

ECOLOGICAL AND BEHAVIORAL IMPACTS OF SNAG DENSITY ON CAVITY-
NESTING BIRDS IN THE OAK SAVANNA

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ABSTRACT

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Natural and anthropogenic disturbances affect the abundance, availability, and distribution of resources within oak savanna, an early successional ecosystem. Disturbance-dependent species, such as cavity-nesting birds of the oak savanna, are experiencing population declines. The cavity-nesting bird guild depends on snags (standing dead trees), which occur naturally, but are also formed as a result of oak savanna restoration practices. In order to understand the role that snag density plays on the ecology and behavior of cavity-nesting birds, we assessed the relative abundance, evidence of reproductive success, activity budgets and substrate use of the guild in five oak savanna sites. We also analyzed the influence of other site characteristics including canopy cover and area on all bird relative abundance, diversity, and cavity-nesting bird behavior. Cavity-nesting bird and all bird abundance were related to snag density by polynomial functions where the relative abundance of birds was highest at either ends of the snag density range. The site without any confirmed nests and the lowest species diversity had the lowest snag density (5.4 snags/ha) and the most homogenous canopy, however, the weight of juvenile Eastern Bluebirds was highest at that site. No differences in activity budgets were found between sites at the guild scale, however, substrate use at the guild and species scale was different between sites. At the guild scale, as snag density increased, snags were used more often and as canopy cover increased, snags and dead wood were used less and live wood was used more often. At the species scale, patterns of substrate use were similar to those of the guild, however, the site with the lowest snag density and homogenous canopy particularly influenced substrate use as canopy cover increased. These results suggest that not only is snag density

important to cavity-nesting bird ecology and behavior, but that the vegetative structural context of snags in oak savanna is an important factor as well and should be considered when oak savanna restoration takes place.

In honor of

Dorothy Irene Johnston

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CHAPTER I

GENERAL INTRODUCTION

Disturbance is a phenomenon in all ecosystems and can be defined as “a relatively discrete event in time that disrupts the structure of an ecosystem, community or population and changes resource availability or the physical environment” (White and Pickett 1985). Disturbances are described in terms of intensity, frequency, and size for any given ecosystem (Turner et al. 1989). Disturbances that occur at moderate intensities, frequencies, and sizes aid in structuring ecosystem diversity at a local scale (Connell 1978). Intermediate disturbance favors colonization of r-selected species but does not favor competitive elimination by k-selected species. An intermediate level of disturbance will allow a diverse composition of r and k-selected species within an ecosystem (Connell 1978). At the scale of a community, various sources (natural and anthropogenic) and levels (frequency, intensity, and size) of disturbance create a mosaic of patches as well as heterogeneity across the landscape (Sousa 1984, White and Pickett 1985). Resource availability and the physical structure of an ecosystem will be influenced by disturbance which will have an impact on the abundance, diversity and fitness of organisms living in those ecosystems.

By impacting physical and biological habitat structure, disturbance changes the diversity and abundance of organisms. In a fire-maintained shrubland ecosystem, the intensity and frequency of fire along with seasonal moisture levels determined the survivorship and diversity of shrubland flora and fauna (Christensen 1985). In stream ecosystems where stream bed movement due to discharge is a form of disturbance, macroinvertebrate taxa were found to be more diverse at areas of moderate stream bed movement (Townsend and Scarsbrook 1997).

Prescribed fires in southern Ohio mixed-oak communities caused a temporary reduction in shrubs, saplings, and leaf litter (Artman et al. 2001). As a result, densities of four ground-nesting bird species declined and densities of two ground-foraging bird species increased. Frequent prescribed fires (10-26 fires in 32 years) in an oak savanna changed the stand structure; northern pin oak and bur oak seedlings were present, there were no saplings, and the basal area as well as overstory tree density were lower compared to plots with infrequent fires (Peterson and Reich 2001). In the same oak savanna, habitat features that resulted from prescribed fires such as densities of trees, shrubs, and snags had a positive effect on particular bird foraging guilds. Abundance of omnivorous (ground and lower canopy) feeders and insectivorous bark gleaners (i.e., woodpeckers) increased and insectivorous species decreased, especially in the upper canopy (Davis et al. 2000). These studies demonstrate that changes in habitat structure due to disturbance also change the diversity and guild structure of ecosystems. In some ecosystems disturbance can create one particular habitat feature that is an important component to the ecosystem.

Disturbance in forest, woodland, and savanna ecosystems can create standing dead or partially dead trees known as snags. In forest ecosystems, a disturbance such as a storm event may cause the death of a single canopy tree and result in a gap that allows colonization of shade-intolerant species (Runkle 1982). Storm events that produce strong winds also create snags in open areas like savannas. Natural or anthropogenic fires aid in creating snags that many organisms utilize. Another cause of snag formation is the spread of a fungus known as oak wilt (*Ceratocystis fagacearum*). Oak wilt is spread by root grafts between oak trees and sap-feeding beetles, which increase the risk for nearby oaks to be infected (Rexrode and Brown 1983). A common management technique for creating snags for habitat is girdling and inoculation of trees.

Girdling and inoculation consists of removing a complete ring of bark from a tree, and then heart rot fungus spores are injected into the live tree tissue (Gary Haase, The Nature Conservancy, personal communication). Although disease, pest infestation, and management may take a few years to create a snag, the disturbance is discreet relative to the age of the tree. Natural and anthropogenic disturbance create snags, thus density and characteristics of snags can be used to represent disturbance.

Snags have many impacts on habitat selection and foraging ecology of cavity-nesting birds. White birch snag density in a Newfoundland forest best predicted habitat selection of Downy and Hairy Woodpeckers, and density of snags greater than 20 cm diameter at breast height (dbh) best predicted habitat selection for Black-backed Woodpeckers (Settingington et al. 2000). Raphael and White (1984) found that cavity-nesting birds preferentially foraged on snags and densities of cavity-nesting birds were positively correlated with densities of snags greater than 38 cm dbh. Hairy Woodpeckers preferred to forage on large diameter, well-decayed snags in Oregon, and they spent 91% of their time foraging on the main stem (bole) of the snag rather than at the top (Weikel and Hayes 1999). Cavity-nesting birds, as a guild, have a range of preferred snag characteristics when used for foraging. For example, woodpeckers in Texas preferred to forage on oak trees and snags that were 3-10 m in height and lacked bark (Conner et al. 1994). Snag age also has an effect on woodpecker foraging; young ponderosa pine snags showed more woodpecker foraging and beetle boring activity than older snags (Farris et al. 2002). The characteristics of snags are important for habitat selection as well as foraging, which implies that snags also play a significant role in reproductive success.

Specific snag characteristics are often related to nest site selection of cavity-nesting species. For example, tree hardness may limit which species are able to excavate nest cavities

based on their excavating ability. Hairy Woodpeckers are able to excavate harder wood than Downy and Red-headed Woodpeckers and Downy Woodpeckers had nests in trees and snags that were softer than nest sites for Hairy Woodpeckers (Jackson and Jackson 2004). The distribution of snags may also play a role in nest selection; woodpeckers preferred to nest in patches of soft trees (Schepps et al. 1999). Ingold (1994) found that Northern Flickers (ground feeder) and Red-headed Woodpeckers (aerial feeder) nested in more open areas than Red-bellied Woodpeckers, a bark-gleaning species. This supports the idea that nest site selection is closely tied to foraging habitat needs. In Missouri, primary cavity-nesting bird weight was correlated with the size of snags used for nesting (Brawn et al. 1984). Cavity-nesting species display a range of morphology, excavating ability, and foraging strategy that result in them nesting in snags with various characteristics.

Snag management for cavity-nesting birds has been well described (Evans and Conner 1979, DeGraaf and Shigo 1985, Bunnell et al. 2002). These studies have focused on distribution, density, and size of snags in forested areas and are based on assessments of abundance, numbers of cavities, and evidence of foraging. In order to support stable cavity-nesting bird populations along with other wildlife, there should be 2-3 large snags (greater than about 30 cm dbh) per hectare and 10-20 smaller snags per hectare in a forest (Cain 1996, Boleyn et al. 2002, Bunnell et al. 2002). Other studies have successfully described or modeled snag densities and characteristics specifically for cavity nesting birds (Evans and Conner 1979, Brawn et al. 1984, Conner et al. 1994, Ohmann et al. 1994, Giese 1999, Schepps et al. 1999, Steeger and Dulisse 2002). Raphael and White (1984) were able to determine that cavities excavated by cavity-nesters were the most important source of nest cavities for non-excavating species. They also found that cavity-nesting birds nested in and foraged preferentially on snags. These studies

demonstrate the depth of knowledge about the importance and use of snags by cavity-nesting birds in forests; however, there is a lack of understanding pertaining to the use of snags, regardless of size, in disturbance-dependent ecosystems.

Oak savanna is a very rare ecosystem dependent on moderately high frequency and intensity of disturbance in order to function (Abrams 1992, Brawn et al. 2001). Oak trees, an herbaceous understory of tallgrass prairie species, and 10-60% canopy cover characterize the oak savannas that grow on outwash ridges formed during the last glaciation event in North America (Anderson and Bowles 1999). The main sources of disturbance in oak savanna are fire and wind. Fire historically occurred frequently (few times every decade), although humans have suppressed natural fires since settlement. The suppression of fire has caused oak savannas to disappear; the total area of oak savanna in the American Midwest has decreased to 0.02% of pre-settlement area (Nuzzo 1986). The frequency of fire in oak savannas has a marked effect on seedling, sapling, and overstory species composition and density (Perterson and Reich 2001). Historically, oak savanna in the Oak Openings Region (northwest Ohio) was described as having 14 trees/ha, whereas a more closed-canopy system, oak woodland, had 90 trees/ha (Brewer and Vankat 2004). The open vegetative structure of oak savanna, which is maintained by disturbance, provides a unique context in which snags, a disturbance-related resource, are valued and used by cavity-nesting birds.

The objective of this thesis was to assess the impacts of snag density on cavity-nesting birds in oak savanna. The ecology and behavior of a guild of six cavity-nesting birds was assessed at five sites of oak savanna, representing a range of snag density. In Chapter 2, cavity-nesting bird abundance was described as a function of snag density and evidence of nesting was measured at all sites. Total bird abundance and diversity was measured at each site as a function

of snag density. Two other site characteristics, canopy cover and area, were also measured and used to describe trends in the data. In order to understand ecological trends of cavity-nesting birds, guild activity budgets were analyzed for differences among sites in Chapter 3. Site characteristics including snag density, canopy cover, and area were used to describe trends in activity budgets as well as behavioral substrate use for Red-headed Woodpeckers and Eastern Bluebirds.

The cavity-nesting bird guild used in this study included four primary cavity-nesters and two secondary cavity nesters. Primary cavity-nesters excavate their own cavities to roost and nest in. Downy Woodpeckers (*Picoides pubescens*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Red-headed Woodpeckers (*Melanerpes erythrocephalus*), and Northern Flickers (*Colaptes auratus*) were the primary cavity-nesting birds in this study. Secondary cavity-nesters need to roost and nest in cavities, though they use previously formed cavities to do so. Eastern Bluebirds (*Sialia sialis*) and Great Crested Flycatchers (*Myiarchus crinitus*) were the secondary cavity-nesting birds used in this study. This set of cavity-nesters also varies in methods of feeding. The Red-bellied and Downy Woodpeckers glean insects off of tree surfaces, such as within the fissures of oak bark. The Red-headed Woodpecker and the Great Crested Flycatcher can chase and capture insects in flight, a technique known as flycatching. Eastern Bluebirds and Northern Flickers mainly forage on the ground. Even though these species have particular methods of feeding, there is still a large variety in the techniques in which they feed. All species are known to live in open areas with some trees during the breeding season (Moore 1995, Lanyon 1997, Gotway and Plissner 1998, Shackelford et al. 2000, Smith et al. 2000, Jackson and Ouellet 2002). The use of a guild of cavity-nesting species provides a broad understanding of the impact of snag density on the ecology and behaviors that contribute to fitness.

CHAPTER II

THE IMPACT OF SNAG DENSITY ON THE BREEDING ECOLOGY OF CAVITY-NESTING BIRDS

Introduction

The cavity-nesting bird guild, by definition, depend upon the unifying resource of snags (standing dead trees), and use snag resources in a variety of ways. Birds within this guild select snags with specific characteristics (height, size, decomposition state) for nesting sites (Raphael and White 1984, Evans and Conner 1979, Brawn et al. 1984, Ingold 1994). Snags are also used as a foraging substrate, either due to increased amount of arthropod communities found in them (Evans and Conner 1979, Weikel and Hayes 1999) or used as a perch for hunting (Rosenberg et al. 1988). In addition, some birds within this guild use snags as a substrate for communication in the form of drumming (e.g., Three-toed Woodpecker, Imbeau and Desrochers 2002). Given the diversity of resource uses that snags provide within this guild, it is apparent that snags are a critical resource and their availability may influence the location, population numbers, and fitness of cavity nesting birds.

As with many critical ecological resources that influence the densities of populations, the availability or limitation of snags has spawned research focused on snag management. It has been suggested that optimal management of snag densities would promote the abundance of cavity-nesting birds (Evans and Conner 1979, Raphael and White 1984, DeGraaf and Shigo 1985, Ohmann et al. 1994). Snag management has most often been limited to the presence of snags large enough to serve as substrates for excavating nests, yet it is clear that this resource is used for more than just nesting. Other studies have investigated an expanded role of snags as a

multifaceted resource and have shown that an increase in abundance and/or species richness of secondary cavity-nesting birds depends upon the spatial distribution of snags (Land et al. 1989, Bunnell et al. 2002, Lohr et al. 2002). Regardless of the perspective on the role that snags play in the ecology of cavity nesting birds, all of these studies show the importance of snags and their management to bird populations.

Before any effective management plan can be developed, it is necessary to understand the processes that form snags and how these different types of snags are perceived or used differently by cavity nesting birds. Snags are primarily formed by natural disturbances such as fire, storms, plant disease, and pest infestation (Franklin et al. 1987). In addition, anthropogenic events such as land management techniques can also generate snags. In a coarse overview of avian responses to fire, which creates snags, 36% of studies reported cavity-nester species to respond positively and only 18% responded negatively to fire (Saab and Powell 2005). Cavity-nesting bird abundance and cavities in the Atchafalaya Basin did not decrease one year after Hurricane Andrew, a severe storm event which increased snag abundance (Torres and Leberg 1996). Outbreaks of mountain pine beetle initially increased the abundance of cavity-nesting birds in coniferous forests of western Canada due to an increase in dead and dying trees (Martin et al. 2006). Natural and anthropogenic disturbances are important for both snag formation and cavity nesting bird populations in specific habitats such as oak savannas.

Disturbance, and in particular fire, plays a functional role in maintaining the structure and composition of oak savannas. The *Quercus* spp.-dominated canopy of oak savannas ranges from 10-60% (Anderson and Bowles 1999). The canopy cover and open structure of oak savannas is maintained by disturbances. Oak savannas that were burned with high frequency (1 fire every 1-3 years), have decreased tree density and older more established trees (20-30 cm dbh size class).

Conversely, in oak savannas that have low (1 fire every 8 years) fire frequency the tree density is higher and younger trees are more dominant (5-10 cm dbh size class; Peterson and Reich 2001). As a result of an open structure with sparse tree density (historically 14 trees/ha, Brewer and Vankat 2004), snags may occur within patches of canopy or isolated along the landscape. This spatial structural will likely influence the resource value of snags for cavity-nesting birds and thus, the general composition of the bird community or density.

Since oak savanna restoration alters the spatial distribution of snags and living trees, restoration will likely alter the structure and composition of bird communities. Abundance of insectivorous bark gleaning birds as well as ground foraging birds increased with savanna restoration that decreased live tree density and increased snag density (Davis et al. 2000). Abundance of the Red-headed Woodpecker, Northern Flicker, and Great Crested Flycatcher all significantly increased in restored savanna as opposed to closed canopy forest (Brawn 2006). These previous studies both cite the disturbance-based restoration process of oak savannas for making suitable habitat, especially since it is a progressive process that promotes a heterogeneous landscape.

Snags in oak savanna may impact cavity-nesting birds differently than snags in forests since the snags are more likely to be in open areas. Therefore, the impact of snag density in oak savannas may be critical to the cavity-nesting bird guild abundance, reproductive success, body measurements, and species diversity as a whole. In this study we investigated, as a guild, how does increasing snag density influence abundance, reproductive success, body size, and species diversity in oak savanna?

Methods

Study Species

Six species of cavity-nesting birds were used in this study including both primary and secondary cavity-nesting birds. Primary cavity-nesters excavate their own cavities for roosting and nesting. Downy Woodpeckers (*Picoides pubescens*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Red-headed Woodpeckers (*Melanerpes erythrocephalus*), and Northern Flickers (*Colaptes auratus*) were the primary cavity-nesting birds included in this study. Secondary cavity-nesters roost and nest in previously-formed cavities. Eastern Bluebirds (*Sialia sialis*) and Great Crested Flycatchers (*Myiarchus crinitus*) were the secondary cavity-nesters included in this study. All species are known to live in open areas with some trees during the breeding season (Moore 1995, Lanyon 1997, Gotway and Plissner 1998, Shackelford et al. 2000, Smith et al. 2000, Jackson and Ouellet 2002).

Study Sites

We conducted this study in restored and managed areas of oak savanna which are characterized by oak trees (*Quercus* spp.), an herbaceous understory of tallgrass prairie species, and 10-60% canopy cover (Anderson and Bowles 1999). Restoration techniques including prescribed burning, snag (standing dead tree) formation, stand thinning, and mowing were used to simulate the oak savanna disturbance regime (Gary Haase, The Nature Conservancy and LaRae Sprow, Oak Openings Metropark, personal communication). These techniques along with natural disturbances created snags and other dead wood that are used by oak savanna species. Over the course of the study, there was a total of 58.24 cm of precipitation; 25.4 cm above normal (NOAA 2006). We determined potential study sites using a Geographic Information Systems (GIS) model that predicted the location of oak savanna in Lucas County,

Ohio based on soil type and elevation. All study sites had an elevation within 202-209 m above mean sea level and had soil types Ottokee, Granby, Oakville B, Tedrow, or Oakville C (Ricci 2006). The five chosen study sites were located within the Oak Openings Metropark of the Toledo Area (lat. 41.5579, long. -83.3531) or the Kitty Todd Nature Preserve (owned by The Nature Conservancy) (lat. 41.699, long. -83.7886). Land managers provided input on the final placement of study sites to reduce conflicts with other studies and land management activities.

Study sites ranged in size from 6.03-13.65 ha and were limited by selecting the largest continuous area with the soil type and elevation that best predicted oak savanna combined with visual confirmation of oak savanna vegetative structure. Study sites were at least 450 m apart to minimize the chance of observing the same birds in different study sites.

Each study site was digitally mapped (ArcGIS 8.3, ESRI, Redlands, California) in a similar manner to Dudley and Saab (2003). A digital image of the Oak Openings region (Lucas County Auditor, 2003) was combined with mapped boundaries of Metroparks of Toledo and The Nature Conservancy and the boundaries of areas determined to be oak savanna as indicated by the predictive model (Ricci 2006). Canopy cover and snag density were visually estimated initially to ensure sites would represent a range of snag density and 10-60% canopy cover.

Snag density was calculated by counting and recording the location of each snag within each site. A snag was considered to be any free-standing dead tree without foliage, regardless of the presence or absence of a crown and/or bark. All snags were marked with a small flag (removed after all snags were counted) and mapped with a global positioning system unit (Garmin eTrex Legend, Olathe, Kansas) throughout all sites.

Canopy cover was estimated similar to the method described by Klingenbock et al. (2000) by photographing the canopy 1.5 m from the ground with a digital camera (Cyber-Shot

DSC-S75, Sony, New York, New York). Photographs were taken along transects every 50m through each site. The digital images were then converted to grayscale and all dark pixels (canopy) were selected and counted using a graphics program (Adobe Photoshop 7.0, San Jose, California). Percent canopy cover was averaged for each site based on the images taken within each site. Canopy cover, area, and snag density values for each site are given in Table 1.

Surveys

Relative bird abundance was measured by conducting line transect surveys. All birds seen and heard within approximately 25m of transects were identified and counted while an observer steadily traversed the transects (Bibby et al. 1992, Gregory et al. 2004). A 25 m belt on either side of the transect allowed the counter to adequately identify birds and reduce the chance of counting birds more than once in a site. Numbered transects were established through the sites 100 m apart oriented either north to south or east to west in order to avoid walking across slopes or through areas with water which would alter walking pace (Dudley and Saab 2000). Odd and even-numbered transects were surveyed every other time in order to decrease the chances of counting the same bird twice. Surveys were conducted between 0600 and 1000 hr on days without inclement weather (i.e., heavy rain) that would have hindered bird detection. Nine surveys were performed throughout May 17 and August 7, 2006 at all sites except for one, Old State Line, which was surveyed 8 times. Relative bird abundance for all birds and cavity-nesting birds, measured as birds detected/km, over time was averaged per week and described with trend lines. Relative bird abundance was described as a function of overall snag density per site. Survey data was also used to determine Shannon-Wiener Index (H) of species diversity at each site and compared using ANOVA. Species diversity was also correlated with survey length using linear regression.

Body Measurements

Cavity-nesting birds were caught in mist nets, identified, banded, and measured at three sites despite efforts to catch birds in all sites. Based on visual observation of areas where cavity-nesting birds were seen close to the ground, we placed a combination of 2.6×6 m and 2.6×12 m (36 mm mesh size) mist nets strung up on 3 m tall aluminum poles within the study units (for a review of mist nets see Keyes and Grue 1982). Mist-netting occurred on thirteen days for a total of 298.5 net-hours. Once birds were caught in the net, they were identified, weighed using a spring scale (Pesola, Switzerland), and banded with an appropriately-sized United States Geological Survey (USGS) band based on techniques described by Gosler (2004). Other criteria for determining age and sex were based on species-specific characteristics described in Pyle et al. (1997). Measurements included wing cord and tail length using a wing rule (AFO Banding Supplies, Manomet, Massachusetts) and bill length, bill depth, and tarsus length using a caliper (Scherr-Tumico, St. James, Minnesota). Average values for similar adult and juvenile species were compared between sites using ANOVA.

Nests were found by observing cavity-nesting bird activity and looking for excavation evidence including woodchips at the base of trees. When a cavity appeared to be a potential active nest (with eggs or chicks), we used a small camera affixed to an extendable pole (TreeTop Peeper, Sandpiper Technologies, Inc., Manteca, California) to observe the contents of the nest. The camera had a light-emitting diode (LED) and the image from the camera was sent to a handheld monitor to allow the operator to see within the nest in real time. Once an active nest was confirmed by the presence of eggs, we used a GPS to mark the location and we recorded characteristics of the nest. All nest searching was performed after 1000 hr because egg-laying generally occurs before that time (Smith et al. 2000).

Results

The relative abundance of birds detected at individual sites ranged from 12 to 100 birds detected/km. Over the thirteen weeks of the study, the relative abundance of all birds detected peaked at approximately the eighth week, early July ($y = -0.0602 x^2 + 9.477 x + 34.37$, $r^2 = 0.5846$, $p = 0.0717$, Figure 1). The average relative abundance of cavity-nesting birds detected peaked slightly earlier at approximately the seventh week ($y = -0.0885 x^2 + 1.274 x + 1.926$, $r^2 = 0.2173$, $p = 0.4796$, Figure 2). For both cavity-nesting birds and all birds combined, average relative abundances were lower at the beginning and end of the study (mid-May and early-August).

Cavity-nesting bird relative abundance was described by a curvilinear relationship with snag density (Figure 3). The relative abundance of cavity-nesting birds was greatest at the lower and upper ends of the snag density range (approximately 6-20 snags/ha) ($y = 0.0514 x^2 - 1.124 x + 9.384$, $r^2 = 0.9112$, $p = 0.0888$, Figure 3). A similar trend was found with the relative abundance of all birds detected across all snag densities ($y = 0.4712 x^2 - 11.86 x + 117.2$, $r^2 = 0.9883$, $p = 0.0117$, Figure 4).

Area and canopy cover estimates were not significantly correlated with cavity-nesting and all bird relative abundances. In general, as area increased, average relative abundance of cavity-nesting and all birds decreased (Table 2). Similarly, as canopy cover estimates increased, both cavity-nesting bird and all bird average relative abundance decreased (Table 2).

Species diversity was calculated for each survey using the Shannon-Weiner Index (H). The diversity of birds (H) was highest at Old State Line with an average H of 2.213 ± 0.0798 (standard error). The diversity was significantly lower at Shaffer ($H = 1.711 \pm 0.1261$) than at Old State Line ($F = 3.317$, $df = 4$, $p = 0.0197$, Figure 5). Surveys were different lengths due to

different transect lengths, a result of oddly-shaped sites, and total survey length was positively correlated with H value, though only slightly ($y = 0.0008x + 1.726$, $p = 0.0158$, Figure 6). Snag density, site area, and canopy cover estimates were not significantly related to H values.

Fifty-nine cavity-nesting birds were trapped, banded, and measured in three of the five sites (North Girdham $n = 8$, Shaffer $n = 16$, and South Girdham $n = 35$). Of the 59 birds, 17 were adults (Northern Flicker = 2, Eastern Bluebird = 8, Red-headed Woodpecker = 2, Downy Woodpecker = 2, Great Crested Flycatcher = 2) and 42 were juveniles (Downy Woodpecker = 5, Eastern Bluebird = 33, Red-bellied Woodpecker = 1, Red-headed Woodpecker = 3).

Juvenile Eastern Bluebird body measurements were only compared between Shaffer, South Girdham, and North Girdham due to sample size. Body weight was significantly higher (Bonferroni corrected, $p < 0.008$) at Shaffer compared to South Girdham, while body length measurements did not differ between the sites (Figure 7).

A total of 13 active nests were located within all sites except Shaffer (Table 3). Five of those nests were bluebird boxes. Only nests of Red-headed Woodpecker, Red-bellied Woodpecker, and Eastern Bluebird were located. Not including bluebird boxes, Old State Line had the greatest amount of nests; one of each species for a total of 3 nests. Seven nests had confirmed hatchlings for a total of 28 hatchings.

Discussion

Several factors impact how many birds are detected in a given area besides the absolute density of birds including, song phenology (Wilson and Bart 1985), observer bias, and weather (Bibby et al. 1992). In general, though, singing increases as the breeding season progresses, then decreases after mating (Slagsvold 1977). The results of this study support what has been shown in previous studies; birds detected throughout the breeding season increased until late June and

then began to decrease in early July (Figure 1). This trend was not as strong in the cavity-nesting bird guild (Figure 2), possibly due to a relatively smaller population and the variability in phenology of the six species. The guild as a whole nests and lays eggs between early April and early July, and more specifically, the cavity-nesting birds may have been more detectable earlier in the season due to frequent territorial displays, which then decrease as the season progresses (Moore 1995, Lanyon 1997, Gotway and Plissner 1998, Shackelford et al. 2000, Smith et al. 2000, Jackson and Ouellet 2002).

Snag density had a significant curvilinear relationship with the relative abundance of all species and a weaker relationship with cavity-nesting guild (Figures 3 and 4). This suggests that the relationship between bird abundance, specifically cavity-nesting bird abundance, and snag density is complex. Previous studies that found positive trends between cavity-nesting birds and snag density have included information regarding snag size. For example, in a Pacific-northwest coastal coniferous forest habitat, Bunnell et al. (2002) recommended at least 2-3 large snags/ha (large snag > 30 cm diameter) and 10-20 small snags/ha (small snags < 30 cm diameter) to promote cavity-nesting wildlife. The suggested snag density range in the northeast is similar; primary cavity-nesters are believed to require 1.2-10 snags/ha between the sizes of 15-60 cm dbh, depending on bird species (Evans and Conner 1979). Raphael and White (1984) recommended 10.4 soft snags/ha (15 years or older) for maximum bird densities in Sierra Nevada forests. Snag density recommendations have not been provided for oak savanna. This study would greatly benefit by having information about each snag that, at a minimum, included size.

Species that live in oak savanna may also be adapted to living in surrounding woodlands. Shaffer had the lowest bird abundance and also had the greatest canopy cover and canopy cover

was weakly correlated with decreasing bird abundance (Table 2). Gunn and Hagan (2000) found a similar negative trend with woodpecker abundance as a function of increasing canopy closure. All sites were adjacent to woodlands, which would have provided habitat for closed-canopy species. In support, the same trend is stronger with the cavity-nesting guild which included species such as the Downy Woodpecker, Red-bellied Woodpecker, and Great Crested Flycatcher which also breed in woodlands (Sibley 2003).

Shaffer ($H = 1.71 \pm 0.13$) and Old State Line ($H = 2.21 \pm 0.08$) were the only sites with significantly different species diversity (Figure 5). Even though survey length was correlated with site area, Old State Line and Shaffer were similar in size (Table 1), implying that site area is only a partial explanation for the difference. The snag density at Shaffer (5.4 snags/ha) was lowest of all sites. Species diversity has previously been positively correlated with snag density (Dickson et al. 1983). Furthermore, Shaffer was most recently restored to be oak savanna and has only been thinned and mowed; Shaffer has never had a prescribed burn (Appendix B). Fire disturbance in oak savanna has been shown to impact plant, invertebrate, and vertebrate species composition (Siemann and Haarstad 1997, Davis et al. 2000, Peterson and Reich 2001). It is possible that Shaffer does not yet have the vegetative structure or composition to support a greater diversity of oak savanna species.

No cavity-nesting birds were captured at Old State Line or Garden which may reflect a lack of cavity-nesting birds flying within 3 m of the ground (where they would fly into the mist nets) or human error. Excluding Eastern Bluebirds, similar numbers of adult (8) and juvenile (9) cavity-nesting birds were caught. The paucity of cavity-nesting birds caught within sites in general may suggest that there are few individuals of each species in each site, or species are using adjacent habitat. When juvenile Eastern Bluebirds were compared among two sites, body

weight was found to be significantly higher at Shaffer than South Girdham, though all other measurements were not significantly different (Figure 7). This suggests that juvenile Eastern Bluebirds may be feeding young similar amounts of food.

Sites provide different nesting opportunities for cavity-nesting birds. Both North Girdham and Old State Line had one nest of each species; Red-headed woodpecker, Red-bellied Woodpecker, and Eastern Bluebird (Table 3). These sites may be optimal for guild-scale reproductive success and probably closely resemble historic oak savanna as a result of the degree of restoration they have received (Appendix B). Bluebird boxes seemed to positively influence Eastern Bluebird nesting, which is not surprising since nest-sites are considered a limiting resource for non-excavating species (von Haartman 1957). Finding a much greater number of active Eastern Bluebird nests along with catching several juveniles is also not surprising; non-excavating cavity nesters tend to have lower adult survivor and higher annual fecundity when compared to other passerines and especially woodpeckers (Martin 1995). No Great Crested Flycatcher, Northern Flicker, or Downy Woodpecker nests were located, either because they were not present, or they were too difficult to be found by observers (i.e., located high in the canopy). Garden was the best site for Red-headed Woodpeckers because two out of three possible nest territories (based on territory size reported by Evans and Conner 1979) were found. All sites were located within 5 km of Toledo Express Airport, which may have hindered nesting (Jackson 1976).

Two nests were found adjacent to sites which suggest that guidelines used to choose oak savanna sites may not be the same used by cavity-nesting birds with access to both oak savanna and woodland ecosystems. A Red-headed Woodpecker nest was found in woodland adjacent to Shaffer. Adult birds from that nest were observed flying into Shaffer to forage and then return to

the nest, which may imply that preferred snags for nesting are more abundant in surrounding woodlands (either due to site fidelity or snag quality). However, Red-headed Woodpeckers may be able to forage more efficiently within Shaffer site. Another Red-headed Woodpecker nest was found in woodland halfway between North Girdham and South Girdham as well.

An interesting finding was a snag with an active Red-headed Woodpecker nest and an active Wood Duck (*Aix sponsa*) nest. The snag was a cottonwood (*Populus deltoides*) without bark. Late seral stage cottonwood woodlands are tightly associated with Red-headed Woodpecker abundance (Rumble and Gobeille 2004). This finding neatly demonstrates that plant species diversity found in oak savannas ecosystems (Brewer and Vankat 2004), has the potential to support many species.

In conclusion, the ecology of cavity-nesting birds is impacted by snag density in a complex way, but is not significantly influenced by canopy cover and site area. Differences in species diversity and nests found between sites suggest that sites do not provide equivalent breeding habitat for cavity-nesting birds. Cavity-nesting birds that live and reproduce in oak savanna are most likely living in and using the resources of surrounding oak woodlands as well. Though this study was limited by subjective boundaries, the species that were surveyed, caught, and found nesting were not limited in the same manner. However, as restoration practices such as snag creation, progress in areas such as Shaffer, bird diversity and cavity-nesting reproduction will probably increase. To gather a further understanding behind the mechanisms that determine abundance, diversity, and reproductive success, this guild should be behaviorally analyzed with attention to substrate use.

CHAPTER III
IMPACT OF SNAG DENSITY, CANOPY COVER, AND AREA ON CAVITY-NESTING
BIRD GUILD ACTIVITY BUDGETS AND SUBSTRATE USE

Introduction

Natural and anthropogenic disturbances affect the abundance, availability, and distribution of resources within oak savanna, a disturbance-maintained ecosystem (Vogl 1974). Fire, drought, herbivory, plant disease, and storm events have historically maintained oak savanna structure and function (Leach and Ross 1995). Restoration techniques such as prescribed burning, snag (standing dead tree) formation, stand thinning, and mowing are used to simulate the oak savanna disturbance regime. These techniques along with natural disturbances create snags and other dead wood that are used by oak savanna species.

The cavity-nesting bird guild utilizes common resources: snags and dead wood. Snags are used by the guild for nesting, foraging, and communicating (Evans and Conner 1979, Raphael and White 1984, Rosenberg et al. 1988, Imbeau and Desrochers 2002). More recently, dead wood has become recognized as an important resource to cavity-nesting birds. Removal of dead wood reduced breeding territory sizes of strong excavators and reduced abundance and richness of both strong and weak excavating birds (Lohr et al. 2002). Retention of decadent trees (snags or trees with dead limbs) on golf courses has been shown to promote Red-headed Woodpecker nesting (Rodewald 2005). In support, King et al. (2007) suggested that Red-headed Woodpeckers may need nesting habitat over a threshold value of clustered decadent trees.

Organisms interact with the environment, and in turn, those interactions impact how time and energy is allocated to activities that improve fitness (Schartz and Zimmerman 1971).

Analysis of activity budgets that include information on substrate or resource use can indicate the value (in terms of behaviors that improve fitness) or preference of that resource. For example, Wolf and Hainsworth (1971) demonstrated that territorial hummingbirds spent variable proportions of their time foraging and defending territories centered on different flower species. For the male and female tropical *Anolis* lizard, *Anolis polylepis*, season and structural habitat were significantly related to time spent socially interacting and foraging (Andrews 1971). A behavioral response to resource distribution and availability in terms of showing a preference, selection, or change in time budget, may demonstrate the importance of a resource to the fitness of an organism. Thus, analysis of activity budgets provides a way to measure the response of organisms to changes in resources.

The impact of disturbance on a particular resource can be examined by quantifying the behavior of a guild of species that use the particular resource in a similar manner. The guild approach is advantageous because guilds group species that compete for the same resource, allowing for a broad assessment of resource use (Root 1967, Simberloff and Dayan 1991). Using a group of four passerine bird species that forage upon leaf surfaces for arthropods, Robinson and Holmes (1984) demonstrated that vertical vegetation structure and composition impacts foraging behavior. At the scale of a guild, activity budgets suggest trends influenced by disturbance-related resources. However, species within a guild may rely on the uniting resource to varying degrees (i.e., using a particular substrate for nesting as well as foraging). Therefore, examining activity budgets at the species scale is valuable as well; the response of a single species may explain variability in trends and provide insight about species dynamics.

In this study, activity budgets were assessed for cavity-nesting birds at five oak savanna sites with various snag density. Six species of birds (four primary and two secondary cavity-

nesting birds) made up the cavity-nesting bird guild and activity budgets were analyzed at both the guild and species scale. Differences in activity budgets of the guild and individual species were compared across various snag densities. As a resource becomes more abundant, there may be shifts in guild behavior that reflect improved fitness. Similarly, time spent on substrates should reflect the value or preference of a resource as its abundance increases.

Methods

Study Species

Six species of cavity-nesting birds were used in this study including both primary and secondary cavity-nesting birds. Primary cavity-nesters excavate their own cavities for roosting and nesting. Downy Woodpeckers (*Picoides pubescens*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Red-headed Woodpeckers (*Melanerpes erythrocephalus*), and Northern Flickers (*Colaptes auratus*) were the primary cavity-nesters used in this study. Secondary cavity-nesters roost and nest in previously-formed cavities. Eastern Bluebirds (*Sialia sialis*) and Great Crested Flycatchers (*Myiarchus crinitus*) were the secondary cavity-nesters used in this study. Though these species all use snags for nesting, they forage differently. The Red-bellied and Downy Woodpeckers glean insects off of tree surfaces, such as within the fissures of oak bark. The Red-headed Woodpecker gleans as well, but can also chase and capture insects in flight (flycatch) in the same manner as Great Crested Flycatchers. Northern Flickers mainly forage on the ground. Eastern Bluebirds employ both flycatching from a perch (sallying) and ground foraging techniques. All species are known to live in open areas with some trees during the breeding season (Moore 1995, Lanyon 1997, Gotway and Plissner 1998, Smith et al. 2000, Jackson et al. 2002, Jackson and Ouellet 2002).

Study Sites

We conducted this study in managed and protected areas of oak savanna which are characterized by oak trees (*Quercus* spp.), an herbaceous understory of tallgrass prairie species, and 10-60% canopy cover (Anderson and Bowles 1999). Prescribed burning, girdling, stand thinning, and mowing were used to simulate the oak savanna disturbance regime (Gary Haase, The Nature Conservancy and LaRae Sprow, Metroparks of the Toledo Area, personal communication). These techniques along with natural disturbances created snags and other dead wood throughout the sites. Over the course of the study, there was a total of 58.24 cm of precipitation; 25.4 cm above normal (NOAA 2006). We determined potential study sites using a Geographic Information Systems (GIS) model that predicted the location of oak savanna in Lucas County, Ohio based on soil type and elevation. All study sites had an elevation within 202-209 m above mean sea level and had soil types Ottokee, Granby, Oakville B, Tedrow, or Oakville C (Ricci 2006). The five chosen study sites were located within the Oak Openings Metropark of the Toledo Area (lat. 41.5579, long. -83.3531) or the Kitty Todd Nature Preserve (owned by The Nature Conservancy) (lat. 41.699, long. -83.7886). Land managers provided input on the final placement of study sites to reduce conflicts with other studies and land management activities.

Study sites ranged in size from 6.03-13.65 ha and were limited by selecting the largest continuous area with the soil type, aspect, and elevation that best predicted oak savanna combined with visual confirmation of oak savanna vegetative structure. Study sites were at least 450 m apart to minimize the chance of observing the same birds in different study sites.

Each study site was digitally mapped (ArcGIS 8.3, ESRI, Redlands, California) in a similar manner to Dudley and Saab (2003). A digital image of the Oak Openings region (Lucas

County Auditor, 2003) was combined with mapped boundaries of Metroparks of Toledo and The Nature Conservancy and the boundaries of areas determined to be oak savanna as indicated by the predictive model. Canopy cover and snag density were visually estimated initially to ensure sites would represent a range of snag density and 10-60% canopy cover.

Snag density was calculated by counting and recording the location of each snag within each plot. A snag was considered to be any free-standing dead tree without foliage, regardless of the presence or absence of a crown and/or bark. All snags were marked with a small flag and mapped with a global positioning system unit throughout all sites.

Canopy cover was estimated similar to the method described by Klingenbock et al. (2000) by photographing the canopy 1.5 m from the ground with a digital camera (Cyber-Shot DSC-S75, Sony, New York, New York). Photographs were taken along transects every 50 m through each site. The digital images were then converted to grayscale and all dark pixels (canopy) were selected and counted using a graphics program (Adobe Photoshop 7.0, San Jose, California). Percent canopy cover was averaged for each site based on the images taken within each site. Canopy cover, area, and snag density values for each site are given in Table 1.

Focal Observations

We conducted focal observations of cavity-nesting birds between 0700 and 1400 hr within the five study sites from May until August of 2006. We searched for and located birds opportunistically and followed them as long as possible while recording a verbal description of their behavior with a microcassette recorder (Sony M-830V, New York, New York) (Hartung and Brawn 2005). The observation ceased when the bird left the study site or flew out of view. The microcassette recordings were transcribed to calculate the amount of time the bird spent

performing each behavior based on how long each behavior was described, along with the location and substrate used during the behavior.

Observed behaviors were classified into five categories; foraging, resting, preening, nest tending, and being territorial/communicating. Definitions for resting, preening, nest tending, and being territorial/communicating were the same for all species. Foraging behaviors were specific for each species (Table 4).

Statistical Analysis

An initial analysis of behavior was completed by averaging the proportions of time a bird of any species performed a particular behavior at each site.

We determined a range of behavioral proportions based on values reported for any species included in the cavity-nesting guild. For example, the range of time a cavity-nesting bird has been reported foraging is 23-67% (Moore 1995, Shackelford et al. 2000). Each proportion of time a behavior was observed was then categorized (less than, more than, or within the range). Only one reported value for territorial/communication was comparable to our study, so territorial/communication proportions were categorized as less than or equal to/more than the reported value. Categorical proportions of time spent performing behaviors (i.e., foraging) were compared across all sites using a contingency table analysis. Trends between categorical proportions and site characteristics (i.e., snag density, estimated canopy cover, and area) were analyzed with a Cochran-Mantel-Haenszel statistic. The categorization scheme for all coded variables is given in Table 5.

Proportions of time spent on live wood and dead wood (including all snags and dead branches) substrates for the guild were categorized (less than or more than half of all time spent on snags, live/dead wood). The categorized proportions were compared between sites using

contingency table analysis. Trends between categorical proportions and site characteristics (i.e., snag density, canopy cover, and area) were analyzed with a Cochran-Mantel-Haenszel statistic.

Multiple regression was used to assess correlations between species' behavior and site characteristics (i.e., snag density, area, canopy cover).

The behavioral observations of the Red-headed Woodpecker, a primary cavity-nesting species, and the Eastern Bluebird, a secondary cavity-nesting species, were analyzed based on substrate (snag, dead wood, or live wood). These were the only two species that had enough observations to perform statistical analysis. Live wood observations included any proportion of time spent performing a behavior on any live tree. Live wood observations were then categorized (less than or more than 50% of the time). Dead wood observations included any proportion of time spent performing a behavior on a snag or dead branch. Similarly, dead wood observations were categorized (less than or more than 50% of the time). Snag observations were the same as dead wood observation, except that only behaviors performed on snags were included. Very few observations occurred on the ground, in the air, or another substrate for either of the species. Categorized proportions of time spent on snags, live or dead wood substrates were compared across sites using a contingency table analysis. Trends between categorical proportions of live and dead wood substrates and site characteristics (i.e., snag density, canopy cover, and area) were analyzed using the Cochran-Mantel-Haenszel statistic.

Results

We performed 206 independent focal observations on a total of 6 cavity-nesting bird species among 5 sites, each with unique values of snag density. The observations varied in duration (17-1759 seconds) and all behavior observations were standardized by being converted

into proportions. Site characteristic values; snag density, canopy cover, and area, were measured for each site (Table 1).

Guild Analysis

An overall description of time spent performing behaviors at each site by the guild suggests that regardless of the site, cavity-nesting birds spend similar amounts of time performing specific behaviors (Figure 8). On average, cavity nesting birds devote 48% of their time foraging and 27% of their time resting. The guild spends about the same time preening (11%) and being territorial/communicating (9%). Only 5% of the time was devoted towards nest tending (Figure 8).

Categorical proportions of time spent performing each behavior were compared between sites at the guild scale and site characteristics were used to describe any trends in the differences. Based on the categories determined for each behavior, there was no significant difference between sites at the guild scale (Table 6). Furthermore, there were no significant trends between snag density, area, or canopy cover and behavior at the guild scale (Table 6). However, most observations did not fall within the categorical parameters described by previous studies (Moore 1995; Lanyon 1997; Gotway and Plissner 1998; Smith et al. 2000; Jackson et al. 2002; Jackson and Ouellet 2002) (Table 7). Across all sites, 28% of cavity-nesting birds foraged between 23-66% of the time, 34% of observations were described as foraging behavior for more than 66% of time. Time spent resting (37%) fell within the reported range of proportion of time resting for the guild, 10-77%. Only seven out of 206 (3%) observations fell within the reported range of preening for the guild, 4-10%. Most (70%) observations of preening were less than the lower value (4%) of the reported range. Being territorial/communicating at least 15% of the time only

described 18% of the observations. Nesting behavior was not observed frequently; only 8% of observations were described by nesting behavior for more than 27% of time (Table 7).

At the guild scale, substrate use was analyzed between sites and site characteristics were used to describe trends. There was a significant difference between sites and proportion (less than half or more than half) of the time spent on live wood substrates ($\chi^2 = 30.50$, $p < 0.0001$), dead wood substrates ($\chi^2 = 13.37$, $p = 0.0094$), and snags ($\chi^2 = 15.61$, $p = 0.0015$) (Table 8). As snag density increased, cavity-nesting birds were more likely to spend more than half of their time on snags (Cochran-Mantel-Haenszel statistic = 3.201, $p = 0.0736$). An increase in canopy cover was significantly correlated with cavity-nesting birds spending more than half of their time on live wood (Cochran-Mantel-Haenszel statistic = 6.636, $p = 0.01$) and spending less than half of their time on snags (Cochran-Mantel-Haenszel statistic = 5.655, $p = 0.0174$). Similarly, there was a strong trend for birds to spend less than half of their time on dead wood (Cochran-Mantel-Haenszel statistic = 2.854, $p = 0.0912$) as canopy cover increased (Table 8).

Species analysis

Linear regression was used to describe relationships between site characteristics (i.e., snag density, canopy cover, or area) and each species' behavior (Table 9). Proportion of time a Northern Flicker spent foraging decreased as site area increased ($r^2 = 0.4346$, $F = 4.61$, $p = 0.0754$). However, as snag density increased, the proportion of foraging behavior of Northern Flickers increased ($r^2 = 0.6904$, $F = 13.38$, $p = 0.0106$). Time spent foraging decreased for Red-bellied Woodpeckers as snag density increased ($r^2 = 0.2972$, $F = 4.65$, $p = 0.0540$). An increase in area was correlated with a decrease in time Great Crested Flycatchers were preening ($r^2 = 0.1599$, $F = 3.62$, $p = 0.0725$) (Table 9).

Red-headed Woodpecker substrate use analysis

Substrate use by Red-headed Woodpeckers was compared between sites and site characteristics were used to describe trends. Snags ($\chi^2 = 15.59$, $p = 0.0033$), dead wood ($\chi^2 = 16.31$, $p = 0.0049$), and live wood ($\chi^2 = 26.86$, $p < 0.0001$) substrates were used by Red-headed Woodpeckers significantly differently across all sites (Table 10). One site, Shaffer, tended to be different than the others, in general. As snag density increased, Red-headed Woodpeckers were more likely to spend less than half of their time on live wood (Cochran-Mantel-Haenszel statistic = 6.449, $p = 0.0111$) and more likely to spend more than half of their time on snags (Cochran-Mantel-Haenszel statistic = 6.092, $p = 0.0136$). An increase in canopy cover had an opposite effect; Red-headed Woodpeckers were more likely to spend more than half of their time on live wood (Cochran-Mantel-Haenszel statistic = 3.588, $p = 0.0582$) and more likely to spend less than half of their time on snags (Cochran-Mantel-Haenszel statistic = 4.982, $p = 0.0256$) or dead wood (Cochran-Mantel-Haenszel statistic = 2.777, $p = 0.0957$). An increase in area was not correlated with a shift in substrate use (Table 10).

In order to determine if values from Shaffer site were influencing the results, the other four sites were analyzed for relationships between substrate and site characteristics without Shaffer using contingency table analysis (Table 11). There were still differences in use of live wood ($\chi^2 = 5.879$, $p = 0.075$) and snags ($\chi^2 = 6.559$, $p = 0.0907$) between sites, though the differences were less pronounced. Similarly, an increase in snag density was still related to Red-headed Woodpecker being more likely to spend less time on live wood (Cochran-Mantel-Haenszel statistic = 2.716, $p = 0.0994$) and more likely to spend more time on snags (Cochran-Mantel-Haenszel statistic = 3.386, $p = 0.0657$), though the trends were not as strong when Shaffer was not included. Any differences described by an increase in canopy cover were no

longer significant. And, without Shaffer, an increase in area was related to Red-headed Woodpeckers spending more time on live wood (Cochran-Mantel-Haenszel statistic = 5.476, $p = 0.0193$) (Table 11).

Eastern Bluebird substrate use analysis

Substrate use by Eastern Bluebirds was compared between sites and site characteristics were used to describe trends. There were differences between sites for Eastern Bluebird use of snags ($\chi^2 = 9.524$, $p = 0.0496$) and live wood ($\chi^2 = 13.14$, $p = 0.0084$) (Table 12). Canopy cover was strongly correlated with substrate use, as opposed to snag density or area (Table 12). As canopy cover increased, Eastern Bluebirds were more likely to spend more than half of their time on live wood (Cochran-Mantel-Haenszel statistic = 8.435, $p = 0.0037$) and less likely to spend more than half of their time on snags (Cochran-Mantel-Haenszel statistic = 6.894, $p = 0.0087$) or dead wood (Cochran-Mantel-Haenszel statistic = 5.320, $p = 0.0211$).

Discussion

At the guild scale, time spent performing any behavior was similar at all sites (Figure 8). Similar activity budgets across the guild imply that either guild scale behavior was not detectably plastic at the spatial or temporal scale used or that the sites provided similar resources. The current study was conducted during one breeding season, which may have been too brief of a temporal scale to detect activity budget differences. Wagner (1981) detected greater differences in foraging site use by an insectivorous bird guild between years rather than within season. Time budgets for a single species may only slightly differ across wide geographic regions as opposed to areas in the same region or ecosystem. For example, Red-bellied Woodpeckers forage 66.9% and rest 32.3% of their time away from the nest in Maryland, though forage 62.3% and rest 35.2% of their time away from nests in Minnesota (Askins 1983). This study was conducted

within a single breeding season and sites were located within a small geographic range. If this study had been conducted over several years and had sites more distant from each other (i.e., > 450 m distance between sites), differences in behavior might have been detected, however, those differences would then be partially accounted for by time and space, rather than snag density.

Guild activity budgets were also similar between sites based on categorical proportions of behaviors (Table 6). The majority of observations were always described by the category that ranged lower than the range proportion reported in literature (Table 7). For many observations of a single bird, only one or two behaviors were seen, causing many zero values in the data set. The range of reported proportions may have also been overestimations for this geographic area and combination of species. Similar activity budgets across sites may be due to factors that were alike at all sites. One factor that was historically extreme at all sites was the amount of precipitation received during the breeding season. Between May and August 2006, the Toledo Express Airport weather station (within 5 km of all sites) reported an additional 25.4 cm of rain over the 30-year average (NOAA 2006). Above-average rainfall may have promoted increased vegetation that could have supported larger arthropod communities. For example, mosquito count data for Lucas County reported the highest mosquito counts in a decade during the summer of 2006 (Lee Mitchell, Toledo Area Sanitary District, personal communication). In this study, an increase in snag density was considered a representation of an increase in resource availability, including food resource availability. Above-average precipitation and mosquito counts (that would have affected all sites) suggest that food may not have been a limiting factor during this study and might have hidden some effects of snag density. Food abundance has long been considered a limit to reproductive success (Lack 1947). For example, Magpies (*Pica pica*) given additional food had greater reproductive success including having larger clutches, heavier eggs,

and producing more fledglings than bird that were not given additional food (Hogstedt 1981). In tropical habitats with wet and dry seasons, avian breeding and molting mostly occurs during the wet season when arthropod abundance is positively associated with rainfall (Poulin et al. 1992).

Three out of the four significant linear correlations of a behavior and site characteristic described foraging behavior which may imply that foraging is the most likely behavior to change with available resources (Table 9). For example, the foraging tactics and capture success of some insectivorous forest birds changed with various vegetative structure, insect abundance, and plant species (Robinson and Holmes 1984). Weikel and Hayes (1999) argued that land management for cavity-nesting birds should be guided by foraging as well as nesting habitat requirements. Using foraging ecology as an approach to analyzing cavity-nesting bird behavior in oak savanna may be useful since foraging was the most prevalent behavior (Figure 8) for the guild. Other than foraging and preening, individual species' behavior was not accurately described by a linear relationship with snag density, canopy cover, or area (Table 9).

The proportion of time cavity-nesting birds performed behaviors on snags alone, dead wood, and live wood was significantly different across all of the sites (Table 8). As predicted, an increase in snag density was correlated with increase in the time cavity-nesting birds spent on snags. Snags are an important resource for nesting; however, snags (regardless of size) in the oak savanna are still a valuable and highly-used resource for cavity-nesting birds. Not surprisingly, an increase in canopy cover is significantly correlated with an increased use of live wood, and a decreased likelihood of using snags and dead wood substrates (Table 8). All of the cavity-nesting birds included in the guild are also known to occur in woodland and even forest ecosystems with greater canopy cover (Sibley 2003). Furthermore, the oak savanna sites used in this study were adjacent to oak woodlands. Therefore, it is likely that birds observed in this

study were also using oak woodlands and not demonstrating a behavioral change in habitat structure use as the woodlands become open savanna. Area of sites did not significantly influence proportions of time using various substrates. Similarly, the size of restored oak savanna sites did not influence the abundance of Red-bellied Woodpeckers, Red-headed Woodpeckers, Northern Flickers, or Great Crested Flycatchers (Brawn 2006).

Investigation of Eastern Bluebird substrate use supports the guild scale trends. Eastern Bluebirds use snags and live wood differently at all of the sites. Rather than snag density or area being correlated with changes in substrate use, an increase in canopy cover is strongly related to an increased use of live wood and a decreased use of snags and dead wood (Table 12). Eastern Bluebirds were often observed foraging from lower branches of trees, and in more open areas of the sites. Eastern Bluebirds are known to perform aerial foraging from higher perches in more open areas during the summer as opposed to the spring (Pinkowski 1977). Substrates without foliage such as dead branches and snags may not be as necessary in open areas where live branches are also suitable for foraging perches. Snag density may not have had an effect on substrate use due to the availability of nest boxes in two of the sites. Eastern Bluebirds were observed, resting, preening, and foraging on the nest boxes themselves, rather than on other substrates.

Red-headed Woodpecker substrate use is strongly influenced by site characteristics. When all sites were compared, there were significant differences in time spent using snags, live wood, and dead wood (Table 10). Snag density was positively correlated with snag use by Red-headed Woodpeckers. Use of live wood also decreased as snag density increased. Similar to the trends seen at the guild level, an increase in canopy cover was associated with an increased use of live wood and a decreased use of snags and dead wood.

Inspection of the Red-headed Woodpecker contingency table analysis suggested that one site, Shaffer, may have been responsible for the differences observed between sites. When the analysis was repeated without Shaffer, many of the trends were not as pronounced or were no longer significant (Table 11). There were still differences in snag and live wood use between sites, but differences in dead wood use were no longer significant ($p < 0.1$). An increase in snag density was still related to an increased use of snags and decreased use of live wood, however, canopy cover was no longer related to substrate use. The persistence of these trends suggests that they are biologically significant; snags of all sizes are an ecologically relevant resource for Red-headed Woodpeckers.

The strong differences observed at Shaffer site pose an interesting question; why do most trends observed at Shaffer seem opposite compared to observations at the other sites? The answer may give insight towards the functional role of disturbance in oak savannas. Shaffer was the most recent site to be actively restored as oak savanna and thus has had the least amount of restoration-related disturbances. The site had been thinned in 2004 and again in 2005, and brush piles were still present throughout the site. Shaffer has never had a prescribed burn, though there was a wildfire that went through the site in 2000 (Appendix B). Every other site has had at least one prescribed burn since 2004, was mowed at least once in the previous year, and had been thinned at least six years before the study. Since the Red-headed Woodpecker is considered a possible savanna specialist (Brawn et al. 2001), and there were less-pronounced differences in substrate use when Shaffer was dropped from the analysis, Shaffer may not have been functioning as oak savanna, even though it fit the physical description. Without frequent (few times a decade), moderate-intensity disturbances such as prescribed burning and mowing, oak savanna may not ecologically function. Fire disturbance in oak savanna has been shown to

impact plant, invertebrate, and vertebrate species composition (Siemann and Haarstad 1997, Davis et al. 2000, Peterson and Reich 2001). It is possible that Shaffer site does not have oak savanna species composition yet and this information would greatly benefit this study.

In conclusion, cavity-nesting birds breeding in northwest Ohio oak savanna have similar activity budgets, regardless of snag density, canopy cover or area. An abundance of resources due to very high levels of precipitation may have made sites similar enough to hide possible behavioral differences. Substrate use was significantly different at sites for cavity-nesting birds. Canopy cover was positively correlated with live wood use and negatively correlated with snag and dead wood use at the guild scale and was also seen at the species level. Snag density was positively correlated with snag use at the guild level and for Red-headed Woodpeckers, demonstrating that snags of any size are an important cavity-nesting guild resource in oak savannas. Increased canopy-cover may have provided similar resources available in adjacent woodlands to which the guild also had access. Finally, Shaffer may not accurately represent functioning oak savanna due to recent restoration activities and a lack of frequent, moderate-intensity disturbance. The cavity-nesting bird guild behavioral analysis was an effective approach to understanding disturbance-related resources use as well as the role of disturbance in oak savanna.

CHAPTER IV

DISCUSSION, SYNTHESIS, AND MANAGEMENT IMPLICATIONS

The goal of oak savanna restoration is to reestablish the ecological processes, vegetative structure, and species composition of historic oak savannas. Land managers have a variety of techniques (i.e., prescribed burning, stand thinning, tree girdling, mowing) at their disposal to accomplish these goals. These techniques generally mimic natural disturbances that historically occurred in oak savannas. For example, fires have been suppressed in the Oak Openings Region since Euro-American settlement (Mayfield 1969, Brewer and Vankat 1995) and prescribed burning has been successfully implemented to restore Midwest oak savanna species composition and stand structure (Perterson and Reich 2001).

Restoration is often guided by the needs of a group of organisms that are threatened due to habitat loss. Disturbance-dependent species that live in early successional ecosystems, such as oak savanna, are experiencing severe population decline (i.e., Red-headed Woodpeckers, Hunter et al. 2001). Cavity-nesting birds of the oak savanna depend on snags and oak restoration techniques often involve snag formation. Therefore, a thorough understanding of the relationship between snags and oak savannas and cavity-nesting bird fitness (the focus of this thesis) would benefit conservation, restoration, and land management efforts.

Relative abundance, diversity, evidence of reproductive success, and behavior was used to measure indirect fitness of cavity-nesting birds since fitness is impossible to measure without knowing exactly how many offspring each bird produces. Cavity-nesting birds, along with all species of birds were significantly ($p < 0.1$) correlated with snag density by a polynomial function (Figures 3 and 4). The results of this study indicate that snags, regardless of size, are

influencing abundance of all birds and cavity-nesting birds in a more complex way. Previous studies (e.g., Raphael and White 1984, Land et al. 1989) have shown that each additional snag of a certain size class in a forest has an equal value in terms of cavity-nesting bird abundance. In oak savanna, each additional snag has a different value, which is dependent on the number of existing snags. This finding suggests that the vegetative structural context of snags, not just the snags themselves, is influencing bird abundance.

Species diversity and substrate use results indicated that one site in this study, Shaffer, was probably not oak savanna. Shaffer probably did not have the species composition and vegetative structure that defines oak savanna (even though the site fit within the definition given for this study). Vegetative species composition and structure measurements for each site would have improved selection of sites by adding another potential level of experimental control. Shaffer also lacked the frequency and intensity of anthropogenic disturbance that other sites had received (Appendix B). The developing oak savanna at Shaffer was most recently part of adjacent woodland. In order to begin restoration, the area was thinned in 2005 and again in 2006 before the study. Two consecutive years of stand thinning is a disturbance in terms of a woodland disturbance regime and woodlands characteristically have a lower intensity and frequency of disturbance compared to savannas (Brawn et al. 2001). Furthermore, the canopy cover at Shaffer appeared more homogenous than any other site; Shaffer lacked large open areas without canopy cover that the other sites had. Low bird diversity at Shaffer may be reflecting a lack of niches due to a lack of structural heterogeneity (Figure 5). And the species present at Shaffer may have been more adapted to woodlands rather than savanna, except potentially for the Red-headed Woodpecker. The differences in substrate use by the Red-headed Woodpecker were no longer described by trends in canopy cover after Shaffer was removed from the

contingency table analysis (Tables 10 and 11). This suggests that substrate use is influenced less by canopy cover when the canopy is patchy.

Abundance of seasonal resources may help to explain why abundance and diversity was similar at four of five sites (Figures 3, 4 and 5), and there were no differences in activity budgets at any of the sites (Table 6). This study was conducted over a single field season and may have been complicated by the effects of extreme weather. During this study, precipitation was 150% of the average, and this undoubtedly impacted vegetation growth and arthropod abundance. Even though snag density was different within each site, the resource value that snags provide may have been less important compared to resources found in lush vegetation.

This study was conducted within pre-determined boundaries in order to differentiate oak savanna from surrounding areas. In reality, the Oak Openings region is a matrix of contiguous ecosystems including oak woodlands, sand barrens, and savanna (Brewer and Vankat 1995). The mobile nature of cavity-nesting birds allows them to travel easily into and out of the sites used in this study. The soil type, elevation, and canopy cover of each site was controlled for, though the site characteristics of adjacent woodlands and sand barrens could not be controlled. For example, two Red-headed Woodpecker nests were found very close to sites, though they were not within boundaries and could not be counted. Likewise, an increase in live wood use with increasing canopy cover implies that cavity-nesting birds were obtaining resources that may be similar in composition to resources in surrounding woodlands.

A novel approach used in this study was counting all snags, regardless of size, when determining snag density. This approach probably inflated snag density when being compared to studies that only include snags large enough for nesting. However, substrate use results suggest that snag density, regardless of snag size, is an important resource for cavity-nesting birds

(Tables 8, 10, and 11). And not only are snags important, but all dead wood as well. Snags and dead wood are a valuable resource to cavity-nesting birds in oak savanna because they are used for much more than nesting. Without having the resources of an area with a closed canopy, such as the forests/timberlands where much of the cavity-nesting research has taken place, the guild is probably more dependent on snag for resting, preening, foraging and communicating on top of the already-known reproductive value of snags and dead wood. However, it is possible that the value of snags can not be realized until an area has the structure and species composition of oak savanna.

Future directions

The results of this study suggest that cavity-nesting ecology and behavior is complex; the trends associated with snag density in forests do not seem to necessarily hold in oak savanna. Instead, other factors such as canopy cover and resource abundance may influence the role of snag density on the ecology and behavior of cavity-nesting birds. Future studies should expand the spatial and temporal scale used; more than five sites should be selected and they should be large (greater than 15 ha) to improve the probability of having more territories included in the study. A study that addresses questions regarding disturbance should also be conducted over several consecutive years to detect differences due to weather anomalies versus long-term trends.

Several factors should be addressed in order to have a better understanding of bird behavior in relation to a disturbance-dependent resource. Color-banding of cavity-nesting birds would allow for individual recognition. Provided that nesting success could be measured effectively, detailed information regarding individual fitness could be obtained and compared between sites and breeding seasons. Color banding would also eliminate doubt about whether individuals were being counted or observed twice. A behavioral study should also focus on a

measure besides time to imply fitness. Instead, a behavioral study should count evidence of success, i.e., number of fledglings or prey type caught. A strength of this study was recording behavioral substrate; this approach should be continued in future studies. Attention should also be paid to interspecific interactions with competitors and predators. Cavity-nesting birds may be potentially competing for nesting sites with invasive species such as European Starlings. Management may also attract predators; hawks seemed more abundant after areas were mowed, though this was not quantified.

There is a need for more basic information on snag density, characteristics, and distribution within oak savannas. This study included sites with snag densities between 5.4-20.4 snags/ha, though this range may not accurately represent historic oak savanna snag density. Furthermore, canopies of forests are different in structure from canopies of savannas. Therefore, snags must be considered in a different context. Future studies should address this issue by using GIS to spatially analyze how snags are distributed within the patches of canopy or isolated along the landscape. As many studies have done before, snag characteristics including height, dbh, species, and decay class should be included in analysis since these measures have been used to describe cavity-nesting bird snag preferences. In order to determine if management impacts snag ecology, a study could compare cavity-nesting bird use of snags with similar characteristics that were formed anthropogenic or natural.

The landscape context should also be considered when selecting study sites. Oak savanna is a successional ecosystem that serves as an ecotone between early successional and mature ecosystems (Temple 1998). Mobile species, such as birds, can easily move into and out of sites, thus an effort should be made to choose sites within similar landscape contexts.

Though spatial distribution of snags was not measured beyond terms of snag density at

each site, some observations may provide insight. Young trees in oak savanna were often growing in patches of similar species. If these trees are not fire tolerant, a prescribed burn may create a cluster of thin snags. Snag management at North Girdham imitated this process; two large clusters of young trees were girdled. Cavity-nesting birds were often observed using these snags for foraging, resting, preening, and communication. Other studies suggest clumping snags or dead wood is beneficial for primary cavity-nesting birds (Bunnell et al. 2000, King et al. 2007). More research should be conducted to determine optimal spatial distribution of different sized snags in oak savanna to benefit cavity-nesting birds and other guilds.

Implications for management

As the canopy is opened, snags become more important for cavity-nesting birds. Severe prescribed burns that maintain oak savanna species composition and also create stands of snags would benefit cavity-nesting birds. Retention of dead branches is also important, when it is safe to do so because dead branches are used for a variety of behaviors. Girdled snags should be large enough for nesting at densities similar to those recommended by forest studies such as Bunnell et al. (2000) and Evans and Conner (1979). A variety of tree species should also be girdled since different species decay at different rates. Finally, restoration techniques that simulate natural disturbances should be continued. Return of ecological processes will aid in returning ecological function, which in turn, will benefit species adapted to the disturbance-dependent oak savanna ecosystem.

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APPENDIX A
TABLES AND FIGURES

Table 1. Measurements of snag density (snags/ha), area (ha), and canopy cover (%) for each study site.

Site Name	Snag Density (snags/ha)	Area (ha)	Canopy Cover (%)
Shaffer	5.4	8.9	26.9
South Girdham	5.6	13.7	13.2
Old State Line	6.7	10.2	24.9
Garden	13.7	12.3	30.5
North Girdham	20.4	6.0	14.0

Table 2. Linear regression analysis of all bird and cavity-nesting bird relative abundance measured as birds detected/km as a function of area (ha) or canopy cover (%). Equation of the line, correlation coefficient (r^2), and p-value are given. There were no significant correlations between all bird or cavity-nesting bird abundance and area or canopy cover.

Independent Variable	Range	Dependent Variable (birds detected/km)	Regression	r^2	p
Area	6.03-13.65 (ha)	All bird relative abundance	$-2.234x + 83.977$	0.3657	0.27996
Area	6.03-13.65 (ha)	Cavity-nesting relative abundance	$-0.4241x + 9.3586$	0.5508	0.15094
Canopy Cover	14.0-30.5 %	All bird relative abundance	$-0.9538x + 82.034$	0.4558	0.21113
Canopy Cover	14.0-30.5 %	Cavity-nesting relative abundance	$-0.1597x + 8.5215$	0.5339	0.16081

Table 3. Total number of active nests per species found within sites and total number of hatchlings confirmed. An asterisk (*) indicates a bluebird box was used for nesting.

Site	Total Nests per Species			Hatchlings
	Red-headed Woodpecker	Red-bellied Woodpecker	Eastern Bluebird	
South Girdham	1	0	4*	11
Old State Line	1	1	1	13
Garden	2	0	0	0
North Girdham	1	1	1*	4
Shaffer	0	0	0	0

Table 4. Definitions of cavity-nesting bird behaviors observed during the study. Definitions based on Moore 1995, Lanyon 1997, Gotway and Plissner 1998, Smith et al. 2000, Jackson et al. 2002, and Jackson and Ouellet 2002.

Behavior	Species	Definition
Resting	All	Perched on a substrate without movement, sometimes bill open in hotter weather, extending wings or legs without flying (stretching)
Preening	All	Using bill to comb through plumage, fluffing plumage, cleaning legs
Territorial/ Communicating	All	Any interaction with other birds and/or calling from a perch
Nest Tending	All	Having any part of the body inside the nest cavity
Foraging	Red-headed Woodpecker	Gleaning, excavating, probing and pecking from bark, flycatching, searching along the ground, feeding on fruits/berries
Foraging	Downy Woodpecker	Gleaning, excavating, and probing prey from live/dead wood surfaces
Foraging	Red-bellied Woodpecker	Gleaning, excavating, probing, pecking on live/dead wood, feeding on fruits/berries
Foraging	Northern Flicker	Probing the ground for prey
Foraging	Eastern Bluebird	Actively searching for prey from a branch and sallies to catch it, flycatching, searching on the ground
Foraging	Great Crested Flycatcher	Flycatching, sallies from perch, short dives to the ground, hovering

Table 5. Variable codes and corresponding categorization scheme used in contingency table analyses at the guild and species scale.

Independent Variable Code	Categorization Scheme
Site	Shaffer, South Girdham, Old State Line, Garden, North Girdham
Snag	(snag density) 5.4, 5.6, 6.7, 13.7, 20.4 snags/ha
Canopy	(canopy cover estimate) 13.2, 14, 24.95, 26.9, 30.5 %
Area	(area of site) 6, 8.9, 10.2, 12.3, 13.7 ha
Behavior variable code	
Forage	[0-.229], [0.230-0.66], [0.670-1] proportions of time foraging
Rest	[0.099], [0.1-0.77], [0.771-1] proportions of time resting
Preen	[0-0.039], [0.040-0.10], [0.101-1] proportions of time preening
Terr/comm	[0-0.149], [0.15-1] proportions of time being territorial/communicating
Nest	[0-0.39], [0.040-0.27], [0.271-1] proportions of time at or in the nest
Substrate variable code	
Live	[0-0.500], [0.501-1] proportions of time on any live tree
Dead	[0-0.500], [0.501-1] proportions of time on any snag or dead branch
Snag only	[0-0.500], [0.501-1] proportions of time on any snag only

Table 6. Contingency table analysis results of activity budgets based on categorical proportions of behaviors of all cavity-nesting birds between all sites. Site characteristics including snag density, area, and canopy cover were used to determine if there were trends in the data. Chi-square (X^2) or Cochran-Mantel-Haenszel Statistic are given along with p-value. There were no significant differences in activity budgets between sites.

Independent Variable Code	Dependent Variable Code	X^2	Mantel-Haenszel	p
site	forage	5.2649		0.7289
site	rest	8.5415		0.3824
site	preen	4.4163		0.8178
site	terr/comm	3.2135		0.5228
site	nest	7.7644		0.4568
snag	forage		0.881	0.3479
snag	rest		0.0735	0.7863
snag	preen		0.0372	0.847
snag	terr/comm		1.3016	0.2539
snag	nest		1.2041	0.2725
canopy	forage		1.0241	0.3116
canopy	rest		0.6822	0.4088
canopy	preen		0.1169	0.7324
canopy	terr/comm		0.0114	0.9149
canopy	nest		0.0203	0.8867
area	forage		0.0016	0.9685
area	rest		1.2752	0.2588
area	preen		0.011	0.9165
area	terr/comm		2.0394	0.1533
area	nest		0.4089	0.5225

Table 7. Percent of observations occurring in proportion categories. The majority of observations occurred below the category ranges used in this study.

Behavior	Proportion Categories		
	Below Range	Within Range	Greater Than Range
Forage	38	28	34
Rest	49	37	14
Preen	71	3	26
Terr/Comm	82	n/a	18
Nest	86	6	8

Table 8. Contingency table analysis results of substrate use based on categorical proportions of behaviors of all cavity-nesting birds between all sites. Site characteristics including snag density, area, and canopy cover were used to determine if there were trends in the data. Cochran-Mantel-Haenszel Statistics are given along with p-value. An asterisk (*) indicates a Fisher's exact test was used in the analysis. Cavity-nesting birds used substrates differently between sites and site characteristics influenced substrate use.

Independent Variable Code	Dependent Variable Code	Cochran-Mantel-Haenszel Statistic	p
site	live		<0.0001*
site	dead		0.0094*
site	snag only		0.0015*
snag	live	1.3187	0.2508
snag	dead	0.6023	0.4377
snag	snag only	3.2008	0.0736
canopy	live	6.6364	0.0100
canopy	dead	2.8536	0.0912
canopy	snag only	5.6548	0.0174
area	live	0.0058	0.9392
area	dead	0.0133	0.9083
area	snag only	0.1174	0.7319

Table 9. Regression analysis of species' behavior as a function of site characteristics including snag density, canopy cover, and area. The correlation coefficient (r^2) and F-value are given along with the direction of the slope which is designated as positive (pos) or negative (neg).

Behavior	Site Characteristic	Species	r^2	F value	p	Slope
Forage	canopy	Downy Woodpecker	0.0029	0.05	0.8323	pos
Forage	canopy	Eastern Bluebird	0.0035	0.22	0.6441	pos
Forage	canopy	Great Crested Flycatcher	0.0618	1.25	0.2772	pos
Forage	canopy	Northern Flicker	0.2588	2.09	0.1980	neg
Forage	canopy	Red-bellied Woodpecker	0.0551	0.64	0.4401	pos
Forage	canopy	Red-headed Woodpecker	0.0051	0.42	0.5194	pos
Forage	area	Downy Woodpecker	0.0143	0.17	0.6858	neg
Forage	area	Eastern Bluebird	0.0052	0.32	0.5733	neg
Forage	area	Great Crested Flycatcher	0.0422	0.84	0.3716	pos
Forage	area	Northern Flicker	0.4346	4.61	0.0754	neg
Forage	area	Red-bellied Woodpecker	0.0087	0.1	0.7624	pos
Forage	area	Red-headed Woodpecker	0.0008	0.06	0.8034	pos
Forage	snag	Downy Woodpecker	0.0153	0.25	0.6251	pos
Forage	snag	Eastern Bluebird	0.0082	0.5	0.4801	neg
Forage	snag	Great Crested Flycatcher	0.0000	0	0.9782	neg
Forage	snag	Northern Flicker	0.6904	13.38	0.0106	pos
Forage	snag	Red-bellied Woodpecker	0.2972	4.65	0.0540	neg
Forage	snag	Red-headed Woodpecker	0.0049	0.4	0.5298	neg
Rest	canopy	Downy Woodpecker	0.0300	0.49	0.4921	pos
Rest	canopy	Eastern Bluebird	0.0000	0	0.9705	pos
Rest	canopy	Great Crested Flycatcher	0.0011	0.02	0.8887	neg
Rest	canopy	Northern Flicker	0.0029	0.02	0.8995	pos
Rest	canopy	Red-bellied Woodpecker	0.0362	0.41	0.5334	pos
Rest	canopy	Red-headed Woodpecker	0.0183	1.51	0.2229	neg
Rest	area	Downy Woodpecker	0.0125	0.2	0.6585	pos
Rest	area	Eastern Bluebird	0.0256	1.6	0.2105	pos
Rest	area	Great Crested Flycatcher	0.0081	0.15	0.6988	neg
Rest	area	Northern Flicker	0.3492	3.22	0.1229	pos
Rest	area	Red-bellied Woodpecker	0.0010	0.01	0.9185	pos
Rest	area	Red-headed Woodpecker	0.0024	0.2	0.6583	neg
Rest	snag	Downy Woodpecker	0.0729	1.26	0.2785	neg
Rest	snag	Eastern Bluebird	0.0019	0.12	0.7321	pos
Rest	snag	Great Crested Flycatcher	0.0067	0.13	0.7235	neg
Rest	snag	Northern Flicker	0.1002	0.67	0.4450	neg
Rest	snag	Red-bellied Woodpecker	0.0218	0.25	0.6303	neg
Rest	snag	Red-headed Woodpecker	0.0026	0.21	0.6477	pos

Table 9. (Continued.)

Behavior	Site Characteristic	Species	r ²	F value	p	Slope
Preen	canopy	Downy Woodpecker	0.0174	0.28	0.6015	pos
Preen	canopy	Eastern Bluebird	0.0314	1.98	0.1647	neg
Preen	canopy	Great Crested Flycatcher	0.0912	1.91	0.1834	pos
Preen	canopy	Northern Flicker	0.0094	0.06	0.8194	pos
Preen	canopy	Red-bellied Woodpecker	0.0000	0	0.0000	n/a
Preen	canopy	Red-headed Woodpecker	0.0012	0.1	0.7523	neg
Preen	area	Downy Woodpecker	0.0586	1	0.3331	neg
Preen	area	Eastern Bluebird	0.0005	0.03	0.8560	neg
Preen	area	Great Crested Flycatcher	0.1599	3.62	0.0725	neg
Preen	area	Northern Flicker	0.0971	0.65	0.4524	neg
Preen	area	Red-bellied Woodpecker	0.0000	0	0.0000	n/a
Preen	area	Red-headed Woodpecker	0.0194	1.6	0.2092	pos
Preen	snag	Downy Woodpecker	0.0073	0.12	0.7364	pos
Preen	snag	Eastern Bluebird	0.0029	0.18	0.6741	pos
Preen	snag	Great Crested Flycatcher	0.0005	0.01	0.9227	pos
Preen	snag	Northern Flicker	0.0017	0.01	0.9236	pos
Preen	snag	Red-bellied Woodpecker	0.0000	0	0.0000	n/a
Preen	snag	Red-headed Woodpecker	0.0201	1.66	0.2006	neg
Territorial/communicate	canopy	Downy Woodpecker	0.0341	0.57	0.4629	neg
Territorial/communicate	canopy	Eastern Bluebird	0.0029	0.18	0.6731	pos
Territorial/communicate	canopy	Great Crested Flycatcher	0.0902	1.88	0.1859	neg
Territorial/communicate	canopy	Northern Flicker	0.0373	0.23	0.6466	pos
Territorial/communicate	canopy	Red-bellied Woodpecker	0.0126	0.14	0.7151	neg
Territorial/communicate	canopy	Red-headed Woodpecker	0.0107	0.88	0.3520	pos
Territorial/communicate	area	Downy Woodpecker	0.0891	1.56	0.2290	pos
Territorial/communicate	area	Eastern Bluebird	0.0017	0.11	0.7454	neg
Territorial/communicate	area	Great Crested Flycatcher	0.0134	0.26	0.6173	neg
Territorial/communicate	area	Northern Flicker	0.0058	0.04	0.8574	pos
Territorial/communicate	area	Red-bellied Woodpecker	0.0234	0.26	0.6179	pos
Territorial/communicate	area	Red-headed Woodpecker	0.0001	0.01	0.9251	neg
Territorial/communicate	snag	Downy Woodpecker	0.0346	0.57	0.4600	neg
Territorial/communicate	snag	Eastern Bluebird	0.0013	0.08	0.7779	neg
Territorial/communicate	snag	Great Crested Flycatcher	0.0211	0.41	0.5301	pos
Territorial/communicate	snag	Northern Flicker	0.0611	0.39	0.5551	neg
Territorial/communicate	snag	Red-bellied Woodpecker	0.0909	1.1	0.3167	pos
Territorial/communicate	snag	Red-headed Woodpecker	0.0021	0.17	0.6795	pos

Table 10. Contingency table analysis results of Red-headed Woodpecker substrate use based on categorical proportions of behaviors between sites. Site characteristics including snag density, area, and canopy cover were used to determine if there were trends in the data. Cochran-Mantel-Haenszel Statistics are given along with p-value. An asterisk (*) indicates a Fisher's exact test was used in the analysis. Red-headed Woodpeckers used substrates differently between sites and snag density and canopy cover influenced substrate use.

Independent Variable Code	Dependent Variable Code	Cochran-Mantel-Haenszel Statistic	p
site	dead		0.0049*
site	live		<0.0001*
site	snag only		0.0033*
snag	dead	1.8168	0.1777
snag	live	6.4485	0.0111
snag	snag only	6.0916	0.0136
canopy	dead	2.7765	0.0957
canopy	live	3.5879	0.0582
canopy	snag only	4.9819	0.0256
area	dead	0.4929	0.4826
area	live	2.0239	0.1548
area	snag only	0.6135	0.4335

Table 11. Contingency table analysis results of Red-headed Woodpecker substrate use based on categorical proportions of behaviors between all sites excluding Shaffer. Site characteristics including snag density, area, and canopy cover were used to determine if there were trends in the data. Chi-square (X^2) or Cochran-Mantel-Haenszel Statistics are given along with p-values. An asterisk (*) indicates a Fisher's exact test was used in the analysis. Red-headed Woodpeckers used substrates differently between sites. Snag density and canopy cover influenced substrate use to a lesser extent when Shaffer was excluded from analysis, and area also influenced substrate use.

Independent Variable Code	Dependent Variable Code	X^2	Cochran-Mantel-Haenszel Statistic	p
site	dead	2.7434		0.1177
site	live			0.075*
site	snag only			0.0907*
snag	dead		0.251	0.6163
snag	live		2.7158	0.0994
snag	snag only		3.3862	0.0657
canopy	dead		0.755	0.3849
canopy	live		0.8494	0.3567
canopy	snag only		2.5737	0.1087
area	dead		1.6391	0.2004
area	live		5.4759	0.0193
area	snag only		1.5236	0.2171

Table 12. Contingency table analysis results of Eastern Bluebird substrate use based on categorical proportions of behaviors between sites. Site characteristics including snag density, area, and canopy cover were used to determine if there were trends in the data. Cochran-Mantel-Haenszel Statistics are given along with p-value. An asterisk (*) indicates a Fisher's exact test was used in the analysis. Eastern Bluebirds used substrates differently between sites and canopy cover influenced substrate use.

Independent Variable Code	Dependent Variable Code	X^2	Cochran-Mantel-Haenszel Statistic	p
site	dead	6.2317		0.1825
site	live			0.0084*
site	snag only			0.0496*
snag	dead		0.0823	0.7742
snag	live		0.6849	0.4079
snag	snag only		0.0087	0.9255
canopy	dead		5.3204	0.0211
canopy	live		8.4349	0.0037
canopy	snag only		6.8937	0.0087
area	dead		0.6258	0.4289
area	live		0.9967	0.3181
area	snag only		2.2002	0.138

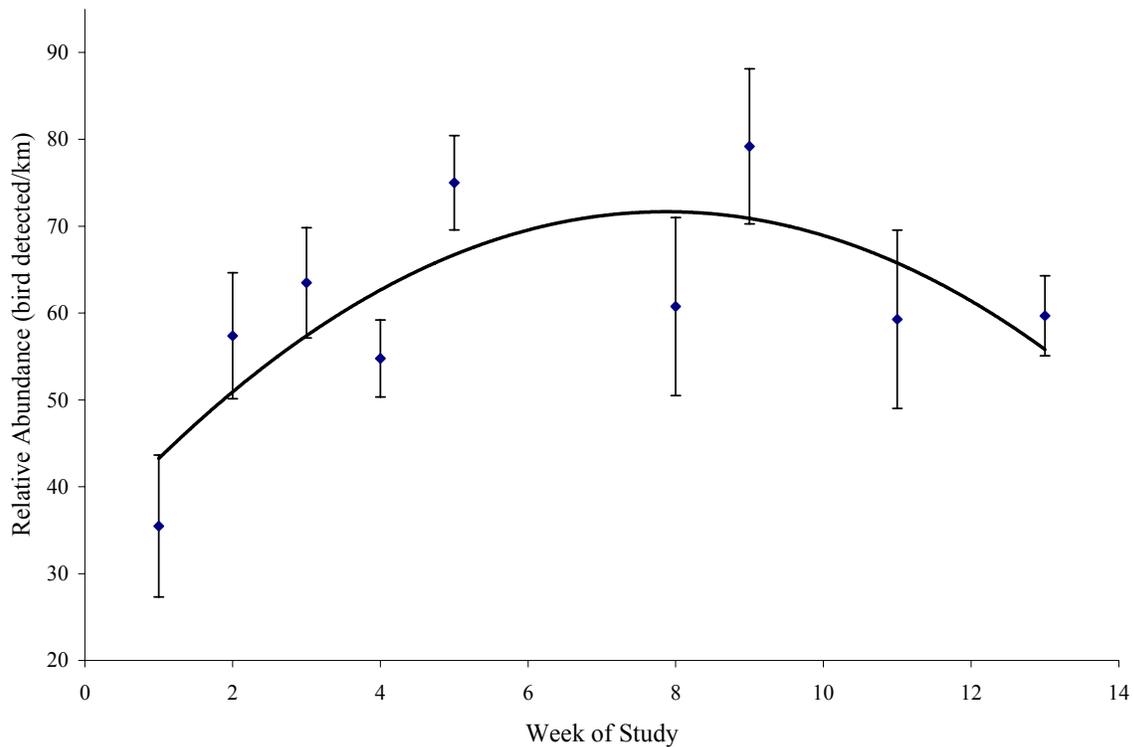


Figure 1. Average relative abundance of all birds detected among survey transects over time at all sites combined. Error bars represent standard error. Polynomial function equation is $y = -0.6022 x^2 + 9.4773 x + 34.371$, $r^2 = 0.5846$, $p = 0.07169$. Peak abundance occurs at approximately the eighth week of the study (early July 2006).

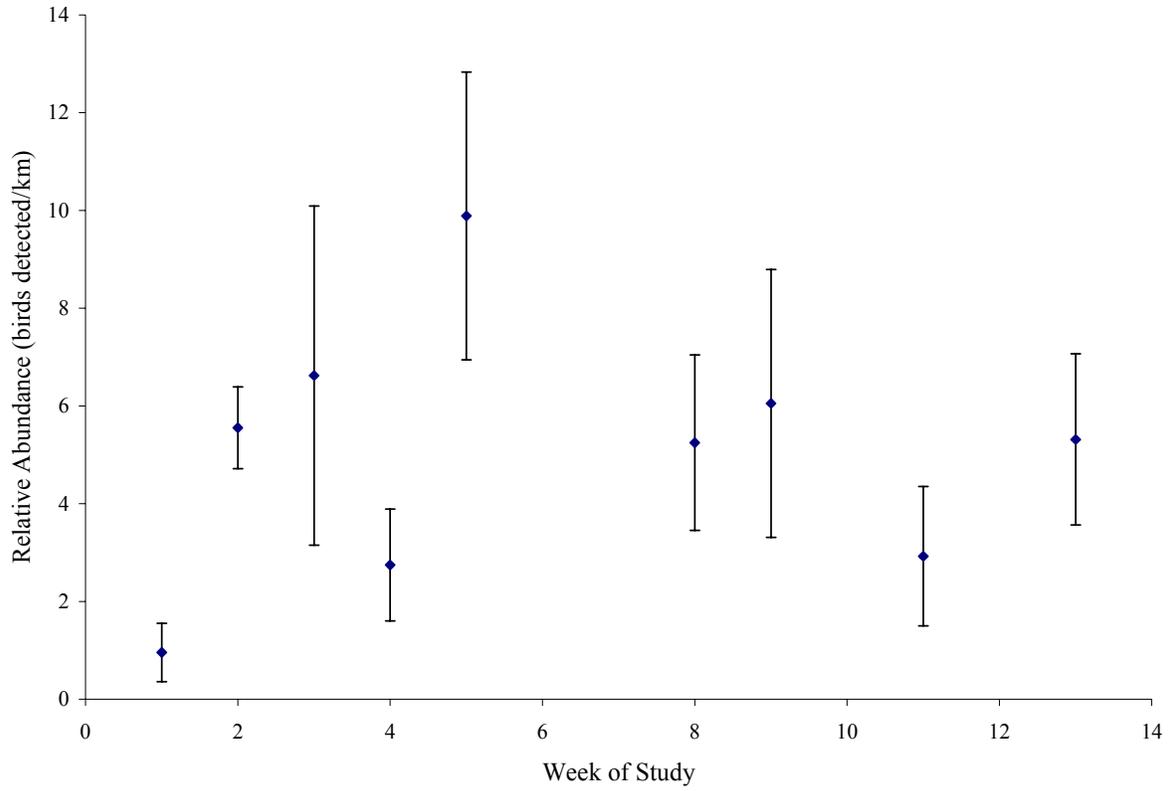


Figure 2. Average relative abundance of cavity-nesting birds detected along transect surveys over time at all sites combined. Error bars represent standard error.

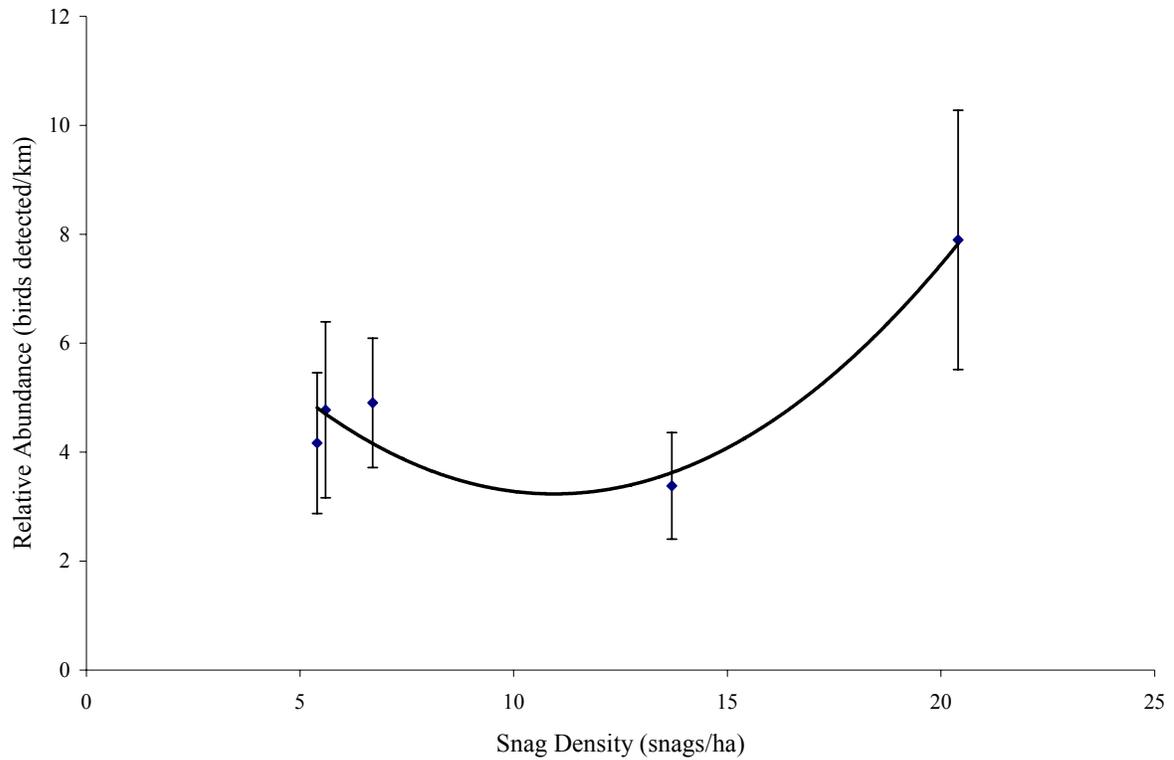


Figure 3. Average relative abundance of cavity-nesting birds as snag density increases. Each point represents a different site with a unique snag density. Error bars represent standard error.

Polynomial function equation is $y = 0.0514 x^2 - 1.1244 x + 9.3868$, $r^2 = 0.9112$, $p = 0.08877$.

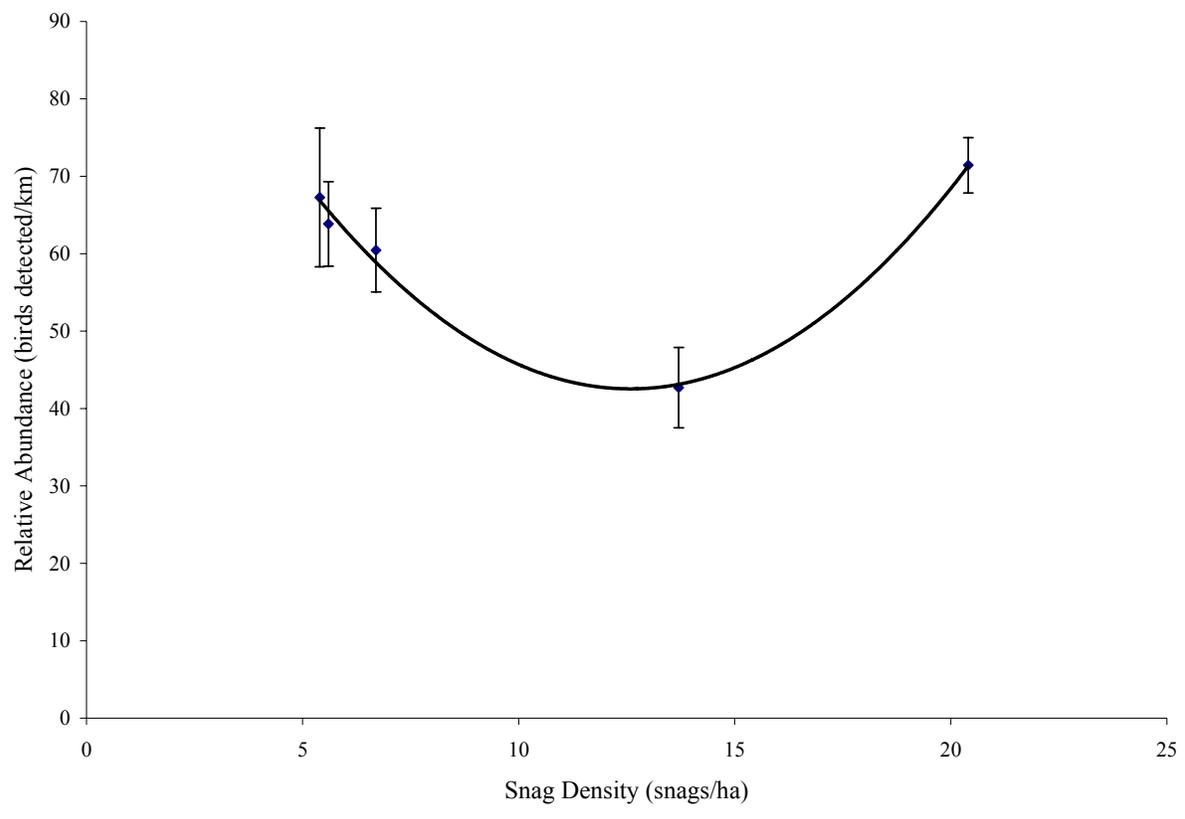


Figure 4. Average relative abundance of all birds as snag density increases. Each point represents a different site with a unique snag density. Error bars represent standard error.

Polynomial function equation is $y = 0.4712 x^2 - 11.863 x + 117.2$, $r^2 = 0.9883$, $p = 0.01169$.

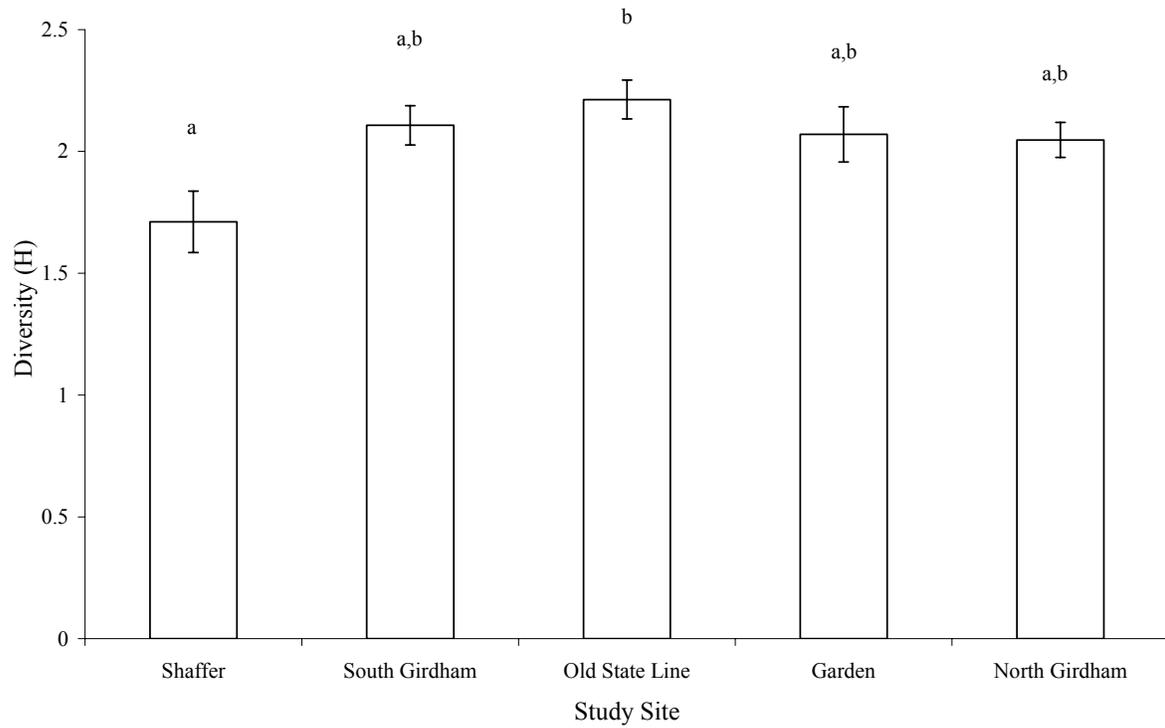


Figure 5. Average Shannon-Wiener Index of diversity (H) values at all sites. Error bars represent standard error, different letters represent a significant difference, $p = 0.0197$. Old State Line had a significantly higher diversity than Shaffer.

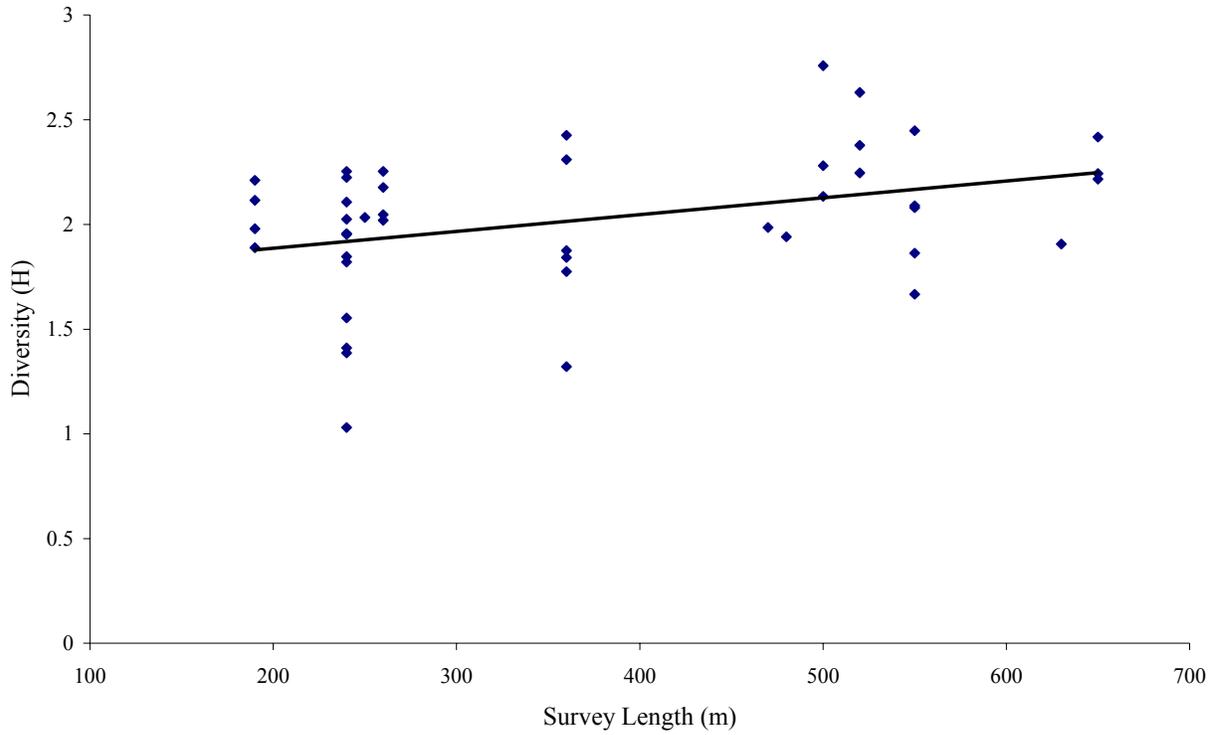


Figure 6. Shannon-Wiener Index of diversity (H) values for each survey length. Linear regression equation is $y = 0.0008x + 1.7256$, $r^2 = 0.1308$, $p = 0.0158$. As survey length increased, diversity of birds increased.

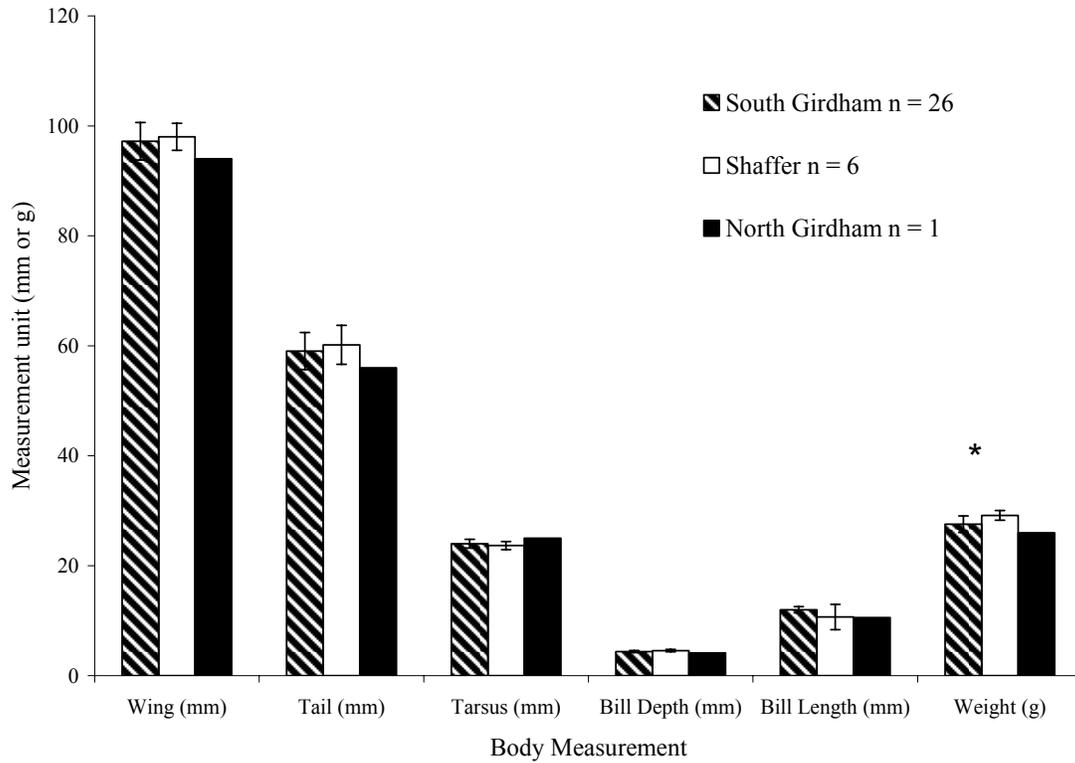


Figure 7. Average juvenile Eastern Bluebird body measurement comparison between South Girdham (diagonal lines, n = 26), Shaffer (white, n = 6), and North Girdham (black, n = 1). An asterisk (*) indicates a significant difference. Error bars represent standard error. Eastern Bluebirds weighed significantly more at Shaffer than at South Girdham, Bonferroni corrected, $p < 0.008$.

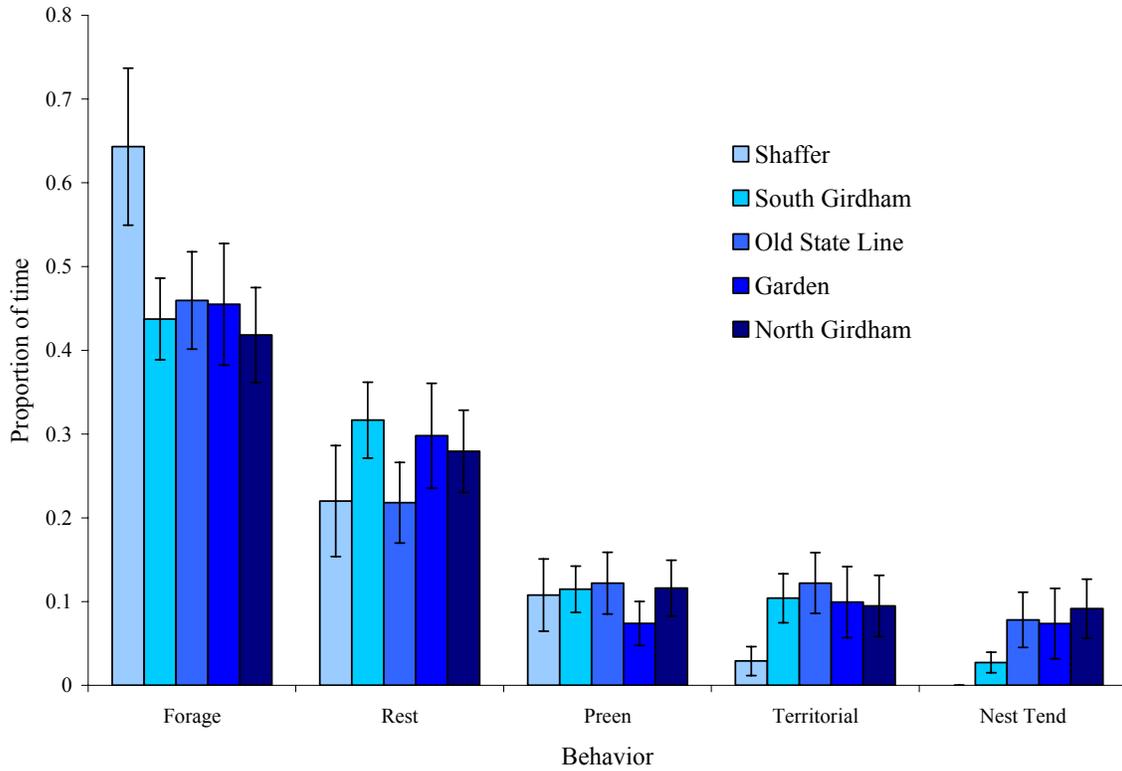


Figure 8. Average proportion of time spent performing behaviors among all sites for cavity-nesting birds. Error bars represent standard error. Proportions of time spent performing behaviors were similar at all sites.

APPENDIX B
SITE RESTORATION HISTORY

Site	Restoration Technique		
	Most Recent Burn (burn history)	Most Recent Thinning	Mowing Regime
Shaffer	2000 wildfire (no prescribed burns)	spring 2005	mowed every year since 2004
Garden	2004 (burned 2x since 2000)	2000	mowed every other year since 2000
OSL	2004 (burned 3x since 1999)	1999	mowed every year since 1996
North Girdham	2003 (burned 3x since 1997)	2002	mowed 2003, 2006
South Girdham	2006 (partially burned 9x since 1995)	2005	mowed 2002, 2006