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## **Effects of Urbanization on the Avian Community of Oak Woodlands**

By

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### THESIS

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For the Degree of Master of Science, With a Major in Environmental Biology

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ABSTRACT — Continued human population growth leads to further expansion of highdensity population centers and agricultural land necessary to sustain them. With this urban expansion comes a myriad of effects on both native habitat and wildlife. In birds, these effects can have a variety of negative impacts on behavior and physical health. Habitat degradation, largely through various forms of pollution, leads to impaired immune responses, increased stress levels, altered behavior, and much more. The wide range of effects impacting wild birds and their habitat can also alter the structure of local communities. Only species that can survive on or adapt to the resources and conditions of the urban landscape fare well, leading to a reduction in avian diversity, and the homogenization of urban avian communities. The city of Chicago, together with the range of land use types around it, makes up an urban-rural gradient, providing an opportunity to study the effects of urbanization. Across this gradient, during the summers of 2018 and 2019, point-count surveys of breeding birds in 28 oak woodland patches were performed to measure the effect of urbanization on the local bird community. Contrary to similar studies, no significant effect of urban development was found on either density or overall species richness of breeding birds. When grouped by guilds, significant impacts on species richness were found. While some results matched expected patterns (omnivore species richness peaks at high levels of development), many did not. Granivores and ground-foragers tend to respond positively to urbanization but showed no significant difference here. The focus of this study on oak woodlands may be responsible, as a single habitat type is far more consistent than the whole of an urban-rural matrix. Additionally, the urban birds typically found in cities across the world do not typically inhabit woodlands, freeing up resources for local natives.

Key words: urban-rural gradient, breeding birds, oak woodlands, density, richness, community.

**Chapter One: Literature Review**

#### **Introduction**

As human populations grow, population centers continue to expand, removing, fragmenting, and degrading the surrounding habitat. The shift from rural to urban life led to high-density living, but the need for large expanses of land for agriculture persists, and land use, for everything from commercial development to housing, continues to grow (Laurence 2010). The single largest effect of this expansion, and the leading cause of the loss of biodiversity worldwide, is the destruction of habitat for urban infrastructure (Pimm et al. 2014, Hanski 2015). Compounding habitat loss is habitat fragmentation. As habitat is removed, relatively small and isolated patches often remain (Rudd et al. 2002, Zuidema et al. 2009). As suggested by island biogeography, smaller habitat patches tend to be less capable of supporting high biodiversity (MacArthur and Wilson 1963, MacDonald et al. 2018). Originally developed to explain the effect of size, distance, immigration, and extinction on biodiversity of marine islands, island biogeography theory has since been adapted to inland habitats (Brown 1978, Samson 1980). In addition to the loss and fragmentation of habitat, urban development brings with it numerous other problems for native habitat and wildlife. Habitat degradation in the form of air, water, soil, light, and noise pollution, as well as countless other smaller effects, introduces new problems, and can negatively impact wildlife in different ways (Longcore and Rich 2004, Chace and Walsh 2006, Rattner 2009, Ortega 2012, Sanderfoot 2017, Sepp et al. 2018). Not only do these negative effects tend to decrease biodiversity, but they can also lead to shifts in species composition (McKinney 2002). In bird communities, changes in food availability and predator assemblage, among others, tend to select for generalists, omnivores, granivores, and exotic species (Lim and Sodhi 2004, Kark et al. 2006, Croci

et al. 2008, Ortega-Álvarez and MacGregor-Fors 2009, Leveau 2013). Over time, these changes can lead to homogenization of bird communities among separate urban environments, as the urban communities begin to more closely resemble one another than those in their respective native habitats (Blair 2001, Morelli et al. 2016).

#### **Habitat area and fragmentation**

Limited area of habitat constrains the maximum number of species an area can support (Gilpin and Diamond 1980, Oertli et al. 2002). Within an ecologically uniform area, observed species richness can increase logarithmically as a function of sampling area, although log-log relationships also occur (MacArthur and Wilson 1963, Matthews et al. 2014). Habitat loss being the leading cause of the loss of biodiversity worldwide further supports this relationship (Pimm et al. 2014, Hanski 2015). The relationship between area and species richness of oceanic islands has shown that a 100% increase in area corresponds to an approximate 25% increase in number of species. This relationship, however, is prone to change as other variables are introduced (MacArthur and Wilson 1963, Gilpin and Diamond 1980). The majority of these fluctuations may be attributed to distances between islands, although competition, predation, immigration rates, and extinction rates can have lesser effects. Distance from the main faunal source has also been shown to have a negative correlation with species saturation of birds in Oceanic and Indonesian island chains (MacArthur and Wilson 1963). With the extent of human influence on the distribution of species, economic factors such as trade and transportation also factor in to the rates at which new species are introduced (Helmus et al. 2014).

The relationship between the size of islands, distance among islands, immigration rates, and extinction rates gives us the concept of island biogeography, which has since been adapted to inland habitats (MacArthur and Wilson 1967, Brown 1978, Samson 1980). Just as island species richness is dependent on these variables, species richness of isolated terrestrial habitats like mountain ranges or patches of habitat among urban landscapes can be affected in a similar manner (Brown 1978, Davis and Glick 1978).

In areas of human development, the division of previously contiguous habitat into several smaller habitat patches results in fragmentation, often reducing biodiversity (Rudd et al. 2002, Zuidema et al. 2009). Fragmentation can have a variety of effects on abundance, species richness, and species diversity. These effects can be both positive and negative, depending on the taxa and habitat type (Knutson et al. 1999**,** Knick and Rotenberry 2002, Fahrig 2003). Fragmentation increases the proportion of edge habitat, as smaller patches have a higher ratio of perimeter to area (Fahrig 2003). This change in edge to interior ratio favors species that are adapted to the conditions of edge habitats, such as increased light levels and a well-developed understory (Fink et al. 2006, Reino et al. 2009). Proximity to edge habitat can be negatively correlated with species diversity of small mammals in forest fragments, while species richness and diversity of birds of coniferous forests has shown both positive and negative responses to edges, depending on the adjacent habitat type (Stevens and Husband 1998, Laiolo and Rolando 2005).

Furthermore, fragmentation into small patch sizes can have a negative effect on the abundance of area-sensitive species. Woodland bird species like the Scarlet Tanager (*Piranga olivacea)* and Pileated Woodpecker (*Dryocopus pileatus*), as well as grassland species like the Greater Prairie-Chicken (*Tympanuchus cupido*) and at least a dozen

others in North America are known to respond negatively to reductions in patch size (Winter and Faaborg 1999, Fraser and Stutchberry 2004, McIntyre 2004, Ribic et al. 2009). In the case of forest-dwelling species, it has been shown that birds in smaller patches are less well-fed and rear smaller nestlings than their counterparts in larger fragments. Zanette et al. (2000) suggests that food shortages, due to the habitat's lessened ability to support sufficiently high biomass of prey species, may be the cause.

#### **Other effects of urbanization**

Urbanization can have a variety of impacts on wildlife populations. As a primary cause of habitat loss, urban development is a major contributor to the extinction of species, which is currently estimated to be 1000 times higher than the natural, pre-human background rates of extinction (McKinney 2002, Seto et al. 2011, DeVoss et al. 2014). Estimates of future urban land cover suggest that between 2011 and 2030, the global area of urban land will increase by  $1,527,000 \text{ km}^2$ , with 81% of the world's population living in cities (Imhoff et al. 2010, Seto et al. 2011). Because habitat loss is often paired with fragmentation, urbanization is also responsible for many of the associated effects of fragmentation. Although urban habitat patches are less isolated than with a strict adherence to the concept of island biogeography, due to the differing permeability of the matrices in which the fragments are embedded, fragmentation in urban areas can cause measurable detrimental effects on wildlife populations and communities (MacArthur and Wilson 1967, Marzluff 2005, Cane et al. 2006). Often these urban matrices are very low permeability, resulting in little dispersal and re-colonization. Although the extent to which permeability is impacted by the urban landscape and fragmentation varies by taxa,

it has been shown to influence the territory parameters and behavior of woodland songbirds (Umetsu and Pardini 2007, Tremblay and St. Clair 2011). Despite the effects of fragmentation varying by taxa or habitat, they may ultimately alter the structure of communities, which can have further unpredictable consequences.

In addition to destroying and fragmenting habitat, urbanization has a wide range of other negative effects on habitat quality and wildlife. Due mainly to traffic and power generation, but also affected by agricultural practices, poor air quality is known to be major factor in a variety of ailments in both humans and wildlife (Newman 1979, WHO 2003, Aneja et al. 2009, Guarnieri and Balmes 2014). In humans, air pollution has been associated with health issues such as increased rates of asthma, cancer, and increased annual mortality (Dockery et al. 1993, Nyberg et al. 2000, Guarnieri and Balmes 2014). Poor air quality can also produce similar effects in wildlife. Proximity to cities has been shown to increase heritable mutation rates in both Herring Gulls (*Larus argentatus*) and lab mice via air-borne chemical pollutants (Sepp et al. 2018). A variety of other health impacts have also been shown in birds, including impaired immunity and reproductive success, increased stress, increased tracheal mucous, increased risk of respiratory infection, and more (Llacuna et al. 1993, Sanderfoot 2017, Sanderfoot and Holloway 2017). Birds have even been suggested as a means of studying the effects of air pollution due to their particular susceptibility to it (Brown et al. 1997).

Likewise, water quality is also impacted by several aspects of development. In urban centers; runoff from concrete surfaces, roads, and other materials used in construction can alter water chemistry. Mineral leeching from concrete used in construction and drainage systems alters the pH of freshwater streams and increases

concentrations of substances like bicarbonate and calcium by as much as 10 times (Wright et al. 2011). Other construction materials can contain biocidal additives which have also been shown to leach into storm water, some of which can bioaccumulate, potentially impacting organisms at various trophic levels (Burkhardt et al. 2011). Even without chemical or mineral leaching, roads and other impervious surfaces change the timing of and reroute runoff which can lead to downstream changes in erosion rates, patterns of sediment deposition, and stream velocities (Klein 1979, Evink 2002).

Farther from the urban center, agriculture can have similar effects as runoff carries fertilizer, pesticides, sediment, nutrients, and more into downstream bodies of water (Dahshan et al. 2016, Mohammadi et al. 2017, Baker et al. 2018). These effects are made even worse by flow reduction in nearby bodies of water which is attributed to the need for irrigation in agriculture (Evans et al. 2019). These changes to local and downstream water systems can then affect the organisms living in or depending on them. Mercury concentrations alone (which can be increased by both industry and agriculture) can impact behavior, hormones, and reproduction in fish, mammals, and birds through bioaccumulation and biomagnification (Scheuhammer et al. 2007, Wolfe et al. 2009). As with air pollution, changes in water quality can also increase rates of cancer in humans, fish, and other mammals (Ebenstein 2012, Sepp et al. 2018).

Land development can have similar impacts on soil quality, which is often linked to the effects seen in air and water systems. Heavy metal (e.g. cadmium, copper, lead, nickel, zinc) concentrations in soil are known to be higher in regions of heavy urban development (Pouyat et al. 1991, Lu et al. 2009). These high soil concentrations have, in some cases, been attributed to high concentrations of these elements in both air (from

traffic emissions and industry) and water (from industrial and household sewage and runoff from roads, parking lots, and roofs) in urban landscapes (Möller et al. 2005). Polycyclic aromatic hydrocarbons (PAH) in the air (which have shown a positive correlation between concentration and urban development) can also be transferred into soil, as well as water, via atmospheric deposition (McVeety and Hites 1988, Wong et al. 2004). Other compounds, such as  $NO_3$ <sup>-</sup>,  $NH_4$ <sup>+</sup>, and  $Ca_2$ <sup>+</sup>, transfer between air and soil via throughfall and particulate dust deposition, as well as atmospheric deposition (Lovett et al. 2000). Many of these soil contaminants have negative impacts on the health of vegetation, wildlife, and humans. Plants grown in contaminated roadside soil have shown not only low germination rates, but also high concentrations of nitrogen and heavy metals (Spencer and Port 1988, Williams et al. 2018). These heavy metals can then inhibit plant growth by impeding the growth of beneficial soil bacteria, damaging plant cells, and interfering with certain enzymes and ion exchange processes (Chibuike and Obiora 2014). Just as contaminants can enter and spread through the food chain in aquatic systems via bioaccumulation and biomagnification, heavy metal contaminants in soil can accumulate in terrestrial frugivores and herbivores and be transferred to higher trophic levels as they are preyed upon by insectivorous and carnivorous species (Wijnhoven et al. 2007, van der Brink et al. 2010, Orta-Martínez et al. 2018). Effects of this contamination vary depending on the metal and can include a variety of ailments such as cardiovascular, nervous, and renal diseases, bone disorders, and impairment of neurological development (Rattner 2009, Burger and Gochfeld 2010, Yarsan et al. 2014). When high concentrations of these metals are present in agricultural crops, they can also pose a threat to humans,

increasing the risk of gastrointestinal cancer, mental retardation, and damage to the central nervous system (Huang et al. 2017, Rai et al. 2019).

While pollution is typically seen as physical or chemical contamination of the environment, there are other known ways of reducing habitat quality, and therefore impacting wildlife. One example is the abundance of artificial lighting that comes with urbanization, specifically that which remains after sunset, illuminating an otherwise dark night (Falchi et al. 2016). Often associated with obscuring astronomical observations (known as astronomical light pollution), light pollution has a wide range of effects on both humans and wildlife (ecological light pollution) (Longcore and Rich 2004, Falchi et al. 2016). Light pollution is strongly associated with urbanization, as artificial light follows human population concentration, but there are factors other than the physical development of an area that can exacerbate the situation (Gallaway et al. 2009). A lack of, or inadequate restrictions on lighting for industrial and residential areas and roadside advertising, plus poor urban planning, and low public awareness all contribute to the issue (Song and Li 2017). Cloud coverage is a natural phenomenon that can alter and amplify the effects of artificial lighting, altering the color and increasing luminance by a factor of ten, with overcast nights in an urban center being brighter than clear moonlit rural areas (Kyba et al. 2011, Kyba et al. 2012). In some cases, bright areas are also associated with less vegetation cover and high-albedo surfaces (Katz and Levin 2016). Light pollution levels vary greatly by location, with some cities having demonstrated not only a change in color temperature between day and night, but also peak nighttime luminance levels of more than 50 times that of dark sky regions (Liu et al. 2017). It is estimated that 83% of the world's population lives in light-polluted areas, with some

locations being over 1300 km from the nearest point of natural nighttime light levels, as the effects can be felt hundreds of kilometers from the source (Duriscoe et al. 2007, Falchi et al. 2016). Effects on wildlife from light pollution are widespread and often involve disorientation or attraction/repulsion by light sources (Longcore and Rich 2004). Nocturnally migrating birds can be attracted to and disoriented by artificial light sources in poor weather conditions and become trapped in brightly lit areas, increasing the risk of collisions with buildings and other birds, as well as risking exhaustion (Longcore and Rich 2004, Van Doren et al. 2017). Light levels can also impact sleep in birds (as well as humans), reducing both quality and quantity of sleep, leading to changes in hormone concentrations and reduced immune responses (Cho et al. 2013, Raap et al. 2015, Ouyang et al. 2017). Some species of birds and other predators living in more brightly lit areas experience altered hunting behavior, including a tendency to hunt later into the night, allowing them and their young better access to food (Longcore and Rich 2004, Gaston et al. 2013, Stracey et al. 2014, Schoeman 2015). Reduced prey activity and increased nighttime vigilance in bright areas indicate a negative impact on prey species (Longcore and Rich 2004, Yorzinski et al. 2015).

Excessive amounts of anthropogenic sound released into the environment can cause noise pollution. Noise in this case can be defined as any unwanted sound, but some researchers specifically characterize it as sounds of high amplitudes and low frequencies (Goines and Hagler 2007, Francis et al. 2009). Like light pollution, noise pollution is both clearly linked with human development and has many potential impacts on the health of humans and wildlife (Buxton et al. 2017). Studies from around the world report ambient noise levels in residential or urban areas in excess of 65dB(A) (Palestine/Brazil),

80dB(A) (Turkey/India), and even 110dB(A) (Nigeria) (Zeid et al. 2000, Sagar and Rao 2006, Zannin et al. 2006, Oyedepo and Saadu 2009, Ozer et al. 2009). With a recommended threshold for residential areas of 50dB(A), and a risk of hearing impairment starting at 70dB(A), many locations far exceed the point at which noise can impact human health (Berglund et al. 1999, Menkiti and Agunwamba 2015). Not only are noise levels high in regions of high population density, but the effects can also be felt outside of urban centers. Buxton et al. (2017) have shown that 63% of protected wildlife areas in the United States experience ambient sound levels of at least double the background levels, while 21% see an increase of 10x or more. Although its effects have gone relatively unstudied, noise pollution is considered to be the third most hazardous type of environmental pollution, behind air and water pollution (Khilman 2004, Barton et al. 2018). Effects of prolonged exposure on humans include sleep disturbance beginning at 30dB, hormonal responses related to stress, blood pressure, and heart rate at 65dB, and hearing damage at 70dB (Berglund et al. 1999, Goines and Hagler 2007).

Similar effects are seen in wildlife. Noise pollution has been shown to damage hearing in birds, to increase nestling stress hormone levels and telomere attrition rates (which suggest lower pre- and post-fledgling survival rates), and even to affect physiology, development, and behavior of aquatic organisms (Ortega 2012, Schroeder et al. 2012, Kunc et al. 2016, Injian et al. 2019). Some behavioral impacts in birds include changes in song timing to avoid peak traffic and airport activity, changes in vocalization frequency to minimize interference from low-frequency noise, and a preference to nest in quieter locations (Francis et al. 2009, Ortega 2012, Dominoni et al. 2016). Nest placement preferences also end up changing urban bird communities, as species with

lower-frequency vocalizations tend to avoid louder areas (Rheindt 2003, Francis et al. 2009, Francis et al. 2011).

 Bird collisions with human structures can cause high mortality rates; collisions with windows, power lines, wind facilities, and vehicles range between approximately 460 million to 1.4 billion birds per year in the United States alone (Loss et al. 2013, Loss et al. 2014a, 2014b, 2014c). These collisions, which affect species differently, having a larger impact on nighttime migrants, are not simply correlated with land development, but affected by factors such as size and proximity of vegetation patches to structures (Hager et al. 2013, Van Doren et al. 2017). Urban development also leads to changes in predator assemblages, tending to hinder larger predators like foxes and coyotes, while allowing mesopredators such as raccoons and domestic cats to thrive (Chace and Walsh 2006, Randa and Yunger 2006, Gehrt et al. 2013). Coyote presence is one of the best predictors of the activity of domestic cats, which kill an estimated 14.2-38.9 prey cat<sup>-1</sup> hectare<sup>-1</sup> year<sup>-1</sup>, matching or exceeding predation rates of wild predators (Chace and Walsh 2006, Kays et al. 2015, Kays et al. 2020). Urban habitat also tends to select for generalists, including corvids, which are known nest predators (Lancaster and Rees 1979, Andren 1992). Ambient temperature in urban centers tends to be higher as a result of increased energy consumption and increased heat dissipation from impervious and lowalbedo surfaces that have replaced vegetation (Oke 1973, Deviche and Davies 2014). This may impact urban birds directly by affecting reproductive hormones and egg-lay dates and can affect them indirectly by impacting local plant growth and insect abundance (Deviche and Davies 2014, Zipper et al. 2016, Singh et al. 2018).

#### **Changes in community structure**

As many studies on the various effects of urbanization suggest, these changes can impact species in different ways, favoring some at the expense of others (Chace and Walsh 2006, Ortega-Álvarez and MacGregor-Fors 2009). Over time, and as land is further developed, this can lead to shifts in the distribution of species in the affected areas. The more developed an area becomes, the closer its communities tend to resemble those in other areas of high urban development, as the urban environment is usually more similar to other cities than it is to the surrounding native habitat (Blair 2001, McKinney 2002, Morelli et al. 2016). This shift was shown in a study which demonstrated an inverse correlation between persistent, low-frequency, ambient noise and nesting bird species with low-frequency vocalizations (Francis et al. 2011). These results suggest not only selection against species with these vocalization characteristics, but also indirect selection against larger birds, as they are more likely to communicate via low-frequency signals. Selection for or against certain traits is seen in other aspects of birds' life history, including diet, nesting behavior, and many others (McKinney 2002).

Based on their response to land development, many species can be categorized into one of three response guilds: urban exploiters, urban adapters, and urban avoiders (Blair 1996, McKinney 2002, Leveau 2013). These guilds represent species that are found in highest abundance in high, intermediate, or low levels of land development, respectively (McKinney 2002, Blair 1996). Although this categorization is likely an overgeneralization, it still allows us to see community patterns in response to urbanization (Fischer et al. 2015). Certain aspects of a bird's life history, such as diet or nesting behavior, may favor reproductive success in urban habitat. Omnivorous,

granivorous, and frugivorous birds tend to fare well in developed areas, whereas insectivorous species do not. Urban-adapted birds also tend to be non-migratory, and capable of nesting on artificial structures such as buildings (Lim and Sodhi 2004, Kark et al. 2006, Croci et al. 2008, Ortega-Álvarez and MacGregor-Fors 2009, Leveau 2013). It is also not uncommon to find a higher proportion of exotic species living in urban areas relative to the less disturbed surrounding habitat (McKinney 2002, Lim and Sodhi 2004).

#### **The urban-rural gradient**

As land use changes and human density declines through the suburbs and into rural and undeveloped areas, some of the effects of urbanization can be lessened (Rosch et al. 2001, Venn et al. 2003, Parris 2006). This gradual change in human population density and the consequences thereof creates an urban-rural gradient. This change may not necessarily mean better habitat, however. While urban areas are more densely packed with roads, buildings, and cars, rural areas can still be far from the natural habitat to which local wildlife is adapted. Where habitat in urban areas is replaced by industrial centers, highways, and housing complexes, rural landscapes are cleared for extensive hectares of row crops. In studies of both birds and mammals, areas with moderate levels of urbanization tend to show the highest levels of species diversity, although there is still a general trend towards higher diversity in less urbanized, lower human density areas (Jokimäki and Suhonen 1993, Chace and Walsh 2006, McKinney 2008, Pal et al. 2019).

This spatial gradient or, in some cases, experimental manipulation, is often used in place of temporal scales, as studies done over time can take decades (Batten 1972, Tait et al. 2005). One such case is a study conducted in the 19th and 20th centuries in

northwest London, in which species richness of breeding birds was measured against increasing levels of urbanization between 1830 and 1970. The urbanization levels reported by this study increased from 10% to 30%, 50%, and finally 65%, while the species richness of breeding birds during these times were 71, 64, 53, and 43, demonstrating a steady decline (Batten 1972). While studies like this show us that they can produce good data, they also emphasize the importance of the urban-rural gradient in research as a short-term alternative.

A critical aspect of the urban-rural gradient is quantifying urbanization, and the subsequent categorization of areas into regions demonstrating different levels of land development. To do this, a wide range of factors are taken into account, often primarily land use type and land use cover (Zhao et al. 2007 and Mao et al. 2019). These data can be sourced from USGS databases, state-level resources such as the IDNR (Illinois Department of Natural Resources), or other sources of aerial images and GIS technology (Medley et al. 1995, Randa and Yunger 2006). A collaboration by USGS and NASA has given rise to Landsat data: a resource for researchers that provides access to long-term, medium spatial resolution imagery of landscapes to monitor spatial and temporal changes in land cover (Hansen and Loveland 2012). As habitat loss and fragmentation are major aspects of land development, land use and percent cover are useful metrics for these studies (Stow and Chen 2001, McKinney 2008, Dewan and Yamaguchi 2009). The resolution at which these measurements are taken then determines how finely an area can be divided (Medley et al. 1995). Many other parameters may also be factored into this process, including human population density, distance from an urban center, road density,

traffic volume, and the number and size of habitat patches (Medley et al. 1995, Hahs and McDonnell 2006).

**Chapter 2: Synthesis of Research**

### **Introduction**

Continued human population growth leads to a shift from low to high density living, resulting in the creation of the urban ecosystem at the expense of previously existing ecosystems (Marzluff 2005). Destruction of habitat for urban and agricultural infrastructure is the single leading cause of the loss of biodiversity worldwide, including widespread impacts on birds (Owens and Bennett 2000, Pimm et al. 2014, Hanski 2015, Piersma et al. 2017). With land development, habitat is not only destroyed, but also fragmented into relatively small and isolated patches that tend to be less capable of supporting high species diversity (MacArthur and Wilson 1963, Rudd et al. 2002, Zuidema et al. 2009, MacDonald et al. 2018). These byproducts of urbanization, in addition to air, water, soil, light, and noise pollution, destroy or degrade habitat, thereby lowering biodiversity and shifting species composition of local avian communities (Longcore and Rich 2004, Chace and Walsh 2006, Rattner 2009, Ortega 2012, Sanderfoot 2017, Sepp et al. 2018).

The tendency of urban development to fragment habitat is detrimental to overall biodiversity but can have a variety of effects depending on taxa and habitat type (Knutson et al. 1999**,** Knick and Rotenberry 2002, Rudd et al. 2002, Fahrig 2003, Zuidema et al. 2009). Fragmentation increases the proportion of edge to interior habitat, favoring species like the Brown-headed Cowbird (*Molothrus ater*) that are adapted to the conditions of edges, such as an increase in light levels and density of woodland understory (Fahrig 2003, Fink et al. 2006, Reino et al. 2009). Fragmentation can also have particularly strong effects on area-sensitive species. Species like the Scarlet Tanager (*Piranga olivacea)*, Pileated Woodpecker (*Dryocopus pileatus*), and at least a dozen other birds in

North America, are known to respond negatively to reductions in patch size, likely due to the habitat's lessened ability to support sufficiently high biomass of prey species (Winter and Faaborg 1999, Zanette et al. 2000, Fraser and Stutchberry 2004, McIntyre 2004, Ribic et al. 2009).

Beyond fragmentation, urbanization has a negative impact on air quality, largely due to traffic and power generation (Newman 1979, WHO 2005, Guarnieri and Balmes 2014). Birds have even been suggested as a means of studying the effects of air pollution due to their particular susceptibility to it (Brown et al. 1997). Poor air quality can impair avian immunity and reproductive success through an increase in tracheal mucous, respiratory infections, stress, and heritable mutation rates (Llacuna et al. 1993, Sanderfoot 2017, Sanderfoot and Holloway 2017, Sepp et al. 2018). Water systems and aquatic habitats are also affected by urbanization, as runoff and mineral leaching from concrete and asphalt surfaces alter water chemistry (Wright et al. 2011). Contaminants like mercury can persist for over 100 km downstream of the site of contamination, biomagnifying through terrestrial food webs and showing up in elevated concentrations in the blood of songbirds, altering behavior and impairing immunity and reproduction (Cristol et al. 2008, Jackson et al. 2011). Agriculture can have similar negative impacts on water resources as runoff carrying fertilizer and pesticides contaminates both water and soil, decreasing the abundance of arthropods that many birds rely on (Dahshan et al. 2016, Egwumah et al. 2017, Mohammadi et al. 2017). Often linked to air and water quality are negative impacts on soil, which can also be detrimental to birds. Effects of soil contamination on birds and other wildlife vary, but can include cardiovascular, nervous, and renal diseases, bone disorders, and impairment of neurological development

(Rattner 2009, Burger and Gochfeld 2010, Yarsan et al. 2014). In some bird species, nestling survival rates have shown a negative response to proximity to soil contaminant release sites (Fair et al. 2003).

Effects other than chemical contamination, such as light pollution, can also have a wide range of impacts on birds, many of which involve disorientation, attraction, or repulsion by light sources (Longcore and Rich 2004, Falchi et al. 2016). Nocturnally migrating birds can be attracted to and disoriented by artificial light sources in poor weather conditions and become trapped in brightly lit areas, increasing the risk of collision with buildings and other birds (Longcore and Rich 2004, Van Doren et al. 2017). Light levels can also impact sleep in birds, reducing both quality and quantity of sleep, leading to changes in hormone concentrations and reduced immune responses (Cho et al. 2013, Raap et al. 2015, Ouyang et al. 2017). Some species of birds and other predators living in brightly lit areas experience altered hunting behavior, including a tendency to hunt later into the night, allowing them and their young better access to food (Longcore and Rich 2004, Gaston et al. 2013, Stracey et al. 2014, Schoeman 2015). In turn, prey species in these affected areas may be forced to reduce their activity and increase nighttime vigilance (Longcore and Rich 2004, Yorzinski et al. 2015). In addition to anthropogenic light, ambient noise levels in residential or urban areas can rise to an excess of 65dB(A) (Palestine/Brazil), 80dB(A) (Turkey/India), and even 110dB(A) (Nigeria) (Zeid et al. 2000, Sagar and Rao 2006, Zannin et al. 2006, Oyedepo and Saadu 2009, Ozer et al. 2009). Noise pollution can damage hearing in birds, increase nestling stress hormone levels, and damage DNA through higher telomere attrition rates, contributing to lower pre- and post-fledgling survival rates (Ortega 2012, Schroeder et al.

2012, Injian et al. 2019). Behavioral impacts can include changes in song timing, vocalization frequency, and a preference to nest in quieter locations (Francis et al. 2009, Ortega 2012, Dominoni et al. 2016).

The physical structures that are part of urban development introduce a risk of collision injury to birds, affecting between 460 million to 1.4 billion birds per year in the United States alone (Loss et al. 2013, Loss et al. 2014a, 2014b, 2014c). Ambient temperature in urban centers tends to be higher than surrounding habitat, which can impact urban birds directly by affecting reproductive hormones and egg-lay dates and indirectly by impacting local plant growth and insect abundance (Oke 1973, Deviche and Davies 2014, Zipper et al. 2016, Singh et al. 2018). Urban development also leads to changes in predator assemblages, tending to hinder abundance and activity of larger predators like foxes and coyotes, while allowing smaller predators such as raccoons and domestic cats to thrive (Chace and Walsh 2006, Randa and Yunger 2006, Gehrt et al. 2013). Coyote presence is one of the best negative predictors of the activity of domestic cats, which kill an estimated 14.2-38.9 prey cat<sup>-1</sup> hectare<sup>-1</sup> year<sup>-1</sup>, matching or exceeding predation rates of wild predators (Chace and Walsh 2006, Kays et al. 2015, Kays et al. 2020). Free-ranging domestic cats kill an estimated 1.3 to 4 billion birds every year in the contiguous United States alone and are responsible, at least in part, for 33 modern bird, mammal and reptile extinctions on islands (Loss et al. 2012). Raccoons also feed on birds, as well as bird eggs, and can, to a lesser extent, further impact bird populations (Mazzamuto et al. 2020).

All of the various impacts of urban development can affect species in different ways, ultimately favoring some at the expense of others (Chace and Walsh 2006, Ortega-

Álvarez and MacGregor-Fors 2009). Urbanization tends to favor certain aspects of a bird's life history, such as a granivorous or omnivorous diet, which can lead to shifts in the distribution of species in the affected areas (Kark et al. 2006, Croci et al. 2008, Ortega-Álvarez and MacGregor-Fors 2009, Leveau 2013). The more developed an area becomes, the closer its communities tend to resemble those in other areas of high urban development, as the urban environment is usually more similar to other cities than it is to the surrounding native habitat (Blair 2001, McKinney 2002, Morelli et al. 2016).

As land use changes and human density declines, some effects of urbanization can be lessened, creating an urban-rural gradient (URG; Rosch et al. 2001, Venn et al. 2003, Parris 2006). In studies of both birds and mammals, areas with moderate levels of urbanization often show the highest levels of species diversity, although there is still a general trend towards higher diversity in less urbanized, lower human density areas (Jokimäki and Suhonen 1993, Chace and Walsh 2006, McKinney 2008, Pal et al. 2019). To measure the effects of urbanization on birds, I conducted a two-year point-count survey of breeding birds in oak woodland patches of northeast Illinois. By surveying along an urban-rural gradient, effects from low to high levels of urban development were assessed, as well as how these impacts are distributed across different functional groups among the avian community. I predicted that the effects on avian species diversity would match the majority of previous findings, showing a significant effect of urbanization with the lowest diversity in the region of highest urban development and the highest diversity at either the lowest or the intermediate levels of development. The effects on specific functional groups were expected to vary greatly, as the resources required by different guilds are affected unevenly.

## **Methods**

#### **Study sites**

This study took place across 28 sites in Cook, Will, Kankakee, and Grundy Counties in northeast Illinois, ranging from Eggers Grove in Chicago (41°41'6.35" N, 87°31'41.11" W) to Coal City (41°19'56.40" N, 88°17'28.36" W; Fig. 1). Four regions were recognized along the urban-rural gradient south-west of Chicago: urban, suburban, rural, and macrosite (Randa and Yunger 2006). Each of the 28 sites is located in one of these four regions, distributed evenly with 7 sites in each. With ten sites in Cook County (the second most populous county in the United States), this study recorded the effects of the county as well as those of the city of Chicago itself, the third largest city in the US (Ratcliffe et al. 2016, USCB 2020). The suburban and rural regions of the matrix are composed of the southern suburbs of Chicago and a large agricultural matrix of Will and Kankakee Counties, made up of mostly farm fields of row crops that alternate yearly between corn (*Zea mays*) and soybeans (*Glycine max*). The majority of the sites in the macrosite region are located within or near Midewin National Tallgrass Prairie, Des Plaines State Fish and Wildlife Area, or Goose Lake Prairie State Natural Area, totaling over 10,000 ha of protected land, plus a number of other protected grasslands and woodlands in the vicinity (IDNR 2020a, 2020b). The survey locations each consist of oak-dominated woodlands ( $\geq$  50% oak trees) of varying sizes, ranging from 17 ha to 720 ha.

#### **Survey methods**

Each site contained four to nine survey points placed at least 200 m from one another along transects established through the habitat, totaling 181 survey points throughout the study. Transects were established to stay 50 m from the edge of the habitat, roads, and water. Due to inconsistencies in area, shape, and terrain of the woodland patches, transects and survey points were determined on a site-by-site basis using satellite images from Google Earth.

Data were collected between May 31st and August 8th, the breeding season of local birds as determined by the latitudinal position of the study location and the MAPS (Monitoring Avian Productivity and Survivorship) breeding bird monitoring protocol (DeSante et al. 2015). At each survey point, following a 3-minute acclimation period, an unsupplemented (no playbacks or other lures) 10-minute point-count survey was performed, during which every individual bird that was seen or heard within a 50-m radius was recorded. Surveys began 30 minutes before sunrise and concluded three hours after sunrise to maintain between-site consistency as well as to survey during peak avian activity.

The order in which the sites were surveyed was determined semi-randomly, ensuring no region would be surveyed more heavily than another at any point during the survey period. This was done to avoid possible temporal effects such as a stint of particularly good or bad weather that could otherwise affect the survey results in one particular region. In addition to recording birds, the level of ambient noise at each point was ranked. These rankings were later assigned numbers for analysis (ranging from silent [0] to very loud [3.5]). Due to low visibility in woodland habitat, observations were

usually by sound rather than by sight. Counts were rescheduled in the case of rain or wind speeds exceeding 16kph. Surveys were performed once at each location in the summer of 2018 and repeated in reverse order during the same period in 2019.

#### **Statistical analyses**

Ambient noise rankings from each point were averaged by site and again averaged over the two survey years to provide a final ambient noise level for each location. These rankings were then analyzed via Analysis of Variance (ANOVA), and ambient noise was determined to be significantly different among regions (Fig. 2). Similarly, the number of survey points among regions was analyzed via ANOVA and also determined to vary significantly (Fig. 2). These were both factored into the subsequent analyses. For all of the following analyses, data from both years were pooled to ensure sufficient sample sizes of less-frequently observed species.

Avian density at the community level (all species combined), species level (density calculated per species), and grouped by guilds was analyzed. Density was used in place of abundance to account for differing numbers of sample points among sites and was calculated as the average number of individuals per 50-meter-radius survey point  $(7854 \text{ m}^2)$ . Total and guild densities were then analyzed using Analysis of Covariance (ANCOVA) and species-level density was analyzed via Multivariate Analysis of Covariance (MANCOVA), each with the ambient noise of sites as a covariate.

Prior to analysis of species richness, an asymptotic richness estimator (Abundance Coverage-based Estimator, ACE) was used to correct for the difference in number of sample points among regions. After this correction, the adjusted richness values were

analyzed via ANCOVA, again with ambient noise as a covariate. In addition to overall species richness, the richness of various guilds was analyzed to emphasize effects of development that may unevenly impact certain groups of birds within the avian community. All analyses in this study were performed in RStudio with the additional packages broom, emmeans, ggpubr, rstatix, tidyverse, and vegan (R Core Team 2019, RStudio Team 2020). All ANOVA and MANOVA tests were type II, using an alpha value of 0.05.

## **Results**

#### **Point-count surveys**

A total of 5286 individual birds of 58 identified species were recorded between 2018 and 2019 (Table 1). The number of individuals per site ranged from 77 to 256, with observed richness ranging between 17 and 34. The most abundant species throughout the study was the American Robin (*Turdus migratorius*), followed by the Eastern Wood-Pewee (*Contopus virens*), House Wren (*Troglodytes aedon*), Northern Cardinal (*Cardinalis cardinalis*), Indigo Bunting (*Passerina cyanea*), Downy Woodpecker (*Dryobates pubescens*), and Blue Jay (*Cyanocitta cristata*). These seven species together accounted for roughly 50% of all observed birds. Less than 4% of birds observed were unable to be identified.

#### **Density**

The density of all species analyzed together was highest in the urban region, and lowest in suburban. An ANCOVA performed on this data, with ambient noise as a

covariate, determined density at the community level to be not significantly different among regions ( $P = 0.343$ ,  $F_{3/23} = 1.169$ ; Fig. 3a). A MANCOVA, again with ambient noise as a covariate, was then performed on the densities of all species for which at least 30 individuals were recorded. This analysis also found no significant difference among regions ( $P = 0.109$ ,  $F_{69/9} = 2.135$ ; Fig. 3b). ANCOVA analyses of the density of each of the ten guilds showed no significant differences among regions for any guild (Figures 4, 5, and 6).

#### **Species richness**

After correcting for differences in sampling effort through the asymptotic richness estimator ACE, mean species richness was found to be highest in the rural region, followed by macrosite, suburban, and urban. Analysis of this corrected richness via ANCOVA, with ambient noise as a covariate, showed no significant difference among regions ( $P = 0.254$ ,  $F_{3/23} = 1.450$ ; Fig. 7). Although there was no difference in total richness among regions, there were clear shifts in species composition. Consequently, birds were subdivided into guilds. These guilds include diet (insectivorous, omnivorous, and granivorous), foraging behavior (foliage-gleaning, flycatching, and ground-foraging), and nesting behavior (ground-, tree-, shrub-, and cavity-nesting).

Of diet guilds, only omnivores showed a significant difference, with the highest richness being in the urban region and the lowest in macrosite ( $P = 0.009$ ,  $F_{3/17} = 5.262$ ; Fig. 8a). Insectivores were nearly so with a p-value of 0.059 ( $F_{3/23} = 2.864$ ), showing the highest richness in the least developed macrosite region (Fig. 8b). One of the foraging styles, foliage-gleaning, showed a significant difference among regions ( $P = 0.033$ ,  $F_{3/23}$ )

 $= 3.445$ ), while the other two showed virtually no change (Fig. 9). Among the nesting types, the only significant result was the tree-nesters  $(P = 0.014, F_{3/22} = 4.449)$ , which showed a pattern similar to that of overall species richness, with the lowest richness found in the urban region, and highest in rural (Fig. 10).

## **Discussion**

### **Density**

The density of birds, particularly those that are exotic or otherwise able to adapt to the urban environment, is typically greater at higher levels of urbanization (McKinney 2002, Lim and Sodhi 2004). Although not statistically significant, the average density was highest in the urban region. Despite previous findings however, this study recorded no significant impact of urban development on overall bird density. In this study, the very low number of exotic species typically found in urban habitat (notably, the House Sparrow [*Passer domesticus*], European Starling [*Sturnus vulgaris*], and Rock Pigeon [*Columba livia*]) may be partially responsible for this result. As Chace and Walsh (2006) state, urban areas are often dominated by introduced species. Here, however, only a total of 5 individuals of these three species (one sparrow, four starlings, and no pigeons) were observed throughout the study. Other species that benefit from urban development are generalists, seen here as omnivores. While omnivore richness was highest in the urban region, not only do they make up less than 10% of observed birds, but omnivore density showed no significant change, and thus did not alter the significance of the overall density.

Even when species were analyzed separately, which may have exposed a change in density in those species more or less suited to urbanization, no significant difference was found. Likewise, the density of guilds compared among regions showed no significant effect of urbanization. While the patterns of mean density among regions vary, and some show higher levels of significance than others, this study ultimately recorded no significant effect of region on any measure of density. The lack of the typical urban exotics, as well as a more consistent habitat across the urban-rural gradient is likely responsible for these results. The lack of large numbers of competitors and relatively consistent food and nesting resources may allow for the density of the avian community to remain consistent despite widespread changes in the surrounding urban matrix.

#### **Species richness**

Similar to density, richness appears, at first, to loosely fit the expected pattern. Mean richness is lowest in the urban region and tends to increase through decreasing levels of development. The ANCOVA of richness among regions, however, yielded a pvalue of 0.254, not statistically significant. There are likely many factors at play here, but among them may be a function of the habitat surveyed, as seen with density. Despite urban regions' tendency to homogenize avian communities, the selection of exclusively wooded habitat in this study avoided that phenomenon as a factor, as the exotic species that are largely responsible for this homogenization do not typically inhabit woodlands (Mao et al. 2019, Pal et al. 2019). The lack of competition with these species may have allowed a larger number of natives to persist where they may not have otherwise.

It is not until we look at avian richness by guilds that the effects of urbanization begin to show significance. Granivores, which previously-published research has shown to respond positively to urbanization, did not match expectations (Kark et al. 2006). While they did show the highest average species richness in the urban region, the difference was not statistically significant. In insectivores, the difference in species richness approached significance, with the lowest mean species richness found in the urban region, the highest in macrosite, and a significant difference between the two from the pairwise analysis. This pattern fits with the expected effects of urban development on this feeding guild, as other studies have seen similar patterns, and is likely due to decreased insect abundance in urban areas (Lim and Sodhi 2004, Chace and Walsh 2006, Kark et al. 2006). Conversely, omnivores are seen at their highest species richness in urban, and the lowest in macrosite, a highly significant result and one that is also supported by previous research (Clergeau et al. 1998, Croci et al. 2008). As Clergeau et al. (1998) state, birds that fare well in the urban environment are either able to find resources that they would normally make use of in their usual habitat or, notably, are able to adapt to the new resources that become available.

Grouped by foraging behavior, ground-foraging birds showed no significant changes along the URG, with no discernible pattern. Ground-foragers, depending on diet, tend to respond positively to urbanization (Chace and Walsh 2006). Again, the habitat surveyed in this study may be responsible for these results for several reasons. In woodlands, ground-level food resources may be more consistent than they would be throughout the rest of the urban-rural matrix, which may have led to a more consistent richness among this guild throughout the gradient. Also, as before, woodlands don't

support the typical exotics found in urban areas. All three of the previously-mentioned exotic species are ground-foragers and, if present, would be expected in high abundance. Similarly, flycatchers showed no significant effect of urbanization. Mean species richness was slightly lower in the urban region, but no other patterns were apparent. While not all flycatchers are insectivorous (the Red-headed woodpecker [*Melanerpes erythrocephalus*] is classified as an omnivore), six of the seven observed here were. Despite this, their response to development was clearly different than the insectivore guild, implying the presence of other underlying effects. Foliage-gleaners, the only foraging guild to do so, did show a significant negative response to development. Similar to flycatchers, foliage gleaners are almost exclusively insectivorous but, in this case, their response was more similar to that of insectivores. Both insectivores and foliage-gleaners show the lowest species richness in urban, followed by suburban, although foliage-gleaners' species richness peaks in rural rather than macrosite.

When grouped by nesting behavior, only the tree-nesting guild was shown to vary significantly with urbanization, with the lowest mean species richness in urban and the highest in rural. While vegetation was not assessed in this study, this result may be due to some measure of tree volume or cover changing throughout the gradient. In addition to tree-nesters, such a change in vegetation structure could be responsible for patterns of foliage gleaners and, while maybe not directly affected, insectivores, as tree volume has been strongly correlated with insectivore abundance (Lim and Sodhi 2004). The three remaining nesting guilds--ground-nesting, shrub-nesting, and cavity-nesting--showed no significant effect of urbanization on species richness.

#### **Conclusions**

While much here did not match with the results one might expect when studying general effects of urbanization on birds, many deviations from these other studies are likely attributable to the limited habitat that this study investigated. One would expect different results from a study of all birds across the entirety of an urban-rural matrix, but this is strictly a measure of breeding woodland birds. Whereas the whole of an urbanrural matrix tends to show significant loss of species richness as well as an increase in avian density, which can have further negative impacts, this study reflected very few of these effects. These results may suggest an inherent value of oak woodland habitat within urban matrices. If these patterns are typical of oak woodland patches, or other habitat islands within areas of urban development, that would indicate an inherent conservation value of these fragments for not only birds, but likely a variety of other plant and animal life.

While ambient noise levels in this study were measured and incorporated into the analysis, it is worth pointing out that noise can have two significant effects on a study such as this. It can, and likely is, impacting birds directly by damaging hearing and increasing stress hormones as discussed earlier (Ortega 2012, Injian et al. 2019). However, it also has a very obvious effect on the survey itself, especially here, where observations were made almost exclusively by song or call. As ambient noise levels increase, the ability of a surveyor to identify or even detect a bird call decreases drastically. Without the ability to separate these two effects, noise can either be left alone, and included with the myriad of environmental effects of urbanization, or factored out, thus compensating for the impact it has on the observations, but also ignoring the impact

on the birds themselves. As I believe ambient noise in this study to have had a larger impact on the observations themselves, the decision was made to treat it as a covariate, factoring it out of the analyses.



**Figure 1.** Map of the northeast Illinois where the study took place, including regions and site locations.



**Figure 2.** ANOVA analyses and post-hoc tukey hsd pairwise comparison of (a) number of point-counts among regions ( $P = 0.003$ ,  $F_{3/24} = 6.205$ ) and (b) ambient noise among regions ( $P < 0.001$ ,  $F_{3/24} = 16.233$ ). Bars above the plots show significance in post-hoc tests between any two regions  $(*<0.05, **<0.01, **<$  $0.001, **** < 0.0001$ ).



**Figure 3.** (a) ANCOVA analysis of density of all species combined among regions ( $P = 0.343$ ,  $F_{3/23} = 1.169$ ) and (b) MANCOVA analysis of individual densities of the top 10 most abundant species among regions ( $P = 0.109$ ,  $F_{69/9} =$ 2.135).



**Figure 4.** ANCOVA analyses and estimated marginal means pairwise comparison of density among regions of species grouped by diet, including (a) omnivores (*P*  $= 0.181, F_{3/23} = 1.768$ , (b) insectivores ( $P = 0.556, F_{3/23} = 0.709$ ), and (c) granivores ( $P = 0.439$ ,  $F_{3/23} = 0.936$ ).



**Figure 5.** ANCOVA analyses and estimated marginal means pairwise comparison of richness among regions of species grouped by foraging behavior, including (a) foliage-gleaners ( $P = 0.319$ ,  $F_{3/23} = 1.238$ ), (b) ground-feeders ( $P = 0.418$ ,  $F_{3/23} =$ 0.983), and (c) flycatchers (*P* = 0.983, *F*3/23 = 0.053).



**Figure 6.** ANCOVA analyses and estimated marginal means pairwise comparison of density among regions of species grouped by nesting location, including (a) tree (*P* = 0.767,  $F_{3/23}$  = 0.382), (b) cavity (*P* = 0.393  $F_{3/23}$  = 1.042), (c) shrub (*P* = 0.115,  $F_{3/23} = 2.199$ ), and (d) ground ( $P = 0.544$ ,  $F_{3/23} = 0.731$ ).



**Figure 7.** ANCOVA analysis of ACE-adjusted species richness among regions (*P*  $= 0.254, F_{3/23} = 1.450$ .



**Figure 8.** ANCOVA analyses and estimated marginal means pairwise comparison of richness among regions of species grouped by diet, including (a) omnivores (*P*  $= 0.009$ ,  $F_{3/17} = 5.262$ ), (b) insectivores ( $P = 0.059$ ,  $F_{3/23} = 2.864$ ), and (c) granivores ( $P = 0.422$ ,  $F_{3/21} = 0.977$ ). Bars above the plots show significance in post-hoc tests between any two regions ( $* < 0.05$ ,  $** < 0.01$ ,  $*** < 0.001$ ,  $*** <$ 0.0001).



**Figure 9.** ANCOVA analyses and estimated marginal means pairwise comparison of richness among regions of species grouped by foraging behavior, including (a) foliage-gleaners ( $P = 0.033$ ,  $F_{3/23} = 3.445$ ), (b) ground-feeders ( $P = 0.737$ ,  $F_{3/22} =$ 0.426), and (c) flycatchers  $(P = 0.904, F_{3/22} = 0.187)$ .



**Figure 10.** ANCOVA analyses and estimated marginal means pairwise comparison of richness among regions of species grouped by nesting location, including (a) tree ( $P = 0.014$ ,  $F_{3/22} = 4.449$ ), (b) cavity ( $P = 0.320$   $F_{3/23} = 1.234$ ), (c) shrub ( $P = 0.710$ ,  $F_{3/21} = 0.465$ ), and (d) ground ( $P = 0.915$ ,  $F_{3/13} = 0.170$ ). Bars above the plots show significance in post-hoc tests between any two regions  $(* < 0.05, ** < 0.01, ** < 0.001, *** < 0.0001).$ 



## **Table 1.** List of all identified birds, including guild assignments and observed abundance.

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