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UNIVERSITY OF NORTHERN COLORADO

Greeley, Colorado

The Graduate School

EFFECTS OF NOISE, LIGHT, AND LANDSCAPE ON BIRDS
IN A RECENTLY URBANIZED COUNTY

A Dissertation Submitted in Partial Fulfillment
Of The Requirements for the Degree of
Doctor of Philosophy

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College of Natural and Health Sciences
School of Biological Sciences
Biological Education

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This Dissertation by: Karina Alejandra Sanchez

Entitled: *Effects of Noise, Light, and Landscape on Birds in a Recently Urbanized County*

has been approved as meeting the requirement for the Degree of Doctor of Philosophy in the College of Natural and Health Sciences in the School of Biological Sciences program of Biological Education

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ABSTRACT

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Anthropogenic activities are drastically and rapidly altering ecosystems. Research has found that urban environments support less biodiversity than non-urban environments. This work has inspired recent interest investigating animal behavior and individual reproductive success in urban wildlife as mechanisms to why biodiversity is lower in urban areas. For my dissertation research, I used three key urban characteristics; noise, light, and landscape composition to study the effects of urbanization on avian species across Weld County, CO. I used these measurements to test the overarching hypothesis that urban land characteristics alter avian community structure and more specific hypotheses regarding how each factor (noise, light, or landscape composition) might contribute to individual reproduction and singing behaviors differently in biologically meaningful ways. My focal study species is the American Robin (*Turdus migratorius*), a bird species common across many habitat types. In Chapter II, I found that landscape composition has a much stronger effect on avian community composition than noise or light. In chapters II and IV, I use measured song characteristics and reproductive success of individual birds to test for the effects of “urbanness”. I hypothesize that all three urban characteristics would have negative impacts on reproductive output measures, but that urban land characteristics and increased noise would have the main effects on song characteristics. Contrary to my hypothesis, none of the urban characteristics measured had an affect on American Robin reproductive output. In fact, most nests had high survival, large clutch sizes, large brood sizes, and high hatching success.

Only minimum song frequency was affected by urbanization and more specifically only be percent developed land. Noise and light did not alter song characteristics. Considering the staggering decline of nearly three billion birds in North America since the 1970's, it is critical that we investigate how anthropogenic changes to habitats may affect wildlife and how wildlife are reacting to these changes. In this dissertation, I discuss the results of this research, the implications of my work, and the importance of connecting the public to the ecosystems in which we all inhabit.

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CHAPTER I

INTRODUCTION TO URBAN ECOLOGY, COMMUNITY STRUCTURE, AVIAN REPRODUCTION, AND BIRD SONG

Introduction to Urban Ecology

Over the past century humans across the globe have moved into cities and away from rural areas at a rapidly growing pace. Today, more than 55% of the world's population resides in urban areas and this is expected to increase to 65% by 2050 (United Nations, 2018). This increase in population will ultimately lead to more developed land surrounding urban areas resulting in even more loss of critical habitat (Chen et al., 2020). For these reasons, the impact of urbanization on biodiversity and wildlife has been the focus of a large volume of research in the area of urban ecology. To date, urbanization has been linked to decreases in biodiversity across the globe and much of this decrease has been attributed to habitat loss (Keil et al., 2015; Rosenberg et al., 2019). Nevertheless, the study of urban ecology is still relatively new, and we have a limited understanding of the extent of the effects of urbanization on wildlife behavior, reproduction, physiology, community dynamics and life history.

In addition to habitat destruction and fragmentation, humans have also introduced selective pressures such as chemical pollution, light pollution, noise pollution, invasive species, and novel predators. Environments are a combination of characteristics including geography, vegetation, structure, and other features such as increased reflective surfaces, noise, light, and climate. Urban characteristics can range in intensity, frequency, and spatial extent, depending on the age of the developed area and human population size. Yet, many studies investigating animal

diversity, abundance, and behavior in urban environments often lump these characteristics to categorically assign sites as “urban”. There is still no consensus on the methods used for describing these environments. In some cases, aerial imagery is used to rank sites by “urbanness” (Blair, 1996) and in others, human population density is used to rank and describe urban versus non-urban areas (Blair, 1996; McDonnell et al., 2008). Not all urban spaces are equal and should not be treated equally in scientific studies. To understand what aspects of urbanicity are affecting wildlife, it is important to separate and measure the variables being used to describe an area as urban. By measuring urban areas categorically, scientists cannot compare studies accurately to find persistent trends. By measuring individual characteristics that urban areas are composed of, such as noise or light levels, we can better address how wildlife may be interacting with cities.

Avian species have received considerable attention in the field of urban ecology (Rivkin et al., 2018) and serve as good models for understanding the effects of urban environments on wildlife. Birds are found in nearly all habitat types. With the current breadth of general knowledge about many avian species, we can evaluate how different environments affect bird populations. Two overarching phenomena relating to urban environments and birds have become apparent through scientific research: 1) bird community composition differs in urban areas when compared to their non-urban counterparts (Chace & Walsh, 2006) and 2) songbirds alter the temporal timing, frequency, amplitude, and duration of their songs in urban areas (Gil & Brumm, 2013). These two phenomena may reflect strategies birds use to cope with altered environments, but little is known about how the two strategies may be related and how they affect reproductive output and evolutionary processes.

Urbanization and Avian Community Structure

Human disturbance can have profound effects on ecosystem functions by altering ecosystem functions. Measuring how communities differ and how they respond to urbanization is important for understanding the consequences of habitat alterations. Disturbed areas often have lower biodiversity and increased prevalence of invasive species (Cadotte et al., 2017; Riley et al., 2005; Shochat et al., 2006). Avian biomass is often higher in urban areas when compared to less urbanized ones; however, species diversity has been shown to decrease with urbanization, resulting in high abundances of the few species that thrive in urban environments (Beissinger & Osborne, 1982; Blair, 1996). These patterns are not limited to avian communities and have been studied in several organisms including birds, butterflies, insects and frogs (Cam et al., 2000; Murgui, 2009; Proppe et al., 2013).

In some cases, species richness can increase with human disturbance, but plateaus at a moderate degree of urbanization, similar to what one may see in the suburbs (Blair, 1996; Cam et al., 2000). This initial increase could be due to new ecological niches opening with the human disturbance, allowing local or adjacent individuals to exploit this new habitat. However, several studies have identified when species richness does increase with urbanization, it is due to the presence of non-native species (Chace & Walsh, 2006; Riley et al., 2005). Further, with time, urban avian communities become distinct from native communities and resemble those of other urban areas (Devictor et al., 2007). Although studies have measured urbanness in different ways, the trends have remained consistent; urbanization alters native community structures and homogenizes the avifauna within cities (McKinney, 2006; Vallejos et al., 2016). Urban conditions are more favorable to invasive species, resulting in the displacement of native species (Cadotte et al., 2017). This displacement may result from behavioral responses to altered habitats

(Blair, 2004; Gil & Brumm, 2013) or the inability of native species to tolerate changes to habitat characteristics. As more land is converted for human use, it is likely that homogenization of the avifauna will continue to occur (Blair, 2001, 2004; McKinney, 2006).

The literature investigating changes in urban avian community structure has continued to grow, yet most studies are still conducted in large and established cities. Few studies have been conducted in areas of recent, rapid urbanization. Measuring community structure in recently established and growing cities will increase our understanding of species *currently* being affected by the process of urbanization. This differs from work in old cities where avian communities are made of species that were able to remain or move into urban areas in the past. In Chapter II, I attempt to fill this gap in the literature by investigating the relationship between avian community assemblages and urban characteristics, specifically noise, light, and landscape composition in an area that has recently begun urbanizing rapidly.

Reproductive Success in an Urban World

Avian reproductive behaviors such as singing for mate attraction, mating-systems and nest building have been shaped by habitat characteristics (Picman, 1988; Verner & Willson, 1966). In today's changing world, these behaviors may not be as effective as they once were. Birdsong is associated with individual fitness, and the ability to sing at high frequencies in the city may become associated with higher or lower reproductive success. Loss of signal transmission may make finding a mate or coordinating nesting behaviors difficult in urban environments, leading to unsuccessful reproductive seasons and decreased fitness for those that do not or cannot alter their songs. Additionally, for those individuals that can alter their songs in urban environments, there may be unexpected trade-offs between efficient communication and parental care. Evidence suggests that song production is metabolically costly, especially when

being produced at a high amplitude or high frequencies (Oberweger & Goller, 2001). After pair bonding, many species use song and other vocalizations to defend their territory and relay important information to their mate but producing these costly songs (and potentially other vocalizations) may take energy away from feeding trips to young and their parental care.

The expansion of urbanization has increased the amount of noise that wildlife are exposed to. Noise pollution has been the main sensory pollutant of exploration for urban ecologists over the last three decades. Noise can affect not only mating success but also survival. While songbirds may be shifting their songs to higher frequencies to be heard above excess noise by other individuals, they still must be able to hear threats within the environment. Vigilance has been demonstrated to increase in birds exposed to excess noise (Meillère et al., 2015) which may lead to differences in parental care, energy and time budgets ultimately affecting survival and nest success. Recent studies have documented both positive and negative effects of noise exposure on reproduction in individual species (Injaian, Poon, et al., 2018; Injaian, Taff, et al., 2018; Meillère et al., 2015; Mulholland et al., 2018). More work is needed to get a comprehensive understanding of how noise may be affecting breeding success and population persistence in urban birds.

Light pollution has also been shown to affect important reproductive behaviors in birds. For example, at dawn, sounds transmit further than at other times of the day (Brown & Handford, 2003), but with the introduction of anthropogenic light, photo cues may be altered and singing may occur at earlier and later hours (Da Silva et al., 2014). Kempenaers and colleagues (2010) found that the timing of the dawn chorus was positively associated with artificial night light and egg laying date. Early or excess singing may alter energy budgets such that individuals reallocate time from other activities like parental care to singing. In addition, the alteration of

egg-laying dates may create a mismatch in ecological timing of important events such as the presence of insects and other food sources (Dominoni et al., 2013; Seress et al., 2020).

Generally, most studies have chosen to isolate one or two urban characteristics to test for effects on reproduction. Few studies have attempted to understand the relative effects that several of these characteristics may have on reproduction. In Chapter III, I measure the reproductive success of individuals and test whether breeding success is related to urban habitat characteristics.

Bird Song in the City

Behaviors associated with mate attraction and reproduction are critically important for population persistence. In birds, song can play a crucial role in sexual selection and consequently the fitness of an individual (Kroodsma & Byers, 1991). In urban habitats, avian species have been observed to alter song behaviors. Studies have shown that birds alter the temporal timing, frequency, amplitude, and duration of their songs to avoid their song being masked by anthropogenic noise (Nemeth & Brumm, 2009; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003), while others have shown that birds shift the dawn chorus timing in areas with anthropogenic light (Kempnaers et al., 2010; Slabbekoorn & den Boer-Visser, 2006). As described above, several studies have shown that avian species richness and abundance is low in urban areas (Marzluff et al., 2001; Proppe et al., 2013) but little is known about the mechanism driving this decrease in richness and abundance. An organism's ability to tolerate anthropogenic environmental changes may be dependent on its ability to communicate effectively in altered environments, and losses of diversity may be due to species' inability to adjust to novel conditions.

The modified habitats that humans are building around the world place unique selective pressures on wildlife. For organisms that rely heavily on acoustic and visual communication, it is important to understand the effects of anthropogenic environmental changes on signaling behaviors and outcomes. The ability to communicate effectively in an environment is critical for the reproductive success of individuals. The “Acoustic Adaptation Hypothesis” (AAH) proposes that environmental selective pressures have shaped acoustic signals to result in the “best” signal for that habitat (Hansen, 1979; Morton, 1975). Evidence from a wide range of habitats supports the AAH with specific song characteristics being found in similar habitat environments. For example, bird species native to closed habitats have lower song frequencies than those found in open habitat species (Boncoraglio & Saino, 2007). In addition, studies have shown that sound degradation differs between habitats (Barker et al., 2017; Dabelsteen et al., 1993). Development of land for human use often results in a drastic alteration of existing habitat structure. An open habitat can quickly become a closed habitat with the introduction of tall buildings. As urbanization alters landscapes, it is important to know how animal signaling is affected by these changes.

Many studies that have investigated the relationship between habitat and acoustic signaling have been done with birds. Most examined the relationships between anthropogenic noise and altered song, and few reflected on how the physical structure of urban habitat may contribute to the propagation or degradation of sounds. Scientists have found that birds can adjust song or vocalization characteristics in a variety of ways (Patricelli & Blickley, 2006), but the most relevant to urban environments is the ability to alter frequency, amplitude, and temporal aspects of song. Cities are often composed of vertical reflective surfaces (buildings) and a great deal of impervious surfaces, both of which affect the acoustic environment. While many studies

acknowledge that the landscape structure likely contributes to the results of their study, only recently have scientists begun to include these measurements in their research (Phillips et al., 2020).

In addition to the physical structures of cities, anthropogenic noise has strong effects on animal communication. Human-generated noise such as traffic noise and oil extraction has increased drastically over the last century. Much of these sounds are generated at low frequencies and overlap with some bird species song frequencies. Several studies have found a positive relationship in bird species between minimum song frequency and the level of urban noise (Peter & Slater, 2006; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003). These studies have found that birds in noisier areas sing with higher frequencies than those in less noisy areas. In addition to changing song frequency, birds in urban areas alter the amplitude of song. It has been suggested that these patterns could be similar to the Lombard effect, a phenomenon where humans alter their volume and associated voice characteristics according to background noise (Pick et al., 1989). For example, a person telling a story in a quiet room will speak at a lower volume than that same person telling a story in a loud busy room, and in the louder room the person with the loud voice will also use higher acoustic frequencies. The Lombard effect has been observed in birds in the laboratory and under natural conditions. Laboratory studies have found that like humans, birds are capable of modifying the amplitude of songs voluntarily in order to be more audible in noisy or loud conditions (Brumm & Todt, 2002; Cynx et al., 1998). Adjusting song characteristics may not, however, be the fix birds hope for. When shifts in song frequencies in urban birds have been observed, they often lead to potentially unfavorable song characteristics. For example, birds may alter their songs to sing at a frequency above the traffic noise, but higher frequencies attenuate faster and degrade more easily

(Dabelsteen et al., 1993) and therefore are unable to travel far in an urban environment (Forrest, 1994; Romer & Lewald, 1992). The inability to adjust songs, or the decreased efficacy in altered songs produced in urban environments where signals are lost, might contribute to the decreased species richness seen in noisy urban areas.

Fewer studies have investigated the effects of light pollution on bird song structure. Most of the work to date has instead examined how light pollution alters the timing of singing behaviors. An overwhelming proportion of the literature has found that populations living in areas with more light pollution start the dawn chorus earlier (Da Silva et al., 2014; Kempenaers et al., 2010). Other work has found that some species even display nocturnal singing behaviors (Miller, 2006). Species that sing earlier, later, or into the night receive less sleep, which ultimately affects daily energy and ability to complete other behaviors during the day (Raap et al., 2015, 2017). A lack of sleep and rest may also result in increased susceptibility to disease (Ouyang et al., 2017). Still, the direct consequences of changing active singing times on fitness is unknown and requires more exploration.

Adjustments in song structure and timing may differ across species and some species may have more vocal constraints than others (Hill et al., 2018; Nemeth et al., 2013; To et al., 2021). Three mechanisms have been proposed and tested to explain vocal shifts in avian species (Moseley et al., 2018). One mechanism is immediate response to conditions, where an individual alters their song in real time (Bermúdez-Cuamatzin et al., 2009), similar to the Lombard effect. Another mechanism is via natural or sexual selection, where genotypes and phenotypes of individuals with songs that are less masked are selected for in urban environments (Endler, 1992). A third mechanism is via cultural selection, where birds either preferentially learn songs that transmit better in urban environments or learn songs that they can simply hear better in

urban environments, leading to an increase in these songs in a population over time (Moseley et al., 2018). These mechanisms each have some evidence to support them but are limited to only a few species, most of which have been studied extensively already. More investigation is needed on a wider range of lesser-studied species. No matter the mechanism, adjusting song characteristics may have functional consequences.

The avian ability to adjust vocalizations may come with many trade-offs, yet in urban areas avian species overwhelmingly adjust their songs to avoid being masked (Duquette et al., 2021). Trade-offs associated with such behavioral alterations are likely to be most influential at the beginning of urban development. As buildings are built, roads fill with cars, and humans move in, populations of birds will be exposed to the selective pressures of these novel urban characteristics and their abilities to adapt will be tested. Most studies where vocal adjustments have been observed took place in large cities that have been established for hundreds of years (Dowling et al., 2012; Hamao et al., 2011; Mendes et al., 2011; Seger-Fullam et al., 2012), and wildlife has had time to adjust to those conditions. What this means is that a large portion of the current evidence for vocal adjustment comes from the oldest urbanized cities. What we do not know is when these vocal adjustments take place and how long it may take to establish within a population. Studying this phenomenon of vocal adjustments in an area of current and rapid urbanization allows an opportunity to assess what stage local populations are at in their ability to withstand urban characteristics. Currently, it seems that being heard (sometimes by making vocal adjustments) takes precedence. Perhaps the effects of these adjustments have yet to affect fitness of individuals in urban populations.

Study Location

The studies reported here were conducted in Greeley Colorado and surrounding areas within Weld County. Weld County was established the 1860s and is composed of active and inactive agriculture land along with natural spaces that are changing rapidly to accommodate the growing population. The city of Greeley is the most populated area in Weld County, and it has a well-established urban center surrounded by newly developed land. With a population of ~108,175 people, Greeley houses one-third of the Weld County population of ~314,305 people (Barnett & Mueller, 2018). Greeley has historically been known as a small town, but over the last forty years has grown immensely with the human population more than doubling in size (Barnett & Mueller, 2018; City of Greeley, 2020). With these expected changes in this metropolitan area, Weld County and the city of Greeley serve as a unique location in which to study the effects of increasing urban noise, light, and landscape compositional changes on birds and their behaviors.

Study Species – American Robins

The American Robin (*Turdus migratorius*) is one of the most common and widely-distributed bird species of North America (Figure 1.1). American Robins are sexually dimorphic: adult males often present with a dark and vibrant red chest and dark crown while females tend to be paler in plumage coloration (Figure 1.2). Males are the primary singers in this species and have a familiar song, described as a caroling “*cheerily, cheer up, cheer up, cheerily, cheer up*” (Figure 1.3). American Robins are year-round residents in the state of Colorado and breed from April to August. They are opportunistic nesters, only needing a firm support or shelf-like structure to build their open-cupped nests. This species offers an excellent test system for my

work due to its apparent success in varied environments, both urban and non-urban, its easily identifiable songs, and accessibility of nests.

Figure 1.1

Distribution of The American Robin. Map From Vanderhoff et al., (2020), Cornell Lab Of Ornithology.



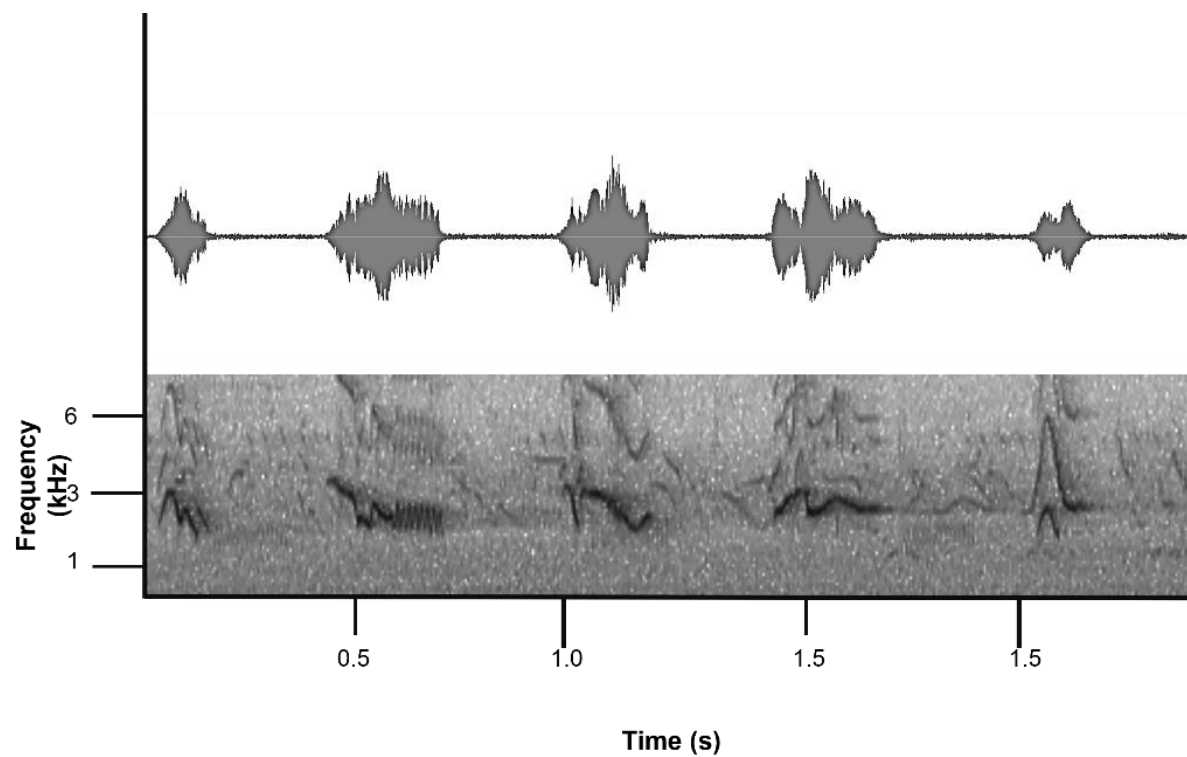
Figure 1.2

Pictures Showing Differences in Adult Male (Left) and Female (Right) American Robin Plumage Coloration. Photographs Copyright Karina Sanchez.



Figure 1.3

Spectrogram of Typical American Robin Male Song.



CHAPTER II

LANDSCAPE IS A STRONGER DETERMINANT THAN NOISE AND LIGHT OF AVIAN COMMUNITY STRUCTURE IN A NEWLY URBANIZED COUNTY.

Contribution of Authors and Co-Authors

Manuscript in CHAPTER II

Author: Karina A. Sanchez

Contributions: Conceived the study topic, developed, and implemented study design, collected data, searched the literature, and wrote the first and final draft of manuscript.

Co-Author: Dr. Lauryn Benedict

Contributions: Helped conceived the study topic and edited drafts of manuscripts.

Co-Author: Dr. Emily Holt

Contributions: Helped conceived the study topic, contributed heavily to data analysis provided edits on manuscripts

Abstract

Urban development has drastically altered ecosystems and in turn, we have seen dramatic effects on avian diversity and community structure. Accordingly, there has been a surge of interest in understanding the effects of urbanization on wildlife, but studies have not been conducted in all urban ecosystems. Most studies are conducted in large and established cities, with fewer conducted in areas of current rapid urbanization. While current anthropogenic development may result in similar habitats as development in the past, the pace at which urbanization occurs today is notably faster. Measuring community structure in recently established and growing cities is necessary to understand what species are currently being affected by the process of rapid urbanization. This study investigated the relationship between avian communities and urban characteristics in one of the United States' fastest growing metropolitan areas. I tested the general hypothesis that avian community assemblages will vary with multiple urban characteristics. I measured noise, light, and landscape composition across 20 sites and paired this data with avian species census data. I used Nonmetric Multidimensional Scaling (NMS) analysis and two-way cluster analyses to examine patterns of species presence and abundances at sites. Results suggest that developed land and water drive community structure in Weld County. Anthropogenic noise and light did not drive patterns as strongly as developed land did and these three urban characteristics did not exist on a linear urban to non-urban gradient, meaning that urbanization can have patchy and unpredictable effects, highlighting the value of measuring urban characteristics separately. Additionally, this study emphasizes how sampling newly developed areas captures the effects of urbanization on species present during the process rather than those who remain or move into urban areas following development.

Introduction

Land cover changes and sensory pollutants have drastically increased in the past century due to urbanization, resulting in worldwide declines of species (Aronson et al., 2014; Rosenberg et al., 2019; Zuñiga-Palacios et al., 2021). Natural habitats have been replaced by human constructions, such as buildings, homes, oil platforms, and roads. With these replacements come novel habitat characteristics such as more impervious surfaces, more vertical surfaces that create closed habitats, and sensory pollutants such as anthropogenic noise and light. As environments change across the planet, scientists seek to understand the consequences of these alterations.

Birds are crucial bioindicators of environmental change (Alexandrino et al., 2017; Gardner et al., 2014; Mehlman, 1997; Mekonen, 2017). North America alone lost 30% of its birds in less than a century (Rosenberg et al., 2019) due in large part to loss of habitat and habitat fragmentation (Aronson et al., 2014). Among all taxa, birds are one of the most well-studied regarding the effects of environmental anthropogenic changes (Zuñiga-Palacios et al., 2021), and bird community response to urbanization has been key to understanding human impacts on ecosystems. Species diversity is essential for healthy ecosystem functions and the literature assessing urban avian species richness, abundance, and diversity is vast. Previous studies report that high urban land cover is associated with decreases in species richness, increases in abundances of generalist species (Melles et al., 2003; Ortega-Álvarez & MacGregor-Fors, 2009), and biotic homogenization of avian species (McKinney, 2006; McKinney & Lockwood, 1999; Reale & Blair, 2006; Vallejos et al., 2016). Moreover, cosmopolitan generalist species in urban spaces (“urban exploiters”) tend to replace specialist and local species (“urban avoiders”) (Devictor et al., 2007; McKinney & Lockwood, 1999; Newbold et al., 2014; Reale & Blair, 2006). While most urban studies of avian diversity have focused on land-use and landcover

changes, there is no clear consensus on how to measure urban-ness. Many studies investigating the effects of urbanization on wildlife categorically assign study locations to “urban” or “rural” based on qualitative data (Blair, 1996; McDonnell & Hahs, 2008). There may, however, be secondary mechanisms associated with land-use change that have received comparatively less attention. Noise pollution and light pollution can result from urbanization and have been demonstrated to affect avian communities (Ciach & Fröhlich, 2017; Perilla et al., 2017; Proppe et al., 2013). It is important that scientists studying urbanization consider a habitat holistically to include multiple anthropogenic factors. Independently, anthropogenic noise, light, and landscape characteristics (such as impervious surface and canopy cover) have been shown to affect wildlife and they respond in different ways, including individual behavior (Lowry et al., 2013; Shannon et al., 2016; Willems et al., 2022) biodiversity, (Aronson et al., 2017; Marzluff & Ewing, 2001), species richness (Carral-Murrieta et al., 2020; Gatesire et al., 2014), abundance, (Gatesire et al., 2014; Wilson et al., 2021) and reproduction (Beck & Heinsohn, 2006; Seress et al., 2020). It is evident that each of these environmental components are impacting wildlife but, the relative impacts of each characteristic are not well understood.

Additionally, most urban wildlife studies worldwide are conducted in large and historically old cities, with fewer studies being conducted in more recently urbanized areas. Today, urbanization occurs at a rapid rate as we attempt to keep pace with populations moving to metropolitan areas. This rapid urbanization may affect species and communities in novel ways. Without disentangling habitat characteristics or studying wildlife in cities at different stages of urbanization, it will be difficult to understand the mechanisms leading to declines in species. The rate of urbanization worldwide is expected to continue to increase with approximately 5 billion people living in urban areas/cities by 2028 (United Nations, 2018). Thus, there is an urgent need

to assess these habitats in recently developed areas, especially as we consider how to build a more wildlife-friendly urban landscape.

The objective of this study was to describe the avian community structure in relation to environmental factors, with a focus on three anthropogenic characteristics: land cover, noise, and light. I conducted this study at variably urban and non-urban sites in an area of recent rapid urbanization: Weld County, Colorado. Based on past research, I hypothesize that community structure will cluster according to landscape characteristics (i.e., land cover, noise pollution, and light). I expect that noise and light will be related to landscape characteristics and therefore will strongly relate to community structure.

Methods

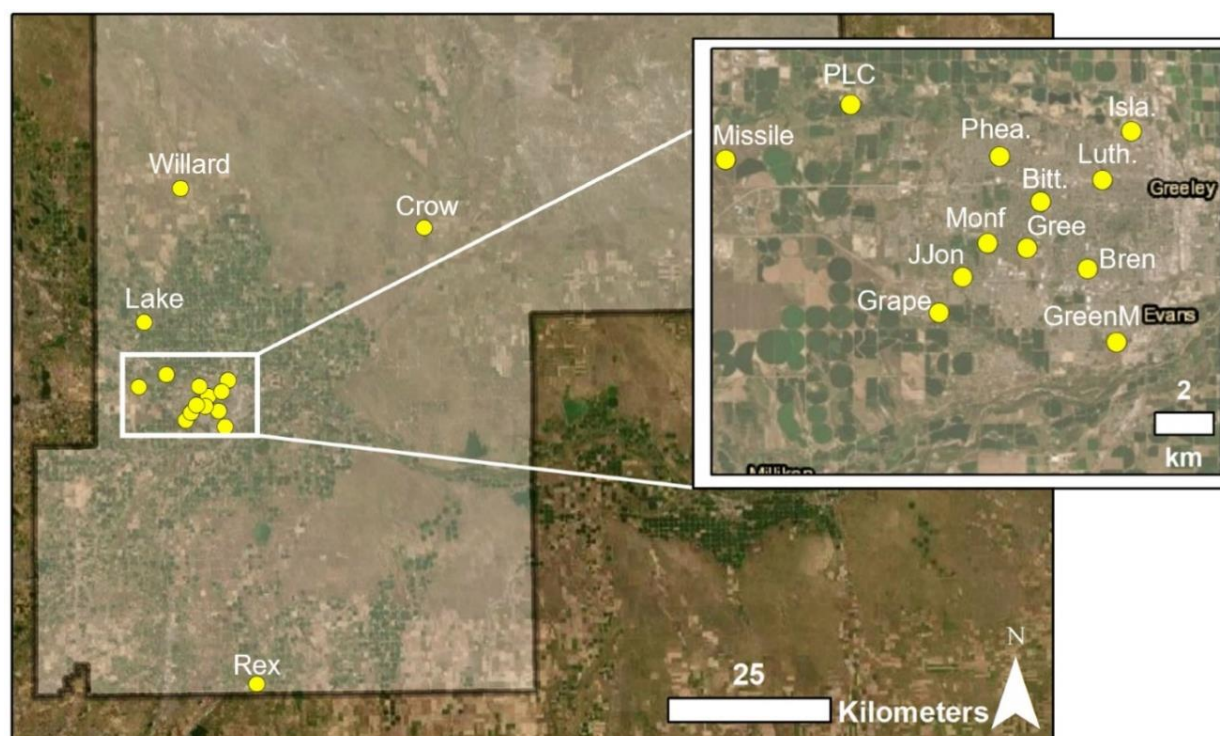
Study Area

Weld County is located on the Northern Front Range of central Colorado. The county spans an area from metropolitan Denver to the Wyoming state line and the Great Plains region. Weld County's 9800 square kilometers are dominated by agriculture, with nearly 75% of land devoted to farming and housing livestock. With a population of 108,795 people, the city of Greeley houses over one-third of the Weld County population (U.S. Census Bureau, 2020). The Greeley Metropolitan Area has consistently remained one of the fastest growing cities in Colorado, which was named the 6th fastest growing state in the United States in the most recent US Census (2020). By 2060, the city of Greeley is expected to nearly double its current population size (City of Greeley, 2020). With these ongoing changes, Weld County served as a prime location in which to study the effects of urban noise, light, and landscape composition on bird community structure.

Sixteen sites were used for this study spanning outward from the city of Greeley representing various degrees of urbanization in the four general cardinal directions (Figure 2.1). For standardization, all sites were required to have trees, the primary avian habitat, and be a minimum distance of 500 m to other sites. In selecting sites, these limitations resulted in most

Figure 2.1

Map of Site Locations Across Weld County.



Note. Sites are shown by yellow dots and labelled with their name or abbreviated name. Maps were created using ArcMap 10.6.1 and the Colorado State Planes FIPS III North projected coordinate system.

Bird Surveys

I conducted bird surveys to determine avian abundance and composition at all sites. I used a modified point count survey protocol adapted from the USGS North American Breeding Bird Survey (Sauer & Droege, 1990). Surveys took place during the avian breeding season in

May and June of 2018. Surveys occurred within 4 hours post-sunrise to coincide with peak bird activity time. A count duration of 7 minutes was used at each site. Birds were identified by sight and sound within a 250 m radius; the number of species and the number of individuals per species were recorded. Individuals flying over the point-location were not counted, as I sought to focus on birds using the local habitat. Each survey location was revisited a minimum of three times and a maximum of four times during the two-month survey period. I rotated timing and day of the week for visits to account for the effects of time and day among sites. For analyses, I took an average across three count visits for each species present to account for all species seen at one site.

Landscape Analysis

Landscape characteristics were extracted using ArcMap and the MRCL 2019 National Land Cover Database layers (Wickham et al., 2021). I created 400 m buffers around each point-count site to capture the variation within the immediate locality. I used the Zonal Statistics tabulate tool to extract a total area represented in these buffers for each established land category (i.e. developed land, agriculture, etc.). All analysis was conducted in the Colorado FIPS III State Plane North projected coordinate system with a 30m resolution. I used these data to obtain a percentage of each land cover type at each site. For simplicity I combined the three highest developed levels determined by the MRLC (22- Developed, low-intensity; 23- Developed, medium intensity; and 24- Developed, high intensity) into one category named “developed” but kept the developed open space category as a separate measure. I also combined the forested areas into one category, the wetlands into one category, and the hay/pasture and cultivated crops into one category.

Sound and Light Measures

All sound and light data were collected in June 2018. Wildlife Acoustics Song Meters (SM2) were used to measure sound at each site. Recorders were set to record continuously for 24 hours over five continuous days at a sampling rate of 48KHz and set to 0 gain (32 bits, waveform audio file format). I used the PAMGuide package (Merchant et al., 2015) in R Studio to batch process sound files and convert all audio data to calibrated 1-s one-third octave band SPLs from 12.5 to 8000Hz (National Park Service, 2013). I extracted unweighted (dB) and A-weighted (dB(A)) L_{eq} SPL measurements (summary of the acoustic energy across a frequency band of interest), a variable commonly used in environmental background noise monitoring (McKenna et al., 2016). Anthropogenic noise typically occurs at ranges below 2000 Hz (McKenna et al., 2016; Merchant et al., 2015). Therefore, I obtained L_{eq} SPL measurements between the frequencies of 31.5 Hz and 1250 Hz (Buxton et al., 2018) in the recordings. Measurements were calculated for 10-minute timesteps and averaged over the five days of collection to obtain a 24 hr mean per site. I calculated descriptive statistics for each site based on these data.

I used Sky Quality Meters (SQM-LU, Unihedron) to measure luminance (brightness) at each site by measuring ground reflectance in magnitudes per square arc second ($\text{mag}/\text{arcsec}^2$). SQMs collected a reading every five minutes over five continuous days which coincided with the noise data collection. From these measures, I converted the logarithmic magnitudes into linear candela per square meter (cd/m^2) for each site. This conversion inverts the scale of the magnitude measurement so that it is more intuitive; brighter sites will have higher values. Equipment was secured in trees close to the center of each site to coincide with the location of each bird survey. I used the `suncalc` package (Benoit & Achraf, 2019) in RStudio to generate the moon altitude, azimuth, and fraction for each SQM reading and classify the lunar phase. I only used data

classified as astronomical twilight and nightfall – the darkest periods of the night. These data were sorted and assessed for potential variation due to cloud cover and moon phase. I only used data that were collected during the new and crescent lunar phases with clear skies. I calculated descriptive statistics for light at night measures over all days for each site.

Multivariate Analysis

To explore relationships between avian community structure and habitat characteristics, I used a multivariate approach in PC-ORD version 7 (McCune & Mefford, 2018). Our main matrix was 16 rows (sites) by 41 columns (species). Species data were relativized by species maximum to account for the influence of hyper-abundant species. I explored removal of rare species (McCune & Mefford, 2018) but negligible improvements in beta diversity and the row and column coefficient of variance suggested I proceed with the full dataset. I evaluated groupings of sites and groupings of bird species using a two-way cluster analysis with a Sørensen (Bray-Curtis) distance measure and Flexible Beta group linkage method, with beta set at –0.25 as recommended by McCune and Mefford (2018).

I used a Nonmetric Multidimensional Scaling (NMS) analysis with a Sørensen (Bray-Curtis) distance measure to summarize the relationships among sites based on avian community compositions. For the NMS ordination I used the autopilot mode under the “slow and thorough” option to identify the solution with the lowest stress and instability. I used a maximum of 500 iteration and ran 250 runs with real data and 250 runs with randomized data. Our final solution included 55 iterations. Ordination plots were rigidly rotated to load the strongest environmental variable onto a single axis. Pearson correlations were calculated between environmental variables or species abundance and each axis to assess relationships among sites and species. To evaluate the quality of ordination results, coefficients of determination (r^2) were calculated in

PC-ORD for each ordination axis. The resulting r^2 values indicate the amount of variation that is represented by each axis. I included joint plots to depict the linear relationships between ordination scores and environmental variables

Results

I recorded a total of 1869 individual birds and identified forty-two bird species across 16 sites in Weld County, CO (Table 2.2). The most frequently occurring species included American Robins (*Turdus migratorius*), Common Grackles (*Quiscalus quiscula*), European Starlings (*Sturnus vulgaris*), and House Finches (*Haemorhous mexicanus*) (Table 2.2). The average species richness (calculated as the total number of species recorded across all visits) was 15.38 per site and varied from the lowest site with 11 species (GREENM and PHEAS) to the most speciose site with 22 species (PLC).

Environmental Characteristics

Developed land levels varied drastically across our 16 sites with an average of 50% developed land per site (including the 400 m buffer zone). Brentwood Park (Brent) and Luther Park (Luther) were our most developed sites with 91% and 90% developed land (Table 2.1). In both parks, the remaining land cover was developed open space meaning that the land was developed by humans to include “green space” such as grasses and Crow Valley Campground (Crow) was the least developed site with 0% developed land and mostly herbaceous, hay/pasture, and wetland landcover in the area (Table 2.1). For 12 out of the 16 sites, developed land was the most common land cover, ranging from 49% to 91%.

Luminance measures from the SQMs ranged across nearly three magnitudes of differences with Bittersweet Park (Bitter) being the brightest at night ($1.26 \times 10^{-2} \text{ cd/m}^2$) and Crow Valley Campground being the darkest ($3.8 \times 10^{-5} \text{ cd/m}^2$; Figure 2.2). Our sites had an

average noise level of 46.9 dB(A)/ 61.5 dB. Luther Park had the loudest background noise with an average of 79.7 dB(A)/ 88.3dB over 24 hours; this level is similar to the sound of a lawn mower or diesel truck. Grapevine Open Space was the quietest site at 37.3 dB(A)/ 51.8 dB, a sound level comparable to that of a library (Figure 2.2).

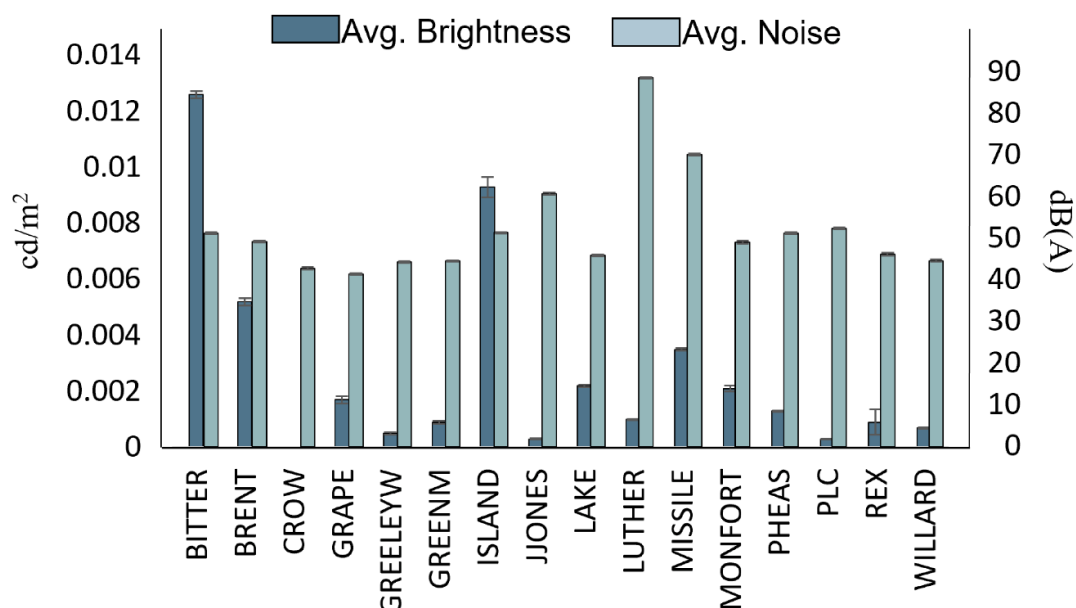
Table 2.1

Proportion of Land Cover for 16 Sites and their Respective 400 m Buffer Zones Using the 2019 Multi- Resolution Land Characteristics Consortium National Land Cover Data.

Site	Water	Developed open space	Developed land	Forest	Shrub & Scrub	Herbaceous	Hay/pasture & cultivated crops	Wetland
Bitter	0.11	0.22	0.60	0.00	0.00	0.00	0.02	0.05
Brent	0.00	0.09	0.91	0.00	0.00	0.00	0.00	0.00
Crow	0.00	0.00	0.00	0.00	0.00	0.67	0.23	0.10
Grape	0.00	0.24	0.52	0.01	0.00	0.10	0.14	0.00
GreenW	0.02	0.20	0.49	0.03	0.01	0.03	0.13	0.08
Green	0.00	0.14	0.64	0.00	0.03	0.16	0.02	0.00
Island	0.00	0.29	0.71	0.00	0.00	0.00	0.00	0.00
JJones	0.00	0.13	0.61	0.00	0.11	0.09	0.05	0.00
Lake	0.00	0.10	0.64	0.00	0.00	0.00	0.19	0.07
Luther	0.00	0.10	0.90	0.00	0.00	0.00	0.00	0.00
Missile	0.00	0.08	0.01	0.00	0.22	0.64	0.05	0.00
Monf	0.00	0.27	0.73	0.00	0.00	0.00	0.00	0.00
Pheas	0.00	0.14	0.85	0.00	0.00	0.00	0.00	0.00
Plc	0.20	0.05	0.14	0.00	0.00	0.04	0.23	0.33
Rex	0.00	0.06	0.01	0.00	0.00	0.70	0.15	0.09
Will	0.00	0.28	0.31	0.00	0.06	0.32	0.03	0.00

Figure 2.2

Average Noise (dark blue bars, right axis) and Light at Night Measurements (light blue bars, left axis) at Each Bird Survey Site.



Community Structure - Nonmetric Multidimensional Scaling Analysis

The three-axis solution constructed by NMS was stronger than expected by chance based on a randomization test ($p = 0.004$). The best solution yielded a final stress value of 6.5. The final instability was < 0.001 following 55 iterations. Cumulatively, the recommended three axes represented 90% of the community variation in our data set. The first axis, which was rotated 40 degrees to maximize its relationship with percent developed land ($r = 0.94$), represented 38% of the variance. The environmental variable with the strongest positive correlation (other than developed land) was the developed open space land category with axis 1 was percent developed land ($r = 0.52$). This land category consists of some constructed features but is predominately covered with vegetation such as lawns (Figure 2.3). Two variables had strong negative associations with this axis including percent herbaceous cover ($r = -0.73$) and hay/pasture and cultivated crops ($r = -0.72$). Few individual species had strong positive correlations with this

axis. The three species with the highest positive correlations included (from highest to lowest correlation) American Crow (*Corvus brachyrhynchos*) ($r = 0.53$), Common Raven (*Corvus corax*) ($r = 0.48$), and American Robin (*Turdus migratorius*) ($r = 0.46$). Fifty-five percent of species had negative correlations with Axis 1, and the top three most negatively correlated with axis one included the Western Meadowlark (*Sturnella neglecta*) ($r = -0.88$), Say's Phoebe (*Sayornis saya*) ($r = -0.70$), and House Wren (*Troglodytes aedon*) ($r = -0.68$). Shannon diversity and total richness measures had strong negative associations with axis 1 ($r = -0.693$; $r = -0.642$). Noise and light both had relatively weak associations with this axis and positive association of light with axis 1 ($r = 0.323$).

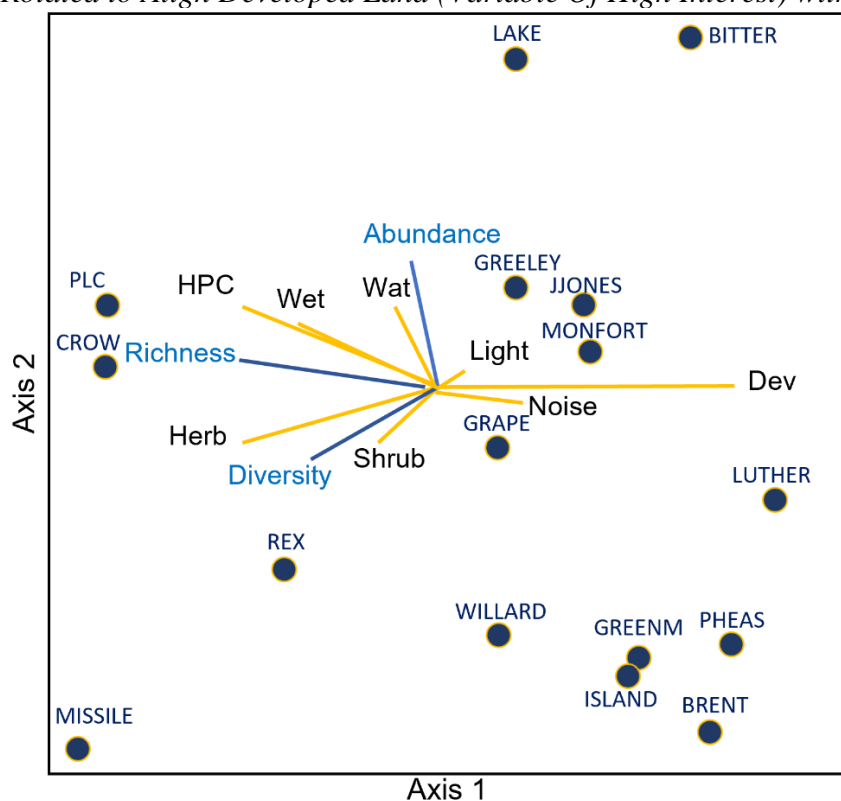
Axis two explained the most variation in our data ($r^2 = 0.419$). Environmental variables most strongly positively associated with this axis included hay/pasture/cultivated crops and water ($r = 0.47$; $r = 0.43$). The most negatively associated environmental variables include herbaceous cover, and shrub/scrub land ($r = -0.34$; -0.31 respectively). The species most positively associated with this axis were Red-winged Blackbirds, Common Grackles, and Barn Swallows ($r = 0.82, 0.76, 0.62$, respectively). Species with negative associations included House Sparrows (*Passer domesticus*), European Starlings (*Sturnus vulgaris*), and American Crows (*Corvus brachyrhynchos*) ($r = -0.73, -0.64, -0.49$, respectively). Shannon diversity had a negative association with axis 2 ($r = -0.340$) while richness had a positive association with axis 2 ($r = 0.253$). As seen in axis 1, noise and light had relatively weak associations with all three axes, with the strongest being a positive association of noise with axis 2 ($r = 0.2$).

The third axis only represented 13% of our variation, with the strongest environmental variables associated with the negative end of this axis being shrub/scrub landcover ($r = -0.46$) and wetlands being most strongly associated with the positive end of this axis ($r = 0.37$).

American White Pelican (*Pelecanus erythrorhynchos*), American Goldfinch (*Spinus tristis*), and Osprey (*Pandion haliaetus*) were the strongest positively associated species with this axis ($r = 0.658; 0.610; 0.678$ respectively) while House Sparrows, European Collared-dove, and Bullock's Oriole were the strongest negatively associated species ($r = -0.518; -0.484; -0.454$ respectively). As seen in axis 1, noise and light had relatively weak associations with all three axes, with the strongest being a positive association of noise with axis 2 ($r = 0.2$)

Figure 2.3

Non-Metric Multidimensional Scaling (NMS) Ordination of Sites in Species Space Rigidly Rotated to Align Developed Land (Variable Of High Interest) with Axis 1.



Note. Sites are depicted in circles. Lines represent joint plots of environmental (yellow lines) and community variables (blue lines) of interest at each site (r^2 cutoff = 0.05). Environmental variables include Developed land (Dev), Shrub/Scrub (Shrub), Herbaceous (Herb), Hay/Pasture and Crops (HPC), Wetland (Wet), Water (Wat), Noise cd/m^2 , and Light at night.

Community Structure - Two-Way Cluster Analysis

For better interpretation, I trimmed both the site and species dendrograms, resulting in three site clusters and six species clusters (Figure 2.4). The species clusters identified through the two-way cluster analysis represent five groups of taxa commonly found at similar sites (Figure 2.4). The three site groups reflect variation in developed (urban) land and presence of water.

The first site cluster (the “Undeveloped Cluster”) contains sites with the least developed land and a range of water features present (Figure 2.4, group 1). All the sites included in this cluster had very low developed land, were dark at night and three of the four were the quietest sites of all. Within this cluster I had two subgroups: one with the site that included a water feature and one with three sites that were mainly herbaceous land. The three undeveloped and herbaceous sites were driven by the black species cluster which mainly included grassland/Great Plains species such as Say’s Phoebe (*Sayornis saya*) and Brown Thrashers (*Taxostoma rufum*). The Poudre Learning Center (PLC) site seems to cluster separately from the other undeveloped sites and is driven by the presence of species commonly found near freshwater lakes and marshes, such as the Great Blue Heron (*Ardea Herodias*) and White Pelicans (*Pelecanus erythrorhynchos*). This site was also our only site classified as undeveloped with a large water feature and was our second darkest site at night, though it was a relatively loud site (Figure 2.4.).

Site cluster two (the “Developed Sites”) contains sites with little presence of water and moderate to the highest levels of developed land (Figure 2.4, group 2, Table 2.1) These sites were clustered primarily by the common avian species (green and purple species). I identified an additionally subgroup in our Developed Sites that clustered separately from the others and was driven by the yellow species group. The yellow species cluster contains three species only found most commonly at Luther Park and Island Grove Park (Figure 2.4). These two parks had

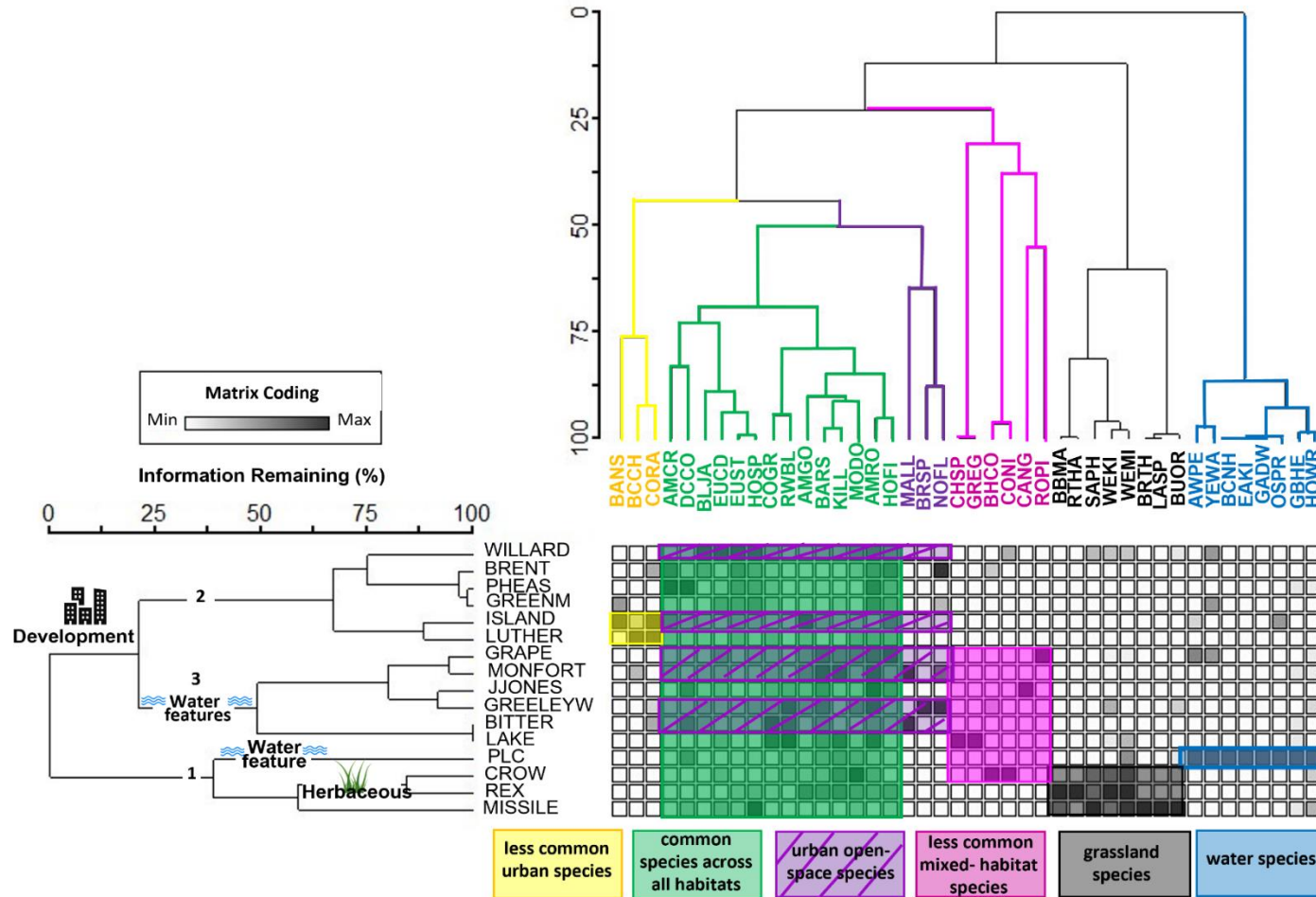
exclusively developed land and developed open space. Overall, the Developed Site cluster did not seem to have commonalities in noise or light at night.

Our final site cluster (the “Developed/Water Sites”) were similarly being driven by the green and purple species including common species (Figure 2.4 group 3). However, these sites were being driven more by common species often associated with water features, including Red-Winged Blackbirds (*Agelaius phoeniceus*), Killdeer (*Charadrius vociferus*), Mallards (*Anas platyrhynchos*). The Developed/Water Sites, were also heavily driven by the American Robin (*Turdus migratorius*). Similar to our Developed Sites cluster, there were no clear trends in landscape composition (other than development), light at night, or anthropogenic noise.

I identified two additional site clusters within our two-way analysis that spanned across the Developed Sites, The Developed Water Sites, and the Undeveloped Sites. First, the pink species group seem to be less-common species that inhabit a variety of different habitat types. These species are not common species across our sites but where they are found, they are found in high abundances such as the Common Nighthawk (*Chordeiles minor*) found at Crow Valley Campground. Second, I found that several of the green and purple species were often found together and in similar abundances (Figure 2.4. purple striped). All of these where these species were found included developed-open space and a mixture of other landscape characteristics. This group was strongly driven by the presence of American Robins, and House Finch (*Haemorhous mexicanus*), two extremely common birds.

Figure 2.4

Resulting Dendrograms from Two-Way Cluster Analysis.



Note. Site clusters are labelled on the left with numbers one through three. Species clusters are coded by color in both the presence matrix and the species dendrogram.

Discussion

The goal of this study was to describe the relationships between avian community structure and environmental factors across Weld County, Colorado. Contrary to our original thoughts, I found that anthropogenic noise, light, and landscape did not covary across our study areas. I did, however, identify patterns of landscape characteristics that may be contributing to community structure.

Backyard Birds are Abundant Across Weld County, and Native Specialists are Sparse

Historically, Weld County is home to a grassland biome that supports ground-nesting bird species, known to be impacted by urbanization (Crocini et al., 2008). Surprisingly, I only identified five ground nesting birds, three of which were water birds, including Mallards (*Anas platyrhynchos*), Gadwalls (*Mareca strepera*), and American White Pelicans (*Pelecanus erythrorhynchos*). With the exception of the Killdeer (*Charadrius vociferus*) and Mallard found in the green species cluster, the remaining ground nesting birds were found at limited sites, most of which are low in developed land. These include Lark Sparrows (*Chondestes grammacus*) and Western Meadowlark, which were present at sites with strong negative associations with Axis 1. In contrast, forty percent of the bird species identified in our study were present at the majority of our sites. This large group of birds (Figure 2.4., green species cluster) consists of many “backyard birds” such as American Robins and American Goldfinches. This group together has a wide range of dietary, nesting, and migratory patterns. Most of these species are not grassland specialists, indicating that the urban areas of Weld County hold bird communities not representative of the historical habitat.

Noise, Light, and Landscape Composition Do Not Contribute Equally to Avian Community Structure

Urbanization is known to influence bird community composition (Francis et al., 2009; Manzanares Mena & Macías Garcia, 2018; Rolando et al., 1997; Verma & Murmu, 2015). However, because urban ecosystems are complex, the extent of the influence of different urban characteristics is less well known. Our findings showed that avian species composition was less associated with anthropogenic noise and light at night than it was with landscape characteristics. I predicted that noise, light, and developed land would covary. However, our results suggest a complex non-linear relationship among these three characteristics which have only been shown in a few other studies (Buxton et al., 2020). The site with the most noise (Luther Park) was relatively dark at night compared to other sites. The brightest site at night (Bitter Park) had moderate noise when compared to other sites. Finally, the most developed sites (Brentwood Park, Island Grove, Luther, and Pheasant Run Park) varied widely in the intensity of noise and light. Additionally, I found that the luminance at night varied much more than the noise measured across our sites. It should be noted that while light varied between sites, I found that our sites overall were darker than other cities (Falchi et al., 2016). This may be due to our decision to measure ground luminance rather than sky illuminance.

Our NMS ordination indicated that noise and light were only weakly associated with site clustering. Recent studies have found that noise and light can have mixed effects on species richness and abundance (Carral-Murrieta et al., 2020; Ciach & Fröhlich, 2017; Wilson et al., 2021). However, there are few studies that have investigated community structure beyond these two measurements. The city of Greeley has grown rapidly over the last decade, and it is possible that responses to noise and light are not as immediate as the response to new habitats. It is

reasonable to predict that habitat changes that deplete say, nesting sites, will affect a species immediately, whereas increased noise and light may disrupt certain behaviors or cycles but not preclude species presence. Additionally, the lack of strong positive relationships among noise, light, and landscape may be due to the population size of Weld County. In the recently urbanized study area, noise and light may not have a large impact on communities as seen in other studies conducted in large, more historic cities. Today, large, and established cities continue to grow in population but likely are not growing in space. Because Weld County and the city of Greeley are still expanding in both space and population, it is possible that the population density has not reached a threshold for which noise and light are maximized, given degree of urban land cover.

Conclusion

I investigated the effects of urbanization on avian community structure by simultaneously measuring three key habitat characteristics: noise, light, and landscape composition. I found that avian community structure is highly associated with landscape composition but not strongly associated with noise or light. Recently, studies investigating the effects of urbanization on wildlife have focused on aspects of the habitat including anthropogenic noise (Jerem & Mathews, 2021) and anthropogenic light (Longcore & Rich, 2004). Although there is interest in understanding the effects of urbanization on wildlife, few studies have incorporated all three key characteristics when studying urban wildlife (Buxton et al., 2020; Carral-Murrieta et al., 2020; Ciach & Fröhlich, 2017). To our knowledge, this study is one of the first to test for the effects of multiple modes of urban disturbance by measuring three top urban characteristics on avian community structure. Our study supports much of the literature in that landscape composition is the most important environmental factor driving reduced diversity and changes to abundance in avian community structure. As we work to create wildlife-

friendly urban ecosystems, it is imperative that we consider the relative importance of multiple urban habitat characteristics and prioritize the management of the most impactful ones.

CHAPTER III
ANTHROPOGENIC NOISE, LIGHT, AND LAND DEVELOPMENT
DO NOT AFFECT AMERICAN ROBIN
(*TURDUS MIGRATORIUS*) BREEDING
SUCCESS IN A RECENTLY
URBANIZED COUNTY

Contribution of Authors and Co-Authors

Manuscript in CHAPTER III

Author: Karina A. Sanchez

Contributions: Conceived the study topic, developed, and implemented study design, collected data, searched the literature, and wrote the first and final draft of manuscript.

Co-Author: Dr. Lauryl Benedict

Contributions: Helped conceived the study topic and edited drafts of manuscripts.

Abstract

Over the last century, avian abundance has decreased drastically in North America. These decreases have been widely attributed to habitat loss, urbanization, and more recently, sensory pollutants such as noise pollution and light pollution. The specific mechanisms of change, however, and their relationships to habitat characteristics are still largely unknown. Urban avian populations may decrease due to lower reproductive success, lower adult survival, or due to migration away from these disturbed habitats. Previous work in urban areas has found mixed effects of urban characteristics such as impervious surface, noise pollution and light pollution on avian reproductive characteristics. These prior studies suggest species-specific responses and even guild-specific responses to urbanization, yet most of the work on urban bird reproductive success has been conducted on only cavity nesters. In this study, I examined the effects of anthropogenic noise, light at night, and developed land on reproductive output measures of a common open-cup nesting bird, the American Robin (*Turdus migratorius*). I monitored 122 nests from 2019- 2021 in a rapidly urbanizing county, Weld County, CO. I used AudioMoth recorders and Sky Quality Meters to measure noise and light at nesting locations, and I measured developed land with MRLC Land Cover Data at 45 nest locations. I used generalized linear mixed-effect models to test for the effects of noise, light, and development on daily survival rates, clutch size, brood size, and hatching success. I found that American Robins are incredibly persistent across a variety of habitats and that none of the urban variables measured in this study affected any measure of reproduction. Additionally, I found that these three urban characteristics did not coincide with one another across the landscape suggesting that compounding effects seen in studies conducted in larger cities may not be present in areas urbanizing today. This study demonstrates the success of a common open-cup nesting bird. I suggest areas of study beyond

nest success that are in need of exploration in order to understand why species such as the American Robin are so successful in urban habitats.

Introduction

Over the last century, urbanization has rapidly spread across the globe. While humans have worked to create an ecosystem that serves their needs in the city, wildlife face the consequences of urbanization. Habitat alterations and habitat loss are among the top contributors to decreases in biodiversity worldwide (Chen et al., 2020; Rosenberg et al., 2019), and the effects of urbanization on avian diversity and community composition have been well documented (Gatesire et al., 2014; Marzluff et al., 2001; Melles et al., 2003; Ortega-Álvarez & MacGregor-Fors, 2009; Rolando et al., 1997; Sol et al., 2020). Research has demonstrated decreased avian diversity in urban areas, lower native species populations, and more introduced species (Cadotte et al., 2017; Riley et al., 2005). Some species seem to thrive in urban ecosystems (Hedblom et al., 2012; Stracey, 2011; Stracey & Robinson, 2012) but others are negatively affected by the changes to their native habitats (Villegas et al., 2010). Urban-positive species (Stracey, 2011) may have traits that allow them to cope with and make use of urban habitats, yet we still do not understand the extent of those traits. It is possible that the increased density of urban-positive birds is due to higher reproductive output, higher survival, or attraction to urban habitats.

Urban habitats can provide some benefits to birds, such as year-round food availability (Chamberlain et al., 2009), increased nesting opportunities, or warmer microclimates (Dhondt & Adriaensen, 1999). However, there are many detrimental components to these systems, including poor food quality, increased predation (Sorace, 2002), chemical pollution (Isaksson, 2015), and sensory pollutants such as noise and light (Senzaki et al., 2020). Because of this, urban habitats may serve as “sink” populations, and the presence or over-abundance of species in urban areas

does not necessarily mean that these species are well adapted. Successful reproduction is essential for sustaining a population and studies have demonstrated reduced reproductive output of several bird species in urban settings (Senzaki et al., 2020; Sumasgutner et al., 2014; Zhou et al., 2019). In contrast, other studies have found that birds nesting in urban and suburban habitats have larger clutch and brood sizes (Senzaki et al., 2020). Overall, habitat characteristics are known to impact reproductive success (Kolbe & Janzen, 2002; Manzer & Hannon, 2005; Paton, 1994). Most of the studies examining this trend in urban areas have used categorical assignments for habitats (e.g. “Urban”, “Rural”) or have assessed the impacts of only one component of urban ecosystems, such as vegetation diversity, habitat fragmentation, or noise pollution.

Today, urban habitats are distinctly different from original or natural habitats, yet they are no less dynamic. In addition to altered landscapes, urban birds must cope with increased novel predators such as cats (Beckerman et al., 2007), noise, and increased light at night (Isaksson, 2018). Songbirds are highly dependent on acoustic communication for signaling information about predator threats, individual quality, and feeding behaviors such as nestling begging calls. Noise pollution can mask these important signals and many studies have demonstrated changes in vocal behavior in the presence of noise (Dorado-Correa et al., 2016; Slabbekoorn & Peet, 2003; Zhou et al., 2019). Furthermore, excess noise may interfere with predator detection, leading to increased vigilance behaviors, alterations in feeding behaviors at the nest, and poor nestling condition (Chan et al., 2010; Injaian, Taff, et al., 2018; Merrall & Evans, 2020). Light pollution has been demonstrated to alter behaviors such as nest initiation that rely on photocues and parental behavioral patterns. In areas with increased light at night, days may seem longer, which may alter time budgets and resting periods (Ouyang et al., 2017; Raap et al., 2017; Senzaki et al., 2020; Stracey et al., 2014).

Urbanization clearly has foreseeable and demonstrated consequences for threatened species. But common species are also susceptible to the threats of habitat urbanization (Rosenberg et al., 2019) and often receive less recognition due to their ubiquity. Additionally, a large bulk of the literature has investigated the effects of urban characteristics on cavity nesting bird species even though open-cup nesters are more likely to suffer from urbanization (Knutson et al., 2004; Máthé & Batáry, 2015). It is understandable that researchers study cavity nesting species due to the advantages of controlling nest locations and accessing nest boxes. However, cavity nests provide different protection from urbanization than open-cup nests. Open-cup nests are exposed to more direct light at night, while cavity nesting species may not be affected by increased light (Raap et al., 2018). Additionally, open-cup nesters are likely more susceptible to predation compared to cavity nesting birds. Acoustic propagation may also differ between the nest types (Grabarczyk & Gill, 2019). To understand the full extent of the effects of urban characteristics on reproduction, we should not generalize findings of cavity nesting birds to other nest-types. With that, more work focused on non-cavity nesting birds is needed.

The American Robin (*Turdus migratorius*) is one of the most common species across North American (Vanderhoff et al., 2020). American Robins are opportunistic nesters in a variety of areas and are often found in urban and suburban regions where they hunt for worms and other invertebrates. Studies have found that American Robins alter their song behaviors in environments with increased noise and light and are negatively affected by noise and light (Miller, 2006; Seger-Fullam et al., 2012). No studies, however, have examined these elements in tandem to understand their relative effects on American Robin breeding biology. Here, I examined the effects of anthropogenic noise, anthropogenic light, and urban landscape on reproductive success (daily survival rate, clutch size, brood size) of American Robins in a county

that is actively urbanizing. Based on prior urban avian reproduction research, I hypothesized that individuals nesting in areas of less noise, less light at night, and less developed land would have higher reproductive success, including higher daily survival rates, larger clutch and brood sizes, and a higher hatching success.

Methods

Study Area

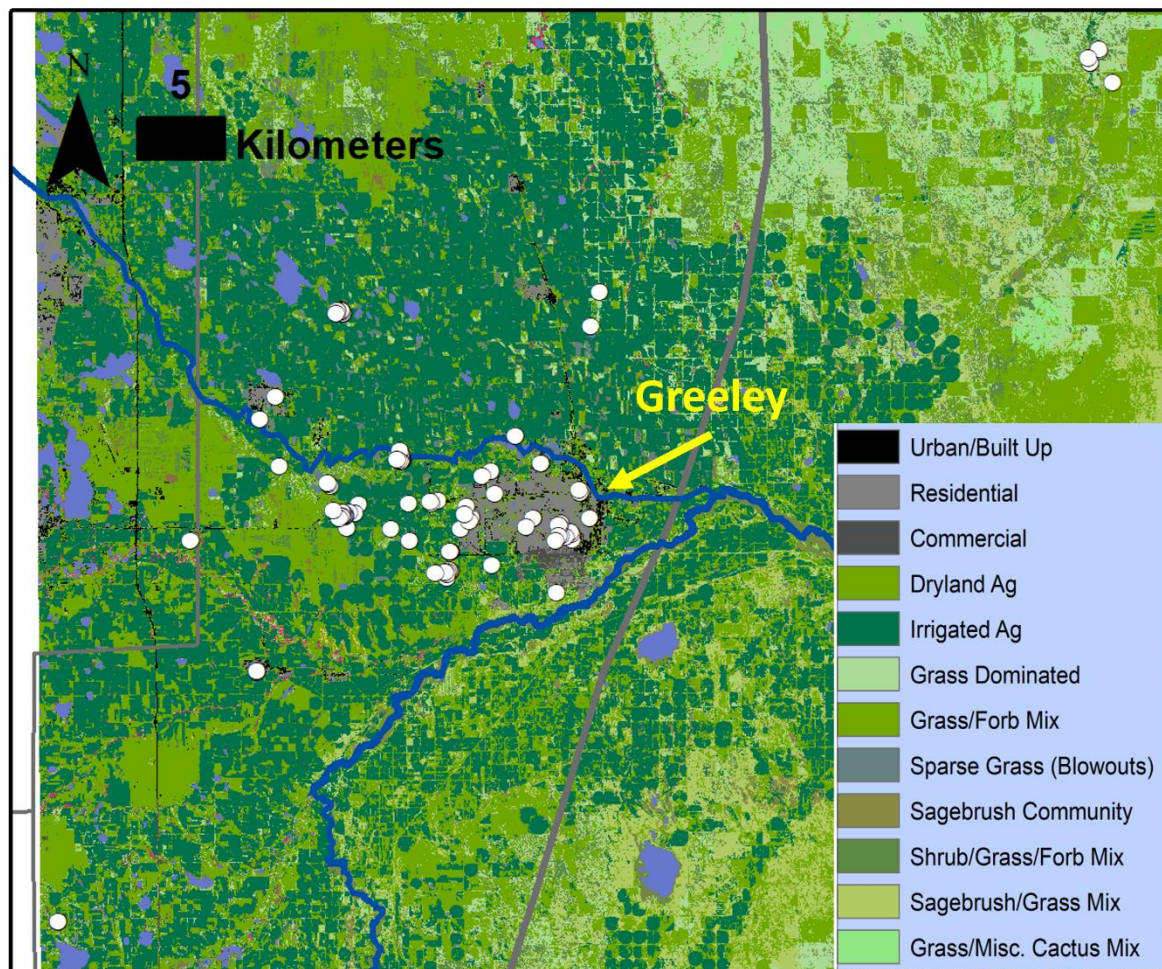
I conducted this research across Weld County, Colorado, a 9,800 square kilometer county dominated by agriculture. My study took place within and around the Greeley Metropolitan area representing various degrees of urbanization in all directions (Figure 3.1).

Nest Monitoring

From May to July during the years 2019, 2020 and 2021, field observers searched for American Robin nests using behavioral cues, and monitored those nests until fledging or failure. In addition, nests were reported by residents of Weld County through an online submission form (urbanbirdnerd.com) and monitored until fledging or failure. I checked nests weekly to count egg and nestling number. Nest check frequency was increased when a transition between stages (lay, hatch, etc.) was expected. I considered nests successfully fledged if chicks were no longer present in the nest after 14 days post hatch with no obvious signs of depredation. All predation events and failures to fledge were recorded. Between 2019 and 2021, I monitored a total of 125 nests to completion.

Figure 3.1

American Robin nesting locations (white circles) across Weld County.



Note. Green color denotes non-urban land while grey-black denotes intensity of developed land.

Landscape Analysis

I used ArcMap (version 10.6.1) and the Multi Resolution Land Consortiums (MRLC) 2019 National Land Cover Database layers (Wickham et al., 2021) to calculate percent developed land at each nesting site (see Chapter II for detailed methods). I created 500 m buffers to capture a wide picture of the landscape. Within each buffer I obtained a percentage of human-developed land around each site. For simplicity I combined the three highest developed levels determined by the MRLC (22- Developed, low-intensity; 23- Developed, medium intensity; and 24- Developed, high intensity) into one category named “developed”. In a previous study (see

Chapter II for methods) developed land was found to have the strongest landcover type effect on avian community structure. Therefore, I felt confident in using the percent developed land as a measure of urbanness.

Sound and Light Measures

Sound and light data were collected during the breeding seasons after nests had fledged. Audiomoth (AudioMoth home page, 2017) acoustic recorders were used to measure the soundscape at each site. I attached recorders to tree/shrub branches within one foot of each nest after fledging was complete to avoid disturbing nestlings. Recorders were set to record a 60 second recording every 6 minutes during the hours of 02:00 – 10:00 and 18:00 – 24:59 for a minimum of four continuous days. Recorders were set to collect data at a sampling rate of 48KHz and gain set at 15 (32 bits, waveform audio file format). For each of the 1 minute samples, I calculated a Normalized Difference Soundscape Index (NDSI) value using the soundecology package (Villanueva- Rivera & Pijanowski, 2018) in R Studio (R Development Core Team, 2020). The NDSI is an acoustic index that estimates the level of anthropogenic disturbance on the soundscape. This is obtained by computing the ratio of human-generated acoustics (anthrophony); defined as sound in the 1000-2000 Hz frequency bin) to the biological acoustics (biophony); defined as sound in the 2000-8000 Hz frequency bin). The resulting NDSI value reflects the dominant frequency within the soundscape from a scale of -1 to +1 with values closer to -1 meaning it is all anthrophony and values at +1 meaning it is all biophony. For each nesting territory, I calculated an “active time” NDSI value using all the collected acoustic data.

I used Sky Quality Meters (SQM-LU, Unihedron) to measure light as ground luminance (the quantity of light that leaves a surface) at each nest site in magnitudes per square arc second ($\text{mag}/\text{arcsec}^2$). SQMs collected a reading every five minutes over five continuous days which

coincided with the noise data collection. I converted the logarithmic magnitudes into linear candela per square meter (cd/m^2) inverting the scale of magnitude to a more intuitive scale where brighter locations have higher values. I used the `suncalc` package (Benoit & Achraf, 2019) in RStudio to generate the moon altitude, azimuth, and fraction for each SQM reading and classify the lunar phase. I only used data classified as astronomical twilight and nightfall – the darkest periods of the night, where the sun is at least 18 degrees below the horizon. These data were sorted and assessed for potential variation due to cloud cover and moon phase. I only used data that were collected during the new and crescent lunar phases with cloud coverage below 3 oktas. Oktas are a unit used to describe cloud cover and ranges from 0 (clear skies) to 8 oktas (completely overcast). I tested for the effects of lunar phase and cloud coverage on cd/m^2 and found no significant effect by either variable. Therefore, I included all samples within these data parameters. I calculated descriptive statistics for light at night measures over all days for each site.

Statistical Analyses

I tested for correlations between all explanatory variables prior to running analyses using Pearson correlation tests. To test for the effects of developed land, anthropogenic noise (NDSI value), and light at night (cd/m^2), I ran models for each of the response variables: daily survival rate, clutch size, brood size, and hatching success. I ran 17 candidate models for each response variable using all combinations of the predictor variables including interaction effects among each independent variable. I calculated daily nest survival rates using the logistic-exposure method (Shaffer, 2004) to model the effects of four explanatory variables: 1) developed land within 500 m, 2) developed land within 500 m, 3) NDSI value, and 4) luminance (cd/m^2). This method accommodates for varying days between nest checks. I used a modified logit-link and set

the four explanatory variables as fixed effects and nest ID and year as random effects to account for annual variation and pairs.

Clutch size and brood size data showed under-dispersion. Therefore, I used the `glmerTMB` function within the `glmerTMB` v 1.1.2.3 package (Brooks et al., 2017) to construct GLMMs with a Conway-Maxwell-Poisson error and log link function to account for under-dispersed data. Hatch success was examined by constructing GLMMs using the `lmer4` package (Bates et al., 2015) and the `glmer` function with a binomial distribution to assess the effects of the explanatory variables. For each model I included Year and Day of Year as random factors to account for annual differences and for variation throughout the breeding season.

I calculated Corrected Akaike's Information Criterion values (AICc) and models were ranked and compared using the ΔAICc values (Anderson & Burnham, 2002). I only report models that had a $\Delta\text{AICc} < 2$ for the most parsimonious models. Prior to model selection, I checked normality by examining residuals q-q plots and histograms. Models that did not meet the model assumptions were discarded. All analyses were completed in R Studio (R Development Core Team, 2020).

Results

Habitat Characteristics

Developed land varied across Weld County with a maximum of 100% developed land and a minimum of 0% developed land around surveyed American Robin nests. The average developed land within 500 m was 55.5% (± 0.337). I also found variation in the soundscape across all territories with an average overall NDSI value of 0.162 (± 0.325). The NDSI ranged from -0.618 (nearly all anthropogenic sound) to 0.605 (very little anthropogenic sound). Nesting locations had nighttime luminances ranging from 0.0005 cd/m^2 to 0.605 cd/m^2 with an average

of $0.068 \text{ cd/m}^2 (\pm 0.149)$. I tested for correlations between independent variables and only found no significant correlations among the variables (Table 3.1).

Table 3.1

Correlation Table of Predictive Variables: Percent Developed Land at 500 M, Soundscape (NDSI), and Luminance (Cd/M^2). I used Pearson's Correlation Test to Measure Correlations.

Habitat Characteristics	Perc. Dev. 500 m	NDSI	cd/m^2
Perc. Dev. 500 m	-	-0.1361	-0.0653
NDSI	-	-	-0.0179
cd/m^2	-	-	-

Nest Survival

From 2019 to 2021, I monitored a total of 122 American Robin nests. Overall, 27% of nests failed, 71% had at least one fledging event, and <2% were abandoned (Table 3.2). Of these nests, I collected noise and light data from 45 nests in 2020 and 2021. I used these 45 nests to examine relationships between daily nest survival, developed land at a 500 m radius, luminance at night (cd/m^2), and the soundscape (NDSI) within the territory. There was an average daily survival rate of 78.5% (± 0.412) across all 45 nests. Two models fit the statistical framework of $\Delta\text{AICc} < 2$ and both included luminance at night and percent developed land as predictors of nest survival (Table 3.3), although neither of these models were of good fit ($\text{cr}^2 < 0.0001$) (Figure 3.2). Large confidence intervals in these models indicate no strong effects on daily survival rates (Table 3.3; Figure 3.2).

Table 3.2*Nest Fates for all Nests Monitored from 2019-2021.*

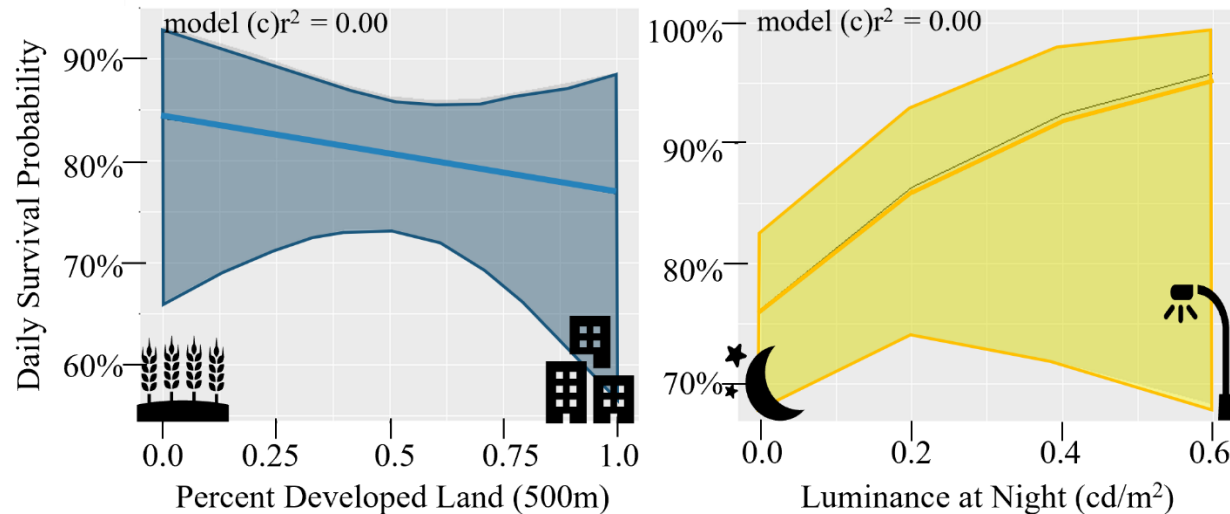
Year	Fledged	Failed	Abandoned	Total N Nests
2019	23	8	1	32
2020	24	12	1	37
2021	40	13	0	53

Table 3.3*Akaike's Information Criterion (Aicc), Delta AICc, Model Weight for Daily Nest Survival Rate of American Robins Nesting in Weld County in 2020 and 2021.*

		Model	Est.	Pr(> z)	(c)r ²	(m)r ²	AICc	ΔAICc	AICc Weight
Daily Survival (DS) N = 45	DS1	Luminance (cd/m ²) + Dev. Land	1.60	0.06	0.00	0.04	189.4	0.00	0.46
			-0.23	0.43					
	DS2	Luminance (cd/m ²) + Dev. Land + Lum. x Dev.Land	2.77	0.26	0.00	0.08	190.7	1.3	0.24
			-0.03	0.93					
			-2.32	0.46					
Clutch Size (CS) N = 36	CS1	Soundscape (NDSI)	0.18	0.52	0.00	0.01	124.7	0.00	0.31
	CS2	Luminance (cd/m ²)	-0.30	0.65	0.00	0.01	124.9	0.2	0.28
	CS3	Dev. Land	-0.01	0.98	0.00	0.00	125.1	0.4	0.43
Brood Size (BS) N = 34	BS1	Dev. Land	0.12	0.37	0.23	0.02	71.7	0.0	0.37
	BS2	Soundscape (NDSI)	0.05	0.64	0.11	0.00	72.3	0.3	0.27
	BS3	Luminance (cd/m ²)	-0.00	0.99	0.06	0.00	73.1	1.4	0.18
Hatch Success (HS) N = 36	HS1	Luminance (cd/m ²)	2.68	0.49	0.00	0.05	48.6	0.4	0.43
	HS2	Dev. Land	0.16	0.89	0.00	0.00	49.2	0.6	0.32

Figure 3.2

Top Predictive Models for Daily Survival Rate Include Developed Land (Left) and Luminance at Night (Right).



Clutch Size

The average clutch size across both years was $3.44 (\pm 0.607)$ and ranged from 2 – 4 eggs laid per nest. Three models fit the ΔAIC criteria, each of these models only included one predictor (Table 3.3). The top model included soundscape and found that clutch size tended to be larger in areas with less anthropogenic noise (Figure 3.3). The second top model included luminance, with clutch size being smaller in areas with more light at night (Figure 3.3). The third model included developed land and found that nests in areas with more developed land had smaller clutch sizes (Figure 3.3). As with daily survival rate, all three top models were weak fits ($cr^2 < 0.0001$). All models had large confidence intervals suggesting that there was little effect on clutch size (Table 3.2).

Brood Size

Average brood size across both years was $2.578 (\pm 1.033)$ and ranged from 1- 4 young per brood. Three models met the ΔAIC criteria and each only included one predictive variable. The top model included percent developed land and suggest a positive relationship of brood size

and developed land (Table 3.2). Soundscape was included in the next best model of fit and suggests a negative effect of anthropogenic noise and brood size (Table 3.2). The third model included luminance only but indicated no directional affect on brood size (Table 3.2). All three brood size models were very weak and large confidence intervals indicate weak effects (Table 3.2; Figure 3.4).

Figure 3.3

Top Three Models for Clutch Size Each Included a Single Explanatory Variable: NDSI (Left), Luminance At Night (Middle), And Percent Developed Land (Right).

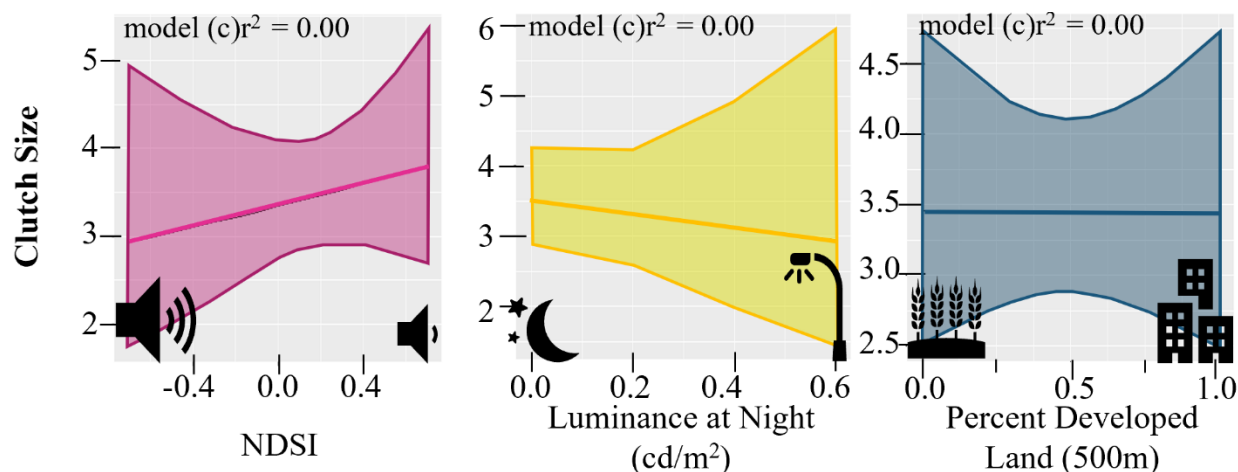
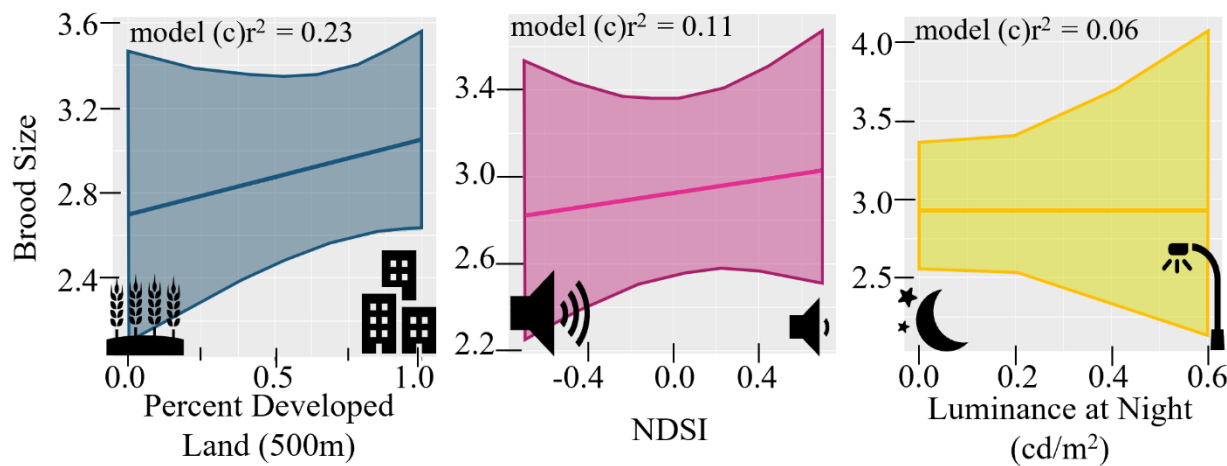


Figure 3.4

Top Three Models for Brood Size Each Included a Single Explanatory Variable: Percent Developed Land (Left), NDSI (Middle), and Luminance at Night (Right).

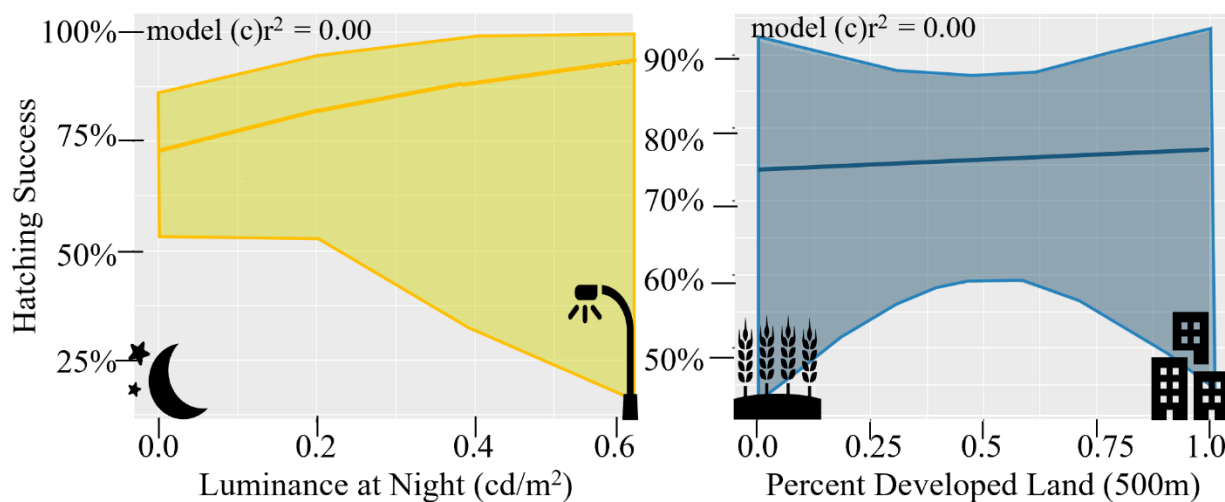


Hatching Success

Average hatching success across both years was 75.7% (± 0.328) and ranged from 0 % to 100%. Hatching success models only had one predictor variable in each; luminance in one and percent developed land in the other (Table 3.3). The top model suggests that birds nesting in areas with more light at night had higher hatching success (Figure 3.5) but had weak predictive power ($cr^2 < 0.0001$). The second-best model suggests that nests in areas with more developed land had slightly better hatching success (Figure 3.4). Large confidence intervals in these models suggest that luminance and developed land did not have strong effects on hatching success (Table 3.2; Figure 3.5).

Figure 3.5

Top Predicted Brood, Clutch, and Hatch Success Models for Each of the Tested Explanatory Variables.



Discussion

The American Robin is a species commonly found in urban and non-urban areas. In this study, I aimed to understand whether their reproductive output was explained by three common urban characteristics. I found minimal effects of increased luminance at night, anthropogenic

noise, and developed land on four measures of reproductive success. The predictor variables used in this study did not explain the variation in reproduction in this sample of birds. These results suggest that American Robins have viable populations across many different habitat types in Weld County, CO. Nest success over the three years varied from 64% in 2020 to 71% and 75% in 2019 and 2021, respectively. These survival rates fall within the reported rates for American Robins (Morneau et al., 1995; Yahner, 1983) in suburbs and non-urban sites. Additionally, I found that the three urban variables did not covary as anticipated. Noise, light and landscape characteristics did not always “match” in the sense that some nest locations were very bright at night but were quiet, and vice versa (see Chapter II for additional examples conducted within the same study area). Perhaps birds in this study area are less affected by urbanization due to this mismatch and a resulting lack of compounding effects of all urban characteristics at once.

Although it was a very weak association, daily nest survival rate was most associated with developed land and luminance at night: higher survival rates were associated with brighter nest locations and areas with less developed land. The brightest nest site measured at 0.605 cd/m^2 , about the brightness of a bike light on the road (average range from 0.3–2.0 cd/m^2) and therefore was not necessarily very bright. This is likely due to my decision to measure ground luminance to represent what wildlife are exposed to in their habitat. Nonetheless, finding the luminance appeared as the most common factor in my models raises the question as to whether light at night might benefit daily nest survival. Russ et al. (2017) studied European Blackbirds (*Turdus merula*) and suggested that increased light may reduce predation risk at night. It may be that nocturnal predators avoid brighter areas at night. A more recent study, (Rodríguez et al., 2021) found that streetlamps were significantly associated with nest site selection because individuals settling next to streetlamps preyed on invertebrates attracted to light. American

Robins will often feed their young insects such as moths during the early stages of nestling growth. Individuals may, thus, nest in brighter areas for immediate access to insect food items that improve nestling survival. Furthermore, other common urban species such as Northern Mockingbirds (*Mimus polyglottos*) exploit excess light in urban areas by feeding young at earlier or later times of the day (Stracey et al., 2014). The present study did not collect data on feeding activities, but this is one of the multiple mechanisms that might lead to increased nest success in brighter areas.

Overall, developed land had minimal effects (Table 3.3). This was surprising because land-use and habitat change have been found to be top contributors to decreases in bird populations (Eglington & Pearce-Higgins, 2012; Rosenberg et al., 2019). Additionally, a previous study conducted in Weld County, CO found that landscape characteristics drive avian community structure (Chapter II). Most of the nests used in this study were found in residential areas in both urban and less-urban locations. American Robins may be nesting in areas with micro-habitats that are conducive for nest survival. Weld County is still urbanizing and compared to other, older cities, has less impervious surfaces overall. There is an abundance of grass lawns that could be offering a stable food supply for American Robins around Weld County. Food availability has been found to be a driving factor in reproduction in other species (Seress et al., 2020) and since there is an abundance of habitat for the robin's main food source (e.g. worms), this could be mitigating nest success within Weld County. I did not measure food availability in this study and direct effects of this factor should be studied in the future in areas with more impervious surfaces.

I predicted that a soundscape with more anthropogenic sounds would negatively impact daily survival, brood size, and clutch size in alignment with recent research (Senzaki et al.,

2020). However, anthropogenic noise did not strongly predict any of these metrics. Since I did not see an effect on daily survival of nestlings or hatching success, it is likely that individuals in noisy areas have success with all clutch sizes. In this study, I did not test for the effects of noise directly on nestling condition or survival post-fledging but other studies have shown a negative impact of anthropogenic noise on nestling body size and stress (Injaian, Taff, et al., 2018) which may result from both noise and disruptions to parental behaviors in noisy areas. I cannot comment on the health of nestlings produced in noisy areas, but we can infer from these results that nests in noisy and less noisy locations have similar success rates.

Evidence from other studies suggests that American Robins show atypical patterns with respect to urbanization: their densities increase with anthropogenic noise, light, and urbanization (Bonnet-Lebrun et al., 2020; Brian Evans et al., 2018; Evans et al., 2015; Pharr, 2021). This discrepancy may be due to the urban landscape offering abundant resources for this species (Morneau et al., 1995). For example, worms are a primary food source for American Robins, and therefore we would expect this species would be attracted to suburban areas with large lawns. American Robins may also be attuned to their local habitats so much that they can select areas of increased noise and light but only experience mild effects of the landscape. Still, the success of this species in urban areas is striking. Being open-cup nesters, American Robin success is expected to be lower in urban areas due to their increased exposure to the elements of their habitats. American Robins have been found to alter their singing behaviors in urban and noisy areas (see Chapter IV). Perhaps there are other behavioral alterations present in urban birds that aid in their persistence in urban areas. More work is needed to understand the mechanisms that allow these birds to have consistent reproduction in areas that other species cannot. In particular,

more work is needed to evaluate the relationship between urban characteristics and parental behaviors, and physiological variables.

Development, anthropogenic noise, and anthropogenic light often coincide with one another. In areas of new development such as Weld County, CO, these correlations are not evident in places where American Robins nest. This may be due to a smaller human population, fewer large roads, the size of the city, or nest site selection by the birds. I did not find that development, noise, and light are proportionate to one another and thus there may have been more variation in the combination of these characteristics across nest sites. Few studies have considered the impacts of all three characteristics and their effects on avian species (Da Silva et al., 2014; Fuller et al., 2007; Senzaki et al., 2020) presumably because they often do coincide with one another. This study demonstrates the importance of measuring these characteristics separately. Finally, this study also highlights the importance of studying native species and open-cup nesters in urban areas. While not as convenient as studying cavity nesters, my study demonstrates that not all open-cup nesters or native species are negatively affected by urbanization.

CHAPTER IV

LANDSCAPE AND ANTHROPOGENIC NOISE DRIVE
HIGHER MINIMUM FREQUENCIES AND
SYLLABLE RATES IN AMERICAN
ROBIN (*TURDUS MIGRATORIUS*)
SONGS.

Contribution of Authors and Co-Authors

Manuscript in CHAPTER IV

Author: Karina A. Sanchez

Contributions: Conceived the study topic, developed, and implemented study design, collected data, searched the literature, and wrote the first and final draft of manuscript.

Co-Author: Lauryn Benedict

Contributions: Helped conceive the study topic and edited drafts of manuscripts.

Abstract

As the human population continues to grow, ecosystems are being modified. These modified environments introduce novel disturbances including noise pollution, light pollution and altered resources. For organisms that rely heavily on acoustic communication, such as birds, it is important to understand the effects of anthropogenic environmental changes on behaviors and the consequences of these behaviors. Bird song is an important behavior for individual fitness, contributing to mate acquisition and resource defense. Recently, studies have demonstrated that birds in urban areas have different song characteristics when compared to populations in rural areas. The most common finding is that minimum frequency increases in urban areas, and this finding has been most linked to increased noise pollution in cities. However, cities are dynamic ecosystems, and habitat structure (open vs. closed habitats) may also affect song characteristics, yet few studies consider this in combination with noise pollution. Additionally, light pollution has been demonstrated to alter the time and length of singing in the day for several species. If individuals alter their singing time-budgets in the presence of light pollution, it is possible that songs characteristics may also change to conserve energy while singing for longer periods of the day. This study investigated the effects of noise, light, and landscape composition on American Robin song characteristics in Weld County, CO. I directly measured the acoustic dynamics and light regimes in combination with landscape and individual behavior within an area currently undergoing rapid urbanization. I found that anthropogenic noise and light do not have an effect on American Robin song characteristics including minimum song frequency, maximum song frequency, duration, syllable rate, inflection rate or peak frequency. I did however find that percent developed land does significantly affect minimum song frequency. Songs recorded in areas with more developed land had higher minimum

frequencies than songs recorded in other areas. This study was conducted in a recently urbanized area in which noise pollution and light pollution do not directly covary with percent developed land. It is possible that these two urban characteristics have yet to “catch up” in magnitude to percent developed land. For this reason, the effects of noise and light may not be as prevalent as percent developed land. Nonetheless, this study demonstrates changes in song characteristics of a common bird in an area with less noise pollution than other large cities suggesting that sensitivity to urbanization may begin at the start of urbanization.

Introduction

Songbirds are heavily reliant on acoustic communication through vocal signals that have been shaped by their habitats (Hansen, 1979; Morton, 1975). Bird song is used for mate-attraction, territory defense/maintenance, and communication between mates (Kroodsma & Byers, 1991), and therefore can have fitness consequences for individuals (Catchpole, 1987). Urbanization has altered the habitats through which these signals travel, including changes in the soundscape, lightscape, and physical landscape (Grimm et al., 2008). One potential consequence of urbanization is the disruption of animal communication via signal masking or changes in temporal patterns.

Noise pollution in urban soundscapes has been intensively studied because noise has the potential to alter animal communication. Generally, anthropogenic noise is any human-caused background sounds that interfere with acoustic signals. Noise can alter our perception of natural sounds by masking these sounds either through amplitude or by overlapping with other sounds in the same frequency band. Most anthropogenic sounds are low frequency (below 2 KHz) in nature and can be both chronic and acute. Anthropogenic noise has increased drastically over the last century in most part to increases in transportation such as automobile traffic and flights

(Barber et al., 2010). Wildlife is exposed to these sounds in ways that differ from humans in that we have ways to mitigate our exposure. Therefore, there are higher consequences for wildlife exposed to noise in that it can have daily interruptions to important communicative signals. Wildlife have responded to increased noise through altering behaviors (Lowry et al., 2013; Shannon et al., 2016). By far, the most common finding is that bird species in urban landscapes with higher anthropogenic noise tend to have songs with higher minimum frequencies (Lazerte et al., 2016; Lowry et al., 2013; Shannon et al., 2016; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003). Songs with higher minimum frequencies are at less risk of acoustic masking by the loud, low-frequency anthropogenic noise found in urban environments (Hu & Cardoso, 2009) and, therefore, can better transmit to a receiver (Cardoso et al., 2020). At the same time, altered signals may carry altered content.

Research has demonstrated a link between animal body size and frequency of vocalizations, such that larger birds produce lower frequency songs than smaller birds (Ballentine, 2009). Because of this, song frequency may carry information about individual's condition or quality relating to size during mate-selection (Conner et al., 1986; Narango & Rodewald, 2018; Rehsteiner et al., 1998; van Oort et al., 2006). If so, we would anticipate that low-frequency songs would be more attractive to mates (Halfwerk et al., 2011; Huet des Aunay et al., 2014). However, as described above, cities also have low frequency anthropogenic noise that is produced at high-energy, leading to masking of low-frequency songs. These opposing selective pressures in urban habitats clash with our traditional understanding of song evolution. Thus, individuals may face consequences by choosing to alter their minimum frequency or not. If they do not, they face the challenge of being drowned out by anthropogenic noise and not being heard. If they do raise their minimum frequency, females may find them less attractive.

Additionally, the alteration of song frequency may mean that this signal is no longer an honest signal relaying the correct information on size or quality of a singing bird. In these situations, females may be faced with the consequences of selecting a male mate that was audible in noise (with higher minimum frequencies) but is not a quality mate.

Light pollution is another conspicuous characteristic of urban habitats. Over the last century, light pollution has become pervasive throughout many habitats and researchers find it to be a threat to biodiversity (Hölker et al., 2010; Smith, 2008). Most organisms have evolved circadian rhythms are founded in light and dark patterns. These patterns have been changed due to the introduction of artificial light at night. Due to the importance of photocues for phenological responses, most of the current literature focuses on the effects of light pollution on the temporal aspects of avian singing behaviors. Several studies have found that the dawn song begins earlier with light pollution (Kempnaers et al., 2010; Marin-Gomez & Macgregor-Fors, 2021). Some species have been observed to sing nocturnally, and others sing for longer periods of the day in the presence of light pollution (Da Silva et al., 2014). Song production can be metabolically costly (Oberweger & Goller, 2001). Individuals who sing longer and non-typical songs at higher frequencies throughout the day could 1) lose time for other important behaviors such as foraging and parental care or 2) alter songs to be less taxing. For example, singing shorter songs with narrower bandwidths, might allow an individual to produce a song with more energy concentrated in a smaller bandwidth. Light pollution may have indirect effects on song structure, but little work has explored this connection.

Finally, the physical structure of habitats affects the propagation of sounds through space (Phillips et al., 2020). Research has found that low-frequency sounds travel farther in closed habitats, such as forests and buildings, while high frequency sounds travel farther in open

habitats, such as the grasslands (Barker et al., 2017; Dabelsteen et al., 1993). Due to the importance of birdsong for avian communication, we would expect selective pressures to act on song structures to increase transmission within their habitats. Accordingly, studies have found that species with low-frequency vocalizations tend to inhabit closed habitats and vice versa for species with high frequency vocalizations (Boncoraglio & Saino, 2007). Urban habitats often include human-structures such as buildings and fences that result in closed habitats. According to the Acoustic Adaptation Hypotheses (Hansen, 1979; Morton, 1975) urban species with low frequency vocalizations *should* have relatively functional communication signals in urban habitats due to their song structure. However, noise has pushed songs frequency in the opposite direction.

Understanding the selective pressures that shape birdsong in a world of rapid land changes is necessary to anticipate and plan for ecological and evolutionary changes to urban species. Existing research confirms that birds change their songs in cities in multiple ways. Altered signaling in urban ecosystems could eventually lead to an evolutionary trap where preferences for altered songs lead individuals to choose poor quality mates and territories. These negative consequences may not, however, be permanent. One recent study, showed that sparrows living in cities quickly resumed species-typical song frequencies in the absence of noise (Derryberry et al., 2020) suggesting that individuals can plastically respond to their environments. Little work has been conducted on the long-term effects of songs alterations on individuals and if these alterations persist within populations via cultural evolutionary processes (Luther & Derryberry, 2012; Moseley et al., 2018). The evolutionary consequences of using these plastic behaviors are still unknown to researchers.

It is clear that landscape and soundscape can affect avian vocal communication, but the effects of light on song structure are less well-studied. In this study, I aimed to test for an effect of these three urban characteristics on song structure. Our research took place within and around the Greeley Metropolitan area in Weld County, Colorado. The Greeley area has been one of the fastest growing metropolitan areas over the last two decades (US Census Bureau, 2020). This growth has resulted in rapid urbanization of the area spanning out from Greeley. Currently, the area includes many degrees of urbanization in all directions (Figure 4.1). In line with much of the work that has been done on urban bird song, I hypothesized that songs recorded in areas with more development and anthropogenic noise, would have higher minimum frequencies. I also predict that if light pollution alters temporal singing behaviors, that songs will be shorter or have higher syllable rates in areas with more light pollution. I predict that both noise and light will be highly correlated with percent developed land.

Methods

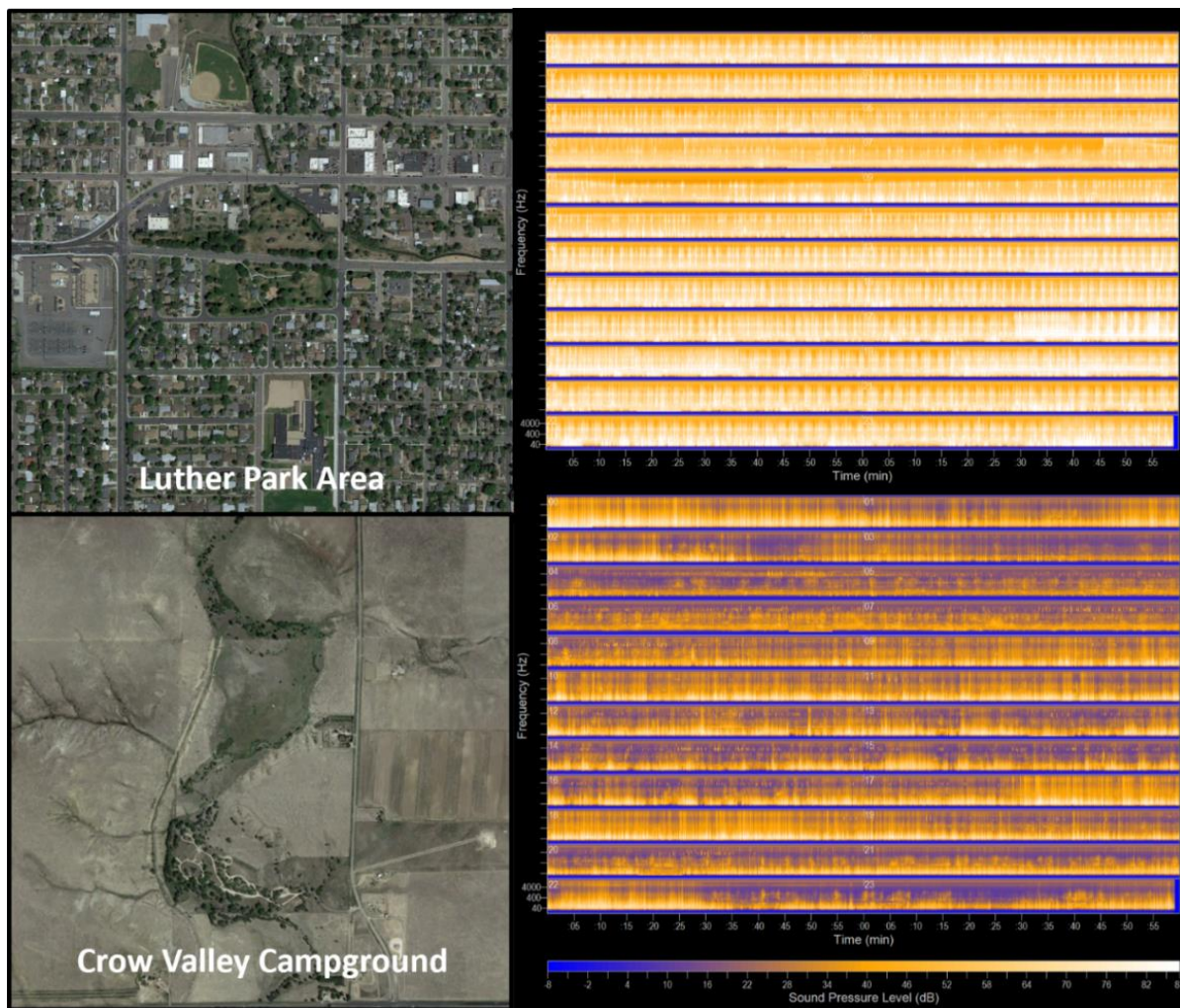
Song Recordings

Song data was collected from recordings of American Robins (*Turdus migratorius*) made during the Colorado breeding season in 2018, 2019, 2020, and 2021. Our analysis included 186 songs from 65 individuals (Table 4.1) At the time of recordings, I marked location using a handheld GPS. Some individuals were trapped and banded as a part of a separate study on this population. Individuals were trapped using mist nets and given federal USGS bands as well as colored bands for identity. I conducted spontaneous audio recordings at and around each location where an individual was trapped or where a nest was identified. When singing banded individuals were heard and located, the recorder moved as close to the bird as possible while minimizing disturbance. Recorders verbally dictated number of songs sung by the target

individual within the recordings as well as provided metadata on time, date, location, context, and other behavioral notes. Songs were recorded for a minimum of one minute and continued until 25 songs were recorded or until 15 minutes had passed or the individual moved out of sight. Recordings were taken typically between sunrise and 10:00 am. All audio recordings were made using a Sennheiser shotgun microphone and a Marantz PMD 661 PMD digital recorder set at a 4800 Hz sampling rate, 24-bit, and WAV file type.

Figure 4.1.

Two Examples of Developed and Non-Developed Locations of American Robin Song Recordings (Left) . 24-Hour Spectrograms of Soundscapes at Luther Park and Crow Valley Campground (Right) Showing Decibels and Frequency Of Sounds (X-Axis)



I inspected recordings acoustically and visually by spectrogram using Raven Pro 1.6 (Charif et al., 2010) and Audacity (<https://audacityteam.org>) version 2.3.3. I selected three high quality songs for each individual for analyses. I considered high quality songs as songs that had the following features: the entire song was clearly visible on a spectrogram with no overlap from other sounds, the waveform clearly indicated the timing of song elements, and the recorder dictation indicated that the vocalization came from the target individual. When three high quality songs were not available, I selected two songs for measurement. Recordings were clipped to include only the selected songs and normalized to -1dB. Songs were high-pass filtered at 1500 Hz to reduce noise below the frequency of American Robin vocalizations and saved as WAV files using Audacity.

Table 4.1

Breakdown of Number of Songs Analyzed from American Robin Individuals for Years 2018, 2019, 2020, 2021 in Weld County, CO.

Year	N Songs	N Males
2018	51	17
2019	24	8
2020	53	18
2021	58	22
Total N	186	65

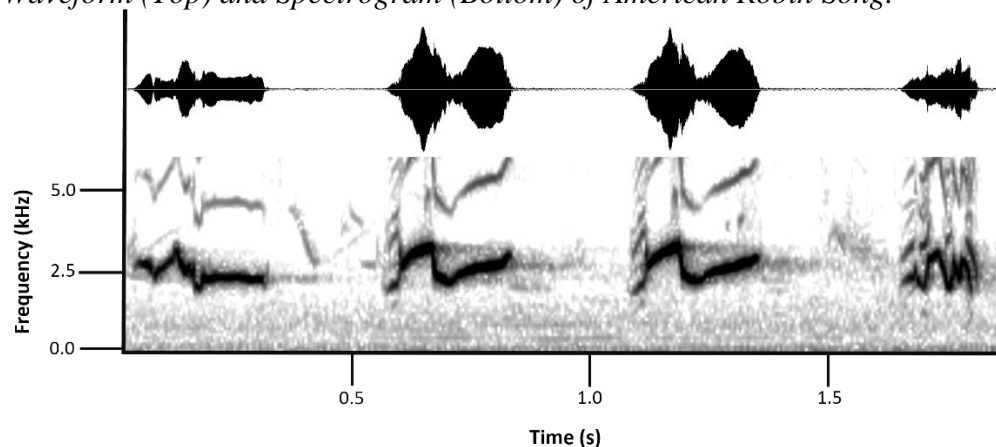
Song Characteristics

I visualized spectrograms in Raven Pro 1.5 using Hanning type spectrograms of 512 samples, a frequency resolution of 135 Hz, and a time resolution of 5.33 ms. American robin songs typically consist of an array liquid tonal syllables that are sang with rising and falling clear

whistles (Figure 4.1). The number of syllables per song varies and there are few resources that identify the average number of syllables per song. I considered a song complete if there was more time between the ending and starting syllables of songs than there are between syllables within one song. From spectrograms, I measured the following song characteristics for each song: PFC minimum frequency, PFC maximum frequency, peak frequency, duration, inflection rate (calculated as number of inflections per second), and syllable rate (calculated as number of syllables per second). I measured frequency features using the Peak Frequency Contour (PFC) Tool. This approach traces the contour of the song by identifying the frequency of peak amplitude at each spectrogram time-step. Therefore, our reported PFC minimum and PFC maximum frequency measures should be consistent across background noise conditions. We used the 90% duration measurement to measure duration for each song; 90% duration reduces the possibility of human error by using the power of the song to determine the length of 90% of the song with the most power. All song measurements were taken by the same observer (KS). Because frequency is non-linear in avian perception of sound, I log-transformed our maximum peak frequency contour measurements prior to analysis (Cardoso, 2013)

Figure 4.2.

Waveform (Top) and Spectrogram (Bottom) of American Robin Song.



Landscape Analysis

I used ArcMap (version 10.6.1) and the Multi Resolution Land Consortiums (MRLC) 2019 National Land Cover Database layers (Wickham et al., 2021) to calculate percent developed land at each recording location (see Chapter II for detailed methods) at a 30m resolution. I created 500 m buffers to capture the variation in landcover within the area of recording. I used the tabulate area tool in ArcMap to extract the number of cells per landcover type within the 500 m buffer. I used these measurements to then calculate a percent human-developed land. For simplicity I combined the three highest developed levels determined by the MRLC (22- Developed, low-intensity; 23- Developed, medium intensity; and 24- Developed, high intensity) into one category named “developed”. In a previous study (see Chapter II for methods) developed land was found to have the strongest landcover type effect on avian community structure. Therefore, I felt confident in using the percent developed land as a measure of urbanness.

Sound and Light Measures

Sound and light data were collected at nests as a part of a co-occurring nest success study conducted on the same American Robin populations (see Chapter III). I used the data collected at nests for songs recorded within 200 m of the noise and light collection sites. Soundscape was measured using Audiomoth (AudioMoth home page, 2017) acoustic recorders attached to branches within one foot of each nest after fledging was complete to avoid disturbing nestlings. Sixty second recordings were taken every 6 minutes during the hours of 02:00 – 10:00 and 18:00 – 24:59 for a minimum of four continuous days (see chapters III for detailed methods). I calculated a Normalized Difference Soundscape Index (NDSI) value using the soundecology package (Villanueva- Rivera & Pijanowski, 2018) in R Studio (R Development Core Team,

2020). The NDSI is an acoustic index that estimates the level of anthropogenic disturbance on the soundscape by computing the ratio of human-generated acoustics, called anthrophony, to the biological acoustics called biophony. NDSI values reflects the dominant frequency within the soundscape on a scale of -1 to +1 with negative values representing more anthrophony in the soundscape and positive values representing more biophony within the soundscape. I calculated an average NDSI value for each nest site representing the typical hours of activity; dawn and dusk (4:00 – 10:00; 20:00 – 21:00). I included a two hour buffer before and after each activity time to capture the soundscape before and after active hours.

Sky Quality Meters (SQM-LU, Unihedron) were used to measure ground luminance (the quantity of light that leaves a surface) at each nest site in magnitudes per square arc second (mag/arcsec^2). SQMs collected a reading every five minutes over five continuous days which coincided with the noise data collection. I calculated linear candela per square meter from the logarithmic magnitudes collected at each location. I used the `suncalc` package (Benoit & Achraf, 2019) in RStudio to generate the moon altitude, azimuth, and fraction for each SQM reading and classify the lunar phase. I only used data classified as astronomical twilight and nightfall – the darkest periods of the night, where the sun is 18 degrees or more below the horizon. I only used data that were collected during the new and crescent lunar phases with cloud coverage below 3 oktas (see Chapters II and III for details). I calculated an average luminance measure (cd/m^2) for each nest site.

Statistical Analysis

I ran linear regressions to examine whether our three urban characteristics co-occur. To test for effects of developed land, and noise, light on song structure, I constructed separate linear mixed models (LMM) using the following measured characteristics as response variables: PFC

min, Log PFC max, peak frequency, 90% duration, inflection rate, and syllable rate. I included developed land, NDSI value, and luminance (cd/m^2) as fixed effect in each model. We nested “Individual” within “Year” and included this as a factor with random effects to account for variable singing behavior by individual birds and differences in years. Following each model, I plotted residuals with explanatory variables to assess the fit of the model and plotted the residuals against the fitted values to determine if there was non-constant error variance. Duration, inflection rate, and syllable rate displayed deviances from normal therefore I performed log transformations on these variables and reanalyzed our models using the log transformed data. Statistical analyses were done using the lmer package (Bates et al., 2015) in R Studio (R Development Core Team, 2020).

Results

The average percent developed land was 44.2% (± 0.328), with a range from 0% to 98% across all recording locations. I found an average NDSI value of -0.06 (± 0.499) suggesting that slightly more sites had higher anthrophony in the soundscape than biophony. NDSI ranged from 0.67 (quietest sites) to 0.99 (loudest sites). Luminance ranged from $0.6 \text{ e-}4$ to 0.28 cd/m^2 with an average ground luminance at night of 0.027 (± 0.065). Overall, I found that bird song locations with more developed land were closest to nests with the most anthropogenic noise and the brightest ground luminance at night (Figure 4.3).

Songs from locations with higher developed land had significantly higher minimum frequencies ($r = 0.326$ $P = 0.024$, Table 4.2, Figure 4.3). The average minimum frequency for all song ($N = 186$) was 1959 Hz (± 126.05). Minimum frequency of songs was not predicted by the soundscape or luminance ($P = 0.941$, $P = 0.418$). The average maximum frequency (PFC maximum) was 3531 Hz (± 243.14) and was not significantly affected by our predictor variables.

Peak frequency (mean = 2851.1 ± 272.14) , 90% duration (mean = $0.22s \pm 0.15$) , and inflection rate (mean = $2.05/s \pm 0.16$) were also not significantly affected by any of our predictors. Syllable rate was significantly affected by the NDSI, but not other predictors, in that songs recorded in areas with more biophony than anthrophony had significantly more syllables per second than songs found in areas with more anthropogenic sounds (mean = $0.94 /s$; $r = 0.13$; $P = 0.020$; Table 4.2, Figure 4.3).

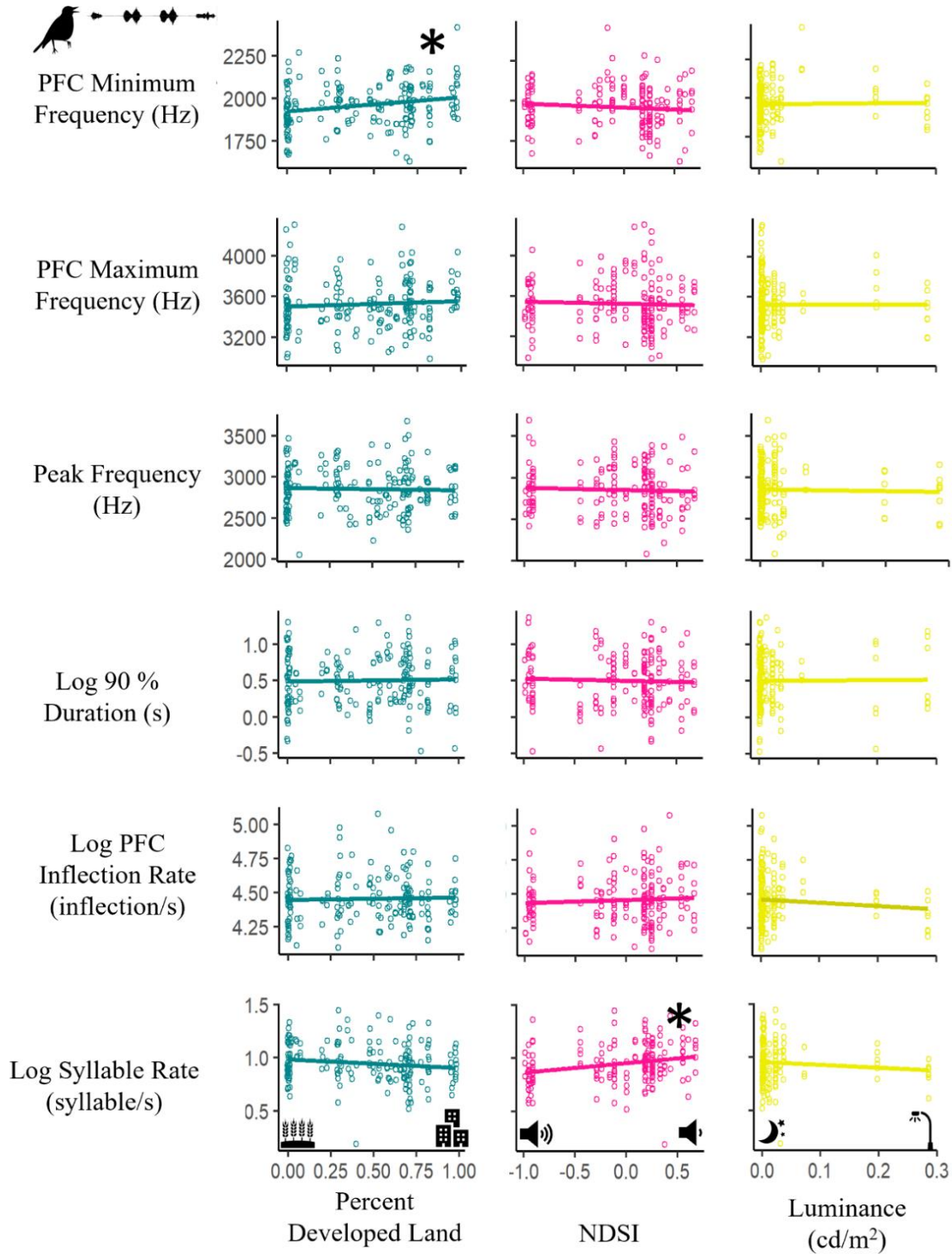
Table 4.2

*Linear Mixed Model Results for American Robin Song Characteristics. Significant Effects at the Level of $\alpha = 0.05$ are Denoted by * and are in Orange.*

	Predictors	Estimates	Confidence Intervals		p
PFC Min	Intercept	1921.52	1881.99	1961.05	<0.001
	cd/m ²	-150.16	-515.24	214.92	0.418
	NDSI	1.91	-48.59	52.41	0.941
	% Development	94.77	12.49	176.75	0.024*
PFC Max	Intercept	3512.82	3424.08	3601.57	<0.001
	cd/m ²	-146.47	963.48	670.48	0.724
	NDSI	-11.60	125.27	102.08	0.841
	% Development	41.52	143.04	226.07	0.658
Peak Frequency	Intercept	2874.10	2794.64	2953.55	<0.001
	cd/m ²	-85.21	-821.63	652.20	0.820
	NDSI	-46.30	-147.60	55.01	0.368
	% Development	-51.27	-215.76	113.21	0.539
Log 90% Duration	Intercept	0.21	0.15	0.27	<0.001
	cd/m ²	-0.04	-0.56	0.49	0.888
	NDSI	-0.02	-0.09	0.05	0.624
	% Development	0.01	-0.10	0.13	0.813
Log Inflection Rate	Intercept	4.44	4.39	4.48	<0.001
	cd/m ²	-0.34	-0.79	0.11	0.137
	NDSI	0.04	-0.02	0.10	0.229
	% Development	0.07	-0.03	0.17	0.196
Log Syllable Rate	Intercept	0.96	0.91	1.02	<0.001
	cd/m ²	-0.19	-0.71	0.33	0.477
	NDSI	0.09	0.01	0.16	0.020*
	% Development	-0.01	-0.13	0.10	0.809

Figure 4.3

*Measured song characteristics for American Robin songs (y-axes) responses to explanatory variables (x-axes). * < 0.05*



Discussion

I tested whether developed land, anthropogenic noise, and/or luminance at night influenced the song structure of American Robins. I predicted based on the literature that we would observe higher minimum frequency in songs recorded in areas with more developed land, and anthropogenic noise. I also predicted that songs in areas with more light pollution will be shorter with a higher syllable rate. I hypothesized that our three urban characteristics would closely covary across the landscape matrix and therefore I anticipated low frequencies would be seen in areas with light and developed land. Our study provides evidence that urbanization does affect song features in ways that were expected and align with much of the recent literature (Dowling et al., 2012; Seger-Fullam et al., 2012). I found that American Robins in areas of more developed land had higher minimum song frequencies than individuals in less developed areas. Furthermore, I saw a significant effect of anthropogenic noise on song syllable rate; songs in places with less anthropogenic sound had more syllables per second. This is somewhat contrary to our prediction, as I thought that light pollution may drive this. American Robin songs are typically relatively low frequency. So, I anticipated that this species would be especially affected by overlapping anthropogenic noise. Yet, I found no effect of anthropogenic noise on minimum frequency. No other song structure measurement (max freq., peak freq., duration, or inflection rate) showed a significant response to developed land, anthropogenic noise, or night brightness.

Interestingly, I found no effect of luminance at night on song structure even though American Robins have been observed to sing nocturnally and are one of the earliest species to sing during the dawn chorus (Miller, 2006). Perhaps American robins do not face tradeoffs between song timing and song form. American Robins are one of the earliest birds to sing (Howell, 1942) and one of the last to be heard singing in the dawn chorus (Wright, 1913).

Robins, therefore, have one of the longest singing periods. Additionally, evidence suggests that American Robin singing times at night are determined by the intensity of light and sunset. This, combined with the fact that American Robin eye structures are adapted for low-light (McNeil et al., 2005) should suggest that light pollution would heavily impact robin singing behaviors and daily activities. The “anti-exhaustion hypothesis (Lambrechts & Dhondt, 1988) was one hypothesis for why birds switch song types – to avoid overuse and exhaustion of motor functions. If we apply this hypothesis to American Robins who sing for longer periods in the presence of light pollution (Miller, 2006), one would hypothesize that robins might alter songs to also conserve energy and avoid motor function exhaustion. I did not find evidence of this in our study. This is an area that has not been studied to our knowledge and deserves further investigation.

Our findings of increased minimum frequencies compliments other studies done on this species (Dowling et al., 2012; Seger-Fullam et al., 2012; Senzaki et al., 2020). However, no studies to our knowledge have tested how different song variations in robins affect mate attraction, territory defense, or species identification. It is possible that individuals may simply be singing louder in urban areas resulting in higher minimum frequencies (Brumm, 2004; Cynx et al., 1998; Pick et al., 1989) but this is only conjecture. I did not measure noise in decibels for this study. It is also possible that the anthropogenic sounds were consistently louder in urban areas which would align with the correlation I found of noise to developed land but would not necessarily be represented in the NDSI index. Most people can recognize the songs of this species, but they have been known to have large repertoires sizes with a variety of song phrases (Borror, 1965; Saunders, 1964; Thomas, 1979). Additionally, American Robins can invent or improvise their song elements (Johnson, 2006). In light of this, one would expect that sexual

selection would act strongly on vocal performance in this species. In other species, research has demonstrated a trade-off between vocal performance and changes in minimum frequency and bandwidth and compromise their vocal performance in the presence of noise (Luther et al., 2016). Individuals might overcome the effects of increasing minimum frequency through increasing song performance by adding more syllables to a song. My results support this hypothesis, as we observed birds in noisier areas sang songs with a faster syllable rate.

Noise, light, and developed land are often correlated in urban habitats. In this study location, I did see a positive correlation of developed land and anthropogenic sounds but the relationship between noise and light did not necessarily align with this. We found that developed land was the strongest predictor of higher minimum frequency songs, not noise. Both noise and development present challenges for acoustic signaling; developed areas with their hard and vertical surfaces, and noise with its amplitude. Yet, few studies separate out the effects of noise and landscape in urban studies. Dowling et al. (2012) demonstrated that impervious surfaces do alter the degree at which song structure changes in the presence of noise. This study population may be experiencing this as we saw only an affect of development. However, our results are contradictory to a more recent study conducted in Southern China on Oriental Magpie-robin (*Copsychus saularis*) (Zhan et al., 2021) which found that noise, not level of urbanization, drives minimum frequency. A previous study conducted on our same population found that, while weakly associated, developed land and NDSI noise values were the most important predictors for overall nest success (see Chapter III). These two characteristics may compound on one another to drive changes in songs.

Because song is linked to reproductive success in songbirds, researchers often assume that song alternations in urban would have fitness consequences. There has been little work to

support these claims, a mixed results in whether nest success is negatively or positively affected by urban characteristics. In this study population, I did see changes in song structure associated with developed land and noise, but we did not find that sound, light, or urban land cover drove differences in nest success in American Robins (Chapter II). For the most part, American Robins were quite successful across a variety of habitat types. The results of the current study might suggest that American Robins in more developed areas successfully mitigate the effects of noise masking by altering their songs to have a successful breeding season (where individuals had at least one young fledge the nest). We did not locate every nest, so it is possible that urban birds might have reduced reproductive output if they lay fewer clutches each year. Conversely, noise, development, and changes to song form may not have as strong of an effect on reproduction as though.

American Robins are one of the most common backyard birds in North America. They are urban-positive species often found in cities and suburban locations. Populations seem to thrive in areas of urbanization but the mechanisms that allow for this success are still unknown. I demonstrated that American Robins in Weld County responded to increased noise and development by altering their songs. Few studies take the approach of measuring multiple urban features and their relative effects on animal behaviors. Here, we illustrate that different urban features affect different song features, and this may be of particular importance for studies taking place in recently urbanized areas. Future studies should be explicit in the habitat characteristics of interest when investigating urban habitats. Our study cannot resolve the argument over whether altered songs in noisy environments are adaptive or non-adaptive, but we add to the literature demonstrating that urbanization alters bird song characteristics. Most importantly, our

results raise questions about whether or not American Robins, and potentially other species suffer negative consequences from altering their songs, as many studies have assumed.

CHAPTER V

SYNTHESIS OF FINDINGS AND CONCLUSIONS

The overarching goal of this research was to measure the effects of landscape, anthropogenic noise, and light at night on birds in Weld County, Colorado. Specifically, I aimed to 1) Identify if and how landscape composition, noise, and light are associated with the Weld County avian community structure, 2) Measure reproductive output of American Robins (*Turdus migratorius*) and test for effects of developed land, noise, and light at night on breeding success, and 3) Measure American Robin song characteristics and test for effects of developed land, noise, and light on song form. I used natural experimental designs, field observations, passive acoustic and light monitoring, GIS analyses, and ornithological field approaches across a gradient of urbanization. Contrary to most of my predictions, I found that all three urban characteristics did not impact avian community structure or American Robin reproduction and song, but some did matter to different behaviors. Results from these studies indicate that landscape composition is the most important habitat feature in driving community structure, reproduction, and song structure. Anthropogenic noise and light had weak associations with avian community structure, reproduction, and song.

Much of the foundational work in modern urban ecology focused on land-use and landscape (McDonnell, 2011; Pickett & Cadenasso, 2009). There has been overwhelming evidence suggesting wildlife is negatively impacted by habitat change associated with urbanization. Recently, the area of sensory ecology has gained traction with more and more studies investigating noise and light pollution (Jokimäki et al., 2011; Madliger, 2012). Despite

this boom in urban ecological studies over the last three decades, the study of urban ecology is still in its infancy. Only recently have scientists begun to identify multiple dimensions of urban ecosystems beyond landscape composition. To create more wildlife friendly ecosystems, it is critical that scientists acknowledge the dynamics between features of these habitat and begin to incorporate these into ecological studies.

On Using a Multimodal Approach to Study Urban Wildlife

Anthropogenic noise, light at night, and developed land often co-vary with one another (Halfwerk & Slabbekoorn, 2015), but few studies have incorporated all three of these urban features into research to examine the relative or compounding effects of these characteristics (Dominoni et al., 2020; Halfwerk & Slabbekoorn, 2015). The few studies that incorporated more than one feature, have found that there may be compounding effects of all of them (Halfwerk & Jerem, 2021; Senzaki et al., 2020). Some of these compounding effects result in stronger effects on behaviors while others are antagonistic, cancelling each other out (Senzaki et al., 2020).

Animals experience the world through multiple senses and are not exposed to these features in isolation of the others. Therefore, many of the studies that have focused on one specific urban characteristic, may not be generalizable to wild populations in areas that differ in urbanness or the degree that noise light and landscape covary. As the technology grows, use of ariel imagery, satellite data, and predictive modelling has become more common for studies investigating noise, light, and landscape (Halfwerk & Jerem, 2021; Senzaki et al., 2020). These studies can detect larger patterns and trends seen often on a country-wide scale. Unfortunately, much of this data is only available at coarse resolutions (e.g. 270 km), effectively lumping many sub and micro-habitats into larger groupings. While these data provide an overall look at what is occurring nationwide, they lack the resolution to understand the scale and degree at which

urbanization becomes problematic for wildlife. Noise and light data in particular can vary wildly across an urban matrix

My doctoral research is one of the first studies to measure multiple natural characteristics within urban and rural habitats and test for effects on avian reproduction and song at a local scale. We found that the urban characteristics do not predictably covary in our study area (see Chapter II). In Chapter III, we found no effect of noise and light at night on reproductive success of American Robins. It is possible though that individuals in this species are selecting the darkest or quietest areas to nest within their local habitats. The discrepancy between our results and general hypotheses in the field could be due to scale differences across studies. Studies at broader scales may overlook the nuances of urban ecosystems, especially new and actively urbanizing ones. Even so, the results in this study provide meaningful information about this assumption often made about urban environments. More on-the-ground studies are necessary to understand if local spatial patterns extend to larger regional and national patterns.

Is Age Just a Number?

One theme that has surfaced from the work presented in this dissertation is that Weld County, may not be “urban enough” to expose trends seen in other cities. For most of Weld County’s history, agriculture dominated the landscape. Changes to the landscape for agriculture are not necessarily considered urbanization, though they are disturbance for human-use. The Greeley Metropolitan area is a relatively new urban area and only in the last two decades has the human population began to rapidly grow. Most urban ecological studies are conducted in old and established cities such as Washington D.C., New York City, Leiden, and Barcelona. These cities are drastically different from Greeley in their amount of impervious surface, noise pollution, and light pollution.

The age of a city has been identified as a key factor in urban ecosystems that affects species richness (Fernández-Juricic, 2000; Sing et al., 2016) however most studies do not incorporate this metric into their study design. More studies in young cities, such as those presented in chapters II- IV are necessary to provide a complete picture of how wildlife respond to urbanization at various stages of establishment. Currently, the metro area of Weld County, does not have a large highway running through it or any tall skyscrapers. These differences could be important in understanding differences among cities. In Weld County, developed land was the most important urban characteristics, however this may change over time as development becomes denser or as species leave urbanized areas and others move in to colonize.

Rockin' Robins - American Robins and the Importance of Studying Common Birds

Urbanization has resulted in a call to action to preserve natural ecosystems and native species. Evidence suggests that losses in diversity and abundance are mostly due to human disturbances world-wide, which has placed focus on native-species conservation. The preservation of diverse native species is critical for ecosystem functions (Sol et al., 2020), and we can certainly learn from those species that are heavily impacted by changes in their environments. However, when we focus solely on species that are at-risk or decreasing in abundance in urban areas, we lose the opportunity to learn from species that are persisting in novel ecosystems such as cities. The American Robin (*Turdus migratorius*) is an extremely common species native to North America. The research presented in this dissertation brings into focus *how* and *why* American Robins succeed in such a variety of habitats.

According to recent literature, native open-cup nesters are at most-risk of population declines in urban habitats (Senzaki et al., 2020). The American Robin seems to defy these claims, however. This species is found across many different habitats in Weld County (Chapter

II) both human-dominated and not. This is in contrast to some other urban-adapted species such as House Sparrows (*Passer domesticus*) which are dependent on human-dominated areas. In Chapter III, we demonstrated the stability of American Robin populations exposed to various degrees of noise, light and developed land across Weld County, Colorado. We found that reproductive output is minimally affected by these variables and that American Robins do well across the entire matrix of Weld County, CO. American Robins may have a high tolerance for urban disturbances that allows them to reside in a variety of habitats. Alternatively, robins may have an inherent ability to select microhabitats within cities that allow them to reproduce successfully all while exploiting urban resources such as lawns with plentiful food.

We note that Weld County is a recently and actively urbanizing area and despite the variance in noise and light seen across the county (Chapter II), this area has relatively lower anthropogenic noise and light compared to other cities. Furthermore, in Chapter IV we found that individuals singing in less developed locations sang songs with higher minimum frequencies, a common finding among urban songbirds. Thus, American Robins *are* affected by urbanization but somehow continue to thrive. Could robins be altering their amplitude in urban areas raising their frequency via the Lombard effect? If so, this plasticity may not be a behavior that affects fitness of individuals in urban areas. To address this, I suggest a study that follows individual song frequencies throughout the breeding season to assess whether frequencies change for paired and unpaired individuals and if individuals use higher frequencies during the song-learning period of their young. American Robins may not face evolutionary consequences by altering their behaviors in urban areas but more work is necessary to full understand this.

Limitations of This Work

This work was conducted in residential, urban, and rural areas inhabited by the Weld County human population. In cases, I had difficulty getting access to private properties and thus were limited to conducting research in many public areas. Residential yards essentially offer micro-habitats which individuals can exploit. Without having access to these areas, we likely missed being able to characterize the populations that reside in these residential sites.

My metrics of noise were valuable but not fully comprehensive. In 2019, I received funding to purchase AudioMoth acoustic recorders to replace the Song Meters used for the 2018 study (Chapter II). AudioMoth are great for field use because they are small, can be placed in a waterproof casing, and can be customized to collect data at intervals of your choice. Due to their size, these recorders are more discrete than Song Meters and can be placed closer to nests without disturbing birds. This recorder however is still a new product that is being updated every year. Because I switched to these recorders, I was unable to calculate noise metrics in decibels for chapters III and IV. This is due to the lack of information from AudioMoth on the specifications of the microphone, voltage, and other measures that are necessary to accurately measure decibels from sound pressure levels. Despite this, I believe the Normalized Difference Soundscape Index captures the information necessary to measure the soundscape at our study sites. While I was able to measure the soundscape that describes whether anthropogenic noise is pervasive in an area based on frequency ranges, I cannot provide specific measures of volume (amplitude).

Measuring light at night is difficult. I wanted to measure brightness at nests across the county rather than using larger satellite data to better understand how brightness within the immediate vicinity may alter reproductive success. However, I was limited in the number of Sky

Quality Meters (n=10) that I had access to throughout the breeding season. This made it difficult to collect data at every nest. Additionally, measuring light at night is restricted to specific conditions. To avoid needing to account for the effect of the moon, I restricted data collection to days that overlapped with the New Moon. This approach made it easier to attribute any light measurements to anthropogenic light at night but limited the number of nests at which we could take measurements (10 nests/ moon cycle). Therefore, we only measured light at a small portion of the nests we monitored and should consider this when interpreting results.

Finally, Weld County is rapidly growing. During our study period, several areas within our study area that rapidly went from low-human population to high-human population and development. The Town of Severance (Figure 5.1) in particular experienced massive alterations to the habitat between the beginning of this project (2018) and the final field season (2021). Because we measured local noise, and light at each nest, we can account for the changes of those factors in our study, but the Multi Resolution Land Consortium only released landscape data every few years. Because Weld County has grown so much over the past four years, there is likely some variation in the landscape that is not represented in our datasets.

Figure 5.1.

Aerial Imagery of Study Location in Severance, CO in 2018 and in 2021



Outcomes and Call for Additional Research

My research adds to the growing literature on wildlife responses to urbanization. I highlight the value of studying common species in areas that are currently undergoing urban expansion. The city of Greeley is only one example of a relatively new urban area. By 2050 it is

projected that 68% of the world will reside in urban areas. Most of this will occur in India, China, and Nigeria. This influx of people will result in even more natural habitat loss as cities continue to expand outward. Studies such as those presented in this dissertation are necessary to understand short term effects of urbanization to complement the work that has been conducted on avian communities well after urbanization. Additionally, as the urbanization continues around the world, it is likely that humans will move more and more into undeveloped lands and understanding the effects of immediate urbanization will be important for city planning and design. Chapter II's results demonstrate the importance of moving away from evaluating changes in community by only using species richness and abundance measures. These two measures tell different stories than when you look at the entire community structure of which you can identify guilds, and functional groups to understand who and what are driving species movements and colonization.

As far as we know, the studies in Chapter II and IV are the first to connect reproductive success with song alterations in urban ecosystems for a wild population at a fine scale. We learned that reproduction and song changes may not be associated as thought or that there may be a disconnect between the two at this stage of urbanization. Scale matters. Finally, we learned from these three studies combined that studying multiple characteristics of urban habitats at the local scale is important. While working with satellite data is convenient and can highlight broad patterns, it should be a compliment, not a substitute for on-the-ground studies during which scientists can identify smaller patterns, such as the use of microhabitats.

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APPENDIX A
INSTITUTIONAL ANIMAL CARE
AND USE COMMITTEE APPROVAL



IACUC Memorandum

To: Lauryn Benedict
From: Laura Martin, Director of Compliance and Operations, ARF
CC: Karina Sanchez and IACUC Files
Date: March 26, 2019
Re: IACUC Protocol 1901C-LB-Bird-22 Approval

The UNC IACUC has completed a final review of your protocol “The Effects of Anthropogenic Noise, Light, and Landscape on American Robin (*Turdus migratorius*) Song, Behavior, and Reproductive Success”. The protocol review was based on the requirements of Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training; the Public Health Policy on Humane Care and Use of Laboratory Animals; and the USDA Animal Welfare Act and Regulations. Based on the review, the IACUC has determined that all review criteria have been adequately addressed. The PI/PD is approved to perform the experiments or procedures as described in the identified protocol as submitted to the Committee. This protocol has been assigned the following number 1901C-LB-Bird-22.

The next annual review will be due before March 26, 2020.

Sincerely,

Laura Martin, Director of Compliance and Operations

A-1 Note. IACUC Approval Letter .

APPENDIX B

SPECIES NAMES AND CODES USED
IN CHAPTER I COMMUNITY ANALYSIS

A-2

Bird Species with Species Codes, Average Number of Individuals Seen During All Surveys and Total Frequency of Each Species Seen During Survey Period

Species Name	Code	Avg	Freq	Species Name	Code	Avg	Freq
American Crow (<i>Corvus brachyrhynchos</i>)	AMCR	2.30	10	Great Egret (<i>Ardea alba</i>)	GREG	1.00	1
American Goldfinch (<i>Spinus tristis</i>)	AMGO	1.71	17	House Finch (<i>Haemorhous mexicanus</i>)	HOFI	2.26	35
American Robin (<i>Turdus migratorius</i>)	AMRO	2.57	60	House Sparrow (<i>Passer domesticus</i>)	HOSP	2.11	47
American White Pelican (<i>Pelecanus erythrorhynchos</i>)	AWPE	2.25	4	House Wren (<i>Troglodytes aedon</i>)	HOWR	1.69	13
Bank Swallow (<i>Riparia riparia</i>)	BANS	1.50	2	Killdeer (<i>Charadrius vociferus</i>)	KILL	1.42	19
Barn Swallow (<i>Hirundo rustica</i>)	BARS	2.88	32	Lark Sparrow (<i>Chondestes grammacus</i>)	LASP	1.50	2
Black-billed Magpie (<i>Pica hudsonia</i>)	BBMA	1.67	3	Mallard (<i>Anas platyrhynchos</i>)	MALL	1.00	2
Black-capped Chickadee (<i>Poecile atricapillus</i>)	BCCH	1.25	4	Mourning Dove (<i>Zenaida macroura</i>)	MODO	1.32	19
Black-crowned Night-Heron (<i>Nycticorax nycticorax</i>)	BCNH	2.00	1	Northern Flicker (<i>Colaptes auratus</i>)	NOFL	1.50	6
Brown-headed Cowbird (<i>Molothrus ater</i>)	BHCO	1.67	3	Osprey (<i>Pandion haliaetus</i>)	OSPR	1.50	2
Blue Jay (<i>Cyanocitta cristata</i>)	BLJA	1.50	12	Rock Pigeon (<i>Columba livia</i>)	ROPI	1.00	1
Brewer's Sparrow (<i>Spizella breweri</i>)	BRSP	5.00	1	Red-tailed Hawk (<i>Buteo jamaicensis</i>)	RTHA	1.00	1
Brown Thrasher (<i>Toxostoma rufum</i>)	BRTH	1.00	1	Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	RWBL	3.74	23
Bullock's Oriole (<i>Icterus bullockii</i>)	BUOR	2.00	7	Say's Phoebe (<i>Sayornis saya</i>)	SAPH	1.50	4
Canada Goose (<i>Branta canadensis</i>)	CANG	4.00	1	Western Kingbird (<i>Tyrannus verticalis</i>)	WEKI	2.11	19
Chipping Sparrow (<i>Spizella passerina</i>)	CHSP	3.00	1	Western Meadowlark (<i>Sturnella neglecta</i>)	WEME	2.27	22
Common Grackle (<i>Quiscalus quiscula</i>)	COGR	6.45	56	Yellow Warbler (<i>Setophaga petechia</i>)	YEWA	1.00	5
Common Nighthawk (<i>Chordeiles minor</i>)	CONI	1.50	2	Unknown Dove	DOVSp.	1.00	6
Common Raven (<i>Corvus corax</i>)	CORA	1.67	9	Unknown Duck	DUCSp.	1.50	8
Double-crested Cormorant (<i>Nannopterum auritum</i>)	DCCO	2.08	13	Unknown Hawk	HAWSp.	1.00	2
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	EAKI	1.33	3	Unknown Sparrow	SPASp.	1.00	1
Eurasian Collared-Dove (<i>Streptopelia decaocto</i>)	ECDO	1.93	30	Unknown Swallow	SWASp.	2.75	4
European Starling (<i>Sturnus vulgaris</i>)	EUST	2.75	36	Unknown Warbler	WARSp.	1.00	1
Gadwall (<i>Mareca strepera</i>)	GADW	4.00	1	Unknown	UNK	3.67	3
Great Blue Heron (<i>Ardea herodias</i>)	GBHE	1.75	8				