarchical suites of variables related to temporal, biological, and microhabitat characteristics. After evaluating each suite, we carried only those models with a $\Delta AIC_c \leq 2$ over to the next suite of models. The first suite included univariate models of temporal covariates: year, a linear date trend, and a quadratic date trend (as well as an intercept-only null model). The second suite, biological variables, included parasitism status (parasitized or not parasitized by Brown-headed Cowbirds) and relative warbler abundance. The third suite, microhabitat variables, added microhabitat characteristics to top equivalent models from the previous two suites. We compared these to a global additive model as well. After we assembled our list of equivalent top models, we assessed the directionality and strength of the relationship between specific variables and DSR by examining the sign of the β coefficient and associated 95% CI for each covariate included in a top model (we did not assess 85% CIs because MARK does not compute them). We considered a variable to be a strong predictor of nest survival when the CI of the β estimate did not include 0. We limited our sample of failed nests to those that were depredated because the mechanisms of nest failure as a result of predation differ greatly from those of flooding (Chalfoun and Schmidt 2012). We performed this modeling procedure for nest boxes and natural cavities separately because of differences in what variables could be measured for each nest type, e.g., nest tree vitality and DBH only apply to natural cavities and mounting substrate only applies to nest boxes. See Table A2.1 and A2.2 (Appendices 1 and 2) for a complete list of models built for natural cavity and nest box nest survival analysis.

Demographic parameters: natural cavities vs. nest boxes

We used the nonparametric Wilcoxon rank sum test to compare demographic parameters (clutch size and number of young fledged from a nest) between natural cavities and nest boxes ($\alpha = 0.05$). To compare DSRs between natural cavities and nest boxes, we used MARK to model nest survival as a function of nest type and compared this to the null model. If the univariate nest type model was > 2 AIC_c units less than the null, we considered DSR to differ between natural cavities and nest boxes. We also compared 95% CIs of DSR for both nest types (if they did not overlap we considered them to differ). We performed this analysis for two subsets of data: one included all nests and the other was a subset that limited our sample of failed nests to those that were depredated. Finally, to assess the biological significance of DSR, we calculated period nest success, which is the likelihood of surviving the entire nesting period (~26 d from the first egg laid to fledge), by taking the product of DSRs across the entire nesting period. All demographic parameter estimates that we present (± 1 SE) are untransformed values.

RESULTS

Over two years, we monitored 144 active Prothonotary Warbler nests, 84 of which were in natural cavities (Table 2). See Tables 3 and 4 for a summary of microhabitat variable measurements recorded for natural cavities and nest boxes, respectively. We monitored 60 nests in boxes, but only three nest boxes were used by Prothonotary Warblers in 2014 so we limited the habitat selection and nest survival analyses to nest boxes from 2015 (*n* = 57). For comparison of demographic parameters, we included nests in boxes from both years, minus one nest that we found too late to make accurate demographic estimates of clutch size (resulting in *n* = 59). We found two nest boxes occupied by another species (Carolina Wren, *Thryothorus ludovicianus*), 13 boxes remained unused for both seasons, and five boxes were removed from habitat selection analysis because they were destroyed by severe flooding before being used and were not able to be repaired or replaced.

Table 2. Summary, by nest type, of nest success rate (raw percent that fledged at least one Prothonotary Warbler, (*Protonotaria citrea*) and Brown-headed Cowbird (*Molothrus ater*) brood parasitism rate for Prothonotary Warbler nests at White River National Wildlife Refuge, Arkansas, USA in 2014–2015.

Year	Nest type	Nests monitored	Nest success rate	Brood parasitism rate
2014	Natural Cavity	46	64.4	13.3
	Nest Box	3	100.0	0.0
2015	Natural Cavity	38	43.6	12.8
	Nest Box	57	56.6	7.5

Habitat selection

Natural cavities

For nest subset A (*n* = 57 nests from 2014–2015), the model that best described selection of natural cavities included absolute nest height ($r^2 = 0.097$; Table 5). Our predicted direction of this relationship (Table 1) was correct; Prothonotary Warblers selected for cavities located higher in trees than available random cavities (Fig. 2, Table 6). A bivariate model with absolute nest height and cavity orientation was statistically equivalent to the above model ($\Delta AIC_c = 1.94$), but the 95% CI for cavity orientation's β included zero (β = -0.12, 95% CI = -0.65 to 0.40), so we do not consider this model to be a strong predictor of habitat selection patterns. For nest subset B (*n* = 23 nests from 2015 only and including the variables water depth, height over water or ground, DBH, and nest tree vitality), the model that best described selection of natural cavities included nest tree vitality ($r^2 = 0.351$; Table 5). Our predicted direction of this relationship (Table 1) was correct; Prothonotary Warblers preferred dead nest trees (Fig. 3, Table 6).

Fig. 2. Prothonotary Warblers (*Protonotaria citrea*) nesting in natural cavities in White River National Wildlife Refuge, Arkansas, USA in 2014–2015 preferred cavities that were higher than nearby available random cavities (β = 1.17, 95% CI = 0.38 to 2.05; ΔAIC_c from Null = -4.56; $r^2 = 0.097$). Dotted lines represent 95% confidence intervals.

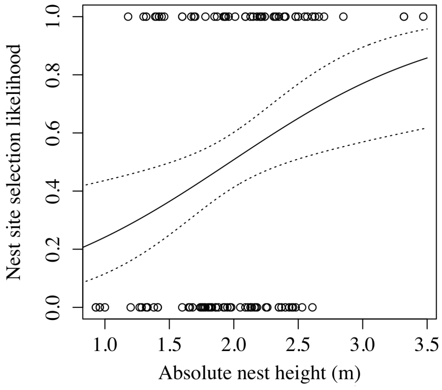

Fig. 3. Prothonotary Warblers (*Protonotaria citrea*) nesting in natural cavities in White River National Wildlife Refuge, Arkansas, USA in 2014–2015 preferred cavities located in dead trees when compared with nearby available random cavities (β = 3.00, 95% CI = 1.20 to 5.97; ΔAIC_c from Null = -8.26; $r^2 = 0.351$).

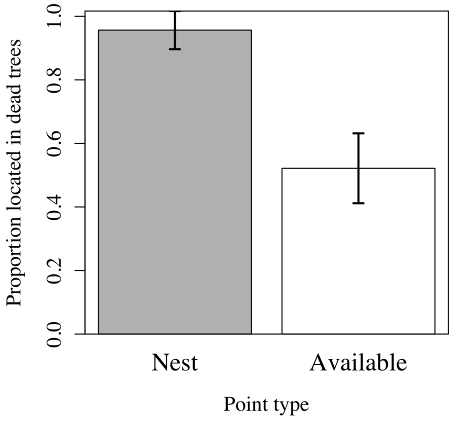

Table 3. Summary of all microhabitat variables measured for Prothonotary Warbler (*Protonotaria citrea*) natural cavity nests found in White River National Wildlife Refuge, Arkansas, USA in 2014–2015. We also present data for random, available cavities measured for habitat selection analysis. Leaf density and vegetation vitality measurements were visually estimated on relative indexes of 0 (low) to 3 (high) and 0 (alive) to 1 (dead), respectively, so we present modes instead of means. Tree vitality was binomial (0 = alive, 1 = dead) and therefore we provide no minimum or maximum value. For Cavity Orientation, we also present the mode. All means are presented ± 1 SE.

Variable	Used natural cavity			Random natural cavity		
	Mean (or mode)	Min	Max	Mean (or mode)	Min	Max
Absolute nest height (m)	2.11 ± 0.07	1.18	3.47	1.83 ± 0.06	0.93	2.61
Distance to cup (cm)	11.3 ± 0.4	4.8	21.5	N/A	N/A	N/A
Cavity Orientation (°)	135–270	N/A	N/A	N/A	N/A	N/A
Cavity Opening Diameter (mm)	46.7 ± 2.39	25	150	47.74 ± 2.67	25	138
Canopy Cover (%)	88.56 ± 0.99	55	100	89.28 ± 1.08	55	100
Leaf Density within 1 m (0–3 index)	0	0	3	0	0	3
Vegetation Vitality within 1 m (0–1 index)	0	0	1	1	0	1
Leaf Density within 5 m (0–3 index)	3	0	3	3	0	3
Vegetation Vitality within 5 m (0–1 index)	0	0	1	0	0	1
Tree Vitality (0–1 index)	0.95 ± 0.06	N/A	N/A	0.52 ± 0.11	N/A	N/A
DBH (cm)	14.97 ± 1.44	7.96	35.65	15.07 ± 1.14	7.8	29.92
Water Depth (m)	0.6 ± 0.1	0.0	2.4	0.5 ± 0.1	0.0	2.4
Height Over Water or Ground (m)	1.6 ± 0.2	0.2	3.5	1.4 ± 0.1	0.0	2.5

Nest boxes

The top model describing nest box use was a bivariate model including box opening diameter and canopy cover (Table 5). However, our predictions that both variables would be positively related to habitat selection (Table 1) were incorrect. Selected boxes tended to have larger cavity openings and be located under less canopy cover than unused boxes (Table 6).

Nest survival

Natural cavities

The only top model describing nest survival of Prothonotary Warbler nests in natural cavities (*n* = 74) was a univariate canopy cover model (Table 7); canopy cover was negatively related to DSR (Fig. 4, Table 6). No temporal or biological variables were included in any of the final top models. Because canopy cover was also related to habitat selection (of nest boxes), Hypothesis 1 was correct: there is a relationship between Prothonotary Warbler habitat selection and nest survival. However, our prediction that canopy cover would be positively related to nest survival (Table 1) was incorrect.

Nest boxes

Two models were equivalent in describing nest survival in nest boxes (*n* = 45 nests): a univariate mount substrate model (Table 7), with pole-mounted boxes having greater nest survival than those on trees (Table 6), and a univariate height-over-water model, with a box's height over the water or ground negatively related to nest survival, however the 95% CI included 0 (Table 7).

Demographic parameters from natural cavities and nest boxes

The portion of Hypothesis 2 regarding clutch size and number of young fledged was correct: these did not differ between natural cavities and nest boxes (clutch size: natural cavities = 4.40 ± 0.11 eggs, *n* = 78 nests, nest boxes = 4.27 ± 0.13 eggs, *n* = 59 nests; *W* = 2565, *P* = 0.22; young fledged: natural cavities = 2.07 ± 0.22 young, *n* = 86 nests, nest boxes = 2.15 ± 0.28 young, *n* = 59 nests; *W* = 2490, *P* = 0.85). However, the portion of Hypothesis 2 regarding nest survival was incorrect: when comparing nest survival between natural cavities and nest boxes (including flooded nests), the univariate nest type model was of equivalent model fit as the null (Table 6) and the 95% CIs of both nest types overlapped, indicating no difference in nest survival between nest

Fig. 4. A negative relationship between canopy cover (within 5 m of the nest tree) and daily nest survival existed for Prothonotary Warblers (*Protonotaria citrea*) nesting in White River National Wildlife Refuge, Arkansas, USA in 2014–2015. This relationship was estimated based on a nest survival model that included percent canopy cover.

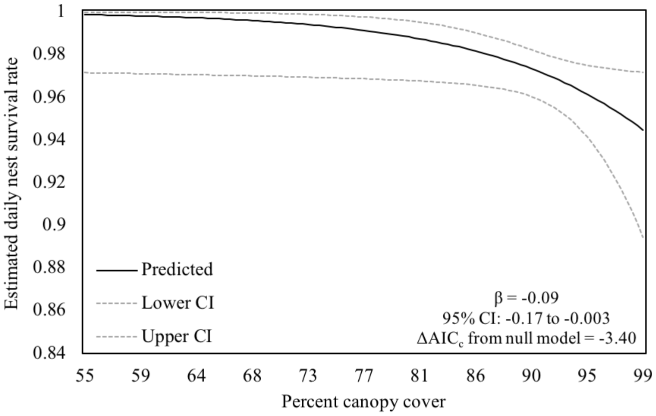

Table 4. Summary of all microhabitat variables measured for nest boxes (used and unused) by Prothonotary Warblers (*Protonotaria citrea*) in White River National Wildlife Refuge, Arkansas, USA in 2014–2015. We present the mode for cavity opening diameter because we had three discrete opening sizes. Leaf density and vegetation vitality measurements were visually estimated on relative indexes of 0 (low) to 3 (high) and 0 (alive) to 1 (dead), respectively, so we present modes instead of means. All means are presented ± 1 SE.

Variable	Used			Unused		
	Mean (or mode)	Min	Max	Mean (or mode)	Min	Max
Absolute nest height (m)	1.55 ± 0.02	1.26	1.76	1.56 ± 0.04	1.14	1.72
Cavity Opening Diameter (mm)	35	32	38	32	32	35
Canopy Cover (%)	91.7 ± 0.95	55	100	94.86 ± 0.48	91	97
Leaf Density within 1 m (0–3 index)	0	0	3	0	0	3
Vegetation Vitality within 1 m (0–1 index)	1	0	1	1	0	1
Leaf Density within 5 m (0–3 index)	3	0	3	3	2	3
Vegetation Vitality within 5 m (0–1 index)	0	0	1	0	0	0

Table 5. Top three models (and null) describing habitat selection of microhabitat features of natural cavity nest sites (vs. random cavity sites; A and B) and nest boxes (C) by Prothonotary Warblers (*Protonotaria citrea*) in 2014–2015 at White River National Wildlife Refuge, Arkansas, USA. All models included a random variable of territory ID to pair used nests with the random cavity within a territory. Subset A included nests from 2014–2015 (n = 57), for which seven microhabitat variables were measured (7 models built, AIC_c of top model = 153.42). Subset B includes nests from 2015 only (n = 23), for which 11 microhabitat variables were measured (11 models built, AIC_c of top model = 57.60). Habitat selection for nest boxes (n = 57) was assessed for nests in 2015 only (8 models built; AIC_c of top model = 60.53).

Model	ΔAIC_c	w_i	k
A. Natural cavities (2014–2015)			
Absolute nest height	0.00	0.55	3
Cavity orientation + Absolute nest height	1.93	0.21	4
Cavity diameter + Absolute nest height	2.11	0.19	4
Null	4.56	0.06	1
B. Natural cavities (2015)			
Tree vitality	0.00	0.98	3
Null	8.26	0.02	1
Cavity diameter	12.31	<0.01	3
Cavity orientation	12.50	<0.01	3
C. Nest boxes 2015			
Canopy cover + Entrance diameter	0.00	0.63	3
Canopy cover	2.75	0.16	2
Canopy cover + Mounting substrate	3.22	0.13	3
Null	6.20	0.03	1

Table 6. Summary of parameter estimates for variables included in the top models describing habitat selection and nest survival of Prothonotary Warblers (*Protonotaria citrea*) nesting in White River National Wildlife Refuge, Arkansas, USA in 2014–2015.

Model set	Parameter	β	95% CI	
Natural cavity habitat selection 2014–2015	Intercept	-2.32	-4.09	-0.71
	Abs. nest height	1.18	0.38	2.05
Natural cavity habitat selection 2015	Intercept	-2.40	-5.30	-0.76
	Nest tree vitality	3.00	1.20	5.97
Nest box habitat selection 2015	Intercept	11.02	-10.90	37.28
	Opening diameter	0.35	0.04	0.73
	Canopy cover	-0.23	-0.51	-0.03
Natural cavity nest survival	Intercept	11.41	3.70	19.11
	Canopy cover	-0.09	-0.17	-0.003
Nest box nest survival	Intercept	3.44	2.63	4.26
	Mount substrate	1.35	2.07	2.50
Nest survival by nest type	Intercept	3.28	2.96	3.60
	Nest type	0.27	-0.02	1.03

types (natural cavities: DSR = 0.964, 95% CI = 0.951 to 0.974; nest boxes: DSR = 0.978, 95% CI = 0.967 to 0.985). However, when we limited the only failed nests to those that were depredated, the univariate nest type model was better than the null (null $\Delta AIC_c = 3.59$), but the 95% CIs of each nest type still overlapped (natural cavities: DSR = 0.972, 95% CI = 0.959 to 0.981; nest boxes: DSR = 0.987, 95% CI = 0.977 to 0.993). Finally, period nest success for natural cavities was 0.41 (95% CI = 0.29–0.52) and 0.56 (95% CI = 0.42–0.68) for nest boxes.

DISCUSSION

We found that, when nesting in natural cavities, Prothonotary Warblers preferred cavities in dead trees that were higher above ground than random cavities, and nests were less successful in areas with greater canopy cover. When using nest boxes, Prothonotary Warblers selected boxes that had larger openings and had less canopy cover surrounding the nest than unused boxes, and nests were more successful in boxes that were mounted on poles (instead of trees). Finally, Prothonotary Warbler nests were less frequently depredated in boxes than in natural cavities, although other demographic parameters did not differ between the two nest types. We discuss the potential ultimate explanations for each result, possible explanations for minor incongruence

Table 7. Top three models (and intercept-only null) describing the relationship between microhabitat variables and daily nest survival of Prothonotary Warbler (*Protonotaria citrea*) nests located in natural cavities (18 models built, AIC_c of top model = 202.60) and nest boxes (20 models built, AIC_c of top model = 101.65) at White River National Wildlife Refuge, Arkansas, USA in 2014–2015.

Model	ΔAIC_c	β	95% CI		k	Deviance
A. Natural cavities						
Canopy Cover	0.00	-0.09	-0.17	-0.003	2	198.58
Height Over Water	2.04	0.001	-0.001	0.001	2	200.62
Multivariate model (variables listed below)	2.93	-	-	-	4	201.35
Canopy cover	-	-0.09	-0.18	-0.01	-	-
Leaf density (1 m)	-	-0.03	-0.33	0.26	-	-
Leaf density (5 m)	-	-0.21	-0.63	0.22	-	-
Null	3.40	1.23	1.17	1.30	1	203.60
B. Nest boxes						
Height Over Water	0.00	-0.16	-1.23	0.90	2	99.65
Mounting Substrate	0.15	1.35	0.21	2.49	2	97.78
Multivariate model (variables listed below)	1.55	-	-	-	5	93.13
Absolute nest height	-	1.99	-3.49	7.47	-	-
Box Orientation	-	-0.01	-0.03	0.004	-	-
Opening Diameter	-	-0.001	-0.05	0.05	-	-
Mounting Substrate	-	1.74	0.50	2.98	-	-
Null	3.15	1.34	1.28	1.41	1	102.80

between habitat selection and nest survival, management implications, and future research directions.

Prothonotary Warblers selected for higher nest cavities relative to available cavities, confirming our hypothesis and prediction regarding nest height (Table 1). They may have done this to reduce the risk of flooding, which is a danger they consistently face because they frequently choose cavities located over water to reduce predation risk (Hoover 2006) and interspecific nest site competition (Cooper et al. 2009), and, possibly, because these territories typically have greater arthropod abundance (Petit and Petit 1996). Water levels in White River NWR, and other low-elevation areas, can change rapidly (≥ 0.25 m d^{-1}; M. C. Slevin, *personal observation*) and severely throughout the season (Cooper et al. 2009), and even temporary inundation can be fatal to eggs and young nestlings (M. C. Slevin, *personal observation*), likely because they are unable to thermoregulate effectively (Dawson and Evans 1957). Accordingly, we observed 100% nest failure for 11 nests where water levels reached the nest cup. Thus, nesting in higher cavities should reduce the likelihood of nest failure caused by flooding. However, we found few nests > 3.5 m (this is also rare in other studies; Hoover 2001, Cooper et al. 2009), so it does not appear nesting in the highest possible cavity would be considered a likely strategy for Prothonotary Warblers. This could be because they are understory foragers and spend most of their time in this canopy stratum (Petit 1999). Nest height may also be constrained by interspecific nest site competition with species such as Tufted Titmice (*Baeolophus bicolor*), which often nest ~11 m above the ground (Ritchison et al. 2015), and Carolina Chickadees (*Poecile carolinensis*), which can nest in Prothonotary Warblers' height range, but often higher (mean = 2.8 m, range = 0.7 - 7.6 m; Albano 1992).

In addition to flooding, a major threat to nest survival for all passerines, and therefore likely a strong pressure on the evolution of nest site selection behavior, is predation (Martin 1993). This is one potential explanation for the preference of higher nests (Nilsson 1984, Albano 1992, Miller 2014), as well as large diameter nest box openings and building the nest cup close to the natural cavity entrance. Although cavities may provide more protection for nestlings than open cup nests (Martin and Li 1992), deep cavities with narrow openings may make escape more difficult for parents on the nest. In the case of Prothonotary Warblers, when approached on the nest, females will often not flush until physical contact with the nest tree or box occurs (Petit 1999). This behavior likely reduces the opportunity for visual predators to locate their nest; however, it may make the female more prone to predation when incubating and brooding. Adult females have been depredated by northern raccoons (*Procyon lotor*; C. M. Tonra, *personal communication*) and possibly American black bears (*Ursus americanus*; M. C. Slevin and T. J. Boves, *personal observation*) while on the nest. Therefore, building the nest cup close to the cavity entrance or selecting boxes with larger openings may help balance the potential trade-off between nestling and adult survival. Also, the opening sizes that we provided on our nest boxes are, in general, smaller than those available naturally (Table 5), and thus our incorrect prediction that warblers would select smaller nest box openings may simply reflect the fact that the species rarely has the option of selecting this cavity size naturally.

Despite evidence of habitat selection behavior occurring, our first hypothesis was partially incorrect because none of the natural cavity nest site features Prothonotary Warblers preferred were related to nest survival, at least for natural cavities. This incongruence may be unexpected because habitat selection behavior should be adaptive (Hildén 1965, Martin 1998, but see Chalfoun and Schmidt 2012, Demeyrier et al. 2016). There are several potential explanations for this lack of clear adaptive behavior. First, natural selection acts on behaviors like habitat selection via variation in lifetime fitness; although nest survival during a single breeding season may be correlated to lifetime fitness, it may rarely be perfect (reviewed in Chalfoun and Schmidt

2012). Additionally, a two-year study may not be able to capture the long-term variation in predation rates and ecological variability, e.g., annual fluctuations in flood severity (Cooper et al. 2009) that have driven the evolution of behaviors, such as nesting over water to reduce predation risk and selecting higher cavities to reduce flood risk. For example, nest survival may be related to some nest site variables only during years of peak predator densities (Schmidt and Ostfeld 2008). This may be the case for hydrological variables, e.g., nest height may be related to nest survival only during years with severe flooding. Finally, because of considerable recent anthropogenic alterations to the region's forests and hydrology, current and historical conditions may differ, which could lead to slightly nonadaptive behavior (reviewed in Chalfoun and Schmidt 2012).

Several of our results, however, do suggest a relationship between nest predation pressure and the nest site preferences we observed. Canopy cover was negatively related to natural cavity nest survival and to nest box selection. Additionally, 95% of natural cavity nests were in dead trees. Together, these results may suggest a historical positive relationship between canopy cover and nest predation, somewhat supporting our first hypothesis. However, the underlying mechanism between canopy cover and nest survival remains unclear. One possibility is a relationship between vegetation density and predator abundance and behavior (Li and Martin 1991), whereby predators are more abundant in areas with more cover and may be more protected from birds that defend their nests by diving aggressively at potential predators. Another possibility is that birds may hedge their bets and select nest sites with habitat characteristics that are ideal for postfledging survival, such as high canopy cover (Jackson et al. 2013), but that may differ from those characteristics ideal for nest survival, such as low canopy cover. Finally, it is unclear if warblers preferred cavities in dead trees for the advantages provided by dead trees, e.g., reduced canopy cover, or if cavities are simply more common in dead trees because of the ease of excavation by primary cavity nesters using trees with softer wood (Lõhmus 2016). Warblers at White River NWR more frequently used cavities excavated by primary cavity nesters (e.g., Downy Woodpecker; *Picoides pubescens*) versus natural tree hollows (M. C. Slevin, *personal observation*), so perhaps warblers' selection patterns are more a reflection of nest tree selection patterns of local primary cavity nesters, but further observation would be necessary. Studies involving experimental forest management and studies of fledgling habitat selection and survival may improve our understanding of the causal mechanisms of the relationships we observed.

The lack of difference we observed in nest survival between nest types (when including all causes of nest failure), suggesting our second hypothesis was incorrect, was likely driven by the increased likelihood of flooding in nest boxes (n = 9, vs. n = 2 for natural cavities). This is explained by the fact that our placement of nest boxes was at a lower height (1.55 ± 0.01 m) than natural cavities used by Prothonotary Warblers at our site (2.11 ± 0.07 m). This further supports our inference regarding the selection for higher nest cavities to reduce flood risk. When excluding flooded nests, i.e., including predation events only, nest survival was greater in nest boxes than in natural cavities, unlike previous work with Prothonotary Warblers that either found nest depredation rates to be equivalent among nest types (Hoover 2006), or that nest boxes provided greater protection from predators only when water around the nest was relatively deep (Petit and Petit 1996). However, based on anecdotal evidence from the breeding season following completion of this study, the benefits that nest boxes provided with respect to depredation may decline quite rapidly as some predators learn to identify nest boxes as a food source. In 2016 (the third breeding season with boxes present on the study area), we observed an increase in predation events at nest boxes by northern raccoons (inferred by scratch marks, removed box lids, and nests disturbed or pulled out of box) and black bears (presence of bear hair and tracks at boxes, boxes completely destroyed, and metal conduit poles bent; M. C. Slevin and T. J. Boves, *personal observation*). This temporally dynamic relationship between the time since nest box installation and predation by some species has previously been observed for Prothonotary Warblers (C. M. Tonra and J. P. Hoover, *personal communication*) as well as other species of birds that readily use nest boxes (Martin 1993, Miller 2002), especially when boxes are installed at high densities (Petit and Petit 1996).

Management implications and future directions

Prothonotary Warblers have been declining by > 1% yr^{-1} over the past half century and possible (mis)management of the limited remaining bottomland forests of the southeastern U.S. may have contributed to this decline (Petit 1999). The habitat features we found Prothonotary Warblers selected for (higher cavities in dead trees), and those related to nest survival (canopy cover), could be provided via a combination of forest and hydrological management strategies.

There are several different management strategies available for providing nesting habitat for Prothonotary Warblers. However, because the causal mechanism(s) explaining the relationship between canopy cover and natural cavity nest survival or nest box habitat selection are unknown, we caution against implementing extensive or invasive forest management before completing further studies aimed at clarifying the cause of these relationships. Therefore, we suggest experimental manipulation of canopy and vegetation (particularly understory; Petit 1999) at multiple scales and measuring effects on both habitat selection and nest survival. Cooper et al. (2009), which also studied Prothonotary Warblers in White River NWR, found no noticeable difference in effect of forest harvest treatment types on productivity, nest predation, or brood parasitism. However, they did report treated plots had lower male breeding densities and available nest cavities than control plots, with 2.1-ha patch cuts per 50-ha plots showing the lowest bird and cavity densities. Therefore, we suggest employing forest management strategies that avoid patch cuts, e.g., single tree or group selection, while attempting to protect likely nest trees. Proposed management scales range from the 5-m radius around nest trees that we studied here, to the size of a typical territory (0.5–1.5 ha; Petit 1999), and therefore less than the 2.1 ha cuts found to be harmful to breeding densities. Other potential methods of improving habitat for Prothonotary Warblers includes girdling small numbers of living trees of appropriate DBH to increase available nest tree numbers by providing dead trees (Fassnacht and Steele 2016) for cavity production by primary cavity nesters, as well as provide targeted small-scale canopy thinning. Once the scale and magnitude of canopy thinning preferred by Prothonotary Warblers are better understood, further forest management could be implemented.

Regarding hydrological management, restoring (or maintaining) natural hydrological regimes where feasible may also lead to increased snag creation through increased flood stress, causing tree mortality (Gee et al. 2014, 2015). In addition, at least partial restoration of the historic hydrology of the region could mitigate problems related to channelization and damming. These practices often result in altered timing, severity, and length of flood events in bottomland forests. Some areas now experience rapid water level fluctuations or increased periods of dry ground during a single nesting attempt (~26 d long; Hoover 2006, Cooper et al. 2009; M. C. Slevin, *personal observation*). Thus, these modern flood regimes increase the likelihood of nest failure by both flooding cavities and, conversely, exposing nests to common shallow-water nest predators such as rat snakes, northern raccoons, and black bears (Hoover 2006, Cooper et al. 2009).

Future directions for management and conservation of Prothonotary Warblers include the development of FAC population models (Hostetler et al. 2015) that would make use of the demographic parameters that we, and others from across the breeding range, have estimated (along with migratory connectivity data obtained from geolocator work). These models will allow us to determine if there are regions that we should target for future conservation and management as well as specific high-risk stages of the annual cycle. Our results suggest that estimates of clutch size and number fledged from nest boxes may be reliable as surrogates for these parameters from natural cavities. However, we caution against using depredation rates from nest boxes in place of those from natural cavities because of the difference in depredation rates we quantified between nest type, as well as the anecdotal annual increase in depredation rates for nest boxes. Finally, we advocate the expansion of our study to additional areas within the LMAV and expanding the study to compare natural cavity habitat selection patterns among different important breeding regions to assess the consistency of the patterns we observed.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1235

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BIRD STUDIES ÉTUDES D'OISEAUX CANADA

Appendix 1.

Table A1.1. List of suites built for hierarchical model selection analyzing habitat selection process of Prothonotary Warblers nesting in natural cavities or nest boxes in White River National Wildlife Refuge, Arkansas, USA in 2014-2015. Each model was a generalized linear mixed model with the random effect of territory identity (not shown). The top model of each suite (†) was carried on to the next suite as the new suite's null model, and parameters from this model were added to the new suite's models. If no model was better than the null model, the null model was carried on to the next suite. In the text, we report the parameters of the final top model or models (‡). All models were built and compared in Program R.

Subset (years sampled)	Suite	Parameters in model
A (2014-2015)	1. Vegetation	None (null model)
		Absolute nest height†
		Canopy cover
		Leaf density (1 m)
		Leaf density (5 m)
	2. Cavity	Absolute nest height (null)‡
		Cavity orientation + Absolute nest height
		Cavity diameter + Absolute nest height
B (2015)	1. Water	None (null model)†
		Water depth
		Height over water or ground
	2. Vegetation	None (null model)†
		Absolute nest height
		Canopy cover
		Leaf density (1 m)
		Leaf density (5 m)
	3. Cavity	none (null model)
		Tree vitality‡
		Opening diameter
		Cavity orientation
		Diameter at breast height

†Top model from suite that we advanced to next suite as new null model.

‡Final top model, reported in text’s Results.

Table A1.2. List of suites built for hierarchical model selection analyzing habitat selection process of Prothonotary Warblers nesting in nest boxes in White River National Wildlife Refuge, Arkansas, USA in 2015 only. Each model was a generalized linear model with the binomial dependent variable of used (boxes that were nested in) versus unused (boxes that were never nested in). The top model of each suite (†) was carried on to the next suite as the new suite's null model, and parameters from this model were added to the new suite's models. If no model was better than the null model, the null model was carried on to the next suite. In the text, we report the parameters of the final top model or models (‡). All models were built and compared in Program R.

Suite	Parameters in model
1. Vegetation	none (null model)
	Canopy cover†
	Absolute nest height
	Leaf density (1 m)
	Leaf density (5 m)
2. Box	Canopy cover (null)
	Canopy cover + Box orientation
	Canopy cover + Opening diameter‡
	Canopy cover + Mounting substrate

†Top model from suite that we advanced to next suite as new null model.

‡Final top model, reported in text's Results.

Appendix 2.

Table A2.1. List of suites built for hierarchical model selection assessing nest survival of Prothonotary Warblers nesting in natural cavities in White River National Wildlife Refuge, Arkansas, USA in 2014-2015. Each model was a logistic exposure model (built in Program MARK) assessing the relationship between daily nest survival rate (dependent variable) and independent variables organized into hierarchical suites of temporal, biological, and habitat variables. Top model of each suite (†) was carried on to the next suite as the new suite's null model, and parameters from this model were added to the new suite's models. If no model was better than the null model, the null model was carried on to the next suite. In the text, we report the parameters of the final top model or models (‡). All models we built and compared in Program MARK.

Suite	Parameters in model
1. Temporal	None (null model)†
	Year
	Date
	(Date) x (Date)
2. Biological	None (null model)†
	Brood parasitism status
	Relative Prothonotary Warbler abundance
3. Habitat	none (null model, same as Suite 2)
	Global model (includes all parameters below)
	Water depth
	Height over water or ground
	Absolute nest height
	Canopy cover‡
	Leaf density (1m)
	Leaf density (5m)
	Cavity orientation
	Opening diameter
	Diameter at breast height
	Tree vitality

†Top model from suite that we advanced to next suite as new null model.

‡Final top model, reported in text’s Results.

Table A2.2. List of suites built for hierarchical model selection assessing nest survival of Prothonotary Warblers nesting in nest boxes in White River National Wildlife Refuge, Arkansas, USA in 2014-2015. Each model was a logistic exposure model (built in Program MARK) assessing the relationship between daily nest survival rate (dependent variable) and independent variables organized into hierarchical suites of temporal, biological, and habitat variables. Top model of each suite (†) was carried on to the next suite as the new suite's null model, and parameters from this model were added to the new suite's models. If no model was better than the null model, the null model was carried on to the next suite. In the text, we report the parameters of the final top model or models (‡). All models we built and compared in Program MARK.

Suite	Parameters in model
Temporal (1st)	none (null model)†
Temporal (1st)	Year
Temporal (1st)	Date
Temporal (1st)	(Date) x (Date)
Biological (2nd)	None (null model)†
Biological (2nd)	Brood parasitism status
Biological (2nd)	Relative Prothonotary Warbler abundance
Habitat (3rd)	None (null model)
Habitat (3rd)	Water depth
Habitat (3rd)	Height over water or ground‡
Habitat (3rd)	Absolute nest height
Habitat (3rd)	Canopy cover
Habitat (3rd)	Leaf density (1m)
Habitat (3rd)	Leaf density (5m)
Habitat (3rd)	Box orientation
Habitat (3rd)	Opening diameter
Habitat (3rd)	Mounting substrate‡

†Top model from suite that we advanced to next suite as new null model.
‡Final top model, reported in text's Results.