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A Comparison of the Singing Activity of Carolina Wrens (*Thryothorus Ludovicianus*) in Urban and Rural Settings

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A COMPARISON OF THE SINGING ACTIVITY OF CAROLINA WRENS 
(*THRYOTHORUS LUDOVICIANUS*) IN URBAN AND RURAL SETTINGS

A Thesis
Presented to
The Faculty of the Department of Biology
Western Kentucky University
Bowling Green, KY

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

By
Shannon R. Trimboli
May 2010
A COMPARISON OF THE SINGING ACTIVITY OF CAROLINA WRENS
(*THRYOTHORUS LUDOVICIANUS*) IN URBAN AND RURAL SETTINGS

Date Recommended 22 April 2010

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Acknowledgements

This research could not have been completed without the assistance and support of many people. First, I would like to thank my advisor and committee members, Drs. Albert J. Meier, Blaine Ferrell, and Ouida Meier, for their help and guidance throughout this process. Each of them provided important input, suggestions, and encouragement on my research. Mr. Wayne Mason was always happy to see me and to share his vast knowledge of birds. I appreciate his kindness and knowledge. Dr. Bruce Kessler was invaluable in analyzing the preliminary time related data associated with this project; I am grateful for his time and expertise.

I am also grateful to Drs. Albert Meier, José Pedro do Amaral, and Rafael Márquez for sharing their amphibian monitoring dataset with me. The Bowling Green City Parks system and the Upper Green River Biological Preserve were kind enough to allow the data loggers to be placed on their property as part of the amphibian monitoring study. The Kentucky Heritage Land Conservation Fund Board and the Ministerio de Ciencia e Innovación CGL2008-04814-C02-02, Spain provided important funding to support the original study.

In addition to the people mentioned above, I am grateful to my fellow graduate students. I knew I could always count on someone to be there to share my successes and my frustrations. Your friendship and support made my years as a graduate student much more fun and enjoyable. I am also very appreciative of the support and encouragement that my supervisors and co-workers at Mammoth Cave National Park provided me. You understood when I needed to take time off to work on my thesis or coursework and gave me the freedom I needed in order to complete my degree. I also thank you for allowing
me to include the Carolina wren data collected as part of Mammoth Cave National Park’s MAPS station from 2007-2009.

Above all, I am eternally grateful to my family. My parents helped instill a love of nature and science in me at a very young age. They always encouraged my curiosity and tolerated my continuous questions of “Why?” I love the fact that the tables have turned and now it is my turn to answer their questions about the different plants and animals they encounter. I thank you for all the encouragement, support, and love that you have given and continue to give me. Most of all, I am thankful to Anthony – my husband, best friend, and often field assistant. You have been there for me through the good times and the bad. Your encouragement and support carried me through when I did not think I had the strength left to continue. Thank you.
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A COMPARISON OF THE SINGING ACTIVITY OF CAROLINA WRENS
(THRYOTHORUS LUDOVICIANDUS) IN URBAN AND RURAL SETTINGS

Shannon R. Trimboli May 2010 98 pages

Directed by: Albert J. Meier, Blaine Ferrell, and Ouida Meier

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As the earth’s landscape becomes increasingly urbanized, local wildlife must adapt to urban conditions or migrate to areas that are more rural. Urban wildlife face challenges such as direct loss of habitat, competition with non-native species, disturbance due to anthropogenic noise, and micro-climatic changes. Factors such as temperature, relative humidity, and noise affect the acoustical environment and may affect the ability of many animals, including birds, to communicate.

Understanding how urbanization affects birds’ singing behavior is critical because singing often plays a vital role in attracting mates and defending territories. In addition, as global climate change occurs it will become increasingly important to understand the influence of abiotic factors such as temperature on the singing behavior of birds. Developing a deeper understanding of how those abiotic factors affect singing and other associated behaviors may help guide future conservation actions.

Carolina Wrens are often used to study the role of singing in defending territories. They are also a common subject for ranging studies. However, surprisingly little research has been conducted on the factors influencing Carolina Wren song activity over the course of a day. No studies have compared the singing activity of Carolina Wrens in urban and rural environments. The purpose of this study was to compare the singing activity of Carolina Wrens in urban and rural areas. Specifically, this study looked for
patterns in the timing of songs throughout the day and examined the effects of season, temperature, and anthropogenic noise on singing activity in urban and rural settings.

I analyzed data from 4 SongMeter\textsuperscript{©} SM2 data loggers (2 located at an urban park in Bowling Green, KY and 2 located at a rural preserve in Hart County, KY). The data loggers were programmed to record ambient sound for 3 minutes at the beginning of every hour. A Hobo\textsuperscript{®} data logger was deployed with each SongMeter\textsuperscript{©} SM2 data logger to record temperature and relative humidity at 15-minute intervals. One week of data in May and one week of data in July were analyzed. Both weeks had similar photoperiods, temperatures, and amounts of precipitation. For each recording, I documented the number of Carolina Wren songs I heard and a categorical assessment of the precipitation and anthropogenic noise due to traffic or machinery.

I conducted Chi-square analyses to compare the seasonal or site-based observed frequencies of singing activity to the corresponding expected frequencies. In May, Carolina Wrens at the urban site sang more than their rural counterparts. Daily activity patterns were visually analyzed using the average number of songs detected for each hour’s sampling period. No Carolina Wrens were heard singing the hour before sunrise or the hour after sunset. In May, the dawn chorus lasted nearly twice as long as in July. Zero-inflated Poisson regressions were used to determine the correlations between Carolina Wren singing activity and temperature or anthropogenic noise. Carolina Wren singing activity had significant correlations with both variables.
Introduction

Influences of Urbanization on Wildlife

Across the world, urban areas are rapidly increasing in size and population. As urban areas grow, wilderness and agriculture lands are converted to urban or suburban uses. In their report, *State of World Population 2007: Unleashing the Potential of Urban Growth* (Martine 2007), the United Nations Population Fund predicted that by 2008 more than half of the world’s population would live in urban environments. They predicted that this number will grow rapidly over the next 2 decades and that by 2030 over 80% of our population will be urban. The United Nations Population Fund (Martine 2007) expects much of this growth to come from the expansion of smaller cities and towns. If realized, these predictions will have tremendous consequences for humans and the plants and wildlife with which we share this planet.

Habitat fragmentation is a major concern with increasing urbanization. Scientists view it as one of the major threats to many ecosystems (e.g., southern California’s Mediterranean scrub habitat: Crooks et al. 2004; Florida’s scrub habitats: Duncan and Schmalzer 2004; southeastern U.S. riparian forests: Burton et al. 2005). Habitat fragmentation due to urbanization can simplify the vegetative structure, reduce biodiversity, allow predators and parasites increased access to breeding sites, or disrupt local ecological processes. For example, fire is an integral part of the ponderosa pine forest ecosystem. However, as suburban and urban areas encroach upon ponderosa pine forests, fire is suppressed in an effort to protect buildings and other human belongings (Marzluff 1997). Forested or planted urban parks also typically lack features such as
standing dead snags (Marzluff 1997) that are necessary for many insectivorous birds and mammals. In Mexico City, only the largest and most vegetated parks support a high diversity of insectivorous bats (Avila-Flores and Fenton 2002). Pets, feral animals, and vehicles take additional tolls on urban wildlife (reviewed in Ditchkoff et al. 2006). Habitat fragmentation also allows native predators increased access to prey.

Ecologists have traditionally looked at urban areas primarily in conjunction with habitat degradation, habitat loss, and related issues. While those issues are important, an increasing number of ecologists are beginning to study urban wildlife and the ecosystems located within urban areas. This has led to the development of new fields such as urban ecology and terms such as synurbanization. Urban ecology is the study of urban environments as functioning ecosystems. Synurbanization refers to the acclimation and adaptation of wildlife living in urban environments (reviewed in Luniak 2004). As scientists pay more attention to urban areas, they have discovered that “green” areas and “wild” places in urban environments are often very different from their counterparts in rural environments. For example, Faeth et al. (2005) found that in the desert southwestern United States, urban parks that looked structurally similar to rural areas often had very different trophic systems. They attributed these differences to the greater availability of limiting resources such as water and nutrients in the urban areas compared to the rural deserts.

Food is often a limiting factor even in more mesic environments than the desert southwest. In urban areas, along roads, and in other areas heavily used by people, anthropogenic food sources can increase the available food supply to a point where it is no longer a limiting factor. One major anthropogenic food source involves the direct
feeding of wildlife. In 2006, 48 million people in the United States identified themselves as birdwatchers and 32% of those people lived in cities with populations of at least 250,000 (Carver 2009). Given the large number of backyard birdwatchers (approximately 42 million, Carver 2009), birdfeeders have the potential to provide a large source of anthropogenic food. In addition, people often intentionally feed other wildlife such as squirrels, raccoons, and deer. Landfills and road kills indirectly provide additional sources of anthropogenic food, which can inflate predator populations. For example, common ravens (*Corvus corax*), an egg predator, use supplemental food from landfills and road kills to encroach into areas of the Mojave desert where they are otherwise unable to survive (Kristan et al. 2004). Although plentiful, many anthropogenic food sources may be lower in energy than natural food sources (Fleischer et al. 2003). Anthropogenic food sources may also result in higher blood cholesterol levels in some species (Gavett and Wakeley 1986).

Regardless of the energy content of the anthropogenic food, the availability of the increased food supplies often leads to life history changes among urban animals. One common life history change is a decrease in home range and territory sizes for urban and suburban animals (e.g., American Crows, *Corvus brachyrhynchos*: Marzluff et al. 2001; Florida Scrub-jays, *Aphelocoma coerulescens*: Fleischer et al. 2003; Northern Goshawks, *Accipiter gentalis*: Rutz 2006; raccoons, *Procyon lotor*: Bozek et al. 2007). This decrease in home range size can lead to increased population densities and a corresponding greater potential for the transfer of diseases between individuals. Food obtained in urban environments can also contain contaminants such as PCBs (Dip et al. 2003), lead (Chandler et al. 2004), and mercury (Hallinger et al. 2010). In some cases, these
contaminants can lead to behavioral changes. For example, Carolina Wrens (Thryothorus ludovicianus) and House Wrens (Troglodytes aedon) with territories on sites containing high levels of mercury sing shorter songs at lower frequencies (Hallinger et al. 2010).

Researchers have repeatedly shown that compared to rural areas, urban and suburban areas typically have increased abundance of a few species, but decreased species richness (e.g., Avila-Flores and Fenton 2002, Fernández-Juricic 2002, Blair 2004, Crooks et al. 2004, Faeth et al. 2005, Burhans and Thompson 2006, Slabbekoorn and Ripmeester 2008). This pattern holds for a variety of taxa. The effects of urbanization on avian and mammalian species are well-studied areas of urban ecology that continue to grow. However, not all taxa, arthropods being one example, have received as much scientific attention (McIntyre 2000). Additional research on these under-represented taxa is still needed.

Often, exotic species of plants and animals will replace native species in urban and suburban areas (Blair 2004, Crooks et al. 2004, Faeth et al. 2005). Many of these species can be found in urban areas that are widely distributed geographically. Blair (2004) found that although her rural California and Ohio study sites shared only 5% of their bird species, 20% of the bird species found in her urban California and Ohio sites were the same. Other researchers have also found that urban areas worldwide tend to share a few common species that thrive in the urban ecosystem, regardless of the geographic location of the ecosystem. This phenomenon has been termed “biotic homogenization” (reviewed by Crooks et al. 2004).

Those species that do survive and thrive in urban areas often exhibit shifts in their daily or seasonal activity patterns. Nutria (Myocastor coypus), a normally nocturnal
South American rodent, will switch to a diurnal pattern of activity in the presence of anthropogenic food sources (Meyer et al. 2005). Several species of birds begin singing earlier in the morning in urban areas compared to rural areas (e.g., European Blackbirds, *Turdus merula*: Nemeth and Brumm 2009). Other birds, like the American Robin (*Turdus migratorius*: Miller 2006) and the European Robin (*Erithacus rubecula*: Fuller et al. 2007) will sing during the night, even though these species are typically diurnal. This behavior has been attributed to light (Miller 2006) and noise (Fuller et al. 2007) pollution in urban environments.

Urban environments also influence seasonal activity patterns such as breeding and migration. Scientists recently discovered that urban birds do not always migrate like their rural counterparts. Partecke and Gwinner (2007) captured newly hatched European Blackbirds from neighboring urban and rural environments. They raised the two groups of birds in identical conditions and monitored their migratory behavior. During the first fall, the male birds hatched in urban environments displayed less migratory behavior than the male birds hatched in the rural environments (Partecke and Gwinner 2007). The next spring those same male urban-hatched birds developed their gonads earlier than their rural-hatched counterparts. Female migratory behavior was the same for both urban and rural-hatched birds (Partecke and Gwinner 2007). The researchers speculated that the sex-specific response was likely due to the ability of male blackbirds to dominate and exclude female blackbirds from the anthropogenic food sources necessary for over-winter survival (Partecke and Gwinner 2007).

Numerous studies have shown that urban birds will often begin breeding before their rural counterparts (e.g., Rollinson and Jones 2002, Fleischer et al. 2003, Burhans
and Thompson 2006, Partecke and Gwinner 2007, Shustack 2008). However, not all species respond the same way. While resident Northern Cardinals (*Cardinalis cardinalis*) on Shustack’s (2008) urban study sites began laying eggs earlier than rural populations, migratory Acadian Flycatchers (*Empidonax virescens*) on his urban study sites initiated nests later than on his rural sites. Shustack (2008) found that temperature in March was the best predictor for clutch initiation in resident Northern Cardinals. It has long been known that many urban areas serve as “heat sinks” and Shustack (2008) found an overall pattern for his urban sites to be warmer than his rural sites. Other researchers have found that increased food supplies from anthropogenic sources are correlated to earlier reproductive activities in many species of birds (Rollinson and Jones 2002, Fleischer et al. 2003, Burhans and Thompson 2006, Shustack 2008).

Starting to breed earlier in the season may result in increased reproductive success; however, that is not always the case. Shustack (2008) found that the Northern Cardinals at his urban sites raised the same number of young as the Northern Cardinals at his rural sites. Blair (2004) found similar results for both Northern Cardinals and American Robins. Increased predation is often suggested as a reason for the lack of increased nest success in urban birds. Recent studies, however, do not always support this suggestion (Rollinson and Jones 2002, Blair 2004, Burhans and Thompson 2006). In fact, Blair (2004) found lower nest predation as urbanization increased along her transects. Cowbird parasitism, on the other hand, appears to increase with increased urbanization (Burhans and Thompson 2006).

Disturbance due to traffic or pedestrians has also been suggested as a possible cause for nest failures in urban birds. In areas with heavy traffic, Willow Warblers
(Phylloscopus trochilus) have lower densities near roads, lower quantities of males near roads, and the males hatched near roads disperse further from their natal site than males hatched further away from the roads (Reijnen and Foppen 1994a, 1994b). The researchers suggested that noise due to traffic likely caused the differences in behavior and nesting success of the birds living at different distances from the roads (Reijnen and Foppen 1994a, 1994b, Reijnen et al. 1996). In contrast, Francis et al. (2009) found increased nest success at their noisier sites. They attributed this finding to decreased predation rates due to scrub-jays avoiding the nosier sites (Francis et al. 2009). Also contradicting studies showing lower nest success in disturbed areas, Smith-Castro (2008) found no difference in the nesting success of Northern Cardinals nesting close to a pedestrian trail in an urban park compared to Northern Cardinals nesting further from the trail. However, Smith-Castro’s (2008) study focused on disturbance due to pedestrian presence and did not look at noise as a possible factor influencing nest success.

Roads can affect, not just reproductive success, but also variables such as species richness, density, and mortality. Disturbance due to both traffic and pedestrian use of an area can also affect the number and types of bird species found in an urban area (Fernández-Juricic 2000, Forman et al. 2002). Grassland birds are present more often in habitat patches that are further from roads used by at least 15,000 vehicles per day than in habitat patches that are closer to equally busy roads (Forman et al. 2002). At distances of 700m or less, grassland birds are practically non-existent near roads travelled by at least 30,000 vehicles per day (Forman et al. 2002). The traffic impacts on grassland bird diversity extend approximately 700m from the road for moderately used roads (15,000 vehicles/day) and approximately 1,200m for heavily used roads (30,000 vehicles/day).
Negative impacts on the breeding activity of grassland birds were observed at even lower levels of traffic (>8,000 vehicles/day) (Forman et al. 2002). Once again, noise was suggested as the most likely cause for the observed results.

Anthropogenic noise caused by traffic, machinery, trains, airplanes, and other human activities is increasingly recognized as a concern for both humans and wildlife. Barber et al. (in press) report that compared to natural levels of low frequency sounds over 83% of the continental United States experiences an increase in low frequency noises due to traffic alone. Many animals use songs, calls, or other acoustical methods to attract mates, maintain territories, communicate with other members of the animals’ social group (i.e. pack, nestmates, pod, etc.), hunt, or avoid predators. The acoustical communications of many wildlife species overlap with the low frequency bandwidths that are predominant in anthropogenic noise. In the past few decades, an increasing number of researchers have begun studying the effects of anthropogenic noise on wildlife, especially in urban areas (e.g., Brumm 2004, Fernández-Juricic et al. 2005, Slabbekoorn and den Boer-Visser 2006, Wood and Yezerinac 2006, Bee and Swanson 2007, Fuller et al. 2007, Swaddle and Page 2007, Leonard and Horn 2008, Parris and Schneider 2008, Francis et al. 2009, Nemeth and Brumm 2009, also reviewed in Brumm and Slabberkoorn 2005, Ditchkoff et al. 2006, Patricelli and Blickley 2006, Warren et al. 2006, Slabbekoorn and Ripmeester 2008). Due partially to the intense human interest in birds and their songs, the ability to find birds in a variety of urban and rural habitats, and the relative ease of studying birds, much of that research has focused on birds.
**Avian Communication**

In order to understand how urbanization and noise affect avian communication, it is necessary to review the literature on bird songs in general. Birds primarily use songs, calls, and other vocal methods to communicate. These communication methods play a vital role in important life history activities such as attracting mates, defending territories, and begging for food by nestlings. While begging sounds and call notes play important communication roles, much of the research on avian communication has focused on bird songs. Singing, although widely used, is a relatively costly activity from a metabolic standpoint (Eberhardt 1994, but see Oberweger and Goller 2001). Much research has gone into studying the dawn chorus, environmental factors (temperature, light, noise, etc.) that influence singing activity, and seasonal fluctuations in singing activity. However, relatively little research has focused on the singing activity patterns over the course of an entire day (Amrhein et al. 2004, Kloubec and Capek 2005).

The dawn chorus is probably the best known and most often studied phenomenon related to bird song. Scientists have long recognized that many species of birds have a daily peak in singing activity that begins shortly before sunrise and lasts for a few hours after sunrise. A smaller peak in singing activity often occurs shortly before dusk. Although, not all birds follow this pattern, it is the most common pattern of singing activity (Stacier et al. 1996). Several hypotheses exist for why birds sing most at dawn. The hypotheses can be grouped into three categories focusing on physiological mechanisms, social functions, and environmental controls (Dabelsteen and Mathevon 2002, Kloubec and Capek 2005). Although these hypotheses were proposed to explain the dawn chorus, many of them can be loosely used to explain singing activity at any
time of day. In fact, Kacelnik and Krebs (1982) concluded that the dawn chorus should be analyzed in relation to other activities throughout the day.

Physiological changes are an important proximate cause of singing. Like all organisms, birds have strong circadian and circannual cycles. In birds, the pineal gland, eyes, and hypothalamic pacemaker serve important roles in maintaining circadian and circannual rhythms (reviewed in Dawson et al. 2001). The location of the hypothalamic pacemaker is currently unknown; however, the medial suprachiasmatic nucleus (mSCN) and the visualSCN appear promising (reviewed in Dawson et al. 2001). Photoperiod is an important zeitgeber for avian circadian and circannual cycles. As day length increases, the release of gonadotropin-releasing hormone (GnRH) by the hypothalamus-pituitary-gonadal axis (HPG) is stimulated resulting in gonad growth and maturation (reviewed in Meier and MacGregor 1972 and Dawson et al. 2001). Interestingly, the retina (eye) and the pineal gland do not appear to be required for photoperiodic control of avian reproductive activities (reviewed in Dawson et al. 2001).

Photoperiod plays a dual role in promoting singing activity. Singing often occurs primarily during the breeding season, and breeding birds have enlarged song control nuclei (Smith et al. 1997, Bentley 1999, Tramontin et al. 1999, Tramontin et al. 2000, Soma et al. 2004, Caro et al. 2005). Plasma testosterone levels are often correlated with growth of the song control nuclei (reviewed in Dawson et al. 2001) and injections or implants of testosterone have long been used to stimulate singing in lab experiments (e.g., Kern and King 1972, Hunt et al. 1997, Sartor et al. 2005). Photoperiod indirectly effects the growth of the song control nuclei through its role in stimulating gonad maturation and thus the production of testosterone. Periods of long photoperiods will also result in
photorefractoriness and gonadal recrudescence causing a decline in the production of testosterone (reviewed in Dawson et al. 2001). In addition, photoperiod has direct effects on the growth of the song control nuclei that are independent of its role in the production of testosterone (Gulledge and Deviche 1998, Caro et al. 2005). In a laboratory experiment, Gulledge and Deviche (1998) found that photoperiod increased song control nuclei volume in adolescent male Dark-eyed Juncos (Junco hyemalis) more than testosterone implants did. Field studies with Corsican Blue Tits (Parus caeruleus) also indicate that the song control nuclei begins increasing up to a month before testosterone levels increase (Caro et al. 2005). Although Caro et al. (2005) suggested that unidentified factors were stimulating, or at least modifying, the growth rate of the song control nuclei, they could not rule out photoperiod as the primary causal factor.

Photoperiod and testosterone are the primary controllers of song control nuclei growth. However, recent research shows that other hormones and testosterone metabolites can have secondary or “fine tuning” effects on various regions of the song control nuclei growth (melatonin: Bentley et al. 1999; dehydroepiandrosterone: Soma and Wingfield 2001, Soma et al. 2002; Aromatase and other neural steroids: Soma et al. 2003; androgen and estrogen: Tramontin et al. 2003; estrogen: Soma et al. 2004). Social interactions can also have “fine tuning” influences on the growth of song control nuclei. Male White-crowned Sparrows (Zonotrichia leucophrys gambelii) housed with females experienced increased growth in the volume of their song control nuclei, but did not experience an increase in plasma androgen levels compared to controls housed with other males (Tramontin et al. 1999). The method for this social stimulation of the song control nuclei is unknown, but appears to be non-auditory. In a separate study, deafened
Gambel’s White-crowned Sparrows experienced the same song control nuclei growth as non-deafened individuals (Brenowitz et al. 2007).

Most research on the physiological changes associated with avian singing behavior focuses on seasonal changes such as an increase in singing at the beginning of the breeding season or a decrease in singing later in the breeding season. I found no studies that monitored changes in hormonal levels or other physiological responses over the course of a day in relation to singing behavior.

The social function of singing can be divided into two sub-categories, intersexual communication (mate attraction, soliciting copulations, maintaining pair bonds, etc.) and intrasexual communication (territory defense). When mate attraction is the primary role for singing, unmated males perform much of the singing. In many species, more males sing earlier in the breeding season compared to later. As more females arrive on the breeding grounds and form pair bonds, the number of singing males decreases (e.g., Sedge Warblers, *Acrocephalus schoenobaenus*: Catchpole 1973; Ovenbirds, *Seiurus aurocapillus*: Lein 1981; Savi’s Warblers, *Locustella luscinioides*: Kloubec and Capek 2005). Reed Warblers (*Acrocephalus scirpaceus*) exhibit a similar seasonal change in singing activity; however, their pattern is not as pronounced because singing also plays a role in territory defense for this species (Catchpole 1973).

Daily singing activity patterns also often vary throughout the breeding period (Amrhein et al. 2004). Kloubec and Capek (2005) reported that at the beginning of the breeding season Savi’s Warblers sang continuously throughout a 24-hour period with distinct dawn and dusk peaks in number of singing males. However, as the season progressed nocturnal singing stopped and the number of singing males decreased until
most of the singing was heard only during the dawn and dusk peaks (Kloubec and Capek 2005). Earlier in the breeding season, the dawn and dusk choruses for Reed Warblers (Catchpole 1973), Ovenbirds (Lein 1981), and Nightingales (Luscinia megarrhynchos: Amrhein et al. 2004) are also longer and periodic singing throughout the day is more common. Singing early in the breeding season has been hypothesized to mainly function in mate attraction and social pair bonding. Mated European Starlings (Sturnus vulgaris: Pinxten and Eens 1998) and Nightingales (Amrhein et al. 2004) have additional seasonal peaks in daily singing activity that occur at approximately the time of egg-laying during their mate’s fertile period. Singing around the time of egg-laying is hypothesized to serve in soliciting within pair and extra pair copulations (Pinxten and Eens 1998, Amrhein et al. 2004).

The intrasexual function of singing is most often territory defense. Many species of birds use singing to announce and defend their territories. Often these territories are short-term territories that last only as long as the breeding season. Other species defend territories year-round or have separate summer and winter territories. The Reed Warbler is one example of a migratory bird that uses song to defend its breeding territory as well as for mate attraction. Paired male Reed Warblers sing sporadically throughout the day during the breeding season, especially when they are challenged by another male (Catchpole 1973).

Determining the function of singing in species like the Reed Warbler can be difficult because it often plays two roles – mate attraction and territory defense. By studying territorial responses during the non-breeding period, scientists can remove the confounding factors associated with mate attraction and copulation solicitation that may
occur during the breeding season. Male Winter Wrens (*Troglodytes troglodytes*) defend separate winter and summer territories. Even during the winter, they have a distinct dawn chorus. Amrhein and Erne (2006) found that predawn intrusions influence singing rates of wintering male Winter Wrens as much as 24 hours later. When they presented the Winter Wrens with a simulated intrusion shortly before dawn, the wrens significantly increased their predawn singing rates the next day (Amrhein and Erne 2006).

Birds that are year-round territorial and year-round pair-bonded also provide important insights into the use of singing to defend their territories. Since pair bonds are maintained year-round, singing is usually thought to serve more of a territorial function than a mate attraction function (e.g., Carolina Wren: Morton and Shalter 1977, Simpson 1985). A detailed discussion of Carolina Wrens and their singing behavior is provided in the following section. The Rufous-and-white Wren (*Thryothorus rufalbus*) is another species that maintains year-round pair bonds and territories. Unlike the Carolina Wren, both male and female Rufous-and-white Wrens sing. Pairs of Rufous-and-white Wrens often participate in duets. In this species, singing and duetting appears to play two distinct roles (Topp and Mennill 2008). Prior to and early in the breeding season, duets and songs appear to play primarily a territorial defense role; however, later in the breeding season these same actions appear to play more of a mate-guarding role (Topp and Mennill 2008). As with the Reed Warblers, determining the exact function of singing in this species can be difficult because it serves multiple purposes at different times of the day or year.

Some researchers have suggested that the dawn chorus in some species is a result of higher numbers of territorial invasions early in the morning compared to other times of day (Kacelnik and Krebs 1982, Staicer et al. 1996). Habitat quality can also influence
territorial response rates. Kacelnik and Krebs (1982) found that Great Tits (*Parus major*) in a lab setting respond more strongly to intrusions when the foraging quality is low. In addition, high population densities may affect singing rates because higher population densities increase territorial encounters. The possible effects of higher densities become especially important to studies in urban areas where population densities are often higher than in rural areas (Nemeth and Brumm 2009).

The environmental controls that influence singing behavior include temperature, relative humidity, precipitation, and light. Because of the pronounced dawn and dusk peaks in singing for many species, light intensity is often hypothesized to play a significant role in controlling song activity (e.g., Leopold and Eynon 1961, Catchpole 1973, Lein 1981, Kloubec and Capek 2005). Precipitation will also affect the daily singing activity of birds. Although heavy rains will keep most birds from singing, many species will continue to sing during light rains especially relatively early in the breeding season (Lein 1981). Temperature will also influence singing behavior. Ovenbirds will not sing during the breeding season in extremely hot or cold temperatures (Lein 1981). Not taking into account extremes in temperature, singing appears to be positively correlated with temperature in many species (e.g., Northern Mockingbirds, *Mimus polyglottos*: Shaver and Walker 1930; Winter Wrens and Great Tits: Garson and Hunter 1979; European Robins, *Erithacus rubecula*: Thomas 1999). However, Catchpole (1973) found that the effects of temperature, relative humidity, and precipitation were secondary to changes in light intensity. Other researchers have found no significant correlation between weather variables and amount of singing (Berg et al. 2005).
Although singing is important for attracting mates and defending territories, birds must participate in numerous other activities each day in order to survive and reproduce. Of those other activities, foraging is arguably the most important. Many species sing more when food availability is higher (e.g., Carolina Wrens: Strain and Mumme 1988; blackbirds: Cuthill and Macdonald 1990; European Robins: Thomas 1999; Australian Reed Warbler, *Acrocephalus australis*: Berg et al. 2005). Several hypotheses and models have been proposed to explain this phenomenon and especially how it relates to the dawn chorus. In diurnal birds, energy reserves are often at their lowest at dawn since the birds have fasted for the overnight hours (Murphy et al. 2008). Singing at dawn, therefore, could be a signal of mate quality (Cuthill and Macdonald 1990, Murphy et al. 2008). In Eastern Kingbirds (*Tyrannus tyrannus*), the largest males begin singing earlier, have higher peak song rates, and have longer song bouts (Murphy et al. 2008). Afternoon foraging success also affects when individual blackbirds join the next dawn chorus (Cuthill and Macdonald 1990).

Other hypotheses focus on the trade-offs of conducting various activities at different times of day. For example, low light levels and cooler temperatures may decrease foraging success at dawn, thus making singing the more energetically efficient activity (Garson and Hunter 1979, Kacelnik and Krebs 1982, McNamara et al. 1987, Hutchinson et al. 1993, Berg et al. 2005). In their discussion Kacelnik and Krebs (1982), compared their observations with reported field studies of arctic birds that are not constrained by the light-dark cycle in the same way as temperate species. Kacelnik and Krebs (1982) concluded that birds sing during the time periods of lowest food availability while they are actively maintaining territories. In species where song is primarily used for
attracting mates, the availability of unpaired females and their willingness to form pair bonds may also affect the timing of activities such as singing and foraging (Kacelnik and Krebs 1982, McNamara et al. 1987, Cuthill and Macdonald 1990, Hutchinson et al. 1993).

It can be somewhat difficult to tease apart exactly what environmental factors are influencing singing. For example, temperature and relative humidity are highly correlated and changes in those factors often correspond with changes in light intensity at dawn and dusk. Also, as previously discussed, singing is only one of many activities that birds participate in during the day. Thus, time devoted to singing is influenced by other activities that are necessary for survival. Regardless of the specific factors that influence singing, the ability to accurately communicate information is the important thing from the bird’s perspective. This has led scientists to study what conditions allow for the most accurate transmission of signals (information).

Water vapor, physical structures (vegetation, the ground, buildings, etc.), wind, or other background noises absorb and degrade soundwaves. This results in a loss of information. Wiley and Richards (1978) provide an in depth review of the types of attenuation and degradation that occur in different habitats and environmental conditions. Often the environmental conditions that affect sound transmission vary throughout the day with atmospheric turbulence being lowest in the early morning (Wiley and Richards 1978). However, Dabelsteen and Mathevon (2002) found that excess attenuation decreased throughout the day.

The physical properties associated with different habitats can have evolutionary impacts on the types of sounds produced by different species of birds (Morton 1975).
Forest, grassland, and edge habitats each have specific frequency ranges and song types that are best adapted for long-range propagation in the given habitat type (Morton 1975). The physical properties of urban environments differ greatly from rural environments and can affect the propagation of bird songs in very different ways than the environments in which the species evolved (Slabbekoorn et al. 2007). However, in natural environments Marten and Marler (1977) found that the height of the singer and the frequency of the song were more important than habitat type for determining how far sound travelled. Either the singer or the listener can increase the distance of sound transmission by increasing their height up to approximately 2m above the ground (Marten and Marler 1977, Wiley and Richards 1978).

Given the relatively close proximity of individual territories, it is likely that evolutionary factors other than simply distance of sound propagation affect the timing of bird songs (Wiley and Richards 1978, Nemeth and Brumm 2009). Brown and Handford (2003) showed that although the average quality of Swamp Sparrow (*Melospiza georgiana*) and White-throated Sparrow (*Zonotrichia albicollis*) songs did not change throughout the day, the consistency of their song quality was significantly better at dawn than later in the day. Songs or song features that degrade at a predictable rate can also be used to judge the distance of the singer or communicate other important information (Wiley and Richards 1978). The Carolina Wren is one example of a bird that uses song degradation for determining the distance of its rivals (Morton et al. 1986, Naguib 1995). Using predictable levels of song degradation to determine the distance of the singer can be complicated by the fact that sounds degrade at different rates in different vegetation
densities (Naguib 1995, 1996). However, Carolina Wrens are able to compensate for differences in the vegetation density due to seasonal changes (Naguib 1995, 1996).

Background noise inhibits the transmission of information through songs resulting in important consequences for attracting mates, defending territories, avoiding predators, and detecting prey (Brumm 2004, Brumm and Slabberkoorn 2005, Slabbekoorn and Ripmeester 2008). The background noise can come from natural sources (other birds singing, insect and anuran calls, waterfalls,) or anthropogenic sources (traffic, machinery, trains, airplanes). As urbanization and anthropogenic noises increase, a growing number of ornithologists are studying the impacts of anthropogenic noise on avian singing behavior. In many cases, birds have developed short-term or long-term methods for dealing with anthropogenic noise (reviewed in Brumm and Slabberkoorn 2005, Warren et al. 2006). Common methods include avoiding areas / times of days with high levels of anthropogenic noise, increasing the volume of songs, singing shorter songs, and shifting the frequency of the notes within their songs. However, each of these methods for overcoming the difficulties associated with communicating through anthropogenic noise has potential energetic and reproductive costs (reviewed in Patricelli and Blickley 2006, Warren et al. 2006).

Many species have a peak in singing activity around dawn or the early morning hours (Leopold and Eynon 1961, Catchpole 1973, Lein 1981, Kacelnik and Krebs 1982, Stacier et al. 1996, Brown & Handford 2003, Amrhein et al. 2004, Kloubec and Capek 2005, Amrhein and Erne 2006, Murphy et al. 2008). The background noise created by so many birds singing at once apparently does not limit a bird’s ability to communicate. Several studies have shown that birds are able to recognize and identify conspecific songs
when other species are singing at the same time (reviewed in Brumm and Slabberkoorn 2005). In many urban areas, rush hour corresponds with the dawn chorus and can reduce the effectiveness of songs at that time of day (Warren et al. 2006, Slabbekoorn and Ripmeester 2008). Some species of urban birds will shift their singing activity to less noisy times of the day, even if that means singing at night. In a field experiment studying nocturnal singing of European Robins, Fuller et al. (2007) found that nocturnal singing was more closely correlated with daytime noise than with nighttime light pollution in a multiple logistic regression. They also reported a lack of nocturnal singing at sites that were relatively quiet during the day, but well lit at night (Fuller et al. 2007). In an observational study on the pitch and speed of urban blackbird songs compared to rural blackbirds, Nemeth and Brumm (2009) reported that blackbirds at their urban sites began singing over an hour before their rural blackbirds. However, they did not attempt to explain the cause of the earlier urban songs. Instead of shifting the timing of their songs, some species will increase the volume of their songs (Brumm 2004, Brumm and Slabberkoorn 2005, Patricelli and Blickley 2006, Warren et al. 2006).

Perhaps the most common method birds use to overcome anthropogenic noise is to shift the frequency of their song notes. Most anthropogenic noise occurs at relatively low frequency levels that overlap with the frequency range of many bird songs (Patricelli and Blickley 2006, Warren et al. 2006, Wood and Yezerinac 2006, Slabbekoorn and Ripmeester 2008, Barber et al. in press). House Finches (*Carpodacus mexicanus*: Fernández-Juricic et al. 2005), Great Tits (Slabbekoorn and den Boer-Visser 2006, Slabbekoorn and Ripmeester 2008), Song Sparrows (*Melospiza melodia*: Wood and Yezerinac 2006), Grey Shrike-thrush (*Colluricincla harmonica*: Parris and Schneider
2008), and blackbirds (Nemeth and Brumm 2009) living in urban areas have higher minimum frequency low notes in their songs than their rural counterparts. The maximum frequency of the high notes in each of these species did not change in noisier environments. Increasing the minimum frequency to combat high levels of low frequency noise appears to be a common strategy at various life stages as well. Nestling Tree Swallows (Tachycineta bicolor) exposed to low frequency white noise also raised the minimum frequency of their begging call and this change persisted for a minimum of two days after the noise was removed (Leonard and Horn 2008). In many species, both females and other males often use low frequency songs as an important indication of singer quality (Patricelli and Blickley 2006). Although a higher minimum frequency appears to correlate with increased anthropogenic noise in a variety of species, it could instead result from increased aggression due to the smaller territories and increased territorial invasions associated with urban environments (Nemeth and Brumm 2009).

**Carolina Wrens**

The Carolina Wren is a relatively common bird in much of the eastern United States. It is most common in the southeastern United States, but its range extends north to Ontario, west to Kansas, and south to Central America (Haggerty and Morton 1995). Male and female Carolina Wrens are sexually monomorphic; however, the male in a given pair tends to be slightly larger than the female of that pair (Haggerty 2006). Carolina Wrens inhabit a wide variety of shrubby habitats ranging from riparian habitats to upland ridges and from natural areas to backyards and urban parks. They are primarily an insectivorous species but will frequent backyard bird feeders during the winter. In fact,
supplemental feeding from bird feeders has been suggested as a possible partial explanation for their northward range expansion.

Unlike most southeastern birds, Carolina Wrens are year-round pair-bonded and year-round territorial (Haggerty and Morton 1995). Also unlike most of their avian counterparts, Carolina Wrens are apparently genetically monogamous (Haggerty et al. 2001). Pair bonds often form in the fall of the birds’ first year and are typically maintained until one of the pair dies (Morton and Shalter 1977, Morton 1982, Haggerty and Morton 1995). Nesting begins in early spring and continues through late fall; multiple clutches are common. Mengel (1965) reported that in Kentucky the earliest known laying date was March 22, 1954. Based on Kentucky Ornithological Society nest card data, Palmer-Ball (1996) reported that active nests have been documented as late as mid-September. Females incubate the eggs for 12-16 days and both sexes feed the young, which typically fledge at 10-16 days old (Haggerty and Morton 1995). Male Carolina Wrens play a vital role in rearing the young and may continue to feed fledglings while the female initiates a second clutch (Haggerty and Morton 1995).

Both sexes defend the territory with individual aggressive actions directed primarily towards members of the same sex (Morton and Shalter 1977, Haggerty and Morton 1995). Most territorial battles are conducted through singing and calls (Simpson 1982, Haggerty and Morton 1995). Simpson (1982) showed that male Carolina Wrens could defend and maintain their territory for at least 30 days through song alone. Only male Carolina Wrens sing. Female Carolina Wrens are physiologically incapable of singing (Nealen and Perkel 2000). In addition to several calls that they share with the
males, female Carolina Wrens have a distinctive female-only call and chatter (Haggerty and Morton 1995).

Male Carolina Wrens are highly vocal and sing year-round. Individual males have a repertoire of 17-55 song-types (Borror 1956, Simpson 1982, Morton 1987). Males appear unable to learn new songs after their first year (Morton et al. 1986). Birds within the same study site (neighbors and near-neighbors) can share up to 80% of their repertoire (Simpson 1982, Morton 1987). The frequency range of their songs falls between 1.8 and 4.5 kHz (Borror 1956, Haggerty and Morton 1995).

Carolina Wrens sing more at the center of their territory than at the edges of their territories (Simpson 1982, 1985). At the edges of their territories and in close-range encounters, Carolina Wrens sing less but use a greater proportion of their repertoire (Simpson 1982, 1985). Regardless of location in territory, hatch-year Carolina Wrens sing a larger number of song-types than older birds (Simpson 1982). Male Carolina Wrens also have a number of calls that are used for close territorial defense and to communicate with their mate (Morton and Shalter 1977, Haggerty and Morton 1995).

Much of the research focused on ranging and the impact of abiotic factors on the acoustical environment used male Carolina Wrens as study subjects (Morton et al. 1986, Naguib 1995, 1996).

The Carolina Wren’s permanent, year-round pair bonds and the early age at which those bonds can form suggest that male song likely plays a greater role in territory defense than in mate attraction (Morton and Shalter 1977, Simpson 1985). Male Carolina Wrens respond well to play backs and do not habituate to repeated playbacks of the same song-type (Simpson 1982, 1984). This makes them a common subject for studies on the

Carolina Wrens apparently recognize neighbors’ songs and respond differently to neighbors vs. strangers (Hyman 2002, 2003; but see Shy and Morton 1986). Territorial intrusions by neighbors are more likely to be tolerated than intrusions by strangers (Hyman 2002). However, Carolina Wrens countersing more aggressively with both neighbors and strangers when they are highly aroused (Hyman 2002, 2003). Responses to neighbors and strangers vary by season. While Carolina Wrens are less aggressive to neighbors than to strangers in the spring, playbacks of neighbor and stranger songs in the fall elicit similar responses (Hyman 2005). This appears to be due to an overall decrease in singing and aggressiveness (Hyman 2005).

Simpson (1982) reported seasonal trends in singing activity. The Carolina Wrens on her study site sang approximately the same number of songs in April, May, and June. Singing activity peaked in July when hatch year birds were seeking new territories. In October and November, singing activity was similar and lower than recorded in the spring. Other researchers have reported similar decreases in song activity between spring and fall (Hyman 2005, Dunaway 2006). Carolina Wrens sing year-round and will continue to sing during the winter, although at lower rates than during the breeding season. Strain and Mumme (1988) showed that winter singing rates of Carolina Wrens are positively correlated with both temperature and the availability of food.

In addition to season, time of day may also affect the singing activity of Carolina Wrens. The dawn chorus is well known in birds and has been discussed above; however, participation in the dawn chorus varies by species. Carolina Wrens are reported to sing
more in the morning (Haggerty and Morton 1995), but I can find no scientific study that records the singing activity of Carolina Wrens over the course of a full day. In fact, the studies I found that take into account possible time of day effects are inconclusive and all the studies were conducted in the morning.

Simpson (1982) reported no time of day effect on the response of Carolina Wrens to playbacks between 07:00 and 09:00 from 23 May through 5 July 1981. She also conducted a series of experiments that used caged wrens located on their own territories instead of playbacks (Simpson 1982). In July 1981, she reported no time of day effect on her caged wrens when she analyzed the singing activity over an unspecified 4-hour experimental period. However, when she broke the 4-hour experiment into a 2-hour early period and a 2-hour late period, she did find a time of day effect between the early and late periods. In a similar study conducted during the fall of 1981, she implemented three 45-minute trials between 06:30 and 09:15. She found no time of day effect between the first two trials (06:30-08:00), but did find a time of day effect between the first two trials and the third trial (08:00-09:15). Shy and Morton (1986) reported that at mid-day Carolina Wrens sang less in response to playbacks than they did earlier in the morning. I found no studies that compared afternoon singing rates to morning sing rates of Carolina Wrens.

**Objectives**

The purpose of this study is to compare the singing activity of Carolina Wrens (*Thryothorus ludovicianus*) in urban and rural areas. Specifically, this study looks for
patterns in the timing of songs throughout the day and examines the effect of season, temperature, and anthropogenic noise on singing activity in urban and rural settings.

**Justification**

As the earth’s landscape becomes increasingly urbanized, local wildlife must adapt to urban conditions or migrate to areas that are more rural. Urban wildlife face challenges such as direct loss of habitat, competition with non-native species, disturbance due to anthropogenic noise, and micro-climatic changes. Factors such as temperature, relative humidity, and noise affect the acoustical environment and may affect the ability of many animals, including birds, to communicate.

Understanding how urbanization affects birds’ singing behavior is critical because singing often plays a vital role in attracting mates and defending territories. In addition, as global climate change occurs it will become increasingly important to understand the effect of abiotic factors such as temperature and relative humidity on the singing behavior of birds. Developing a deeper understanding of how those abiotic factors affect singing and other associated behaviors may help guide future conservation actions.

Carolina Wrens are often used to study the role of singing in defending territories. They are also a common subject for ranging studies. However, surprisingly little research has been conducted on the factors influencing Carolina Wren song activity over the course of a day. No studies have compared the singing activity of Carolina Wrens in urban and rural environments. Although Carolina Wrens are common and face no known conservation threats, understanding how various factors affect the singing activity of this
model species in urban and rural settings may help conservation efforts for rarer and less understood species.

Questions

My research focused on four categories of questions. Those categories were:

1. Differences in singing activity between sites and seasons,
2. Daily singing activity patterns,
3. Correlations between singing activity and temperature, and

Specific questions and associated hypotheses for each category of questions are discussed in the Materials and Methods section of this paper.

Materials and Methods

Study Sites

Urban study site:

The urban study area was located at Weldon Peete Park in Bowling Green, Kentucky (Figure 1). Bowling Green is located in south-central Kentucky and is the 5th largest city in the state. According to the U.S. Census Bureau (2009), Bowling Green had a population of 49,296 during the 2000 census and an estimated population of 53,176 in 2006. In 2000, Bowling Green had a land area of 90.65 square kilometers with 1,392.1 people per square mile (U.S. Census Bureau 2009). Two hospitals, a university, and numerous manufacturing and retail centers are located within the city limits.
Weldon Peete Park is on the Barren River and consists of 2.02 hectares of mixed deciduous hardwoods and open fields. A paved trail loops through the park. The park is bordered by a main road through town, is approximately 0.5 km from a hospital, approximately 0.63 km from a major railroad line, and is across the river from the water treatment plant (Figure 3). The Barren River is a tributary of the Green River and is in the Upper Green River watershed.

Two SongMeter© SM2 data loggers (BG-01 and BG-02) were placed in riparian corridors at Weldon Peete Park. BG-01 (Figures 1, 4 - 6) was located across the trail from the river. BG-02 (Figures 1, 7 - 9) was located on the same side of the trail as the river and almost immediately across from the water treatment plant. BG-02 was also closer to the main road than BG-01. Basic vegetation surveys were conducted for each site (Table 1) in October 2009.
Figure 1: Orthophoto showing the location of SongMeter\textsuperscript{©} SM2 data loggers BG-01 and BG-02 in Weldon Peete Park, Bowling Green, KY.
Figure 2: Paved trail through Weldon Peete Park.

Figure 3: Barren River and Bowling Green’s water treatment plant.
Figure 4: Overview of the area where data logger BG-01 is located.

Figure 5: Data logger BG-01.
Figure 6: Vegetation at BG-01 (A: view facing north of the data logger, B: view facing south of the data logger, C: view facing east of the data logger, D: view facing west of the data logger, E: canopy above the data logger, F: groundcover below the data logger).
Figure 7: Overview of the area where data logger BG-02 is located.

Figure 8: Data logger BG-02.
Figure 9: Vegetation at BG-02 (A: view facing north of the data logger, B: view facing south of the data logger, C: view facing east of the data logger, D: view facing west of the data logger, E: canopy above the data logger, F: groundcover below the data logger).
**Table 1:** Habitat survey for urban sites (BG-01 and BG-02).

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<tbody>
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<td>N36° 59' 58.2''</td>
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<td></td>
<td>W86° 25' 24.6''</td>
<td>W86° 25' 33.00''</td>
</tr>
<tr>
<td>Estimated distance to river</td>
<td>69m</td>
<td>10m</td>
</tr>
<tr>
<td>Estimated distance to field</td>
<td>8.5m</td>
<td>4.5m</td>
</tr>
</tbody>
</table>
| Estimated % canopy cover; 3 most abundant plants | 1-25%  
   *Acer rubrum*  
   *Liquidambar styraciflua*  
   *Fraxinus pennsylvanica* | 1-25%  
   *Acer rubrum*  
   *Ulmus sp.*  
   *Celtis sp.* |
| Estimated % midstory cover; 3 most abundant plants | 26-50%  
   *Acer negundo*  
   *Fraxinus pennsylvanica*  
   *Celtis sp.* | 1-25%  
   *Acer negundo*  
   *Acer rubrum* |
| Estimated % shrub cover; 3 most abundant plants | 51-75%  
   *Ligustrum sp.*  
   *Rosa sp.*  
   *Arundinaria gigantea* | 76-100%  
   *Lindera benzoin*  
   *Acer negundo* |
| Estimated % ground cover; 3 most abundant plants | 1-25%  
   *Euonymus sp.*  
   *Poaceae* | 76-100%  
   *Poaceae*  
   *Urtica dioica*  
   *Verbesina sp.* |
Rural study site:

The rural study area was located at the Upper Green River Biological Preserve (UGRBP) in Hart County, Kentucky (Figure 10). The UGRBP is located in south-central Kentucky and is approximately 2 km from Mammoth Cave National Park. The nearest town is Horse Cave, which had a population of 2,252 in 2000 (U.S. Census Bureau 2008), an estimated 2008 population of 2,326 (U.S. Census Bureau 2008), and is 5 km from the UGRBP. Most of the land surrounding the UGRBP is used for agriculture.

Western Kentucky University owns and manages the UGRBP. The UGRBP serves as a center for conservation, education, and research. It is located on the Green River and consists of approximately 405 hectares of deciduous hardwoods, old fields, and restored prairies. The Green River is the most biologically diverse tributary of the Ohio River (Commonwealth of Kentucky 2008).

Two SongMeter© SM2 data loggers (BP-01 and BP-02) were placed in riparian corridors along the Green River. Young saplings had been planted in the field closest to BP-01 (Figures 10, 11 - 13). Most of the saplings were between 1.5 and 2m high. The field closest to BP-02 (Figures 10, 14 - 16) was grass that was cut for hay in the fall of 2009. In October 2009, I conducted basic vegetation surveys for each site (Table 2).
Figure 10: Orthophoto showing the location of the SongMeter® SM2 data loggers BP-01 and BP-02 in the Upper Green River Biological Preserve, Hart County, KY.
Figure 11: Overview of the area where data logger BP-01 is located.

Figure 12: Data logger BP-01.
Figure 13: Vegetation at BP-01 (A: view facing north of the data logger, B: view facing south of the data logger, C: view facing east of the data logger, D: view facing west of the data logger, E: canopy above the data logger, F: groundcover below the data logger).
Figure 14: Overview of the area where data logger BP-02 is located.

Figure 15: Data logger BP-02.
**Figure 16:** Vegetation at BP-02 (A: view facing north of the data logger, B: view facing south of the data logger, C: view facing east of the data logger, D: view facing west of the data logger, E: canopy above the data logger, F: groundcover below the data logger).
Table 2: Habitat survey for rural sites (BP-01 and BP-02).

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<td>Estimated distance to field</td>
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<td>5m</td>
</tr>
<tr>
<td>Estimated % canopy cover; 3</td>
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<td>1-25%</td>
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<tr>
<td>most abundant plants</td>
<td>Acer rubrum</td>
<td>Acer negundo</td>
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<tr>
<td></td>
<td>Acer negundo</td>
<td>Acer rubrum</td>
</tr>
<tr>
<td></td>
<td>Ulmus sp.</td>
<td>Celtis sp.</td>
</tr>
<tr>
<td>Estimated % midstory cover; 3</td>
<td>1-25%</td>
<td>1-25%</td>
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<td>most abundant plants</td>
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</tr>
<tr>
<td>Estimated % shrub cover; 3</td>
<td>1-25%</td>
<td>1-25%</td>
</tr>
<tr>
<td>most abundant plants</td>
<td>Lindera benzoin</td>
<td>Acer negundo</td>
</tr>
<tr>
<td></td>
<td>Acer negundo</td>
<td></td>
</tr>
<tr>
<td>Estimated % ground cover; 3</td>
<td>76-100%</td>
<td>51-75%</td>
</tr>
<tr>
<td>most abundant plants</td>
<td>Poaceae</td>
<td>Verbesina sp.</td>
</tr>
<tr>
<td></td>
<td>Urtica dioica</td>
<td>Poaceae</td>
</tr>
<tr>
<td></td>
<td>Verbesina sp.</td>
<td>Glechoma hederacea</td>
</tr>
</tbody>
</table>

Data Collection

As part of an anuran bioacoustics study, 4 SongMeter© SM2 data loggers were placed in riparian habitats in urban and rural settings in the spring of 2009. SongMeter© SM2 data loggers consist of dual SMX-II weatherproof acoustic microphones connected to a weatherproof unit that houses the unit’s electrical components including 4 interchangeable flashcards for storing recordings (Wildlife Acoustics, Inc. 2010). Each SongMeter© SM2 data logger was attached to a tree at a height of approximately 1.5m.
The SongMeter© SM2 data loggers were configured to record ambient sound in *.wav format for 3 minutes at the beginning of every hour. Batteries and flashcards were changed every 3-4 weeks throughout the spring, summer, and fall to ensure a nearly continuous dataset. A Hobo® data logger was deployed in conjunction with each SongMeter© SM2 data logger. The Hobo® data loggers monitored and recorded temperature and relative humidity at 15-minute intervals.

I used online weather data to choose 7 consecutive days in May and 7 consecutive days in July that appeared to have similar daily temperatures (minimum and maximum) and precipitation between both sites and months. For the rural site, I used online data from the Mammoth Cave National Park NOAA Climate Reference Station located near Pig, KY (National Climate Data Center 2009a, b). For the urban site, I used online data from the Kentucky Mesonet site located at the WKU farm in Warren County (Kentucky Mesonet 2009a, b).

I chose the months of May and July because they are both within the breeding season of Carolina Wrens, but the two months represent different stages of the breeding season. In May, most Carolina Wrens in south central Kentucky are still on nests and actively breeding. However in July, hatch-year birds are abundant and fewer actively breeding adults are caught during banding operations. These comments are based on data collected while working for 3 years on an unrelated project at Mammoth Cave National Park. Each year, Mammoth Cave National Park participates in the Monitoring Avian Productivity and Survivorship (MAPS) program that is overseen by The Institute for Bird Populations. MAPS stations represent a continent-wide network of banding stations that are operated each year during set banding periods. Each MAPS station is located at the
same spot every year. Mammoth Cave’s station is located on the Green River and is approximately 2 km from the Upper Green River Biological Preserve. During the 3 years that I worked at the Mammoth Cave MAPS station, the earliest banding period in which hatch-year Carolina wrens were captured was the June 20-29 banding period (Figure 17). In addition to species and age of the birds, data on sex and breeding status were also recorded for the birds captured during the MAPS program. Those data for Carolina wrens caught during the 2007, 2008, and 2009, MAPS banding seasons are presented in Table 3. Detailed background and methodology for the MAPS program are described in DeSante et al. 1993.

Photoperiods during the chosen weeks were nearly identical. Sunrise for the week in May varied between 05:31 and 05:28; in July, it varied between 05:30 and 05:33 (U.S. Navy Observatory 2009). Sunset for the same week in May varied between 19:54 and 19:59; for the same week in July, it varied between 20:09 and 20:08 (U.S. Navy Observatory 2009). The primary difference in photoperiod between the two sampling periods was that in May, day length was getting slightly longer and in July, it was getting slightly shorter.

From the anuran bioacoustics dataset, I downloaded the data for 24 May 2009 to 30 May 2009 and 1 July 2009 to 7 July 2009. This provided me with a total of 168 3-minute recordings / week / data logger for a total of 1,344 recordings or 4,032 minutes of sound. I listened to each recording using Audacity software on a desktop computer with the speakers set to a constant volume. For each recording, I documented the singing activity of Carolina Wrens (defined as the number of Carolina Wren songs heard), and a
Comparison of hatch-year to after-hatch-year Carolina wrens captured at Mammoth Cave National Park’s MAPS banding station

Figure 17: Comparison of hatch-year (HY) to after-hatch-year (AHY) Carolina wrens caught at the Monitoring Avian Productivity and Survivorship (MAPS) banding station located at Mammoth Cave National Park. Data from the 2007-2009 banding seasons were combined to produce this graph. The total number of Carolina wrens (Total) caught during each banding period are also shown for comparison purposes. There were no Carolina wrens caught during any of the three banding seasons (2007, 2008, or 2009) for the MAPS banding period of June 10-19. The MAPS banding periods that correspond to my May and July sampling periods are marked by an *. Background and methodology for the MAPS program are described in DeSante et. al 1993.
Table 3: Data on the sex and breeding status of adult (after-hatch-year) Carolina wrens caught at Mammoth Cave National Park’s Monitoring Avian Productivity and Survivorship (MAPS) banding station. Data from the 2007-2009 banding seasons were combined to produce this table. Brood patches are only found on the females and are scored from 0 (none) to 5 (starting to grow pin feathers). A brood patch score of 3 is considered heavy; scores of 1 or 2 are increasing in size while scores of 4 or 5 are declining. Cloacal protuberances are scored from 0 (none) to 3 (large) and are only found on the males. Since Carolina wrens are sexually monomorphic, they cannot be sexed unless they have either a brood patch or a cloacal protuberance. If a Carolina wren is captured and does not have either a brood patch or a cloacal protuberance, it is recorded as an unknown sex. The MAPS banding periods that correspond to my May and July sampling periods are marked by an *. Background and methodology for the MAPS program are described in DeSante et. al 1993.

<table>
<thead>
<tr>
<th>MAPS banding period</th>
<th>Number of after-hatch-year Carolina wrens caught</th>
<th>Score for brood patches (females) and cloacal protuberances (males)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Males</td>
</tr>
<tr>
<td>May 21-30 *</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>May 31-Jun 9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Jun 10-19</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Jun 20-29</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Jun 30-Jul 9 *</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Jul 10-19</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Jul 20-29</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Jul 30-Aug 8</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
categorical assessment (Table 4) of the precipitation and anthropogenic noise due to traffic or machinery. I made no attempt to differentiate between song types. No call notes made by either sex were counted. In order to limit listening fatigue, I took a minimum of a 10-minute break after every five recordings and a minimum 1-hour break after every day’s worth of recordings. Difficult or faint songs were listened to no more than 2 times. I also downloaded the associated temperature data from the Hobo® data loggers.

Table 4: Assessment categories for precipitation and anthropogenic noise data

<table>
<thead>
<tr>
<th>Code</th>
<th>Precipitation</th>
<th>Anthropogenic Noise</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>1</td>
<td>Light mist; cannot hear individual drops.</td>
<td>Slight; Distant traffic, faint machinery, or a few close vehicles.</td>
</tr>
<tr>
<td>2</td>
<td>Light rain; does not interfere with ability to hear birds singing.</td>
<td>Medium; Nearby traffic, machinery that is medium in volume</td>
</tr>
<tr>
<td>3</td>
<td>Steady medium rain; getting hard to hear the birds sing.</td>
<td>Heavy; Nearly constant traffic, loud machinery, getting hard to hear the birds sing.</td>
</tr>
<tr>
<td>4</td>
<td>Downpour; barely hear anything but rain.</td>
<td>Excessive; Hard to hear anything but traffic / machinery.</td>
</tr>
</tbody>
</table>

Hypotheses

Differences in singing activity between sites and seasons

Question 1: Between seasons, is the frequency of Carolina Wren singing activity out of proportion with the expected?

\( H_0: \) The frequency of Carolina Wren singing activity between seasons will be within the expected proportion.
$H_1$: The frequency of Carolina Wren singing activity between seasons will not be within the expected proportion.

Question 2: Between urban and rural areas, is the frequency of Carolina Wren singing activity out of proportion with the expected?

$H_0$: The frequency of Carolina Wren singing activity between urban and rural sites will be within the expected proportion.

$H_1$: The frequency of Carolina Wren singing activity between urban and rural sites will not be within the expected proportion.

Question 3: In May, is the frequency of Carolina Wren singing activity out of proportion with the expected for urban and rural areas?

$H_0$: In May, the frequency of Carolina Wren singing activity will be within the expected proportions for the urban and rural sites.

$H_1$: In May, the frequency of Carolina Wren singing activity will not be within the expected proportions for the urban and rural sites.

Question 4: In July, is the frequency of Carolina Wren singing activity out of proportion with the expected for urban and rural areas?

$H_0$: In July, the frequency of Carolina Wren singing activity will be within the expected proportions for the urban and rural sites.

$H_1$: In July, the frequency of Carolina Wren singing activity will not be within the expected proportions for the urban and rural sites.

Question 5: In each season, is the frequency of Carolina Wren singing activity out of proportion with the expected within the urban sites (i.e. BG-01 and BG-02)?
\( H_0 \): In each season, the frequency of Carolina Wren singing activity will be within the expected proportions for the urban sites.

Prediction 1: In May, the frequency of Carolina Wren singing activity will be within the expected proportions for the data loggers at the urban site.

Prediction 2: In July, the frequency of Carolina Wren singing activity will be within the expected proportions for the data loggers at the urban site.

\( H_1 \): In May, the frequency of Carolina Wren singing activity will not be within the expected proportions for the data loggers at the urban site.

\( H_2 \): In July, the frequency of Carolina Wren singing activity will not be within the expected proportions for the data loggers at the urban site.

**Question 6:** In each season, is the frequency of Carolina Wren singing activity out of proportion with the expected within the rural sites (i.e. BP-01 and BP-02)?

\( H_0 \): In each season, the frequency of Carolina Wren singing activity will be within the expected proportions for the rural sites.

Prediction 1: In May, the frequency of Carolina Wren singing activity will be within the expected proportions for the data loggers at the rural site.

Prediction 2: In July, the frequency of Carolina Wren singing activity will be within the expected proportions for the data loggers at the rural site.
$H_1$: In May, the frequency of Carolina Wren singing activity will not be within the expected proportions for the data loggers at the rural site.

$H_2$: In July, the frequency of Carolina Wren singing activity will not be within the expected proportions for the data loggers at the rural site.

**Daily singing activity patterns**

*Question 7:* Is there a non-random pattern to the daily singing activity of Carolina Wrens?

$H_0$: There will be no patterns in the daily singing activity of Carolina Wrens.

**Prediction 1:** There will be no difference in the number of songs that Carolina Wrens sing during any given hour of the day (sampling period). *Or*

**Prediction 2:** The number of songs may vary over the course of the day, but there will be no consistent pattern to the variation.

$H_1$: A peak in song activity will be found in the sampling period closest to sunrise.

$H_2$: A peak in song activity will be found between the sampling period closest to sunrise and the sampling period closest to four hours after actual sunrise.

$H_3$: Singing activity will be lowest at mid-day.

$H_4$: Around dusk, a smaller peak in song activity may occur that is similar to the peak in song activity seen at dawn.
**Question 8:** Do the daily singing activity patterns of Carolina Wrens vary between seasons?

- **H₀:** There will be no difference in the daily singing activity patterns (or lack of) in May and July.
- **H₁:** The amplitude of peaks (number of calls at any given sampling period) will decrease in July compared to May.
- **H₂:** The amplitude of peaks will increase in July compared to May.
- **H₃:** The timing of the peaks will shift to track the changes in the time of sunrise and sunset.

**Question 9:** Do the daily singing activity patterns of Carolina Wrens vary between urban and rural sites?

- **H₀:** There will be no difference in the number of songs that Carolina Wrens sing during any given hour of the day at the urban sites compared to the rural sites.
- **H₁:** Singing activity will begin earlier in the day at the urban sites compared to the rural sites.
- **H₂:** Singing activity will continue later in the day at the urban sites compared to the rural sites.
- **H₃:** The amplitude of peaks will be greater at the urban sites than at the rural sites.
Correlations between singing activity and temperature

Question 10: Is Carolina Wren singing activity correlated with temperature within a given season?

H₀: Carolina Wren singing activity will not be correlated with temperature within a given season.

Prediction 1: There will be no correlation between singing activity and temperature in May.

Prediction 2: There will be no correlation between singing activity and temperature in July.

H₁: In May, singing activity will be positively correlated to the temperature regardless of time of day as long as it is between sunrise and sunset.

H₂: In July, singing activity will be positively correlated to the temperature regardless of time of day as long as it is between sunrise and sunset.

Question 11: Does the correlation between Carolina Wren singing activity and temperature vary between seasons?

H₀: There will be no difference in the correlation (or lack of) between singing activity and temperature in May and July.

H₁: Any correlation between singing activity and temperature will be greater in May than in July.

H₂: Any correlation between signing activity and temperature will be greater in July than in May.

Question 12: Does the correlation between Carolina Wren singing activity and temperature vary between urban and rural sites?
**H0:** There will be no difference in the correlation (or lack of) between singing activity and temperature in urban and rural sites.

**H1:** Any correlation between singing activity and temperature will be greater in urban than in rural sites.

**H2:** Any correlation between singing activity and temperature will be greater in rural than in urban sites.

**Correlations between singing activity and anthropogenic noise**

**Question 13:** Is Carolina Wren singing activity correlated with anthropogenic noise within a given season?

**H0:** There will be no correlation between Carolina Wren singing activity and anthropogenic noise within a given season.

**Prediction 1:** There will be no correlation between singing activity and anthropogenic noise in May.

**Prediction 2:** There will be no correlation between singing activity and anthropogenic noise in July.

**H1:** In May, singing activity will be positively correlated to anthropogenic noise.

**H2:** In July, singing activity will be positively correlated to anthropogenic noise.

**Question 14:** Does the correlation between Carolina Wren singing activity and anthropogenic noise vary between urban and rural sites?
$H_0$: There will be no difference in the correlation (or lack of) between singing activity and anthropogenic noise in urban and rural sites.

$H_1$: Any correlation between singing activity and anthropogenic noise will be greater in urban than in rural sites.

$H_2$: Any correlation between singing activity and anthropogenic noise will be greater in rural than in urban sites.

**Statistical Analysis**

I used SPSS statistical software (PASW Statistics 2009) to conduct Chi-squared tests on the frequency of songs per 3-minute sampling period and the frequency of a singing Carolina Wren’s presence/absence for the same 3-minute sampling periods. Only the recordings made between 05:00 and 20:00 were used for the presence/absence Chi-squared analyses. All of the Chi-squared analyses had expected values greater than 5. No post-hoc tests were conducted on the Chi-squared results because each Chi-squared analysis only had 2 categories. Preliminary analyses on the daily singing activity patterns of Carolina Wrens used Fourier transforms. I used PROC NLMIXED in the SAS statistical software package (SAS Institute 2000) to conduct zero-inflated Poisson regressions on the number of songs compared to temperature and compared to the level of anthropogenic noise. Zero-inflated Poisson regressions are designed to deal with overdispersed count data with excess zeroes. My data fit these characteristics.
Results

Differences in singing activity between sites and seasons

I used Chi-squared analyses to determine whether the observed singing frequencies were out of proportion with the expected frequencies for the various sites and seasons. For each question, I conducted 2 analyses. The first Chi-squared analysis compared the frequency of songs (number) for each site or season to the frequency of songs expected. The second Chi-squared analysis compared the frequency of a singing Carolina Wren’s presence to the expected frequency. This resulted in 16 Chi-squared analyses, of which, 7 were significant (Table 17). Significant results were obtained from the frequency of songs analyses for the between seasons, overall between sites, between sites in May and July, urban within site during May, and rural within site during May. In addition, the frequency of a singing Carolina wren being present analysis for between sites in May produced significant results.

Between seasons, is the frequency of Carolina Wren singing activity out of proportion with the expected?

In May, 4,064 Carolina Wren songs were detected and 3,002 songs were detected in July. I analyzed the frequency of Carolina Wren songs in each month and found that the observed frequency of songs was out of proportion with the expected frequency \( \chi^2_{(7066, \text{df} = 1)} = 159.616, p < 0.0001 \). In May, 235 recordings had Carolina Wrens singing and 204 recordings in July had singing Carolina Wrens. I analyzed the frequency of singing Carolina Wren presence for each month and found that the observed frequency was in proportion with the expected frequency \( \chi^2_{(439, \text{df} = 1)} = 2.189, p = 0.139 \).
Between urban and rural areas, is the frequency of Carolina Wren singing activity out of proportion with the expected?

I detected a total of 3,978 Carolina Wren songs at the urban sites and 3,088 songs at the rural sites. I analyzed the frequency of Carolina Wren songs in the urban and rural areas and found that the observed frequency of songs was out of proportion with the expected frequency \( \chi^2(7066, \text{df} = 1) = 112.10, p < 0.0001 \). In the urban area, 236 recordings had Carolina Wrens singing and 203 recordings in the rural areas had singing Carolina Wrens. I analyzed the frequency of singing Carolina Wren presence for the urban and rural areas and found that the observed frequency was in proportion with the expected frequency \( \chi^2(439, \text{df} = 1) = 2.481, p = 0.115 \).

In May, is the frequency of Carolina Wren singing activity out of proportion with the expected for urban and rural areas?

Within the May samples, I detected 2,701 Carolina Wren songs in the urban area and 1,363 songs in the rural area. I analyzed the frequency of Carolina Wren songs in each area and found that the observed frequency of songs was out of proportion with the expected frequency \( \chi^2(4064, \text{df} = 1) = 440.513, p < 0.0001 \). Within the May samples, 139 urban recordings had singing Carolina Wrens and 96 rural recordings had singing Carolina Wrens. I analyzed the frequency of Carolina Wren presence in each area and again found that the observed frequency was out of proportion with the expected frequency \( \chi^2(235, \text{df} = 1) = 7.868, p = 0.005 \).
In July, is the frequency of Carolina Wren singing activity out of proportion with the expected for urban and rural areas?

Within the July samples, I detected 1,277 Carolina Wren songs in the urban area and 1,725 songs in the rural area. I analyzed the frequency of Carolina Wren songs in each area and found that the observed frequency of songs was out of proportion with the expected frequency ($X^2_{(3002, df=1)} = 66.857, p < 0.0001$). Within the July samples, 97 urban recordings had singing Carolina Wrens and 107 rural recordings had singing Carolina Wrens. I analyzed the frequency of Carolina Wren presence in each area and found that the observed frequency was in proportion with the expected frequency ($X^2_{(204, df=1)} = 0.490, p = 0.484$).

In each season, is the frequency of Carolina Wren singing activity out of proportion with the expected within the urban sites (i.e. BG-01 and BG-02)?

In May, I detected 1,131 Carolina Wren songs on the BG-01 data logger and 1,570 songs on the BG-02 data logger. I analyzed the frequency of Carolina Wren songs at each data logger and found that the observed frequency of songs was out of proportion with the expected frequency ($X^2_{(2701, df=1)} = 71.352, p < 0.0001$). In May, singing Carolina Wrens were detected in 69 of the recordings for BG-01 and in 70 of the recordings for BG-02. I analyzed the frequency of singing Carolina Wren presence for each data logger and found that the observed frequency was in proportion with the expected frequency ($X^2_{(139, df=1)} = 0.007, p = 0.932$).

In July, I detected 646 songs on the BG-01 data logger and 631 on the BG-02 data logger. I analyzed the frequency of Carolina Wren songs at each data logger and found
that the observed frequency of songs was in proportion with the expected frequency
\( \chi^2_{(1277, \text{df} = 1)} = 0.176, p = 0.675 \). In July, I detected singing Carolina Wrens on 42 of the
BG-01 data loggers and 55 of the BG-02 data loggers. I analyzed the frequency of
singing Carolina Wren presence for each data logger and again found that the observed
frequency was in proportion with the expected frequency \( \chi^2_{(97, \text{df} = 1)} = 1.742, p = 0.187 \).

In each season, is the frequency of Carolina Wren singing activity out of proportion with
the expected within the rural sites (i.e. BP-01 and BP-02)?

In May, I detected 586 Carolina Wren songs at BP-01 and 777 songs during the
same period at BP-02. I analyzed the frequency of Carolina Wren songs at each data
logger and found that the observed frequency of songs was out of proportion with the
expected frequency \( \chi^2_{(1363, \text{df} = 1)} = 26.765, p < 0.0001 \). In May, 42 of the BP-01
recordings had singing Carolina Wrens and 54 of the BP-02 recordings had singing
Carolina Wren songs. I analyzed the frequency of singing Carolina Wren presence for
each data logger and found that the observed frequency was in proportion with the
expected frequency \( \chi^2_{(96, \text{df} = 1)} = 1.5, p = 0.221 \).

In July, I detected 880 songs at BP-01 and 845 at BP-02. I analyzed the frequency
of Carolina Wren songs at each data logger and found that the observed frequency of
songs was in proportion with the expected frequency \( \chi^2_{(1725, \text{df} = 1)} = 0.710, p = 0.399 \). In
July, I detected singing Carolina Wrens on 58 of the BP-01 recordings and 49 of the BP-
02. I analyzed the frequency of singing Carolina Wren presence for each data logger and
again found that the observed frequency was in proportion with the expected frequency
\( \chi^2_{(107, \text{df} = 1)} = 0.757, p = 0.384 \). These results were similar to the urban results.
Daily singing activity patterns

Daily singing activity patterns were visually analyzed; results are summarized in Table 17. Carolina wrens do not sing in the hour before sunrise or after sunset. They have a distinct peak in singing activity during the dawn chorus and a smaller peak during the dusk chorus. The dawn and dusk choruses are greater in May than in July and the May dawn chorus lasts twice as long as in July. Urban and rural daily singing activity patterns are similar.

Is there a non-random pattern to the daily singing activity of Carolina Wrens?

During the study, sunrise occurred at approximately 05:30 and sunset occurred at approximately 20:00. No songs were detected between the hours of 21:00 and 04:00 at any of the data logger locations or during either of the two study periods. Visual analysis of the average number of songs recorded at all of the sites and in both seasons indicates an early morning peak in singing activity (Figure 18). The early morning peak in singing activity lasts for approximately the first 4 hours after sunrise and then a slow, general decline in singing activity begins. The lowest level of singing activity is found in the hours leading up to the hour before sunset. A small peak in singing activity occurs in the hour immediately prior to sunset and then drops rapidly at sunset.
**Figure 18:** Average number of Carolina Wren songs detected at each hour. Data from all 4 data loggers and both sampling periods were compiled in this graph.

Do the daily singing activity patterns of Carolina Wrens vary between seasons?

In May, day length increased by approximately 8 minutes from the first day of the sampling period to the last day. In July, there was an approximately 4 minute decrease in day length from the beginning to the end of the sampling period. Sunrise and sunset were within a few minutes of each other during both May and July. The overall day length, therefore, was relatively constant during both sampling periods. No songs were detected before 05:00 or after 20:00 in either month.

Visual analysis of the average number of songs recorded during each hour at all data logger locations for each of the months indicates that in general singing activity is
greater in May than in July (Figure 19). Both months show an early morning peak in singing activity; however, in May the peak covers the first 6 hours after sunrise, while in July the peak lasts only for the first 3 hours after sunrise (Figure 19). After the early morning peak in singing activity, the number of songs recorded generally drops in both months with relatively minor fluctuations. The fluctuations appear similar in both months, but the timing of the May fluctuations lag slightly behind the July fluctuations.

The sunset peak in singing activity is much more pronounced in May and occurs much closer to sunset than it does in July (Figure 19). In fact, based on visual analysis of the data it is difficult to say whether the July sunset peak in singing activity actually exists.

**Figure 19:** Comparison of the average number of songs detected during each hour for the months of May and July. Data from all 4 data loggers were combined.
Do the daily singing activity patterns of Carolina Wrens vary between urban and rural sites?

Visual analysis of the average number of songs detected over the course of a day at the rural site compared to the urban site indicate relatively similar overall patterns (Figure 19). In general, Carolina Wrens at the urban locations appear to sing more songs at any given hour than their rural counterparts. The midday decline in singing activity in rural Carolina Wrens is also more pronounced than in urban Wrens, which appear to sing at a more constant rate throughout the day (Figure 20).

![Comparison of the average number of songs per hour at the rural and urban sites](image)

**Figure 20:** Comparison of the average number of songs detected during each hour at the urban and rural sites. The urban data were compiled from both urban data loggers during both months. The rural data were compiled in the same way using data from the rural data loggers.
Correlation between singing activity and temperature

Note for interpreting zero-inflated Poisson parameter estimates: “Estimates” are the regression coefficients for the model; “b_0” is the intercept, “b_1” is the log linear slope, and “a_0” is the linear predictor for the inflation probability (UCLA 2010a, b).

My results indicate that temperature is a highly significant predictor of singing activity. The relationship is positive and is similar between seasons and between sites. Table 17 provides a summary of the results.

Is Carolina Wren singing activity correlated with temperature within a given season?

I used a zero-inflated Poisson regression to analyze whether Carolina Wren singing activity is correlated with temperature in May and in July. The zero-inflated Poisson regression model predicting singing activity from temperature was significant in both months (May: t_{665} = -8.02, p < 0.0001, Table 5; July: t_{663} = -7.34, p < 0.0001, Table 6). For these data, the expected change in log (singing activity) for a one degree increase in temperature in May was -0.038 and in July it was -0.036. This fails to support the null hypothesis that there would be no relationship between singing activity and temperature. However, in contrast to my alternate hypotheses H_1 and H_2, which stated that singing activity would be positively correlated with temperature, my results indicate that singing activity is negatively correlated with temperature (May: b_1 = -0.038; July: b_1 = -0.036).
**Table 5:** Parameter estimates for zero-inflated Poisson regression analyzing the correlation between Carolina Wren singing activity and temperature in May.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>3.655</td>
<td>0.101</td>
<td>665</td>
<td>36.34</td>
<td>&lt;0.0001</td>
<td>3.457</td>
<td>3.852</td>
<td>-0.008</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.038</td>
<td>0.005</td>
<td>665</td>
<td>-8.02</td>
<td>&lt;0.0001</td>
<td>-0.047</td>
<td>-0.029</td>
<td>-0.200</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.604</td>
<td>0.081</td>
<td>665</td>
<td>7.45</td>
<td>&lt;0.0001</td>
<td>0.445</td>
<td>0.764</td>
<td>-0.002</td>
</tr>
</tbody>
</table>

**Table 6:** Parameter estimates for zero-inflated Poisson regression analyzing the correlation between Carolina Wren singing activity and temperature in July.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>3.464</td>
<td>0.106</td>
<td>663</td>
<td>32.68</td>
<td>&lt;0.0001</td>
<td>3.256</td>
<td>3.672</td>
<td>0.001</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.036</td>
<td>0.005</td>
<td>663</td>
<td>-7.34</td>
<td>&lt;0.0001</td>
<td>-0.045</td>
<td>-0.026</td>
<td>0.008</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.811</td>
<td>0.084</td>
<td>663</td>
<td>9.64</td>
<td>&lt;0.0001</td>
<td>0.646</td>
<td>0.976</td>
<td>-0.0002</td>
</tr>
</tbody>
</table>

Does the correlation between Carolina Wren singing activity and temperature vary between seasons?

Temperature is a highly significant predictor for Carolina Wren singing activity in both months and the confidence intervals for both months greatly overlap (Tables 5 and 6). These data support the null hypothesis and indicate that the correlation between singing activity and temperature does not vary between seasons.
Does the correlation between Carolina Wren singing activity and temperature vary between urban and rural sites?

The zero-inflated Poisson regression model predicting singing activity from temperature was significant in both urban and rural areas (Rural: $t_{671} = -9.78$, $p < 0.0001$, Table 7; Urban: $t_{657} = -6.30$, $p < 0.0001$, Table 8). At both sites, there is a negative relationship between singing activity and temperature (Rural: $b_1 = -0.044$; Urban: $b_1 = -0.033$). For these data, the expected change in log (singing activity) for a one degree increase in temperature at the rural site was -0.044 and at the urban site it was -0.033. The confidence intervals for both sites overlap (Tables 7 and 8) supporting the null hypothesis that the correlation between singing activity and temperature does not vary between urban and rural sites.

Table 7: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between rural Carolina Wren singing activity and temperature.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>3.645</td>
<td>0.095</td>
<td>671</td>
<td>38.56</td>
<td>&lt;0.0001</td>
<td>3.460</td>
<td>3.831</td>
<td>0.00001</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.044</td>
<td>0.004</td>
<td>671</td>
<td>-9.78</td>
<td>&lt;0.0001</td>
<td>-0.053</td>
<td>-0.035</td>
<td>0.0003</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.835</td>
<td>0.084</td>
<td>671</td>
<td>9.94</td>
<td>&lt;0.0001</td>
<td>0.670</td>
<td>1.000</td>
<td>5.401E-6</td>
</tr>
</tbody>
</table>
Table 8: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between urban Carolina Wren singing activity and temperature.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>3.544</td>
<td>0.115</td>
<td>657</td>
<td>30.96</td>
<td>&lt;0.0001</td>
<td>3.320</td>
<td>3.769</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.033</td>
<td>0.005</td>
<td>657</td>
<td>-6.30</td>
<td>&lt;0.0001</td>
<td>-0.044</td>
<td>-0.023</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.579</td>
<td>0.081</td>
<td>657</td>
<td>7.12</td>
<td>&lt;0.0001</td>
<td>0.419</td>
<td>0.739</td>
</tr>
</tbody>
</table>

**Correlation between singing activity and anthropogenic noise**

The results indicate that anthropogenic noise tends to be a significant predictor of singing (Table 17). In May, anthropogenic noise is positively related to singing activity and in July it is negatively related to singing activity. It is also positively related to singing activity in both urban and rural sites. However, post hoc analysis by season and site indicates that it is not significant in either month at the rural site but is significant in both months at the urban site.

Is Carolina Wren singing activity correlated with anthropogenic noise within a given season?

I used a zero-inflated Poisson regression to analyze whether Carolina Wren singing activity is correlated with anthropogenic noise in May and in July. The zero-inflated Poisson regression model predicting singing activity from anthropogenic noise was significant in both months (May: $t_{665} = 10.30$, $p < 0.0001$, Table 9; July: $t_{662} = -3.22$, $p = 0.001$, Table 10). However, singing activity in May appears to be positively related to anthropogenic noise ($b_1 = 0.159$), while in July it is negatively related to anthropogenic noise ($b_1 = -0.058$). For these data, the expected change in log (singing activity) for a one
category increase in anthropogenic noise in May was 0.159 and in July it was -0.058. The analysis supports the alternate hypothesis $H_1$ that singing activity would be positively correlated to anthropogenic noise in May. However, it fails to support both the null hypothesis and the alternate hypothesis $H_2$, which stated that singing activity would be positively correlated to anthropogenic noise in July.

**Table 9:** Parameter estimates for zero-inflated Poisson regression analyzing the correlation between Carolina Wren singing activity and anthropogenic noise in May.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.54</td>
<td>0.035</td>
<td>665</td>
<td>72.49</td>
<td>&lt;0.0001</td>
<td>2.472</td>
<td>2.610</td>
<td>1.794E-6</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.159</td>
<td>0.015</td>
<td>665</td>
<td>10.30</td>
<td>&lt;0.0001</td>
<td>0.129</td>
<td>0.189</td>
<td>1.227E-6</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.604</td>
<td>0.811</td>
<td>665</td>
<td>7.45</td>
<td>&lt;0.0001</td>
<td>0.445</td>
<td>0.764</td>
<td>9.719E-6</td>
</tr>
</tbody>
</table>

**Table 10:** Parameter estimates for zero-inflated Poisson regression analyzing the correlation between Carolina Wren singing activity and anthropogenic noise in July.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.783</td>
<td>0.034</td>
<td>662</td>
<td>82.15</td>
<td>&lt;0.0001</td>
<td>2.716</td>
<td>2.849</td>
<td>-0.00007</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.058</td>
<td>0.018</td>
<td>662</td>
<td>-3.22</td>
<td>0.0013</td>
<td>-0.093</td>
<td>-0.023</td>
<td>0.0001</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.809</td>
<td>0.084</td>
<td>662</td>
<td>9.61</td>
<td>&lt;0.0001</td>
<td>0.644</td>
<td>0.974</td>
<td>-0.00001</td>
</tr>
</tbody>
</table>
Does the correlation between Carolina Wren singing activity and anthropogenic noise vary between urban and rural sites?

The zero-inflated Poisson regression model predicting singing activity from anthropogenic noise was significant at both sites (Rural: $t_{671} = 2.71$, $p = 0.007$, Table 11; Urban: $t_{656} = 5.15$, $p < 0.0001$, Table 12). For these data, the expected change in log (singing activity) for a one category increase in anthropogenic noise at the rural site was 0.093 and at the urban site it was 0.162. These results fail to support the null hypothesis of no correlation between singing activity and anthropogenic noise. At both sites, the relationship between anthropogenic noise and singing activity is positive (Rural: $b_1 = 0.093$; Urban: $b_1 = 0.162$). The confidence intervals for the two sites barely overlap (Tables 11 and 12), suggesting that there is a difference in the correlation between singing activity and anthropogenic noise in urban and rural areas.

**Table 11:** Parameter estimates for zero-inflated Poisson regression analyzing the correlation between rural Carolina Wren singing activity and anthropogenic noise.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.648</td>
<td>0.033</td>
<td>671</td>
<td>79.79</td>
<td>&lt;0.0001</td>
<td>2.582</td>
<td>2.713</td>
<td>-0.003</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.093</td>
<td>0.034</td>
<td>671</td>
<td>2.71</td>
<td>0.007</td>
<td>0.026</td>
<td>0.160</td>
<td>0.007</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.835</td>
<td>0.084</td>
<td>671</td>
<td>9.94</td>
<td>&lt;0.0001</td>
<td>0.670</td>
<td>1.000</td>
<td>-0.009</td>
</tr>
</tbody>
</table>
Table 12: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between urban Carolina Wren singing activity and anthropogenic noise.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>b₀</td>
<td>2.399</td>
<td>0.085</td>
<td>656</td>
<td>28.28</td>
<td>&lt;0.0001</td>
<td>2.232</td>
<td>2.566</td>
</tr>
<tr>
<td>b₁</td>
<td>0.162</td>
<td>0.031</td>
<td>656</td>
<td>5.15</td>
<td>&lt;0.0001</td>
<td>0.100</td>
<td>0.224</td>
</tr>
<tr>
<td>a₀</td>
<td>0.576</td>
<td>0.081</td>
<td>656</td>
<td>7.09</td>
<td>&lt;0.0001</td>
<td>0.417</td>
<td>0.736</td>
</tr>
</tbody>
</table>

Does the correlation between Carolina Wren singing activity and anthropogenic noise vary between seasons (May, July) and sites (urban, rural)?

I conducted a post-hoc zero-inflated Poisson regression to analyze the interactive effect of season and site on the correlation between singing activity and anthropogenic noise. The zero-inflated Poisson regression model predicting singing activity from anthropogenic noise in May was not significant for the rural site ($t_{336} = 1.56$, $p = 0.1188$, Table 13), but was significant for the urban site ($t_{329} = 3.99$, $p < 0.0001$, Table 14). For these data, the expected change in log (singing activity) for a one category increase in anthropogenic noise at the rural site was 0.089 and at the urban site it was 0.160. The zero-inflated Poisson regression model predicting singing activity from anthropogenic noise in July was not significant for the rural site ($t_{335} = 1.83$, $p = 0.0681$, Table 15), but was significant for the urban site ($t_{327} = 1.98$, $p = 0.0484$, Table 16). For these data, the expected change in log (singing activity) for a one category increase in anthropogenic noise at the rural site was 0.079 and at the urban site it was 0.103. It is interesting to note that although the July results were non-significant at the rural site and significant at the
urban site, neither the July urban nor the July rural results were strongly significant / non-significant.

Table 13: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between rural Carolina Wren singing activity and anthropogenic noise in May.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.587</td>
<td>0.051</td>
<td>336</td>
<td>50.87</td>
<td>&lt;0.0001</td>
<td>2.487</td>
<td>2.687</td>
<td>0.00004</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.089</td>
<td>0.057</td>
<td>336</td>
<td>1.56</td>
<td>0.1188</td>
<td>-0.023</td>
<td>0.200</td>
<td>9.174E-6</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.916</td>
<td>0.121</td>
<td>336</td>
<td>7.59</td>
<td>&lt;0.0001</td>
<td>0.679</td>
<td>1.154</td>
<td>-2.8E-6</td>
</tr>
</tbody>
</table>

Table 14: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between urban Carolina Wren singing activity and anthropogenic noise in May.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.541</td>
<td>0.109</td>
<td>329</td>
<td>23.24</td>
<td>&lt;0.0001</td>
<td>2.326</td>
<td>2.756</td>
<td>0.00002</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.160</td>
<td>0.040</td>
<td>329</td>
<td>3.99</td>
<td>&lt;0.0001</td>
<td>0.081</td>
<td>0.239</td>
<td>0.00005</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.313</td>
<td>0.112</td>
<td>329</td>
<td>2.80</td>
<td>0.0054</td>
<td>0.093</td>
<td>0.532</td>
<td>-3.43E-6</td>
</tr>
</tbody>
</table>
Table 15: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between rural Carolina Wren singing activity and anthropogenic noise in July.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.714</td>
<td>0.044</td>
<td>335</td>
<td>&lt;0.0001</td>
<td>2.627</td>
<td>2.800</td>
<td>-1.64E-6</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.079</td>
<td>0.043</td>
<td>335</td>
<td>0.0681</td>
<td>-0.006</td>
<td>0.164</td>
<td>-5.82E-7</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.757</td>
<td>0.117</td>
<td>335</td>
<td>&lt;0.0001</td>
<td>0.526</td>
<td>0.987</td>
<td>-1.22E-7</td>
</tr>
</tbody>
</table>

Table 16: Parameter estimates for zero-inflated Poisson regression analyzing the correlation between urban Carolina Wren singing activity and anthropogenic noise in July.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t</th>
<th>p</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>2.311</td>
<td>0.138</td>
<td>327</td>
<td>&lt;0.0001</td>
<td>2.039</td>
<td>2.583</td>
<td>0.0005</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.103</td>
<td>0.052</td>
<td>327</td>
<td>0.0484</td>
<td>0.001</td>
<td>0.206</td>
<td>0.001</td>
</tr>
<tr>
<td>$a_0$</td>
<td>0.863</td>
<td>0.121</td>
<td>327</td>
<td>&lt;0.0001</td>
<td>0.625</td>
<td>0.625</td>
<td>-0.0001</td>
</tr>
</tbody>
</table>
Table 17: Summary of results.

<table>
<thead>
<tr>
<th>Differences in singing activity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Comparison</strong></td>
</tr>
<tr>
<td>Between seasons: Frequency of songs</td>
</tr>
<tr>
<td>Between sites: Frequency of songs</td>
</tr>
<tr>
<td>In May, between sites: Frequency of songs</td>
</tr>
<tr>
<td>In May, between sites: Frequency of a singing Carolina wren’s presence</td>
</tr>
<tr>
<td>In July, between sites: Frequency of songs</td>
</tr>
<tr>
<td>In May, within the urban site: Frequency of songs</td>
</tr>
<tr>
<td>In May, within the rural site: Frequency of songs</td>
</tr>
<tr>
<td>Between seasons: Frequency of a singing Carolina wren’s presence</td>
</tr>
<tr>
<td>Between sites: Frequency of a singing Carolina wren’s presence</td>
</tr>
<tr>
<td>In July, between sites: Frequency of a singing Carolina wren’s presence</td>
</tr>
<tr>
<td>In May, within the urban site: Frequency of a singing Carolina wren’s presence</td>
</tr>
<tr>
<td>In July, within the urban site: Frequency of songs</td>
</tr>
</tbody>
</table>
In July, within the urban site: Frequency of a singing Carolina wren’s presence

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Statistical Test</th>
<th>Significant? (Y/N)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chi-squared</td>
<td>N</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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In May, within the rural site: Frequency of a singing Carolina wren’s presence

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Statistical Test</th>
<th>Significant? (Y/N)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chi-squared</td>
<td>N</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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In July, within the rural site: Frequency of songs

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Statistical Test</th>
<th>Significant? (Y/N)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chi-squared</td>
<td>N</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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In July, within the rural site: Frequency of a singing Carolina wren’s presence

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Statistical Test</th>
<th>Significant? (Y/N)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chi-squared</td>
<td>N</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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### Differences in daily singing activity

**Comparison** | **Statistical Test** | **Significant? (Y/N)** | **Notes** |
--- | --- | --- | --- |
Overall daily singing activity | Visual analysis | No singing 21:00 – 04:00. Dawn chorus peak. Smaller dusk chorus peak. Mid-day lull in singing activity. |
May vs. July daily singing activity | Visual analysis | Dawn and dusk chorus greater in May than July. Dawn chorus in May lasts twice as long as in July. |
Urban vs. rural daily singing activity | Visual analysis | Patterns generally the same at both sites. |

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### Correlations between singing activity and temperature

**Comparison** | **Statistical Test** | **Significant? (Y/N)** | **Notes** |
--- | --- | --- | --- |
Between seasons | Zero-inflated Poisson regression | Y | Temperature is highly significant predictor in both months. Singing activity is negatively correlated with temperature in both months. Relationship the same in both months. |

65
<table>
<thead>
<tr>
<th>Between sites</th>
<th>Zero-inflated Poisson regression</th>
<th>Y</th>
<th>Temperature is highly significant predictor at both sites. Singing activity is negatively correlated with temperature at both sites. Relationship the same at both sites.</th>
</tr>
</thead>
</table>

**Correlations between singing activity and anthropogenic noise**

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Statistical Test</th>
<th>Significant? (Y/N)</th>
<th>Notes</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between seasons</td>
<td>Zero-inflated Poisson regression</td>
<td>Y</td>
<td>Anthropogenic noise is highly significant predictor in both months. May: singing activity positively correlated with anthropogenic noise. July: singing activity negatively correlated with anthropogenic noise.</td>
<td>68</td>
</tr>
<tr>
<td>Between sites</td>
<td>Zero-inflated Poisson regression</td>
<td>Y</td>
<td>Anthropogenic noise is significant predictor at both sites. Singing activity positively correlated with anthropogenic noise at both sites. Relationship appears to be different at the two sites.</td>
<td>70</td>
</tr>
<tr>
<td>May urban vs. July urban (Post hoc analysis)</td>
<td>Zero-inflated Poisson regression</td>
<td>Y</td>
<td>May: Anthropogenic noise is highly significant predictor. July: Anthropogenic noise is barely significant predictor. Both months: singing activity positively correlated with noise.</td>
<td>71</td>
</tr>
<tr>
<td>May rural vs. July rural (Post hoc analysis)</td>
<td>Zero-inflated Poisson regression</td>
<td>N</td>
<td></td>
<td>71</td>
</tr>
</tbody>
</table>
Discussion

Differences in singing activity between sites and seasons

I analyzed the singing activity between sites and seasons in two different ways. The first method used the number of songs in each recording to determine the frequency of singing activity. The second method focused on the frequency of a singing Carolina Wren being present. Simpson (1982) found considerable variation in the number of songs individual Carolina Wrens sang per hour. Given that Carolina Wrens are year-round territorial, it is likely that each data logger recorded songs from a very small number of Carolina Wrens. Much of the variation in number of songs from each data logger, therefore, could be due to variation in singing activity of individual birds and not to variation among sites or seasons. For that reason, I consider the presence / absence data for singing Carolina Wrens to be the more robust dataset. Analysis of within-site variation supports this conclusion. At both the urban and rural sites in May, the observed frequency for number of songs at the two data loggers was significantly different from the expected frequency, but the observed frequency of the presence of singing Carolina Wrens did not differ from the expected. However, at both sites in July there was no within-site deviation from the expected frequencies for either method of analysis.

The two methods (frequency of songs vs. frequency of singing presence) for analyzing the data answer slightly different questions. The questions in which I am most interested deal with the frequency of singing activity defined by the number of songs per recording. My discussion, therefore, focuses on the results involving the frequency of songs. However, recognizing that this is the less robust dataset, I also compare those findings to the results from the more robust presence / absence dataset.
Carolina Wren singing activity in North Carolina peaks in July when hatch-year males are establishing and defending territories (Simpson 1982). This peak in singing activity is due in part to increased territorial interactions between hatch-year and after-hatch-year birds and partly due to variations in singing activity between hatch-year and after-hatch-year birds (Simpson 1982). Although the frequency of songs recorded in May and July were out of proportion with the expected frequency, the more robust presence / absence dataset failed to detect a difference in the two months. Increasing the sample size to account for individual variation in singing activity among Carolina Wrens, may allow for a more confident analysis of the number of songs detected in each month. However, the fact that I made my July observations during the first week of the month, suggests an alternative explanation that supports the presence / absence results. Simpson (1982) found no difference in the number of songs that her Carolina Wrens sang in April, May, and June. It is possible that I simply sampled too early in July to detect a difference in singing activity. In other words, my early July 2009 Kentucky-based Carolina Wrens could have been acting more like Simpson’s June 1982 North Carolina-based wrens than her July wrens.

A multitude of studies shows that wildlife can respond in a variety of ways to noise. Urban environments are typically noisier than similar rural environments. One relatively simple way of dealing with noisy environments is to increase the number of times the information is sent (reviewed in Brumm and Slabberkoorn 2005). This could take the form of increasing the number of songs / calls or increasing the number of syllables within a song / call (reviewed in Brumm and Slabberkoorn 2005, Warren et al. 2006). However, in the presence of anthropogenic noise, some species actually decrease
their calling rates (3 species of anurans: Sun and Narnis 2005) or the number of notes within their songs (house finch: Fernández-Juricic et al. 2005). I compared the frequency of singing activity at the urban site and rural sites to see if the observed frequencies would be out of proportion with the expected frequencies. More songs occurred in the urban site than the rural site, and the frequency of songs was out of proportion with the expected frequency. However, the more robust presence / absence data detected no difference in the observed and expected frequency of singing Carolina Wrens at the urban and rural sites.

I was also curious about the interactive effect of season and site. To look for differences in the interactive effect, I compared the frequency of rural and urban singing activity in each of the two months. In July, Carolina Wrens sang more songs at the rural site than the urban site and the observed frequency of those songs was significantly different from the expected frequency. This is what would have been expected based on Simpson’s (1982) findings. The MAPS data indicates that hatch-year Carolina wrens typically begin appearing in Mammoth Cave National Park a week and a half to 2 weeks before my July sampling period. Simpson attributed her findings of increased singing activity in July to hatch-year birds which sing more than after-hatch-year birds and which are beginning to establish territories, thus creating more territorial interactions. This might also explain my finding of increased singing activity at the rural site in July; however, there is no way to test this based on the data collected as part of this study. On the other hand, the observed presence of singing Carolina Wrens was not different from the expected frequency.
The May analyses, however, indicate that the observed frequencies are out of proportion with the expected frequencies for both methods of analysis. In May, the Carolina Wrens at the urban site sang more songs than their rural counterparts did. One possible reason for urban Carolina Wrens singing more than rural Carolina Wrens in May could be that urban wrens experienced higher mortality, and thus were singing both to defend their territories and to attract new mates. Increased mortality among urban animals has been documented in other species, and the dual purpose of singing could result in increased singing activity. Another possible explanation could be that the urban Carolina Wrens began breeding earlier than the rural wrens, as has been shown in other locations with other species. This could have allowed the first fledglings to start singing by the time my observations were made in late May, but I consider this an unlikely explanation. Very few of the recordings made by the data loggers at BG-01, BP-01, or BP-02 had more than one Carolina Wren singing during a given sampling period. I frequently noted 2 Carolina Wrens singing at the BG-02 data logger during a sampling period. The presence of 2 singing Carolina Wrens on so many of the BG-02 recordings is most likely due to its location being at the edge of 2 territories. With such a small sample size, it is possible that the presence of an “extra” wren at the BG-02 site in May could explain a large amount of the difference in singing activity between the urban and rural site. A third explanation could be that the urban Carolina Wrens, like many other urban animals, had smaller territories and those territories were more densely packed than the rural wrens. This could have led to increased territorial interactions (i.e. singing) in the urban wrens during a crucial time in the breeding season. All of the above explanations,
however, are purely speculative since the data necessary for analyzing the different possibilities were not gathered.

**Daily singing activity patterns**

Preliminary analysis of the daily patterns of Carolina Wren singing activity used Fourier transforms to compare the average number of songs detected over the course of a 24-hour day to what was observed (unpub. data). This analysis was conducted separately for each data logger for each week analyzed, resulting in 8 analyses using Fourier transforms. The correlation coefficients for each analysis were very low and ranged from $r = 0.3208$ to $r = 0.5337$. Much of the correlation between the expected and observed activity patterns can be attributed to the 8 hours each day between sunset and sunrise when no Carolina Wrens were heard singing. This suggests that as long as it is daylight, other variables besides time of day are likely to play a larger role in determining the daily singing activity patterns of Carolina Wrens. However, time of day may influence or covary with those other variables. It is therefore useful to visually analyze the daily activity data for general patterns even if the patterns are statistically weak.

Visual analysis of the average number of songs recorded during each sampling period over the course of a 24-hour day suggests that in general Carolina Wrens follow the most common pattern of singing activity described by Stacier et al. (1996). The wrens in my study have a morning peak in activity that corresponds to the dawn chorus and then a slow decline throughout the day. A small peak in singing activity can also be found in the hour immediately preceding sunset. Simpson (1982) observed a decline in singing activity in response to playbacks later in the morning compared to earlier in the morning. Shy and Morton (1986) also reported that at mid-day Carolina Wrens sing less in
response to playbacks. However at mid-day, the wrens in their study increased the amount of time they spent searching for the “intruder” and more closely approached the speaker or edge of their territory. Amrhein and Erne (2006) obtained similar results with Winter Wrens. Shy and Morton (1986) suggested that this behavior may have developed because after fasting overnight, singing is less energetically costly than other forms of territorial defense and the early morning acoustical environment is better for singing than at other times of the day.

In both May and July, sunrise and sunset occurred at approximately the same time. Any seasonal shifts in the beginning or ending of singing activity due to shifts in the time of sunrise or sunset would likely have been relatively small. Sampling for only 3 minutes at the beginning of each hour is unlikely to have detected any such minor shifts in timing of first or last song. The most interesting observation from comparing average singing activity in May and July is that in May the dawn chorus lasts almost twice as long as it does in July.

One common explanation for the dawn chorus is that it serves as a territorial defense mechanism. However, several studies have documented increased dawn and dusk singing activity earlier in the breeding season compared to later in the breeding season (Reed Warblers: Catchpole 1973; Ovenbirds: Lein 1981; Nightingales: Amrhein et al. 2004). Those researchers hypothesized that the increased singing early in the breeding season functioned primarily in mate attraction and social pair bonding. Singing in Carolina Wrens is often considered to play a greater role in maintaining territories than in mate attraction; however, this does not preclude a possible pair bonding or mate guarding role early in the breeding season. Many passerines lay their eggs before mid-day. Male
European Starlings (Pinxten and Eens 1998) and Nightingales (Amrhein et al. 2004) increase their singing rates around the time that the female lays her egg. The increased singing at this time is thought to serve in soliciting copulations (Pinxten and Eens 1998, Amrhein et al. 2004). Typically, more Carolina Wrens are actively maintaining nests in May than in July. One possible explanation for the longer dawn chorus in May is that male Carolina Wrens may use song to solicit copulations from their mate after she has laid her egg for the day. Under this hypothesis, the first 3 hours of singing which are common to both May and July would be attributed to territorial defense. The second 3 hours of the dawn chorus, which are found only in May, would be attributed to maintaining pair bonds and soliciting copulations.

Also of note is the large peak in singing activity immediately prior to sunset in May. This large peak is absent in the July data. Both Reed Warblers (Catchpole 1973) and Nightingales (Amrhein et al. 2004) sing more at dusk early in the breeding season compared to later in the breeding season. Catchpole (1973) reported that paired Reed Warblers contributed more to the dusk chorus than unpaired Reed Warblers. However, he was unable to identify the causal factor for the difference between paired and unpaired contributions to the dusk chorus. Amrhein et al. (2004) found that the Nightingale peak in dusk singing activity was correlated with the egg-laying period. It is possible that the apparent peak in dusk singing activity that I observed in May is also related to the egg-laying period. Although Carolina Wrens can still be laying eggs in July, most eggs are laid before then. It will be interesting to see if future research supports this hypothesis.

Although other species of birds may temporally shift their singing activity to predawn or nighttime hours in urban areas (e.g., American Robin: Miller 2006; European
Robin: Fuller et al. 2007; European Blackbirds: Nemeth and Brumm 2009), Carolina Wrens on my urban study site did not exhibit this behavior. In general, the urban birds in my study had similar singing activity patterns to the rural birds in my study (Figure 19). Visual analysis of the average number of songs at the rural and urban sites suggests that the major difference between urban and rural wrens is that urban wrens sing more than rural wrens. This observation supports the earlier Chi-squared analysis based on number of songs detected that indicated a difference in the observed and expected frequencies of singing activity in urban compared to rural Carolina Wrens. However, once again the small sample size and frequent presence of more than one Carolina Wren singing during individual sampling periods at BG-02 could have skewed the results.

*Correlation between singing activity and temperature*

Previous studies show mixed results for the correlations between singing activity and temperature for other species. Extreme temperatures tend to have a negative influence on the singing activity of birds (Lein 1981). In Winter Wrens and Great Tits, singing activity is not correlated with temperature during observation; however, minimum overnight temperature is correlated with dawn chorus activity the following morning (Garson and Hunter 1979). Singing activity in other species is positively correlated with temperature (Shaver and Walker 1930, Thomas 1999); however, these influences may be secondary to changes in light levels (Catchpole 1973). Still other researchers have found no significant correlation between weather variables and amount of singing (Berg et al. 2005).
Carolina Wrens sing year-round, although winter singing rates are lower than during the breeding season. In winter, Carolina Wrens exhibit a positive relationship between singing and temperature (Strain and Mumme 1988). My study, however, indicates a highly significant and negative effect of temperature on Carolina Wren singing activity in both May and July. Extremes in temperature could explain the contradictory results. In Strain and Mumme’s (1988) study, mean morning temperatures ranged from -10 °C to approximately 20 °C. Temperatures during my study periods in May and July ranged from 11°C to 32 °C. (Both the low and high temperatures in my study occurred during daylight hours.) It is possible that Strain and Mumme’s sample included the effects of “extreme” low temperatures on Carolina Wren singing activity, while my study included the effects of “extreme” high temperatures on Carolina Wren singing activity. In other words, we sampled different tails of the singing-temperature distribution curve. If so, then this could be one explanation for why they found a positive relationship with temperature and I found a negative relationship.

In this study, I specifically chose weeks in May and July that had similar temperatures in order to hold the temperature variable as constant as possible in a field study. A comparison of the correlation between temperature and singing activity in May and July shows that it has the same relationship in both months. This finding supports my conclusion that the contradictory results between Mumme and Strain’s 1988 winter study and my 2009 summer study of Carolina Wren singing activity are due to sampling at different extremes of temperature. It also suggests that in Carolina Wrens, temperature may be a very important predictor for singing activity. My finding that temperature appears to have a highly significant negative relationship with singing activity in both
urban and rural areas provides additional support for the conclusion that temperature is an important predictor for singing activity in a variety of settings and seasons. It also suggests important behavioral implications as temperatures change locally due to urbanization and the associated “heat sink” effect and globally due to climatic changes.

**Correlation between singing activity and anthropogenic noise**

Many recent studies have shown that anthropogenic noise can have a variety of effects on the singing behavior of birds and the communication strategies of other animals. I conducted zero-inflated Poisson regressions to determine whether Carolina Wren singing activity and anthropogenic noise are correlated at my urban and rural site and between seasons. At both the urban and the rural site, anthropogenic noise had a significant positive relationship with singing activity, but the confidence intervals and p-values suggest that anthropogenic noise may have slightly different effects in the two areas. One possible explanation for this difference can be attributed to the different levels of anthropogenic noise at the urban and rural sites. At the rural site, anthropogenic noise was most often coded as 0 or 1. On the other hand, anthropogenic noise at the urban site was most often coded as 2 or 3 with several 4s also being recorded. I never recorded a 4 at the rural sites or a 0 at the urban sites. It would be much harder to detect a relationship between singing activity and anthropogenic noise at the rural site, because anthropogenic noise is so rare. However, at the urban site where anthropogenic noise was common, the relationship may be much easier to detect.

The correlation between singing activity and anthropogenic noise also varies by season. In May, anthropogenic noise has a highly significant positive relationship with
singing activity, while in July the relationship is negative. Reviewing the anthropogenic noise levels by month did not reveal any obvious differences in the amounts of noise in May compared to July. One possible hypothesis for the different effects of anthropogenic noise in May and July could relate to the different breeding stages of the birds. In May, singing may serve a pair bonding and mating role in addition to a territorial role. The possible pair bonding and mating role of the singing activity would make “being heard” much more critical for individual males. Thus, one way to combat increasing anthropogenic noise could be to sing more often. This would result in the observed positive relationship between anthropogenic noise and singing activity.

In July, singing activity likely serves primarily a territorial role. Although Carolina Wrens are still nesting at this time, nesting activity typically is much lower in July compared to May. Mammoth Cave National Park’s MAPS banding station did not catch any breeding female Carolina wrens in 2007, 2008, or 2009 before the first hatch-year wrens were caught for the year. It can be speculated that this was due to the females spending most of their time incubating the eggs. After hatch-year-birds began to be caught, adult female Carolina wrens also began to be captured. Based on their brood patches, it can be speculated that some of the birds were done breeding for the season while one may have been starting a new clutch.

Singing and countersinging are the primary ways in which Carolina Wrens maintain their territories. Simpson (1982) found that caged wrens can maintain their territories through song alone for at least 30 days. However, free Carolina Wrens also utilize other methods such as physically seeking out intruders and will often do so during mid-day when singing activity drops (Shy and Morton 1986). It is, therefore, possible that
“being heard” is not as important in July as it is in May because the wrens have other methods of maintaining their territories while they do not have other methods for soliciting copulations. If this hypothesis is true, as anthropogenic noise increases in July, Carolina Wrens may simply “shut up” and switch to methods of territory guarding that do not rely on competing with excess anthropogenic noise.

My post hoc analysis of the interactive effects of site and season provide preliminary support for this hypothesis. Anthropogenic noise was not a significant predictor for singing activity during either month at the rural site. It was a significant predictor during both months at the urban site. At the urban site, anthropogenic noise was a highly significant predictor of singing activity in May; however, in July it was barely significant. This is exactly what one would expect to find if 1) there was very little anthropogenic noise in rural areas to affect singing activity, and 2) if “being heard” was more important in May than in July. It is important to keep in mind that the post hoc analysis is purely preliminary because with only 2 data loggers at each site, it is possible that the observed variation in singing activity could be attributed to a more vocal individual or an “extra” wren as was often observed in the May BG-02 dataset. More research needs to be done to test this hypothesis.

**Limitations of this project**

The biggest limitation of this study was the small sample size. Only 4 data loggers (2 at the rural site and 2 at the urban site) were used to record the data. The analyses looking at overall trends in singing activity or comparing singing activity between seasons is more statistically robust than the data comparing urban and rural sites. This is
because the overall and seasonal data have larger sample sizes (n = 8 and n = 4, respectively). However, the analyses comparing urban and rural singing activity only have a sample size of 2 data loggers within 1 urban site and 1 rural site. Since a sample size of 2 is not statistically acceptable, it is important to view all of the urban and rural data as preliminary until the results can be tested using more data loggers and preferably more than 1 urban and 1 rural site.

Carolina Wrens are year-round territorial so it is likely that the same individual or small group of individual birds were repeatedly sampled at each of the data logger locations. Singing activity is highly variable among individual Carolina Wrens (Simpson 1982). This high individual variation in singing activity could have highly skewed my results. In addition, Carolina Wrens sing more at the center of their territories than at the edges of their territories (Simpson 1982), yet I had no way of knowing where the data loggers were located in relation to the recorded Carolina Wrens’ territories.

**Directions for future research**

Future research using similar methods to explore the effects of temperature and anthropogenic noise on avian singing activity in urban and rural areas should be conducted with an increased number of sites, more data loggers, and fewer days of sampling. This modified methodology should allow for better statistical analysis of the data. It would also be helpful to map the territories of the observed focal species. Mapping of the territories would allow the location of the data loggers within the territories to be controlled for during the analysis. Conducting nest searches to identify
the stage of the breeding cycle that the individual wrens are in would provide additional important information.

My data suggest two interesting lines of future research. The first direction for future research suggested by my results is to determine how the singing activity of individual Carolina wren males correlates with the timing of their mate’s egg laying or with attempts to solicit copulations. Research in this direction could help explain why Carolina Wrens have a dawn chorus in May that is nearly twice as long as their dawn chorus in July. It may also help explain why in May Carolina Wren singing activity is positively correlated with anthropogenic noise while it is negatively correlated with anthropogenic noise in July. The second direction for future research suggested by my results is determining the importance of singing and “being heard” early in the breeding season compared to later in the breeding season. This research may help explain the preliminary results I obtained from my post hoc analysis of the interactive effects of site and season on the correlation between singing activity and anthropogenic noise.

Common adaptations to anthropogenic noise in other species include preferences for specific song types in noisy versus more quiet areas, varying the number of notes per song, increasing the amplitude of songs, and raising the minimum frequency of lower frequency notes. All of these would be interesting lines of research to pursue for Carolina Wrens. In addition, knowing how changes in those song characteristics affects other behaviors and life history choices would provide a valuable component to understanding how urbanization and the associated increases in anthropogenic noise is affecting this common southeastern bird.
Literature Cited


