THE DIFFERENT USE OF AN URBAN AND RURAL HABITAT BY WINTERING AND RESIDENT SONG SPARROWS (*Melospiza melodia*): A CASE STUDY FROM WESTERN NORTH CAROLINA.

A thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science in Biology.

By

Meredith Layne Carroll

Advisor:
Dr. Jeremy Hyman
Assistant Professor of Biology
Biology Department

Committee Members:
Dr. Sean O'Connell, Biology
Dr. Joseph H. K. Pechmann, Biology

June 2010

Acknowledgments

I would like to thank Dr. Jeremy Hyman for his advice and support. His knowledge and insight into the lives of song sparrows have been invaluable to my research. I greatly appreciate the time and expertise of my committee members, which include Dr. Jeremy Hyman, Dr. Joe Pechmann, and Dr. Sean O'Connell. I have received a wonderful educational opportunity from the Biology Department and the Graduate School of Western Carolina University and its faculty and staff including Dr. Sabine Rundle, Dr. Tom Martin, Dr. Laura DeWald, Dr. Jeremy Hyman, and Dr. Beverly Collins.

I would also like to thank Western Carolina University and the Eastern Band of Cherokee Indians for allowing me to conduct this research on their land. Other individuals have contributed to the final product of this work through banding birds, locating territories, and aiding in collecting survey data: Dr. Jeremy Hyman, Kyle Boudreau, Jackson Evans, Trey Bellows, Ashley Houston, and Andi Garcia.

Lastly, I would like to recognize my parents, Dr. Karen Carroll and Eddie Carroll, my first teachers, whose financial and moral support throughout the course of my life have made this possible, and who have taught me to challenge myself and reach for my dreams.

Table of Contents

List of Figures

List of Tables

List of Appendixes

Abstract

Differences in environments have the potential to affect the behaviors of animals within these areas. In comparison to rural environments, urban environments provide a warmer microhabitat, different predation risk levels, more anthropogenic food opportunities, and artificial light sources. Non-migratory song birds within urban environments have been shown to have a higher local survival rate, earlier gonad development, and better mating success. For this research, weekly point count surveys were conducted at an urban and a rural site in western North Carolina from October 2009 to April 2010 to count and identify banded and non-banded individuals in order to determine if a difference existed between the proportions of migrating individuals. Each site contained a partial migratory population of song sparrows (*Melospiza melodia*), that have already been shown to differ in their average levels of aggression and boldness. Results showed that significantly more males remained as yearlong residents in the urban population than in the rural population ($p = 0.024$), while all females from each population migrated over the winter. Nearly ten times as many migrating song sparrows on average were observed on the rural site than on the urban site during the survey months of November 2009 to January 2010 than within the urban site ($p < 0.001$). These results, in conjunction with the higher abundance of summer territories in the urban site, may mean that song sparrows have different criteria for evaluating what is considered a good summer territory versus a good wintering area. The higher number of yearlong resident males at the urban site may be due to these individuals occupying their summer territory areas so that these prime sites are not taken by other males during the course of the migration period.

Keywords: urbanization, song sparrow, Melospiza melodia, migration, partial migration

The Different Use of an Urban and Rural Habitat by Wintering and Resident Song Sparrows (*Melospiza melodia*): A Case Study from Western North Carolina.

Animals in different environments face different selective pressures. Environmental differences between two different sites could include temperature, elevation, ecosystem type, and land use, to name a few. For animals inhabiting both urban and rural habitats, the urban habitat can present selective pressures very different from those in the animal's natural habitat.

Urbanization can be defined as a concentrated human presence in industrial and residential settings and the associated affects, and for the purposes of ecological studies, urban centers have been quantified as an area containing more than 2,500 people (Chace & Walsh, 2006). Urban environments provide an array of different features than rural environments. For many bird species, urbanization has little to no effect on reducing abundance (Hostetler *et al.,* 2005). In fact, an urban environment can offer many benefits to song birds.

The large amount of reflective surfaces, including asphalt, cement, buildings, and cars, within an urbanized area creates a warmer microclimate than surrounding rural areas; this is known as an urban heat island (Terjung & Louie, 1973; Shochat *et al.,* 2006). Predation risks can vary between rural and urban environments, with some research supporting a higher to equal survival rate for song birds in urban settings compared to rural environments (Whittaker & Marzluff, 2009), while other studies suggest lower levels (Schmidt & Whelan, 1999; Borgmann & Rodewald, 2004). McCleery *et al.* (2008) found that fox squirrel (*Sciurus niger*)

predation accounted for more than 60% of deaths in rural environments while it only accounted for approximately 5% of deaths in urban environments. Collisions with motor vehicles were the most common cause of fatality in the urban environments at a frequency of more than 60%.

Urbanization alters the dynamics of food availability and even foraging behaviors for animals living within these urban environments by providing anthropogenic food sources such as feeders and trashcans (Fleischer *et al.,* 2003). Urbanization also provides artificial light from streetlights, car lights, and windows. This can increase the time available for diurnal animals to continue foraging and other activities that typically must rely on a natural photoperiod.

Differences between these two types of environments have the potential to affect the behaviors of animals living within them. Estes and Mannan (2003) found that Cooper's hawk's (*Accipiter cooperii)* rate of prey delivery to young and prey variety was higher at urban nests resulting in delivery of greater biomass. Surprisingly, they also observed greater prey diversity delivered at urban nests.

Song sparrows (*Melospiza melodia*) at an urban site in western North Carolina showed higher levels of aggression and boldness than those at a rural site (Evans *et al.,* in press). During playback experiments, urban individuals were more likely to show a high level of aggression, measured as the minimum distance the individual got from the speaker during the experiment. Urban individuals were also found to be bolder on average, or had a lower flight initiation distance (as measured by distance the bird allowed researchers to approach before fleeing). With this evidence of aggression and boldness between these two populations, this provides a prime opportunity to examine other possible behavior differences.

Differences in aggression and boldness between these rural and urban North Carolina populations raised the question of whether they might differ in migration behaviors. Although in previous years specific birds were not banded for individual identification, birds were seen in the same general territory areas throughout the winter months at the urban site. This led me to ask if these individuals were in fact yearlong residents, and if so, could this also be the case for individuals of the rural population.

Migration, a bidirectional seasonal movement between geographic areas, is an important behavior in the life history of many animals (Baker 1978; Gauthreaux 1982; Taylor 1986). The majority of migration research conducted has concentrated on the long-distance movements of obligate migrants (Iverson *et al.*, 1996; Stokes *et al.*, 1998; Martell *et. al*, 2001; Kamiya & Ozaki, 2002; Bêty *et al.,* 2004; Landys *et. al*, 2005). However, populations and individuals of many species are only short distance or partial migrants (Adriaensen & Dhondt, 1990; Belthoff & Gauthreaux 1991; Chan, 2001; Forchammer *et al.*, 2002; White *et al.* 2007; Partecke & Gwinner, 2007; Boyle, 2008). Partial migration occurs when not all individuals of a local group or population migrate and this behavior can vary within a species and population (Adriaensen & Dhondt, 1990; Gill, 1995; Chan, 2001; Pérez-Tris *et al.,* 2004).

Environmental factors can affect migration behaviors. Global climate change has been shown to alter bird migration patterns via extended breeding seasons and delayed or advanced autumn migrations (Sokolove *et al.* 1999; Bairlein & Winkel, 2001; McCarty, 2001; Jenni & Kery, 2003; Marra *et al.,* 2005). The level of seasonality of an area has been shown to affect the migration behaviors of black caps *(Sylvia atricapilla)* and European robins (*Erithacus rubecula)*, with lower seasonality leading to decreased migratory restlessness (Pérez -Tris & Telleria,

2002). This research also found a difference in effect across species, with seasonality differences having a stronger effect on black caps than on robins.

Land use differences, specifically those between urban and rural environments, are another environmental factor with the potential to affect migration behavior. Two song sparrow populations from western North Carolina, one urban and one rural, both appear to be partially migratory (J. Hyman, personal communication), although different song sparrow populations may exhibit different migratory behaviors including full sedentariness, partial migration, and full migration (Wingfield & Soma, 2002; Sandercock & Jaramillo, 2002; Arcese *et al.,* 2002). Because these particular populations appear to be partially migratory, it is possible to examine if differences exist between the two populations in the number of birds that are yearlong residents and migrants. In addition, the two sites are located within a range that serves as the wintering ground for other migrating song sparrows. This allows for the documentation of the number of migrating song sparrows that choose either environment type for their wintering ground.

No previous research exists that examines the possible differences in migration by song sparrows in these two different environment types. However, a limited number of studies in other species have looked at the effects that the differences between urban and rural environments can have on bird migration behaviors. Adriaensen & Dhondt (1990) examined the difference in European robin migrations within three different environments in close proximity in Belgium: park lands, gardens, and woodlands. Both park land and gardens were considered urbanized sites, and the neighboring woodland area was defined as a rural site. Males from the two urbanized environments were less likely to migrate over the winter when

compared to those with summer territories in the woodlands. Non-migratory males experienced a higher local survival rate, although cold winters decreased this benefit. A later settling date correlated with a decrease in mating success for males, and the probability of breeding was two to four times greater for residents then for migrant European robins.

Partecke and Gwinner (2007) observed hand-raised European blackbirds (*Turdus merula*) in Germany from both urban and forest environment. The researchers found a decrease in migratory restlessness and fat deposition for urban, male individuals; a trend that continued across years for the same individuals. In addition, these more sedentary males showed earlier gonad development. In fact, urban blackbirds developed gonads an average of three weeks before their rural counterparts, while the timing of their gonad regression did not differ across environment types (Partecke *et al.,* 2005).

These studies and others suggest that early arrival is important to a male's reproductive success for that breeding season by extending the length of the breeding season. Florida scrub-jays (*Aphelocoma coerulescens*), dark-eyed juncos (*Junco hyemalis*), and song sparrows have been observed nesting earlier in urban habitats when compared to individuals within rural habitats of the same general proximity (Schoech & Bowman, 2001; Yeh & Price, 2004; J. Hyman personal communication). This longer breeding season can lead, in some cases, to greater mating success (Yeh & Price, 2004).

Remaining as a yearlong resident, assuming survival, would appear to be a successful strategy to insure the earliest arrival possible onto a territory. I examined if the strategy of remaining as a yearlong resident, as opposed to migrating over the winter, is employed at a different rate between an urban and rural population. I simultaneously examined the use of

these two different environments by wintering migrant song sparrows to determine if there were differences in settling locations for these individuals.

Methods

I conducted winter bird surveys at a rural and an urban site in western North Carolina. The urban site was located within the center of the Western Carolina University (WCU) campus in Cullowhee, North Carolina and the rural site was the Kituwah Farm and flying fields in Bryson City, North Carolina. These sites are 23.74 km apart and are at elevations of 641m and 549m, respectively. Western Carolina University has a total of nearly 9,500 students. There are 22 buildings within the central main campus area of approximately 4.405 km^2. The Kituwah site is 4.425 km^2 of farmland with hedge rows, bordered by the Tuckasegee River and the Nantahala National Forest as well as a light traffic railroad. Boundaries of the WCU site for this research were selected to include the most central sections of the main campus. The Kituwah site boundaries were defined by the area's natural borders and the locations of previously mapped song sparrow territories. Aerial views of the two sites show the differences in land use and the location of summer territories (Figures 1 & 2).

Song sparrows were selected as the species for this study based on some of their general traits as well as the knowledge that there were previously documented behavioral differences between two particular populations (Evans *et al.,* in press). Song sparrows are omnivorous song birds that are wide spread throughout Canada, the United States, and Northern Mexico. They are an edge species, preferring habitat that contains both open foraging areas, low dense brush for cover and nesting, and taller structures from which to sing.

Males are territorial and sing to attract females and defend their territory. Both sexes have similar physical characteristics and can be differentiated between by examining the gonads during the breeding season. Populations of song sparrows may be migratory, partially migratory, or non-migratory (Arcese *et al.,* 2002).

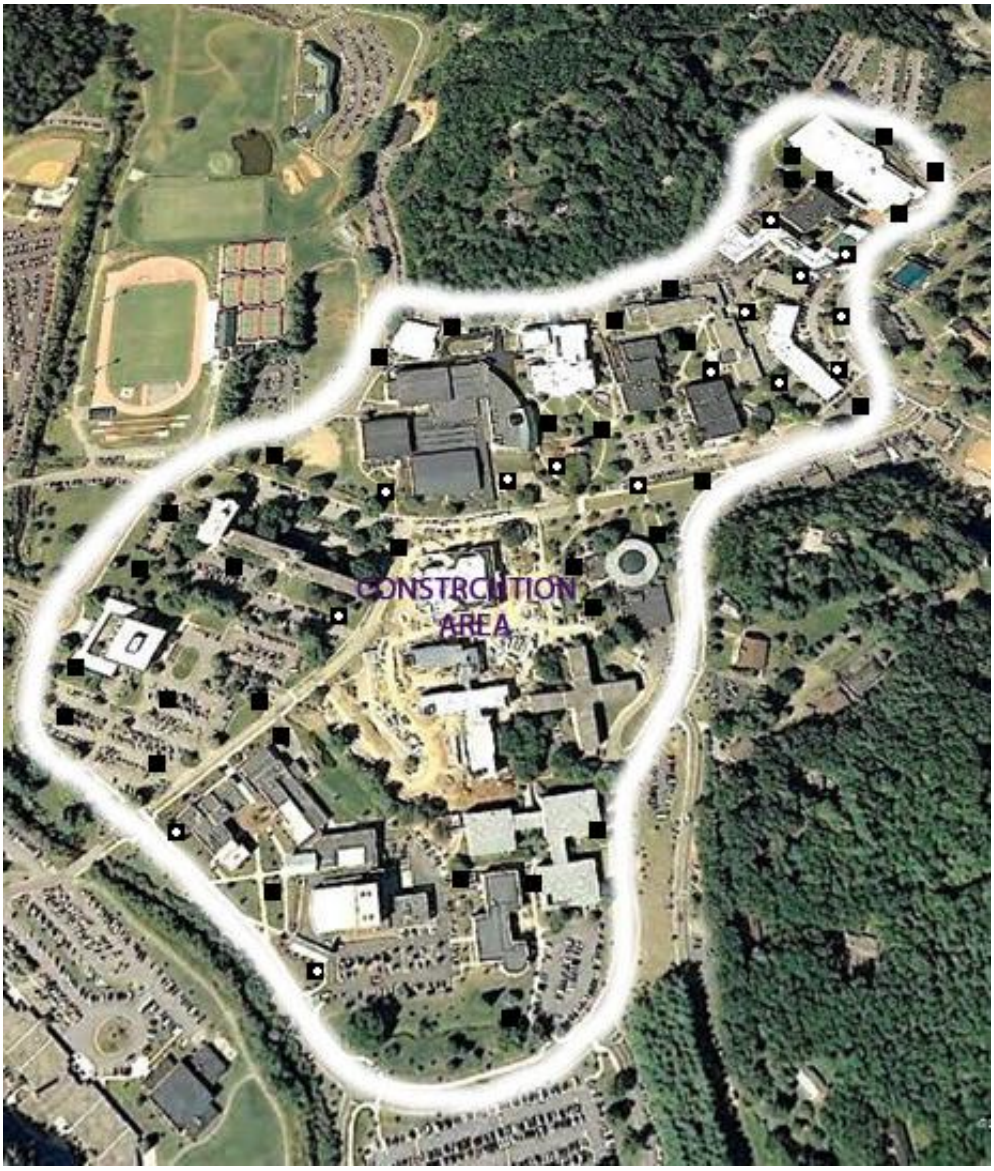

Figure 1. Aerial view of central Western Carolina University campus in Cullowhee, North Carolina. The study site is outlined in white and the central locations of 2009 summer territories have been marked with a black square. The summer territories of yearlong residents have been marked with a white circle within the black square.

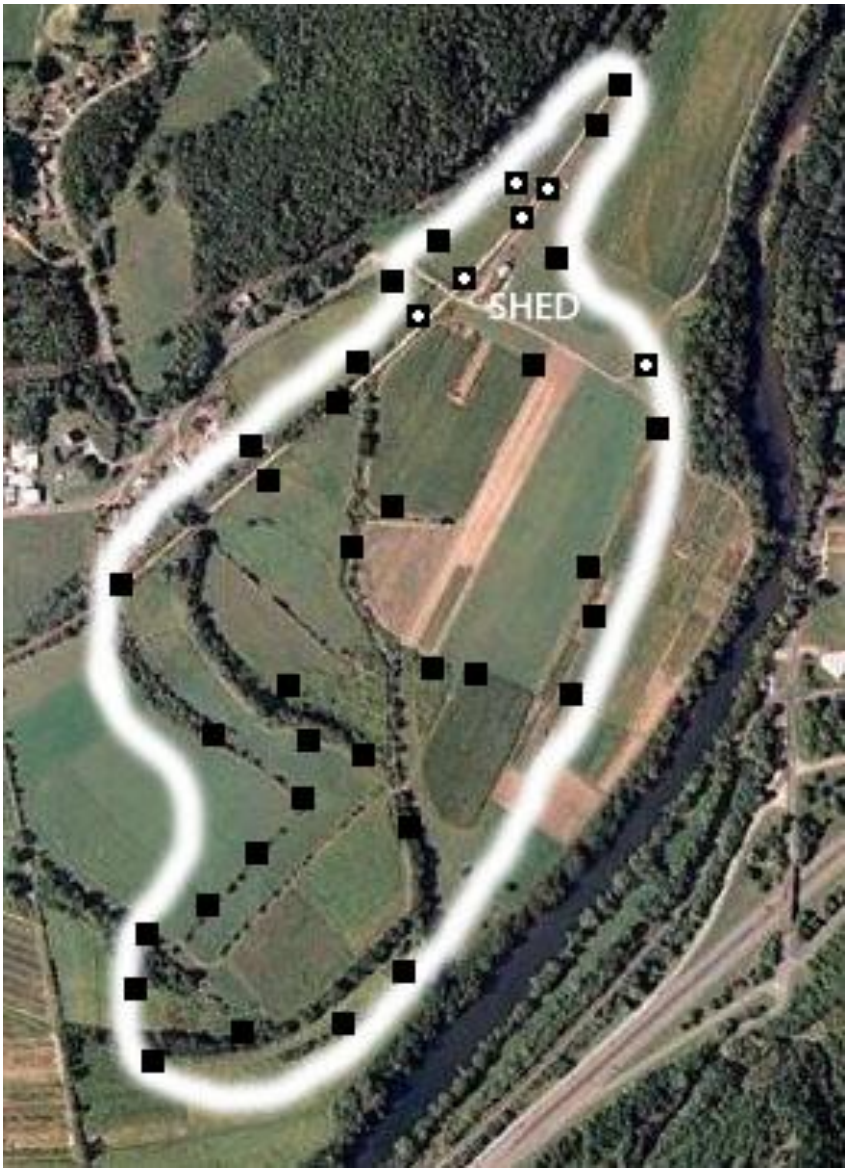

Figure 2. Aerial view of Kituwah Farm and flying fields in Bryson City, North Carolina. The study site is outlined in white and the central locations of 2009 summer territories have been marked with a black square. The summer territories of yearlong residents have been marked with a white circle within the black square.

From May 2009 to July 2009 song sparrows were caught and banded at both sites. They were attracted by song playback and caught in mist nets. Each individual was banded with a specific color combination of three color bands and one US Fish and Wildlife metal identification band. Along with banding, general measurements of wing length, tarsus length,

weight, and bill dimensions (depth, width, and length) were recorded for each individual. Also during the summer of 2009, play back experiments were used at each site to determine the territories of the summer resident song sparrows. The WCU site had 41 summer residents (26 males, 15 females) with summer territories within the area selected for this research. Only the individual territories located within the most central section of the WCU campus were used in order to reduce any effects from the less urbanized edges of the campus. The Kituwah site had 32 (26 males, 6 females) color-banded summer residents for the summer of 2009. All of the Kituwah summer residents were included in this study.

Weekly point count surveys were conducted between October 1st 2009 and April 30th 2010 at each site. These point count surveys were conducted along a predetermined path that allowed all areas of a site to be assessed while reducing the amount of time spent backtracking. Song sparrows seen while walking through an area previously surveyed were not counted again. Due to the lower activity of song sparrows during the winter months and particularly in colder temperatures, a combination of the point count survey method and more invasive methods were used when conducting surveys. Observers disturbed areas of thick shrubs and underbrush that appeared to be preferable song sparrow habitat, and performed alarm calls, known as pishing, were used in an attempt to lure birds out of hiding. It is common for song sparrows to react to these alarm calls by jumping up into sight (Zimmering & Ankney, 2000). In addition to weekly surveys, some information was gathered from *ad lib* observers at both sites.

Weekly point count surveys were conducted by three individuals, one for the rural site and two for the urban site. Surveyors only worked at one location to reduce errors that may have occurred during initial surveys of a novel environment. The two urban surveyors each had

a specified area that they walked weekly. These areas did not overlap and observers did not switch survey locations within the site. All surveyors were given the same training on survey methods and bird identification along with maps of breeding territories and a list of the band combinations of all color-banded individuals.

To ensure that all observers were recording similar data, the rural observers periodically did surveys at the urban site and compared their results. Similarly, the original survey trainer surveyed both sites several times. All compared results were similar and showed that survey data is comparable across surveyors and locations.

Surveys were conducted before noon unless the forecasted temperature high for the day did not exceed 0^{o}C. In those cases, the survey was conducted during the warmest forecasted time of the day. Playback experiments are not reliable in the winter because the song sparrows of these two populations are not territorial during the winter months and would therefore show little to no reaction to the singing of another individual near or on the area of their summer territory (J. Hyman, personal communication). Also, any summer residents that remain through the winter do not stay exclusively on their summer territory but will commonly forage outside of their territorial range.

Observers identified song sparrows during the surveys by viewing their color bands with binoculars. All but one individual retained all four bands from when they were banded during the summer of 2009. One song sparrow from the Kituwah site lost one color band, but was still identifiable by the locations of the remaining colors.

If a song sparrow was identified as having color bands, then their band combination and location was recorded. If the sighting occurred between November 14th 2009 and January 15th

2010, the individual was classified as a yearlong resident. These dates were chosen based on the timing of song sparrow migration. Nice (1933) reported that migratory individuals left their summer territories in October and returned from late February to early April. At the WCU urban site some song sparrows have been observed with fledglings as early as May (J. Hyman, personal communication). Taking this information into consideration, the migration period reported by Nice (1933) was narrowed to a more conservative estimate of November 14th 2009 to January 15th 2010, in order to ensure that individuals sighted during this study were yearlong residents.

During surveys, song sparrows without color bands seen between November 1st 2009 and February 1st 2010 were classified as winter migrants. These dates are a slight expansion of the cutoffs for yearlong residents because the yearlong resident dates are defined to ensure an accurate yet conservative estimate. In a small number of cases, a song sparrow was heard but could not be located visually. In those cases, the bird was not included in counts because their identity as either a color-banded or non-color-banded bird could not be determined. This only occurred on five occasions, four of which were during the months of March and April.

The four weekly surveys conducted during the month of October were not included in any calculations but allowed the surveyors to become familiar with the surveying site and process. Likewise, the continuation of surveys through February, March, and April were not used in all calculations but were important in ensuring that the number of non color-banded song sparrows decreased after the migration time period (Figure 3). Similarly, during these later surveys, it was observed that many summer residents were returning to both sites.

Proportions of migratory and yearlong residents were analyzed using a z-test for proportions. A paired two tailed t-test was used to determine the difference between migratory individuals at the urban and rural site using weeks as the replicates.

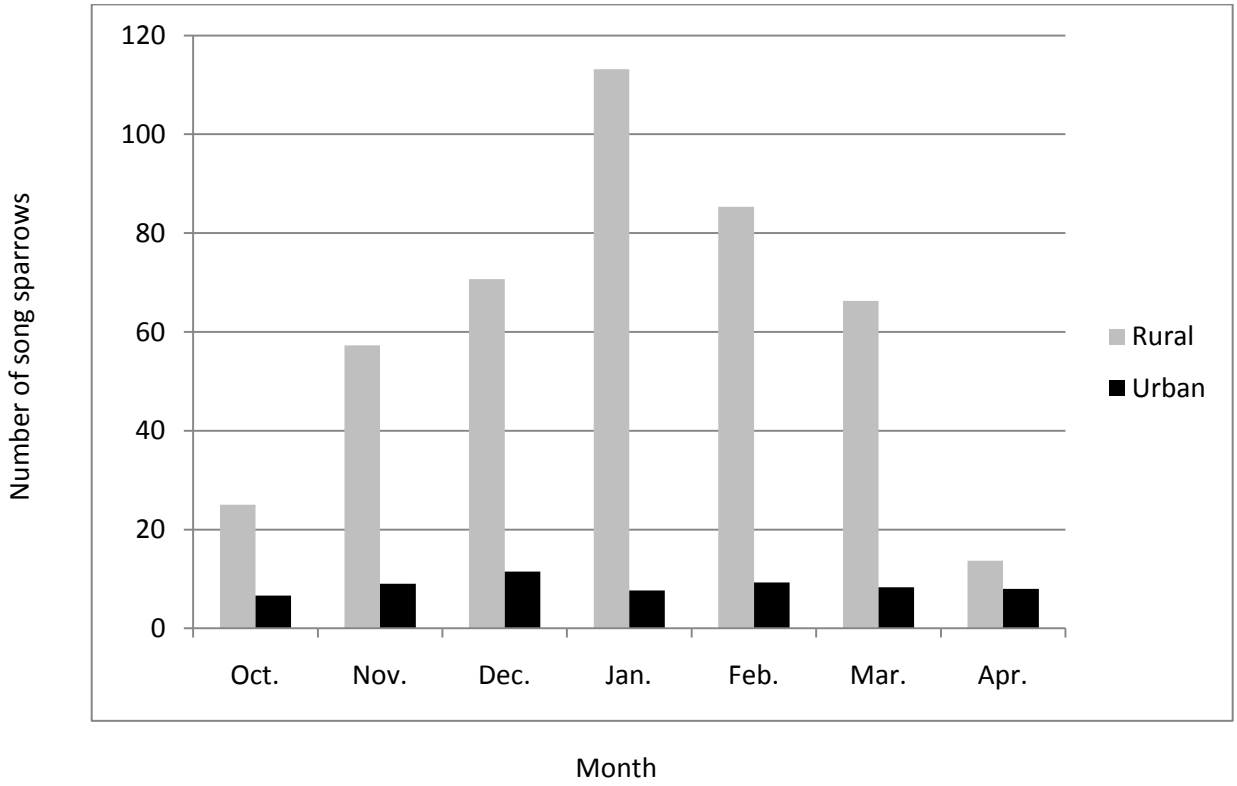

Figure 3. Average number of non-banded song sparrows seen monthly on each site between October 2009 and April 2010.

Results

Yearlong Residents

Color-banded song sparrows seen between November 14th 2009 and January 15th 2010 were categorized as yearlong residents. At the rural site, 6 color-banded individuals (6 males, 0 females) were classified as yearlong residents. At the urban site, 15 individuals (15 males, 0 females) were classified as yearlong residents. A two-tailed z test for proportions on the overall population difference between yearlong residents and summer residents showed no significant

difference (z = 1.41, p = 0.158, Table 1). When analyzed separately for sex, a two-tailed z test for proportions revealed that a significantly higher proportion of males in the urban population stayed year round. Six of the 26 total males from the rural site did not migrate while 15 of the 26 total males from the urban site did not migrate (z = 2.261, p = 0.024, Table 1). The locations of the summer territories of each yearlong resident were marked on aerial views of the two sites (Figure 1 & 2). Yearlong residents were sighted either on or within 100m of their territory in more than 90% of total observations.

Table 1. The proportions of summer resident song sparrows that were yearlong residents, separated by sex and environment type. (p-values are for two tailed z-tests for proportions.)

Environment	Females	Males	Total
Rural	0/6	6/26	6/32
Urban	0/15	15/26	15/41
		p = 0.024	p = 0.158

Winter Migrants

Non color-banded song sparrows seen between November 1st 2009 and February 1st 2010 were considered winter migrants, or song sparrows with a summer territory in a location different from either of the sites included in this research, though these counts could have included young birds born in the previous summer. The average number of winter migrants at the urban site was 9.083 song sparrows per week (SD = 3.175; SE = 0.917) while the average number of winter migrants at the rural site was 83.92 song sparrows per week (SD = 38.30; SE = 11.06). A paired two tailed t-test showed a significant difference between the numbers of winter migrants at each site (t = -6.745, p < 0.001). This significant difference still held when the average number of non color-banded birds seen in the rural site in April 2010 (13.67) was deducted from the average number seen between November 1st 2009 and February 1st 2010 (t

= -5.513, $p < 0.001$). This is an important consideration because all non color-banded birds could not be positively verified as winter migrants due to the lack of the ability to differentiate them from a small number of individuals with summer territories at the rural site who did not receive color bands as well as some non banded juveniles from the previous season. This misidentification is also a possibility at the urban site, but the April average of the urban was not deducted from the average between November 1st 2009 and February 1st 2010 because these numbers only slightly differed (April = 8; November-February = 9.37).

Discussion

I found that significantly higher numbers of male song sparrows remained as yearlong residents within the urban site than within the rural site. These results are consistent with previous research that identified that the benefits of not migrating are for the most part sex specific (Adriaensen & Dhondt, 1990; Partecke & Gwinner, 2007). Song sparrow populations may exhibit different migratory behaviors (migratory, partially migratory, and non-migratory) and this research is the first study to examine the difference in migration between an urban and rural population of these song birds. Additionally, this study points out that even populations within the same general geographic area may employ different types of migration behavior based on a difference in habitat type.

There was not a single color-banded female from either site seen between November 14th 2009 and January 15th 2010. However, only 6 of the 32 total banded individuals from the rural site were females. Sexes of the urban population were slightly more even, with 15 females from 41 total individuals. The sex of color-banded individuals was biased because

males were much more responsive to playback experiments during the capture and banding work due to their territorial nature.

Although we found a significant difference between the numbers of yearlong resident males at the two sites, with more urban birds remaining year round, this difference between urban and rural sites may have even been stronger. The rural site did have one building, a large open shed located within the survey area where farm equipment, hay, and corn were stored. Two of the six rural yearlong residents were observed foraging within this area on multiple occasions and five of the six yearlong residents had summer territories and were observed within 100m of the shed (Figure 2). If this area were excluded from the study site due to its more urban nature there would be an even stronger difference between the numbers of yearlong residents at each site.

Similarly, the difference between the numbers of yearlong residents at each site might be stronger if short distance migration could be taken into account. Some individuals of partially migratory populations may be short distance migrants. It has been observed that short distance migrant white-crowned sparrows (*Zonotrichia leucophrys oriantha*) will winter close enough to their territory to make periodical, even daily, trips back, possibly gathering information on the migratory and territorial choices of past neighbors and future rivals while being able to retreat to more favorable conditions between trips (Hahn *et al.,* 2004). If this were the case for an individual song sparrow, I would expect observations of the individual to be possible, but not common, during weekly surveys. Three of the six yearlong residents from the rural site were only seen once from November 14th 2009 to January 15th 2010. These three

individuals may well have been observed during a visit to their territory as opposed to being a yearlong resident within the rural site.

The large standard deviation (38.03) for the observations of non color-banded song sparrows at the rural site is due to the differences in observations over time, illustrated in Figure 3. This statistic is not a problem because we would expect the number of migrants to rise over time, peak during the winter months, and then recede as summer approaches. In fact, the absence of this pattern in the observations of non color-banded birds on the urban site most likely means that many of these individuals were summer residents of the urban site who were not banded, which included some adults and several juveniles.

During the winter, the overall density of non color-banded song sparrows at the rural site was nearly 10 times that of the urban site. However, urban areas often have denser populations of breeding song birds than rural areas and this was the case for these two populations. This density discrepancy across seasons may mean that song sparrows have different criteria for evaluating what they consider a good breeding territory versus what is considered a good wintering ground. There are different ecological aspects that may be beneficial during each period. During the breeding season, territories should contain a nesting area and perch from which to sing. It should also be located in close proximity to nesting material, and food for both adults and young. During the winter season, an area needs to provide food and cover during harsh weather. For individuals that are not territorial year round, these winter resources may be spread across a large area.

If the rural site is a more beneficial wintering site based on the results of this study, there must be a motivation for the larger number of males that remain within the urban site

separate of wintering ground quality. The denser summer populations in the urban site and the higher level of territory aggression may imply that the urban site is seen as a better quality breeding territory. The higher number of yearlong resident males at this site may then be due to these individuals occupying the area of their summer territories so that these prime sites are not taken by other individuals over the course of the migration period.

It is evident from previous research that sedentary individuals experience earlier gonad development, extending their breeding season, which can lead to greater reproductive success (Adriaensen & Dhondt, 1990; Partecke & Gwinner, 2007; Yeh & Price, 2004). By not migrating, yearlong residents are ensuring that they will not be beat out for a territory or female by an earlier arriving male along with taking advantage of conditions that lead to extended breeding opportunities. The different aspects of an urban environment such as anthropogenic food resources, a warmer microclimate, and possible reduced predation risks may enable an individual to attempt to survive the winter on their breeding territory in order to best be prepared for the next breeding season. From this, it appears that urbanization may alter the evolution of migratory behavior in the Song sparrow.

However, it is important to note that conclusions made based on this research only extend to these two particular song sparrow populations at the time of the study and can be used in the future to serve to help predict possible patterns of behavior in conjunction with the results from similar studies. This study is the first to find this trend in migration behavior in North America but echoes the results from European studies (Adriaensen & Dhondt, 1990; Partecke & Gwinner, 2007).

Research should continue into the future implications of this behavioral trend, examining the alternate strategy choices of the same individuals across seasons. Migration behaviors of song sparrows in urban and rural environments outside of western North Carolina as well as the migration behaviors of different song bird species should be inspected. Future research can be designed to help specifically define the costs, benefits, and drivers for the evolution of partial migration and how it is affected by the environmental differences between urban and rural areas. Additional studies may be conducted that attempt to determine specifically which aspects of an urban environment make it favorable to yearlong residents. Previous research suggests that anthropogenic food sources may directly lead to the extension of breeding periods by providing essential nutrients to individuals earlier than they would typically be available (Schoech & Bowman, 2001).

References

Adriaensen, F., & Dhondt, A. A. (1990). Population dynamics and partial migration of the European robin in different habitats. *Journal of Animal Ecology*, *59(3),* 1077-1090.

Arcese, P., Sogge, M. K., Marr A. B., & Patten. M. A. (2002). Song Sparrow (*Melospiza melodia*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/704

Bairlein, F. & Winkel, W. (2001). Birds and climate change. In Climate of the 21st century: changes and risks (ed. J. L. Lozan, H. Grassl & P. Hupfer), *Hamburg: Wissen- schaftliche Auswertungen*. 278-282.

Baker, R. R. (1978). *The Evolutionary Ecology of Animal Migration*. Hodder & Stoughton, London.

Belthoff, J. R., & Gauthreaux, S. A. (1991). Partial migration and differential winter distribution of house finches in the Eastern United States. *The Condor, 93,* 374-382.

Bêty, J., Giroux, J., & Gauthier, G. (2004). Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology*, *57(1),* 1-8.

Borgemann, K. L. & Rodewald, A. D. (2004). Nest predation in an urbanizing landscape: The role of exotic shrubs. *Ecological Applications, 14(6),* 1757-1765.

Boyle, W. A. (2008). Partial migration in birds: tests of three hypotheses in a lekking frugivore. *Journal of Animal Ecology*, 77, 1122-1128.

Chace, J. F. & Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landscape and Urban Planning, 74(1),* 46-69.

Chan, K. (2001). Partial migration in Austrailan landbirds. *Emu*, *101(4),* 281-292.

Estes, W. A. & Mannan, R. W. (2003). Feeding behavior of Cooper's hawks at urban and rural nests in southeastern Arizona. *The Condor, 105(1),* 107-116.

Evans, J., Boudreau, K., & Hyman, J. Behavioral syndromes in urban and rural populations of song sparrows. *Ethology, 116*, 588-595.

Fleischer Jr., L., Bowman, R., & Woolfenden, G. E. (2003). Variation in foraging behavior, diet, and time of breeding of the Florida scrub-jays in suburban and wildland habitats. *The Condor, 105(3),* 515-527.

Forchhammer, M. C., Post, E., & Stenseth, N. C. (2002). North Atlantic oscillation timing of long- and short-distance migration. *Journal of Animal Ecology, 71(6),* 1002-1014.

Gauthreaux Jr., S. A., (1982). The ecology and evolution of avian migration systems. *Avian Biology*, *6*, 93-167.

Gill, F. B. (1995). *Ornithology*: Second Edition. New York: W. H. Freeman and Co. 287-307.

Hahn, T. P., Sockman, K. W., Breuner, C. W., & Morton, M. L. (2004). Facultative altitudinal movements by mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. *Auk, 121*, 1269-1281.

Hostetler, M., Duncan, S., & Paul, J. (2005). Post-construction effects of an urban development on migrating, resident, and wintering birds. *Southeastern Naturalist, 4(3),* 421-434.

Iverson, G. C., Warnock, S. E., Butler, R. W., Bishop, M. A., & Warnock, N. (1996). Spring migration of western sandpipers along the pacific coast of North America: A telemetry study. *The Condor*, *98(1),* 10-21.

Jenni, L. & Kery, M. (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings: Biological Sciences*, *270(1523),* 1467-1471.

Kamiya, K. & Ozaki, K. (2002). Satellite tracking of Bewick's Swan migration from Lake Nakaumi, Japan. *Waterbirds: The International Journal of Waterbird Biology*, *25,* Special Publication 1: Proceedings of the Fourth International Swan Symposium 2001, 128- 131.

Landys, M. M., Piersma, T., Guglielmo, C. G., Jukema, J., Ramenofsky, M., & Wingfield, J. C. (2005). Metabolic profile of long-distance migratory flight and stopover in a shorebird. *Biological Sciences,* 272(1560), 295-302.

Marra, P. P., Francis, C. M., Mulvihill, R. S. & Moore, F. R. (2005).The Influence of Climate on the Timing and Rate of Spring Bird Migration. *Oecologia*, *142(2),* 307-315.

Martell, M. S., Henny, C. J., Nye, P. E., & Solensky, M. J. (2001). Fall migration routes, timing, and wintering sites of North American ospreys as determined by satellite telemetry. *The Condor, 103(4),* 715-724.

McCarty, J. P. (2001). Ecological consequences of recent climate change. *Conservation Biology, 15,* 320-331.

McCleery, R. A., Lopez, R. R., Silvy, N. J., & Gallant, D. L. (2008). Fox squirrel survival in urban and rural environments. *The Journal of Wildlife Management, 72(1),* 133-137.

Nice, M. M. (1933). Migratory behaviors in song sparrows. *The Condor, 35,* 219-224.

Partecke, J. & Gwinner, E. (2007). Increased sedentariness in European Blackbirds following urbanization: A consequence of local adaptation? *Ecology, 88(4),* 882-890.

Partecke, J. T., Van't, H, & Gwinner, E. (2005). Underlying physiological control of reproduction in urban and forest-dwelling European blackbirds *Turdus merula. Journal of Avian Biology, 36,* 295-305.

Pérez-Tris, J., Bensch, S., Carbonell, R., Helbig, A. J., & Tellería, J. L. (2004). Historical diversification of migration patterns in a passerine bird. *Evolution, 58(8),* 1819-1832.

Pérez-Tris, J. & Telleria, J. L. (2002). Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines. *Acta Oecologica, 23(1),* 13-21.

Sandercock, B. R. & Jaramillo, A. (2002.) Annual survival rates of wintering sparrows: assessing demographic consequences of migration. *Auk, 119(1),* 149-165.

Schmidt, K. A. & Whelan, C. J. (1999). The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. *Conservation Biology, 13(1),* 46-57.

Schoech, S. J. & Bowman, R. (2001). Variation in the timing of breeding between suburban and wildland Florida scrub-jays: Do physiologic measures reflect different environments? 291-308 Marzluff, J. M., Bowman, R., & Donnelly, R. E., (ed.) *In Avian Ecology and Conservation in an Urbanizing World.* Kluwer Academic, Norwell, Massachusetts, USA.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution, 21,* 186–191.

Sokolov, L.V., Markovets, M. Y. & Morozov, Y. G. (1999). Long-term dynamics of the mean date of autumn migration in passerines on the Courish Spit of the Baltic Sea. *Avian Ecological Behavior*, *2,* 1-18.

Stokes, D. L., Boersma, P. D., & Davis, L. S. (1998). Satellite tracking of magellanic penguin migration. *The Condor*, *100(2),* 376-381.

Taylor, L. R. (1986). Synoptic dynamics, migration and the Rothamsted Insect Survey. *Journal of Animal Ecology, 55,* 1-38.

Terjung, W. H. & Louie, S. S-F. (1973). Solar radiation and urban heat islands. *Annals of the Association of American Geographers, 63(2),* 181-207.

White, P. J., Davis, T. L., Barnowe-Meyer, K. K., Crabtree, R. L., & Garrott, R. A. (2007). Partial migration and philopatry of Yellowstone Pronghorn. *Biological Conservation, 135(4),* 502-510.

Whittaker, K. A. & Marzluff, J. M. (2009). Species-specific survival and relative habitat use in an urban landscape during the postfledging period. *The Auk, 126(2),* 288-299.

Wingfield, J. C. & Soma, K. K. (2002). Spring and autumn territoriality in song sparrows: same behavior, different mechanisms? *Integrative and Comparative Biology*, 42(1), 11-20.

Yeh, P. J. & Price, T. D. (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. *American Naturalist, 164(4),* 531-42.

Zimmering, J. R. & Ankney, C. D. (2000). A technique that increases detectability of passerine species during point counts. *Journal of Field Ornithology, 71(4),* 638-649.

Appendix A: Sex and band combinations for all individual song sparrows in each environment.

Rural: Sex	Band Combo
M	GOWF
M	RBIF
F	GOWF
M	YYYF
M	OOOF
M	YGWF
M	IYIF
M	RROF
M	WWRF
M*	IOYF
F	RWRF
M*	BGGF
F	RIWF
M	WWYF
M*	OIOF
M*	RGBF
M	GWOF
M*	BRYF
M	YOIF
M	IBBF
M	YGIF
M	RRBF
M	BWRF
M	BYRF
M	OGGF
M	OWYF
F	YRGF
M	RIIF
M	YOGF
F	IOYF
F	RRGF
M*	OWBF

*Yearlong Resident

Urban: Sex	Band Combo
F	OYWF
M	GBBF
M	YRGF
M	BIWF
M*	IRWF
F	WYBF
M	RYRF
M*	YOBF
M*	OGRF
F	IYWF
F	OYGF
M	BBBF
M*	OGGF
M	WGGF
F	WOWF
F	IGIF
F	YWWF
M	YRBF
M*	GBRF
M*	OOIF
M	WBRF
M	WGRF
M	IOOF
F	OWRF
M*	YRRF
F	IIRF
M	WWOF
M	OIGF
M*	Fish only
M	WRRF
F	IIYF
M*	IBWF
F	BIIF
M	YWYF
F	IYGF
F	GYWF
F	BRGF
M*	GIRF
F	YIOF
M*	IWRF
M*	ROWF
M*	OWOF

Appendix B: Observation data on sightings of song sparrows at rural site.

Date	Total number non-banded	OIOF*	RGBF*	YOIF	BRYF*	BGGF*	OWBF*	IOYF*	YGOF	RIWF	BRIF	GOWF
10.24.09	25				X (<100m)							
11.1.09	19											
11.13.09	30											
11.21.09	97											
11.23.09	83		X (<100m)									
12.6.09	62				X (<100m)							
12.12.09	57	X (<100m)	X (100-300m)		X (<100m)	X (0 m)						
12.29.09	93	X (<100m)					X (<100m)	X (<100m)				
1.4.10	120											
1.11.10	76	X (<100m)	X (<100m)									
1.18.10	127	X (<100m)										
1.23.10	94	X (<100m)										
1.30.10	149		X (<100m)	X (100-300m)					X (<100m)			
2.12.10	71	X (<100m)	X (<100m)									
2.19.10	99	X (<100m)	X (<100m)	X (0 m)								
2.27.10	86	X (<100m)	X (0 m)									
3.7.10	85	X (<100m)		X (<100m)		X (<100m)		X (<100m)		X (<100m)	X (<100m)	
3.13.10	85		X (0 m)			X (<100m)						X (>300m)
3.24.10	29		X (<100m)			X (0 m)		X (<100m)				X (>300m)
4.7.10	20	X (0 m)	X (0 m)	X (>300m)		X (0 m)		X (0 m)				

* Yearlong Resident

X = seen on site during survey

() = Parentheses shows distance individual was seen from their summer territory or location where caught in some cases when no territory could be established for an individual.

** Data on observations of banded birds at the urban site is not complete in a way that can be represented in this fashion.