WRENS ON THE EDGE: DO HUMANS HELP CAROLINA WRENS (*THRYOTHORUS LUDOVICIANUS*) SURVIVE AT THE NORTHERN EDGE OF THEIR RANGE?

by

Jacob Randall Job

Thesis

Submitted to the Department of Biology

Eastern Michigan University

In partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

in

Biology with a concentration in Ecology and Organismal Biology

Thesis Committee:

Peter Bednekoff, PhD, Chair

Steven N. Francoeur, PhD

Ulrich Reinhardt, PhD

Michael A. Kielb

November 5, 2008

Ypsilanti, Michigan

THESIS APPROVAL FORM

Wrens on the edge: Do humans help Carolina wrens (*Thryothorus ludovicianus*) survive at the northern edge of their range?

by

Jacob Randall Job

APPROVED:

Peter Bednekoff, PhD Thesis Chair	Date
Steven N. Francoeur, PhD Committee Member	Date
Ulrich Reinhardt, PhD Committee Member	Date
Michael A. Kielb Committee Member	Date
Marianne Laporte, PhD Department Head	Date
Deborah de Laski-Smith, PhD Dean of the Graduate School	Date

DEDICATION

I would like to dedicate this to all those who waited patiently for me to finish my degree. It was just as hard on me as it was you when we could not be together. I sincerely thank you all.

ACKNOWLEDGMENTS

I would like to thank my committee, Dr. Peter Bednekoff, Dr. Steven N. Francoeur, Dr. Ulrich Reinhardt, and Michael A. Kielb for their continued assistance throughout the completion of my thesis. Without their continued support and guidance, I would not have been able to accomplish what I have in conducting my research and writing my thesis. I would like to also express my gratitude to Kelly McKinne, Josh Perrin, and Jamie Lee Koleth for their assistance in helping me collect my data. Without them there is no way I could have finished in a reasonable amount of time.

I would like to also thank Dr. Deborah deLaski-Smith and the Graduate School for awarding me two research grants. Without these, life would have been very difficult during data collection. This financial aid helped alleviate the costs of research and allow me to concentrate on my research without the burden of an additional job. Additional support for this study was provided by the Meta Hellwig Scholarship Fund of the Department of Biology, Eastern Michigan University.

ABSTRACT

Northern populations of Carolina wrens (*Thryothorus ludovicianus*) have undergone drastic population changes during the last half century. It is widely accepted that understanding winter survival is the key to explaining these changes. Historical climactic and wren data (1959-2007) for Ann Arbor, MI, were analyzed to determine which aspect of winter weather is most detrimental to Carolina wren populations. It was found that snow cover duration was the best predictor of population change. Following up on these findings, we surveyed Carolina wrens on 21 transects. Human influence was hypothesized to be the main factor in population trends. Urban warmth and supplemental feeding were measured and analyzed against winter survival. Carolina wrens survived when they had access to winter bird feeders, regardless of temperature. Winter feeding by humans may help to further increase Michigan Carolina wren populations.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 2

LIST OF FIGURES

CHAPTER 1

Introduction

Carolina wrens (*Thryothorus ludovicianus)* have exhibited dramatic changes at the northern edge of their range over the last century. They are the only *Thryothorus* wrens whose range extends north from tropical latitudes (Morton 1982). Their range extends from the Yucatan Peninsula north to southern Michigan and from eastern Kansas to the Atlantic coast (Haggerty and Morton 1995). Northern populations increased from 1970-1976 when temperatures were above average (Haggerty and Morton 1995). During the winters of 1976-1977 and 1977-1978, heavier than normal snowfall and unusually cold temperatures were prevalent (Bystrak 1979). Sauer et al. (1996) found high mortality rates throughout the northern edge of their range during these winters, with some populations experiencing close to 100% declines (Bohlen 1989). Michigan populations saw major declines following the winters of 1977 and 1978 (Brewer et al. 1991). In Michigan, Carolina wren populations have rebounded and surpassed pre-1977 numbers (National Audubon Society Christmas Count Data). Currently their northern range extends beyond Lansing (Ingham county) (Kielb pers.comm).

Carolina wren population declines are attributed to extremely cold and snowy winters (Townsend 1909, Bystrak 1979, Robbins et al. 1986). Declines are caused by their biology: 1. They are non-migratory throughout their range (Haggerty and Morton 1995) 2. The majority of their food is insects 3. They are ground foragers (Bent 1948). It is thought that prolonged periods of snow cover hinder the ability to find sufficient food for survival (Robbins et al. 1986).

It is widely accepted that severe winter weather is limiting Carolina wren populations, but few studies have specified what aspect of winter weather is most limiting. Root (1988a) stated that Carolina wren populations at the northern edge of the range are limited by January mean minimum temperatures. Using Christmas Bird Count data and historical weather data associated with range boundaries of 90% of wintering birds in the United States, Root (1988b) suggested that January mean minimum temperatures below -9.4°C put metabolic constraints on thermoregulation in Carolina wrens (Root 1988a). During years when snow cover is abundant and prolonged, finding enough food items to meet these metabolic demands can prove difficult, leading to high mortality rates. Another study attempted to quantify a specific aspect of winter weather that led to population declines in Carolina wrens (Link and Sauer 2007). They identified snow as the limiting factor: For every day with 4cm of snow cover, a 1.1% decrease in the Carolina wren population followed. The snow depth 4cm was arbitrarily selected without specific biological reasoning (Link pers.comm).

This study analyzed historical weather and Carolina wren data for Ann Arbor, MI (1959-2007). Ann Arbor is typical in the northern range of the Carolina wren. The purpose of this study was to gain a better understanding of the relationship between Carolina wren population change and winter weather, and to determine which aspects of winter weather explained winter mortality best. This was accomplished by comparing already established weather models from Root (1988a) and Link and Sauer (2007) with two novel models. Models were compared using Akaike's Information Criterion to determine which was the best in predicting population change. We hypothesized that change in the Carolina wren population in Ann Arbor is driven by the amount of snow combined with the duration of cover and developed a snow cover index to test this hypothesis. This model was predicted to perform the best for two reasons. Snow cover is negatively related to food intake in wrens (Morton and Shalter 1977). Snow cover can lead to decreased energy stores for thermoregulation due to the lack of food (Labisky and Arnett 2006). The number of days with 4cm of snow of the ground as proposed by Link and Sauer (2007) was also predicted to perform similarly to the snow cover index. These models are similar measures of snow cover and duration. The snow cover index is a more general model because it does not place an emphasis on any particular snow depth. January mean minimum temperature as proposed by Root (1988a) was not predicted to be a suitable predictor of Carolina wren population change in Ann Arbor. This model does not take into account snow cover duration. General total yearly snowfall was also tested against the other models since declines in Carolina wren populations are often attributed to unusually snowy winters (Bystrak 1979, Robbins et al. 1986). This model was also not predicted to perform well since it does not take into account the duration of snow cover.

Methods

Population Data

Data on the Carolina wren population in Ann Arbor, MI, were obtained from the Christmas bird count (CBC) database (National Audubon Society Christmas Count Data). The CBC has been conducted in the United States every year since 1900 (Butcher et al. 1990). The first CBC in Ann Arbor was conducted in 1940 but was not regularly conducted until 1947 (French et al. 1997). Data from 1959 to 2007 were analyzed. The first consecutive years where Carolina wrens were found was 1957 and 1958. In 1959 wrens were once again absent from the Christmas count. This time period is a good start date for this study since wrens were present consecutively and thus could show population changes due to inclement winter weather.

Christmas Bird Count effort varies from year to year (Link and Sauer 1999). This analysis controlled for effort by dividing total wren counts by the total party hours for each year. Data on the number of party hours were available for all years included in this study. Party hours were first recorded for the Ann Arbor Christmas Bird Count in 1944.

Weather Data

Climatic data were collected from National Climatic Data Center (NCDC) found on the National Oceanic and Atmospheric Administration website. Weather data for Ann Arbor were collected from the Ann Arbor, University of Michigan weather station. This particular weather station has collected data from January 1 1948 to present. Weather data from 1959 to 2007 were used in this study. For this study, each year began on January 1 and ended the day of the following Christmas Bird Count. For those years that the Christmas Bird Count occurred after January 1, the study year began the day after. Only the months of January-March and November-December were analyzed, since severe winter conditions that are thought to have negative impacts on northern wren populations occur during these months (Sauer et al. 1996). A total of 235 months of data were obtained.

Data were organized into four categories based on the four models being compared in the study: January mean minimum temperature (ºC), number of days with ≥4cm of snow cover, total yearly snowfall (cm), and snow cover index (cm). The snow cover index is the sum of daily snow depth measurements. For example, if 10cm of snow fell and melted in a day, that contributes 10cm/days to the snow cover index. If 10cm of snow falls and does not melt until day 10, that contributes 100cm/days to the snow cover index. After all the data were collected and organized into the four categories, they were sorted by year.

Statistical Analysis

Weather data were correlated against time to illustrate any trends during the 48 years of the study (1959-2007) using simple Pearson correlations. Years were correlated with the four weather variables of the four models: number of days with ≥4cm of snow cover, yearly snow fall (cm), January mean minimum temperature (ºC), and the snow cover index (cm). The statistical analysis was performed using Systat®.

All Christmas Bird Counts were increased by one so that count effort could be illustrated, even for those counts where no wrens were found. Once this was done, the new counts were divided by the previous year's count to get the proportion of change in wren counts from year to year. To equalize the variances, a log transformation was performed on all standardized data. We modeled a linear relationship between this measure of population change and each of the four weather variables, then compared the four models using Akaike's Information Criterion within JMP® statistical software.

Results

Population Data

Population trends over the course of the study (1959-2007) revealed two main colonizations by Carolina wrens in Ann Arbor (Figure 1). The first colonization began in 1972 and reached peak wren counts of 4 birds in 1977. Up until 1977, one wren was found for each of the four prior Christmas counts. Except for 1960 (1 wren), there were no wrens located prior to 1972. After 1978, wrens were not found during Christmas bird counts in consecutive years until 1988. This was the start of the second colonization. The last year when wrens were absent from the Christmas count was 1990. Wrens surpassed their 1978 totals once again in 1992. From that year, Carolina wren counts increased to a high count of 62 in 2006.

Weather Data

Trends in yearly snowfall show an increase of 85cm from 1959-2007 (Figure 2). There was a strong correlation between time and yearly snowfall ($r = 0.592$). There was also fairly strong positive correlation between January mean minimum temperature (°C) and time ($r = 0.273$). A 3°C increase was observed for the duration of the study (Figure 3). The coldest January during the period of the study occurred in 1978 (-15.2°C). The number of days with ≥4cm of snow cover has for the most part remained unchanged, showing only slight increases from 45 days to 48 days ($r = 0.033$) (Figure 4). The snow cover index showed slight increases for the duration of the study ($r = 0.063$). Trends show an increase in the snow cover index of 50cm (Figure 5).

Model Analysis

The snow cover index model was the best predictor of wren population change in Ann Arbor (null AIC = -54.80, test AIC = -60.41, R^2=0.147). The number of days with ≥4cm of snow cover was the second best predictor model for wren population change (test AIC = -57.73, R^2 =0.098). Both January mean minimum temperature (°C) (test AIC = -53.08, R^2 =0.0058) and total year yearly snowfall (cm) (test AIC = -53.19, R^2 =0.0079) were shown to be poor predictor models of wren population change.

Discussion

Population Data

Carolina wren populations fluctuate in conjunction with winter weather. Populations often expand northward following winters with above average temperatures (1970-1976) (Bystrak 1979). Populations show marked decreases during unusually cold and snowy winters. The winters of 1976-1977 and 1977-1978 resulted in significant declines in Carolina wren populations (Bystrak 1979, Bohlen 1989). This was evident with wren populations in Ann Arbor, MI. Wrens were present during consecutive CBC's for the first time in 1973. They first reached their peak numbers in 1977, and the population crashed in 1979. The winter of 1976-1977 exhibited the coldest January during the study period. The following winter exhibited the largest snow cover index and number of days with ≥4cm of snow cover. These data are consistent with the literature that severe winter weather has negative impacts on northern Carolina wren populations (Townsend 1909, Bystrak 1979, Robbins et al. 1986).

Weather Data

The 48-year trends of the four weather variables revealed changes in winter weather patterns for Ann Arbor. Temperature and snowfall have shown substantial increases, but the snow cover index and the number of days with ≥4cm of snow cover have shown minimum increases. The relative stability of the snow cover index is most likely attributed to the warmer temperatures negating the effects of the increased yearly snowfall.

Model Analysis

Changes in the Carolina wren population in Ann Arbor, MI, are best predicted by the yearly snow cover index, supporting the hypothesis presented by this study. It was also shown that the number of days with ≥4cm of snow cover is a predictor of wren population change (Link and Sauer 2007). These two models are highly correlated with each other (Pearson =0.862). This reflects the nature of the two measurements. This study proposes that the snow cover index is a more suitable predictor of wren population change since it does not put an emphasis on any particular snow cover depth. It may be that any amount of snow is detrimental to Carolina wren winter survival, so a general model is more appropriate. Link and Sauer's (2007) proposal of 4cm may misrepresent the importance of snow cover to wrens. Carolina wrens are small birds (10-12cm long) and 20g. Their ability to uncover foraging areas under 4cm of snow may be limited at best. Their model also suggests that there is a homogenous distribution of 4cm of snow across a wren's entire territory. Vegetation, particularly in combination with wind, however, can create a heterogeneous landscape of snow cover and bare ground. As snow cover increases, these bare areas begin to fill in. The snow cover index inherently takes this into account.

To illustrate the importance of snow cover duration, this study presented a total yearly snowfall model. This model was based solely on snowfall totals and not duration. This model did not perform well. Root (1988a) proposed that Carolina wrens are metabolically limited by the January mean minimum temperature. This study predicted that Root's model would be the best predictor of wren population change since it is not related to food availability. During years with large amounts of snow cover, wrens can have trouble finding adequate amounts of food to meet daily metabolic demands (Robbins et al. 1986). It was found that Root's (1988a) model performed the worst out the four weather models.

Conclusion

The study illustrates the importance of snow cover duration, presented as the snow cover index, on Carolina wren populations in Ann Arbor, MI. Our findings suggest that for other ground foraging birds wintering in northern regions, the snow cover index may be the best model for population change in these species. The severe winter of 1977 resulted in declines of ≥80% for ground foragers in Illinois (Graber and Graber 1979). The snow cover index is not species specific, so we feel it would perform well for other ground foraging species.

We feel that although periods of critically low temperatures may be harmful to certain species, the availability of food is the primary determinant of survival. In regions where the snow cover index is sufficiently high to inhibit population growth, other human influenced variables may negate the effects of snow cover. These variables may include urban heat islands and the presence of supplemental feeding. The 48-year trend revealed that the snow cover index is relatively unchanged. This could suggest that humans are responsible for the population increases. As with many ecological models, it is likely that Carolina wren populations are affected by a combination of many biotic and abiotic factors.

References

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. United States National Museum Bulletin **195**:475.

Bohlen, H.D. 1989. *The Birds of Illinois*. Indiana University Press, Indianapolis, IN.

Brewer, R., G. A. McPeek, and R. J. Adams Jr. 1991. *The atlas of breeding birds of Michigan*. Michigan State University Press, East Lansing, M.I., USA.

Butcher, G. S., M. R. Fuller, L. S. McAllister, and P. H. Geissler. 1990. An evaluation of the Christmas Bird Count for monitoring population trends of selected species. Wildlife Society Bulletin **18**:129-134.

Bystrak, D. 1979. The breeding bird survey. Sialia 1: 74-79.

French, R., M. Kielb, and N. French. 1997. *Fifty Years and Counting*. Washtenaw Audubon Society, Ann Arbor, MI.

Haggerty, T. M. and E.S. Morton. 1995. *Carolina Wren: Thryothorus Ludovicianus*. American Ornithologists' Union; The Academy of Natural Sciences.

Kielb, M.A. Pers. Comm.

Labisky, R.F. and Arnett Jr., J.E. 2006. Pair roosting of nesting Carolina wrens (*Thryothorus ludovicianus*). The Wilson Journal of Ornithology **118**: 566-569.

Link, W.A. Pers. Comm.

Link, W. A. and J. R. Sauer. 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. Ecology **88**:49-55.

Link, W. A. and J. R. Sauer. 1999. Controlling for varying effort in count surveys: An analysis of Christmas Bird Count Data. Journal of Agricultural, Biological, and Environmental Statistics **4**:116-125.

Morton, E. S. and M. D. Shalter. 1977. Vocal response to predators in pair-bonded Carolina wrens. Condor **79**:222-227.

Morton, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules. Acoustic communication in birds **1**:183-212.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: Its first fifteen years, 1965-1979. U.S. Fish and Wildlife Service Resource Publication. 157.

Root, T. 1988a. Energy Constraints on Avian Distributions and Abundances. Ecology **69**:330-339.

Root, T. 1988b. Environmental factors associated with avian distributional boundaries. Journal of Biogeography **3**: 489-505.

Sauer, J. R., G. W. Pendleton, and B. G. Peterjohn. 1996. Evaluating causes of population change in North American insectivorous songbirds. Conservation Biology **10**:465-478.

Townsend, C. W. 1909. A Carolina wren invasion of New England. The Auk **26**:263-269.

Introduction

Carolina wrens, *Thryothorus ludovicianus*, are members of the wren family *Troglodytidae*. They are the only members of the genus *Thryothorus* that are found north of tropical latitudes (Morton 1982). Historically, their range has extended from the Yucatan Peninsula northwards to the southern counties of Michigan and from eastern Kansas to the Atlantic coast (Haggerty and Morton 1995). Carolina wren populations from southern Ohio northward into Michigan and east into the New England states have fluctuated greatly over the last century (Bent 1948). During this same time period, global surface temperatures have increased by 0.6ºC, with most of the temperature increases occurring since 1976 (Walther et al. 2002). Organisms and ecological processes are exhibiting the effects of this continued warming. Most obviously, many species of animals and plants have expanded northward in the northern hemisphere during this period. Among Michigan birds, northern cardinals, *Cardinalis cardinalis,* tufted titmice, *Baeolophus bicolor,* mourning doves, *Zenaida macroura,* turkey vulture, *Cathartes aura*, and Carolina wrens, *Thryothorus ludovicianus,* have shown notable northward expansions (Brewer 1991). These species were observed only as non-breeding accidentals in Michigan prior to 1900, but after the 1930s, all species had breeding records for Michigan (De Vos 1964). These species have continued to increase in numbers throughout Michigan (National Audubon Society, Christmas Count Data).

Carolina wrens have undergone northward range expansions during the twentieth century (Townsend 1909, Bent 1948, Brewer et al. 1991). A recent expansion into Michigan occurred in the early 1970s, until a string of harsh winters in 1976 and 1977 severely decreased their populations to the extent that the new northern edge of the population was in the Ohio River Valley (National Audubon Society, Christmas Count Data). In 1991, their populations began to rebound in Michigan and have been expanding ever since (National Audubon Society Christmas Count Data). The current range expansion is attributed to infrequent severe winters (Andrle and Carroll 1988, Haggerty and Morton 1995). Currently, the northern limit of the Michigan population lies just north of Lansing (Ingham county) (Kielb pers.comm).

The biology of Carolina wrens makes them susceptible to population declines during particularly harsh winters. Many species of birds migrate in order to seek out more favorable living conditions during the winter, but Carolina wrens are the only wren species east of the Mississippi River that does not migrate (Sibley 2000, Haggerty and Morton 1995). This limits their ability to escape harsh winter conditions. Secondly, Carolina wrens are insectivorous birds that forage on or near the ground (Haggerty and Morton 1995). Their diet consists of 94% animal matter and 6% vegetable matter (Bent 1964). This quality increases their death rate during harsh winters for two reasons. In areas where sub-zero (^{o}C) temperatures are the norm during winter months, insect food items can be rare (Somme and Zachariassen 1981). During years with large amounts of snow cover, wrens can have trouble finding adequate amounts of food on the ground to meet daily metabolic demands (Robbins et al. 1986). Carolina wrens, however, also visit feeders with suet, peanuts, and various seeds, most frequently during the winter months (Bent 1964, Brewer et al. 1991, Kaufman 1996, Link and Sauer 2007).

The purpose of this study was to understand the role humans have in influencing the northward expansion of Carolina wrens in Michigan. Human influence is measured separately here using two factors: urban warmth and supplemental feeding. We studied Carolina wrens in three habitat types (residential, city park, and rural) that differed in how they were influenced by humans. We set up 21 transects in these three habitats. Wren densities in these habitats were monitored for 15 months across the study site using a Carolina wren vocal playback technique developed by the researcher. It was hypothesized that Carolina wrens take advantage of urban warmth and bird feeding stations, leading to greater densities and higher rates of winter survival in the residential and city park habitats. We predicted that the residential and city park habitats would be warmer than rural areas due to heat release from manmade structures. Bird feeder data were collected using door to door surveys. Carolina wren survival was analyzed against the presence of bird feeders in the winter, along with temperature covariates. It was hypothesized that supplemental feeding alleviates the harshness of winter. From that, it was predicted that the survival rates of wrens on transects with higher numbers of winter feeders should be higher than rates on transects with fewer winter feeders present.

Methods

Study Species

Carolina wrens, *Thryothorus ludovicianus*, are non-migratory and maintain their small territories year-round (Brewer et al. 1991, Granlund et al. 1994, Haggerty and Morton 1995). Carolina wrens maintain lifetime pair-bonds and are thought to be monogamous (Morton and Schalter 1977, Verner and Wilson 1969). Pairs aggressively defend their territory year-round, with males responding strongly to conspecific songs (Haggerty and Morton 1995, Morton 1982). Females without a mate may not be able to maintain a territory and are often forced from their territory by neighboring pairs (Morton and Schalter 1977). All breeding behavior occurs within the territory (Haggerty and Morton 1995). Territory size ranges from 4.1 ha in Tennessee (Strain and Mumme 1988) to 1 ha in North Carolina (Simpson 1984) and is inversely correlated with conspecific density (Morton 1982).

Carolina wrens inhabit a wide range of habitats. Hardwood forests provide acceptable habitat, but the presence of moderate to dense shrub or bushy cover is the most important aspect of Carolina wren habitat (James 1971, Dickson and Noble 1978, Hamel et al. 1982). In essence, it is the presence of a well developed understory and not big trees that the wrens prefer. Carolina wrens seem to be comfortable inhabiting areas close to humans. Several studies have shown that wooded residential areas also support populations of Carolina wrens, including those in Michigan (Beissinger and Osborne 1982, Hamel et al. 1982, Brewer et al. 1991). They are abundant in parks (Brewer 2001) and are also often found in suburban areas with dense undergrowth and tangles (Kaufman 1996). In Florida, urban areas (commercial and residential zones) may have the highest densities of any other habitat (Rusnak and Labisky 2003).

Study Site

The study was conducted in Washtenaw County, Michigan, USA (42°15′N 83°50′W). The majority of the transects were located near Ann Arbor, MI (42°16′N 83°43′W).

Carolina Wren Surveying Protocol

To determine Carolina wren density for the 21 transects, conspecific playbacks were conducted. Wrens perceive conspecific songs as intruders and will readily respond to these playbacks (Hyman 2003). Unlike most bird species, Carolina wrens aggressively respond to conspecific playbacks during the non-breeding season as well as the breeding season (Morton 1982). This allowed for the study to be conducted nearly year-round. Surveys began in January 2007 and continued through April 2008. During the first year, surveys were attempted during the first half of the breeding season, but were halted after that, due to inconsistent vocalizations (Kielb pers.comm). A total of six survey series (all 21 transects) were completed during this time period. The order of surveying was randomized for each survey series. Surveys were not conducted in weather that included any rain or winds in excess of 6m/s as these conditions can lead to poor detectability (Conway 2005). All surveys were conducted between 0600-1100, the time of day that wrens are at their most active (Bibby et al. 1998, Shy and Morton 1986).

Transect surveys utilized a Creative Zen Micro mp3 player, Creative Travelsound portable speakers, and Carolina wren vocalizations from Stokes Field Guide to Birds CD 3. The volume of the playback apparatus was set to mimic that of a Carolina wren singing (92dB at 1m). To survey each transect, an initial playback was performed upon arrival to the site. Each playback lasted 0:51 seconds. Once the playback was over, 80m was walked before performing the next playback. This distance was within the broadcast range of a Carolina wren that the surveyor could perceive in each habitat type. This process continued until the entire transect was covered. Whenever a Carolina wren was heard or seen the number of individual wrens present was recorded.

Transect area determination

Use of a playback survey protocol resulted in detection of wrens that was not limited to the central line of each transect, but instead extended laterally from the center line of each transect. The extent to which detection was possible away from the center line of each transect was equal to the distance the observer could detect a Carolina wren singing. Once this distance was calculated, an area for each transect was determined. From this area, the density of wrens per area (km^2) could then be determined.

To determine the lateral distances, first, the maximum distance a Carolina wren could be heard by the observer was determined. In order to do this, the observer measured the intensity (dB) of three Carolina wrens singing in the field using an Extech model 407706 analog sound level meter. Once the intensities were found, the distance from the three singing wrens was measured. The three intensities had to be standardized, that is, the intensities were converted to intensities as if they were recorded at 1m. To do this, the equation ΔL (intensity) = -20 log N1/N2 was used (Miler 1982), where N1 = 1m and N2 = the distance the singing intensity was originally measured. This provided a change in intensity, which could be then added to the original intensity measurement to give the intensity of that wren at 1m. The three measured wren intensities after standardization averaged 92±3 dB at 1m. Naguib (1995) found that a singing Carolina wren has a song intensity of 86 dB at 1m. That study was conducted in North Carolina, which could account for the difference in intensities. Regional dialects can vary within a species, including intensity and frequency (Haggerty and Morton 1995). Vegetation, temperature, and the height at which singing occurs can also affect the intensity level of the song (Morton 1975).

Next the mp3 player/external speaker apparatus was set up so that it would play back a Carolina wren singing at the same intensity (92 dB at 1m). The decibel meter was 1m from the playback apparatus. The volume on the apparatus was placed at 100% and scaled down until the intensity of the playback was the same as the wrens in the field.

Using the setting that mimicked a singing Carolina wren in the field, the playback apparatus was set to repeat. The observer then walked away from the apparatus until detection of the playback was no longer possible. This is the distance that the observer could detect a singing Carolina wren in the field. This was performed on three transects, one for each habitat type. The playbacks all occurred on the same day within a one hour period. This was done to account for the different background noise in each habitat type. It was found that the observer could detect a Carolina wren at 198.5m on the residential transects, 134m for the city park transects, and 140m for the rural transects.

To calculate the area of each transect, all transects were mapped using Google Earth Pro. Using the Carolina wren detection distances found for each habitat type, lateral lines were drawn from the center line of each transect. The length of the lateral line depended on the habitat type. Using the polygon tool, the ends of the lines were connected and the area within the polygon was the area that was covered by the observer while walking each transect (Figure 1). The mean area of the transects were as follows: residential 0.66km^2, city park 0.48km^2, and rural 0.39km^2 (Table 1).

Carolina wren survivorship

Carolina wren population densities were measured over the course of 15 months, from January 2007 to April 2008. Populations were observed using standard playback protocol. Study areas were selected on the basis of different human influenced habitat types: residential, city park, and rural. All residential and city park transects were suggested by and selected with the advice of Michael Kielb, local ornithologist. The size criterion for each transect included a minimum length of 0.75km and minimum area of 0.25 km^2. The residential and city park habitats were chosen with the possibility of receiving benefits of human activity in the form of urban warmth and/or bird feeders. The rural areas were selected with the intent of excluding these potential benefits from those transects.

The residential habitat type is defined here as any area with one or two story houses, located at intervals no greater than 75m apart. Non-residential urban areas were excluded from this study because of the lack of suitable habitat (hardwood trees with moderate to dense shrubby undergrowth) for the wrens (James 1971, Dickson and Noble 1978, Hamel et al. 1982). When selecting areas for transects, a map of the city of Ann Arbor was divided into quadrants so that the eleven residential transects were evenly spaced throughout the city. The selection of transects was not performed in random order. Ten of the eleven residential transects were established within the three major highways that border Ann Arbor. The eleventh transect was setup 1.15km Northwest from the Miller Road exit on M-14

City parks were defined as any parkland area free from residential/commercial development. The parks for inclusion into the study were to be no further than 0.5km from urban or residential areas. This would theoretically allow them to receive heat from the urban areas, but also provide ample habitat to possibly support a large population of wrens.

Five transects were established in city parks -- Dolph Nature Area, Barton Park, Bird Hills Park, County Farm Park, and Nichol's Arboretum. Dolph Nature Area, County Farm Park, and Nichol's Arboretum all have residential areas directly bordering on one or more sides. The city of Ann Arbor was divided into quadrants and the parks were divided evenly throughout the quadrants.

The rural habitat type was defined as any area with no housing or business structures for at least 0.5 km. For those transects in which the center line was a road instead of a hiking trail, that road could not be paved. Rural areas had to have suitable wren habitat located along the transect as defined by James 1971, Dickson and Noble 1978, Hamel et al. 1982. This excluded areas that were solely defined by agricultural use. It was hypothesized that wrens found in these areas would not receive any direct benefit from humans in the form of added heat from the urban areas or supplemental feeding from bird feeders. Five transects were located around Washtenaw County (Table 2). One of the transects in the Waterloo-Pinckney Recreation area is located on public land heavily used for hunting, so surveying during firearm deer hunting season (November 15-30) was not feasible.

Temperature Measurements

In order to quantify the extent of urban warmth in Ann Arbor, all transects were outfitted with temperature data loggers. Dallas thermochron iButtons (DS1921G-F5) were used to record the temperature data. Each iButton was housed in an 8oz aluminum can to prevent damage from precipitation. Each can was painted white in order to reduce the effects that solar radiation might have on the temperature readings. The iButtons were attached to the cans with double-sided insulating weather stripping. Five 0.635cm holes were drilled in the sides of each can to allow air to circulate around the temperature loggers. All iButtons were hung on the north-facing side of trees, 0.6m off the ground.

All iButtons were placed in the field on December 18, 2007. To ensure that data recording began at the same time, all recording times were delayed until the following day after all were placed in the field. The iButtons were set up to record the temperature every hour. Data collection ended on April 7, 2008.

Bird Feeder Data

All residential transects were located in areas comprised primarily of one/two story houses. Three of the five city park transects (County Farm Park, Dolph Park, Nichol's Arboretum) had houses that directly bordered them (<15m). Wrens on these transects could potentially survive prolonged periods of snow cover if these houses provided food at bird feeding stations. To understand if such a relationship existed, houses were selected at random to be surveyed about their use of bird feeders. None of the rural transects had houses close enough to supply supplemental feeding in the form of bird feeders, assuming 4.1ha as the size of a Carolina wren territory (Strain and Mumme 1988) and the transect center line was the edge of the territory.

Maps of all transects to be included in this portion of the study were obtained using Google Earth Pro. All houses that were directly bordering (<15m) the walking path of the residential transects or the boundaries of the city parks were potential participants in this portion of the study. Participating houses on each residential transect were sequentially labeled. Using a random number generator and depending on the number of houses per transect, a random set of 100 numbers was generated, with the highest possible number being the number of houses bordering that transect. A maximum of 30 responses were collected per transect.

All houses that bordered the city parks were surveyed since none of the three parks had more than 25 bordering houses. To account for people who were not home, three total trips were made to each of these transects. The survey was terminated after all households responded, or after three visits.

Surveys were conducted on the weekdays from 530pm to 8pm or on the weekends from 1100am to 800pm, in order to maximize the possibility of the residents being home. Each participant was presented with the same greeting before the survey began in order to prevent any bias in data collection. Only resident adults were allowed to participate. Once consent was given, two questions were asked to the participants. These included: "Do you provide food to birds?" and "Did you provide food throughout this past winter?" Surveying began in June 2008 and was completed in August 2008.

Statistical Analysis

Temperature data were analyzed using a one-way ANOVA. The temperature data that were analyzed were proportion of hours below freezing (0°C), daily mean minimum temperature (°C), and January mean minimum temperature (°C). Bonferroni style multiple comparisons was used to locate the significant differences between habitat types.

Bird feeder survey data were used to examine the relationship between winter mortality and winter bird feeding. The winter bird feeding data were treated as a binary set of data with either a "yes" or "no" response of winter bird feeding presence per transect. All 21 transects were included in this analysis. These data were analyzed along with proportion of hours spent under 0°C, daily mean minimum temperature, and January mean minimum temperature for the transects. Those weather criteria were selected on the basis of Root's (1988) proposal of January mean minimum temperature being most important in Carolina wren distribution. This study proposes that these temperature parameters are the most important weather criteria since these are the coldest and therefore most critical to the wrens. An analysis of covariance was used to show the importance of winter bird feeding to Carolina wrens. January mean minimum temperature was used as the covariate in the analysis. Snow cover data for each transect were not available for this analysis.

Carolina wren survey data, wrens/area (km^2), were analyzed using repeated measures ANOVA. A log transformation was required to equalize the variances. Bonferroni style multiple comparisons were used to locate the significant differences in Carolina wren densities for the three habitat types within a single transect series over the entire study.

Carolina wren survivorship was calculated using the peak wren count for all transects during the fall (September-November) of 2007 and the data from the last survey series (March/April 2008). Percent survival was found using these values. A Kruskal-Wallis test was used to look for significant differences in winter survival for the three habitat types. This test was used instead of an ANOVA because of the many 0% survivorships that were measured.

All data were analyzed using Systat®.

Results

Carolina Wren Density

Carolina wren population density differed among habitat type (Repeated measures ANOVA $F_{2,16}$=3.855, P=0.043). It was found that there were two significant differences (Figure 2). The residential and rural transects were found to exhibit the largest significant difference throughout the study (Repeated measures ANOVA $F_{1,11}$=7.580, P=0.017). Over the course of the study, the average density of Carolina wrens in the residential habitats was 4.19 wrens/km^2 (SEM = 0.519, n=66). The rural habitats had an average wren density of 1.01 wrens/km^2 (SEM=0.405, n=29). It was also found that the city park and rural habitats had Carolina wren densities that were significantly different (Repeated measures ANOVA $F_{1,11}$=5.945, P=0.045). City park habitats had an average density of 7.63 wrens/km^2 (SEM=1.55, n=30).

The time of year also had significant effects on population densities of Carolina wrens (Repeated measures ANOVA $F_{5,80}$=5.741, Greenhouse-Geisser adjusted P=0.001). However, Carolina wren populations responded to seasonal conditions similarly throughout the study, regardless of habitat (Repeated measures ANOVA $F_{10,80}$=0.865, Greenhouse-Geisser adjusted P=0.547) (Figure 3). Wren populations in general were at their peak in late summer/early fall and at their lowest during the winter months, regardless of habitat.

Wren Winter Survival Rates

Wrens had a significantly higher survival rate in residential habitats than rural habitats (Kruskal-Wallis chi sq.=5.357, df=1, P=0.016) (Figure 4). Differences in survival rate were on the verge of being significant between the city park and rural habitats (Kruskal-

Wallis chi sq.=3.716, df=1, P=0.054). Carolina wrens had similar survival rates in the city park and residential habitats (Kruskal-Wallis chi sq.=0.119, df=1, P=0.730). The post winter survival rate of the residential habitats was 37%±8.73_{SError}. The post winter survival rate of the city park habitats was 39%±15.2_{SError}. Finally, the post winter survival rate of wrens in the rural habitats was 0%±0_{SError}.

Temperature

Three different temperature parameters were compared in three different habitat types (residential, city park, and rural). All three parameters were significantly different, revealing that residential areas in Ann Arbor were warmer than rural areas (Table 3). Daily mean minimum temperatures were significantly different between habitats (ANOVA $F_{2,18}$=9.011, P=0.002). A significant difference existed between the rural habitats and the residential habitats (Bonferroni P=0.001). The rural habitats exhibited the lowest temperatures. The proportion of hours ≤0ºC for the three habitat types was found to be significantly different (ANOVA $F_{2,18}$=5.591, P=0.013). Rural habitats exhibited the greatest proportion of hours under 0ºC from December 19, 2007, to April 7, 2008. This difference was significant between the residential habitats (Bonferroni P=0.017) and city park habitats (Bonferroni P=0.036). Finally, January mean minimum temperature was found to be significantly lower in rural areas (ANOVA $F_{2,18}$=8.028, P=0.003). The difference was found to exist between residential and rural habitats (Bonferroni P=0.003).

Bird Feeder Data

The survey data were organized into categories based on the responses of participants. These categories were percent of respondents who feed birds and percent of respondents who feed birds during the winter. Fourteen transects were surveyed (11 residential, 3 city park). The remaining seven transects did not have houses that directly bordered them, so surveying was not required. Six out of the 11 residential transects had the maximum of 30 respondents (Table 4). None of the three city park transects surveyed had 30 houses bordering them, so 30 responses were not possible. Of the houses surveyed on all transects, 39±11% (136 houses) provided food specifically for birds, and 30±8% (101 houses) provided food specifically for birds throughout the winter.

Winter Survival and Bird Feeding

To determine if winter bird feeding had a greater impact on winter survival than any temperature aspect, an ANCOVA was performed. The availability of bird feeders during the winter had the largest impact on Carolina wren winter survivability (ANCOVA $F_{1,18}$=9.922, P=0.006). The covariate January mean minimum temperature (ANCOVA $F_{1,18}$=0.632, P=0.437) showed no significant effect on Carolina wren winter survival.

Discussion

Carolina Wren Density

Habitat played a major role in determining Carolina wren density throughout the study. Wren densities in residential and city park habitats were significantly greater than those in rural habitats, supporting the prediction that wren numbers in these areas would be greater. Mean Carolina wren density in city park habitats was almost double that of residential areas and seven times greater than rural areas.

Carolina wren populations fluctuated similarly throughout the study, regardless of habitat type. Populations were at their greatest for all habitats during the fall of 2007. This is undoubtedly due to breeding season that occurred during the spring and summer. All populations showed marked decreases in populations during the winter that followed. That winter was the snowiest winter on record (1880-present) for Ann Arbor, MI (Jesse 2008). Total wren counts declined by 65% from peak numbers of 88 in the fall 2007 to 31 wrens present post-winter 2008. Despite the benefits that Carolina wrens received in the residential and city park habitats, winter weather still negatively affected their populations. The heat islands and supplemental feeding appear to alleviate, not negate, the harshness of winter.

One possible difference that could explain the difference in densities between city park and residential habitats but was not measured during this study is habitat quality. City parks had wren densities almost double of residential areas. These two habitats both received heat from urban areas and supplemental feeding. However, habitat quality in city parks seemed to be better suited for Carolina wrens. Most residential areas were groomed yards that lacked any dense undergrowth or shrubs, which are important characteristics of wren habitat (James 1971, Dickson and Noble 1978, Hamel et al. 1982, Kaufman 1996), while city parks remained ungroomed. The two residential transects that had the highest wren densities appeared to be characterized primarily by yards that met Carolina wren habitat requirements the closest. However, because no measurements were taken on vegetative habitat quality, any conclusions about this are purely speculative.

Carolina Wren Survival

Carolina wren populations as a whole declined by 65% during the winter of 2007-2008. Wrens in rural areas apparently suffered 100% mortality rates, while wrens in residential and city parks suffered similar mortality rates (63% and 61%, respectively). This supported the prediction that Carolina wrens in residential areas and city parks would have higher survival rates than those in rural areas.

Mortality of wrens in rural areas could have been largely influenced by juvenile birds. It is possible that first year birds were chased from prime habitat in the residential areas and city parks and forced into subprime habitat in the rural areas. One study released a captive Carolina wren and tracked its movement by its vocalizations as it was chased from territory to territory by other males (Morton and Schalter 1977). It has been hypothesized that winter survival is tied to the ability of the male to obtain and defend a territory with sufficient food (Strain and Mumme 1988). In areas of higher wren densities (residential and city parks), juveniles may be forced out to rural areas where there is not enough food to survive during harsh winters.

Bird Feeding

The presence of supplemental feeding through bird feeders was quantified during the study. Almost 40% of the houses surveyed fed birds at some time during the year, with 30% of people saying they continued feeding throughout the winter. A quarter century ago, 21 million or 12% of the U.S. population showed an interest in birds through some form of bird related activity. Since then, that number has grown to 70 million or 33% of the population (Cordell and Herbert 2002). In 1995, 26.7% of the U.S. population showed an interest in birds. Of those interested showing an interest in birds, 19.5% stated that the interest remained at the home, with most people providing bird feeders (Cordell et al. 1999). Cordell et al. (1999) reported that 63.1 million residential bird feeders were in place in 1991. So although impossible to extrapolate the 40% feeder rate found in this study onto the rest of Michigan, there seems to be a growing interest and therefore greater amount of supplemental feeding available to birds.

Winter Survival and Bird Feeding

It was found that winter survival was most strongly related to having bird feeders present on a transect during winter. This supported our hypothesis. None of the five rural transects had feeders available to Carolina wrens. The wrens on these transects had 100% mortality rates. The two city park transects that had no feeders available to the wrens also had wren mortality rates of 100%. Root (1988) states that Carolina wren populations are metabolically limited at the northern edge of their range by January mean minimum temperatures. It has also been stated that low ambient winter temperatures in general are limiting to northern Carolina wren populations (Brooks 1936). However, through the use of an analysis of covariance, this study showed that the presence of bird feeders during the winter best predicts survival for Carolina wrens in our study. Thus we need to focus on food supply, not simply energy expenditure. It has been shown that some species of birds that overwinter at northern latitudes have survival rates influenced by food availability (Lack 1954, Fretwell 1972). Brittingham and Temple (1988) have shown that supplemental feeding decreased winter mortality rates of Black-capped chickadees by half. They also showed that during times of severely cold temperatures, survival of chickadees with access to supplemental food decreased only slightly from 96% to 93%, illustrating the benefits of supplemental feeding over any aspect of winter temperature. The benefits of supplemental feeding depends on what food is offered at a feeding station. A single peanut offers 29kJ of energy. The daily metabolic rate of a Carolina wren at the northern edge of its range is 76.2 kJ/d (Root 1988). Eating one peanut is the equivalent of over a third of its daily metabolic needs. For those wrens with access to feeders, this has important implications. Consuming one peanut before roosting all but ensures that it can properly thermoregulate and survive the night.

While this study does not disagree with Root (1988) that metabolic limits are reached during extremely cold periods, it does find that the presence of bird feeders on a Carolina wren territory allows them to survive during these periods. This supports the hypothesis that wrens living in residential areas and city parks take advantage of human activities to survive through the winter.

Conclusions

The findings of this study illustrate the effects of winter weather on Carolina wren populations at the northern edge of their range. While wrens in the three populations were adversely affected by harsh winter weather conditions, the beneficial effect of human influence could be observed through the residential and city park habitats. Supplemental feeding was found to decrease winter mortality of wrens in these areas despite the weather conditions. The continued growing interest in birds will help Carolina wrens and possibly other species of birds survive particularly harsh winters at the northern edge of their ranges.

This study has also shown that Carolina wrens can survive harsh winters and therefore expand their range northward through humans providing a bird feeder with various seeds throughout the winter. The ranges of tufted titmice and northern cardinals have also expanded northward during the same time period as Carolina wrens. Humans may also be influencing the northward advancement of these songbirds. Further study into that may reveal the extent of human influence on other songbirds struggling to survive at the northern edge of their range. In a time when human influence, through global warming, is having negative effects on many species, Carolina wrens seem to be directly benefitting from the actions of humans.

References

Anderson, S. H. and H. H. Shugart Jr. 1974. Habitat selection of breeding birds in an East Tennessee deciduous forest. Ecology **55**:828-837.

Andrle, R. F. and J. R. Carroll. 1988. *The Atlas of Breeding Birds in New York State*. Cornell University Press, Ithaca, N.Y., USA.

Beddall, B. G. 1966. Range expansion of the Cardinal and other birds in the northeastern states. Wilson Bulletin **75**:140-158.

Beissinger, S. R. and D. R. Osborne. 1982. Effects of urbanization on avian community organization. Condor **84**:75-83.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. United States National Museum Bulletin **195**:475.

Bent, A. C. 1964. *Life histories of North American nuthatches, wrens, thrashers, and their allies*. Dover Publications, Mineola, N.Y., USA.

Bibby, C., M. Jones, and S. Marsden. 1998. *Bird Surveys*. Expedition Advisory Centre London.

Bornstein, R. D. 1968. Observations of the urban heat island effect in New York City. Journal of Applied Meteorology **7**:575-582.

Brewer, D. 2001. *Wrens, dippers and thrashers*. Yale University Press, New Haven, C.T., USA.

Brewer, R., G. A. McPeek, and R. J. Adams Jr. 1991. *The atlas of breeding birds of Michigan*. Michigan State University Press, East Lansing, M.I., USA.

Brittingham, M. C. and S. A. Temple. 1988. Impacts of supplemental feeding on survival rates of black-capped chickadees. Ecology **69**:581-589.

Brooks, M. 1936. Winter killing of Carolina wrens. The Auk **53**:449.

Butcher, G. S., M. R. Fuller, L. S. McAllister, and P. H. Geissler. 1990. An evaluation of the Christmas Bird Count for monitoring population trends of selected species. Wildlife Society Bulletin **18**:129-134.

Bystrak, D. 1979. The breeding bird survey. Sialia 1: 74-79.

Chandler, T. J. 1962. London's urban climate. Geographical Journal **128**:279.

Christman, S. 1984. Plot mapping: Estimating densities of breeding bird territories by combining spot mapping and transect techniques. Condor **86**:237-241.

Conway, C. J. 2005. Standardized North American marsh bird monitoring protocols. Wildlife Research Report **4**:466-473.

Cordell, H. K. and N. G. Herbert. 2002. The Popularity of Birding is Still Growing. Birding **34**:54-61.

Cordell, H. K., N. G. Herbert, and F. Pandolfi. 1999. The growing popularity of birding in the United States. Birding **31**:168-176.

De Vos, A. 1964. Range changes of birds in the Great Lakes region. American Midland Naturalist **71**:489-502.

Dickson, J. G. and R. E. Noble. 1978. Vertical distribution of birds in a Louisiana bottomland hardwood forest. Wilson Bulletin **90**:19-30.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monographs in Population Biology **5**:1-217.

Gibson, C. 1998. Population of the 100 largest cities and other urban places in the United States: 1790 to 1990. US Bureau of the Census.

Graber, J. W. and R. R. Graber. 1979. Severe winter weather and bird populations in southern Illinois. Wilson Bulletin **91**:88-103.

Granlund, J. 1994. *Birds of Michigan*. Indiana University Press, Bloomington, I.N., USA.

Haggerty, T. M. and E.S. Morton. 1995. *Carolina Wren: Thryothorus Ludovicianus*. American Ornithologists' Union; The Academy of Natural Sciences.

Hamel, P. B., N. Station, and N. C. Asheville. 1982. Bird-habitat relationships on southeastern Forest Lands. US Dept. of Agriculture, Southeastern Forest Experiment Station, Forest Service.

Hinkel, K. M., F. E. Nelson, A. E. Klene, and J. H. Bell. 2003. The urban heat island in winter at Barrow, Alaska. International Journal of Climatology **23**:1889-1905.

Hyman, J. 2003. Countersinging as a signal of aggression in a territorial songbird. Animal Behaviour **65**:1179-1185.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin **83**:215-236.

Jesse, D. "It's a record year for snowfall." The Ann Arbor News 22 March 2008.

Karl, T. R., H. F. Diaz, and G. Kukla. 1988. Urbanization: Its detection and effect in the United States climate record. Journal of Climate **1**:1099-1123.

Kaufman, K. 1996. *Lives of North American Birds*. Houghton Mifflin Company, Boston, M.A., USA.

Kielb, M.A. Pers. comm.

Labisky, R. F. and J. E. Arnett Jr. 2006. Pair roosting of nesting Carolina wrens (*Thryothorus ludovicianus*). The Wilson Journal of Ornithology **118**:566-569.

Lack, D. L. 1954. *The Natural Regulation of Animal Numbers*. London: Oxford.

Link, W. A. and J. R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. Ecological Applications **8**:258-268.

Link, W. A. and J. R. Sauer. 1999. Controlling for varying effort in count surveys: An analysis of Christmas Bird Count Data. Journal of Agricultural, Biological, and Environmental Statistics **4**:116-125.

Link, W. A. and J. R. Sauer. 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. Ecology **88**:49-55.

Mehlman, D. W. 1997. Change in avian abundance across the geographic range in response to environmental change. Ecological Applications **7**:614-624.

Miller Jr., F. 1982. *College Physics 5th edition.* New York: Harcourt Brace Jovanovich, Inc.

Morton, E. S. 1975. Ecological Sources of Selection on Avian Sounds. The American Naturalist **109**:17.

Morton, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules. Acoustic communication in birds **1**:183-212.

Morton, E. S. and M. D. Shalter. 1977. Vocal response to predators in pair-bonded Carolina wrens. Condor **79**:222-227.

Mugaas, J. N. and J. R. Templeton. 1970. Thermoregulation in the red-breasted nuthatch (*Sitta canadensis*). Condor **72**:125-132.

Naguib, M. 1995. Auditory distance assessment of singing conspecifies in Carolina wrens: The role of reverberation and frequency-dependent attenuation. Animal Behaviour **50**:1297-1307.

Oke, T. R. 1973. City size and the urban heat island. Atmospheric Environment **7**:769-779.

Repasky, R. R. 1991. Temperature and the northern distributions of wintering birds. Ecology **72**:2274-2285.

Richards, D. G. 1981. Estimation of distance of singing conspecifics by the Carolina wren. Auk **98**:127-133.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: Its first fifteen years, 1965-1979. U.S. Fish and Wildlife Service Resource Publication. 157.

Root, T. 1988. Energy Constraints on Avian Distributions and Abundances. Ecology **69**:330-339.

Rusnak, C. M. and R. F. Labisky. 2003. Carolina Wren (*Thryothorus Ludovicianus*). University of Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, EDIS.

Sauer, J. R., G. W. Pendleton, and B. G. Peterjohn. 1996. Evaluating causes of population change in North American insectivorous songbirds. Conservation Biology **10**:465-478.

Shy, E. and E. S. Morton. 1986. The role of distance, familiarity, and time of day in Carolina wrens responses to conspecific songs. Behavioral Ecology and Sociobiology **19**:393-400.

Sibley, D. A. 2000. *The Sibley Guide to Birds*. Alfred A. Knopf. Inc., N.Y., USA.

Simpson, B. S. 1984. Tests of habituation to song repertoires by Carolina wrens. The Auk **101**:244-254.

Somme, L. and K. E. Zachariassen. 1981. Adaptations to low temperature in high altitude insects from Mount Kenya. Ecological Entomology **6**:199-204.

Strain, J. G. and R. L. Mumme. 1988. Effects of food supplementation, song playback, and temperature on vocal territorial behavior of Carolina wrens. The Auk **105**:11-16.

Townsend, C. W. 1909. A Carolina wren invasion of New England. The Auk **26**:263-269.

Verner, J. and M. F. Willson. 1969. Mating Systems, Sexual Dimorphism, and the Role of Male North American Passerine Birds in the Nesting Cycle. Ornithological Monographs **9**.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Yoda, T., L. I. Crawshaw, K. Yoshida, L. Su, T. Hosono, O. Shido, S. Sakurada, Y. Fukuda, and K. Kanosue. 2000. Effects of food deprivation on daily changes in body temperature and behavioral thermoregulation in rats. American Journal of Physiology- Regulatory, Integrative and Comparative Physiology **278**:134-139.

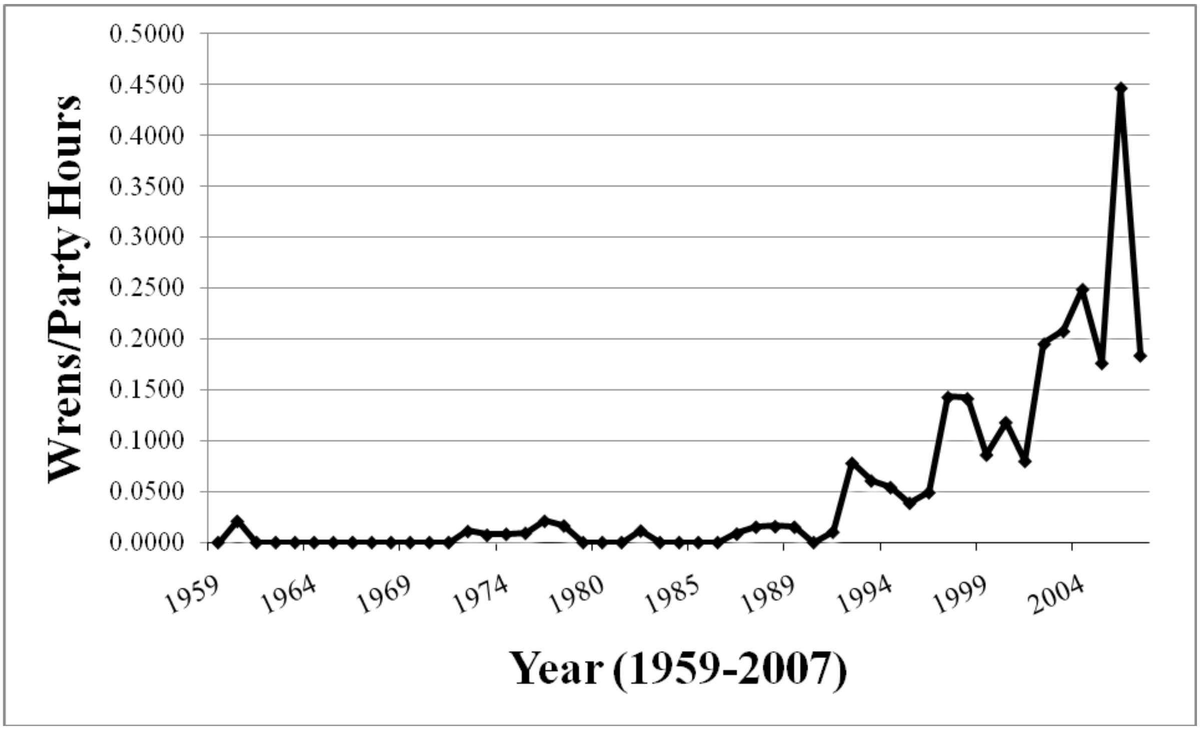

Figure 1: Carolina wren (*Thryothorus ludovicianus*) Christmas Bird Count data from 1959-2007. The original colonization peaked in 1977. The second colonization began in 1991. Wren counts were divided by party hours to account for effort.

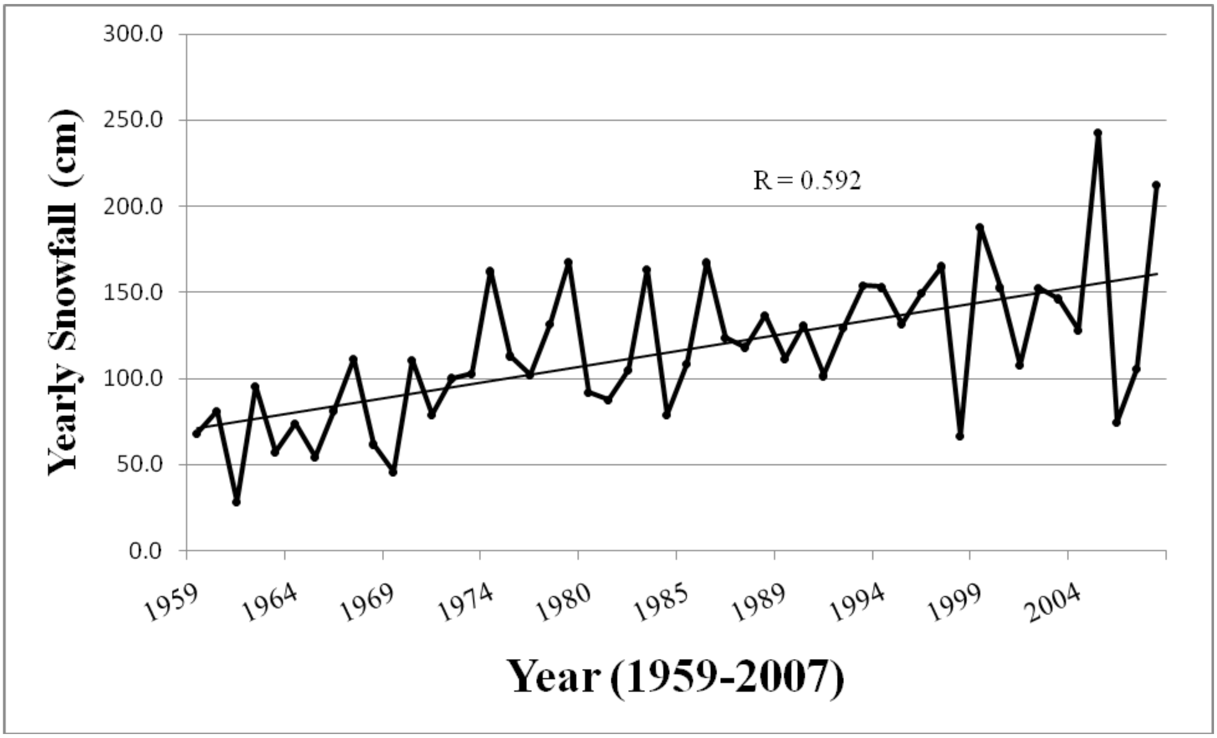

Figure 2: Yearly snowfall data from 1959-2007. Trends from 1959-2007 show an increase in yearly snowfall of 80cm. A simple correlation revealed a strong relationship between yearly snowfall (cm) and year (Pearson =0.592).

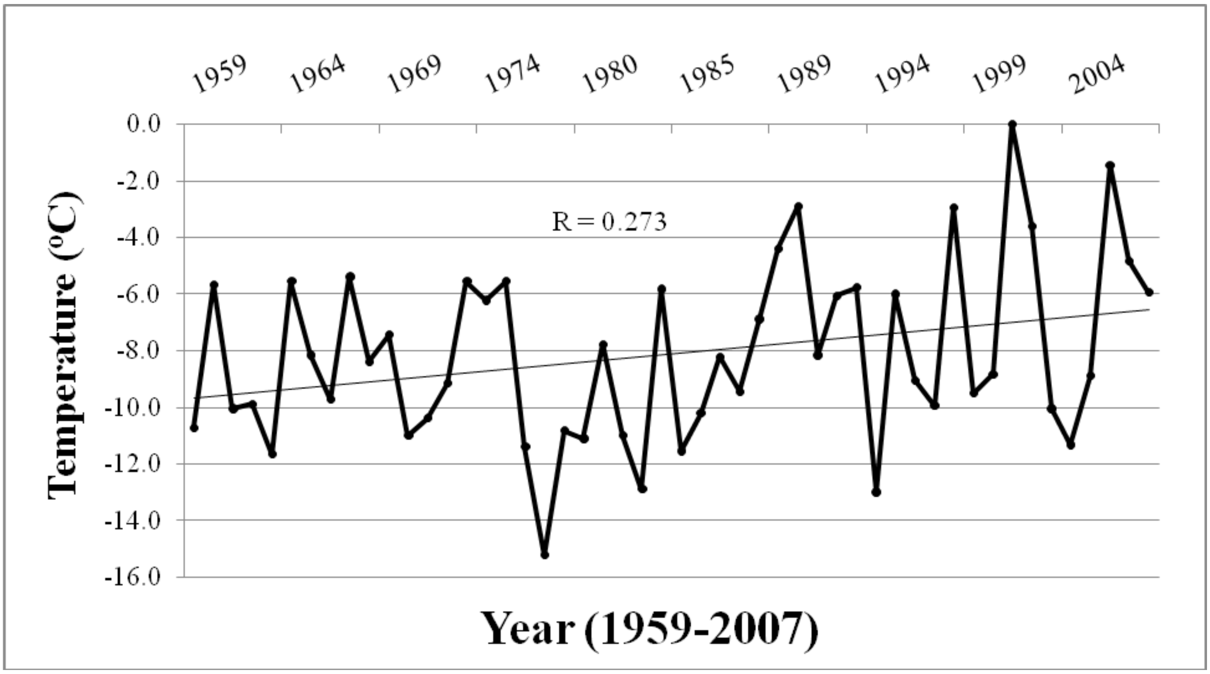

Figure 3: January mean minimum temperature (ºC) for the duration of the study as proposed by Root (1988). Trends from 1959-2007 show an increase of 3ºC (Pearson =0.273). The low peak (-15.2ºC) occurred in 1978 and corresponds to the original population crash.

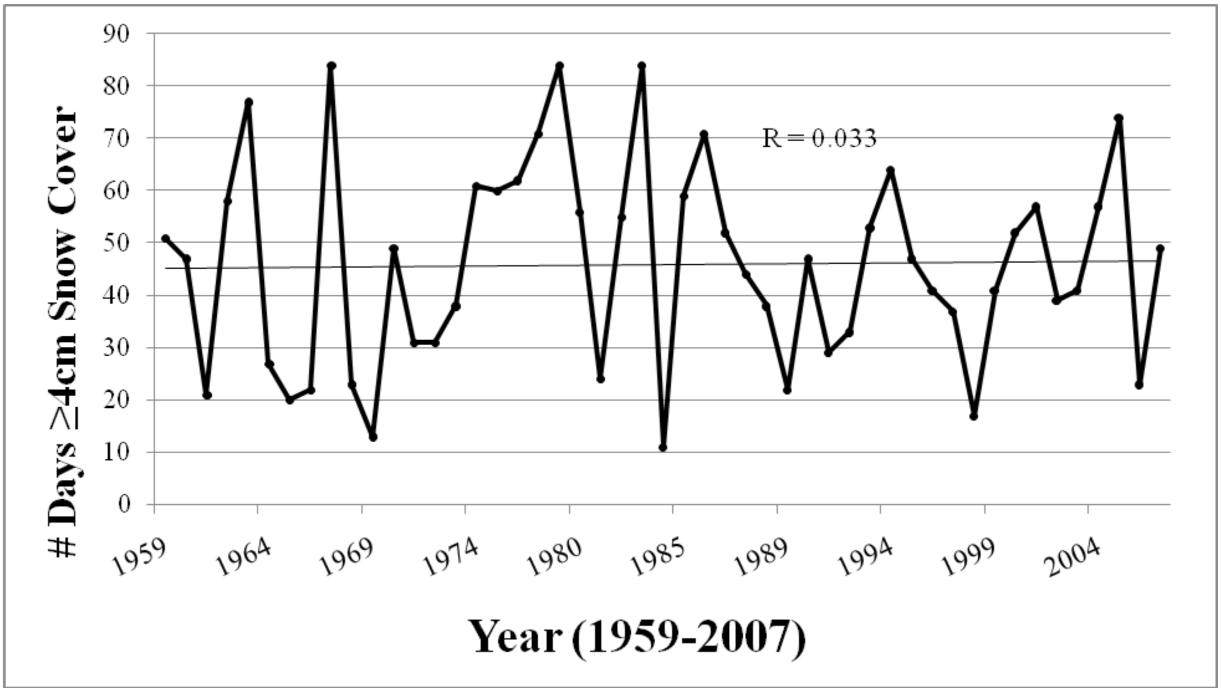

Figure 4: The number of days with ≥4cm of snow cover per year for the entire study as proposed by Link and Sauer (2007). Trends from 1959-2007 show an increase in days with ≥4cm from 45 days to 48 days (Pearson =0.033). Prior to the second colonization, there were five winters with over 70 days with ≥4cm of snow cover. Since the second colonization began, there has only been one.

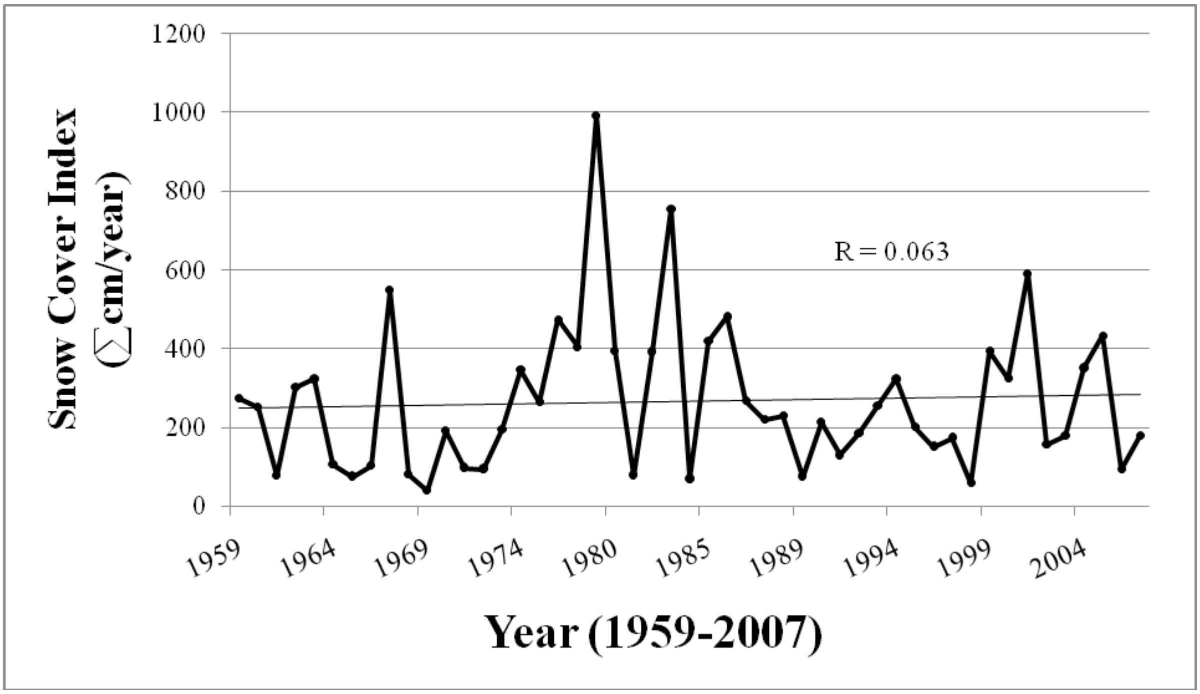

Figure 5: Snow cover index from 1959-2007. The snow cover index in a measure of snow cover combined with its duration for the year. Trends from 1959-2007 show a slight increase around 50cm in the snow cover index (Pearson =0.063). The tallest peak (994 cm) occurred in 1978, the time of the first population crash.

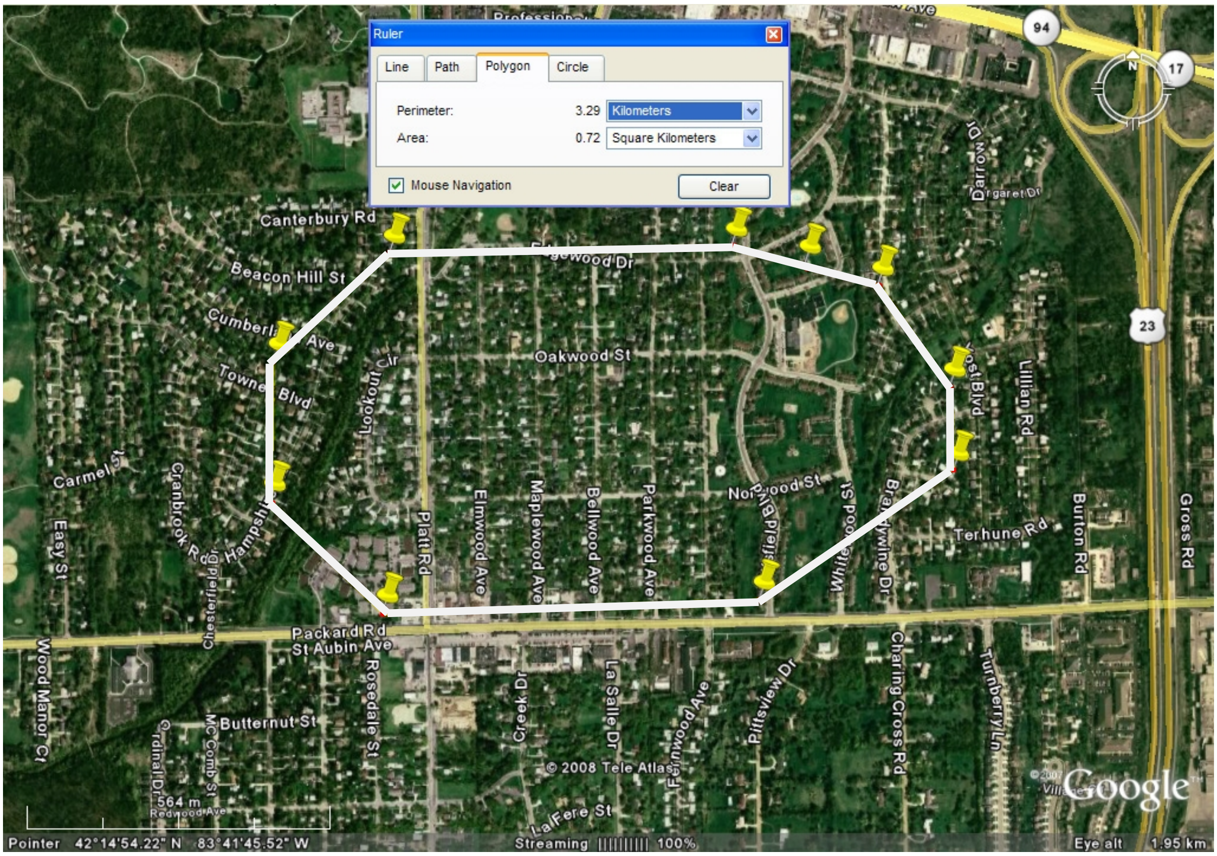

Figure 1: Residential transect (7) as shown in Google Earth Pro. A polygon has been drawn connecting the ‘untitled placemarks’ so that the area could be determined. Each place mark was placed 198m from the transect. The area for residential transect ‘7’ was 0.72 km^2.

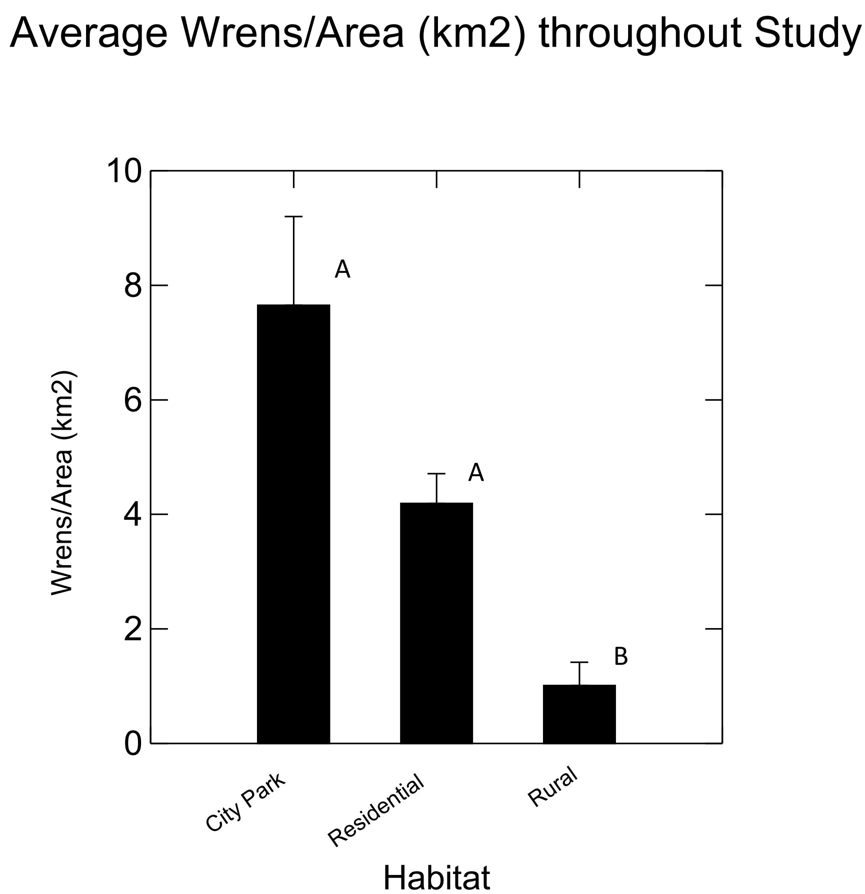

Figure 2: Mean Carolina wren densities for all three habitats throughout the entire study. Repeated measures ANOVA showed significant differences between the residential and rural habitats (F=7.580, df=1, P=0.017) and between the city park and rural habitats (F=5.945, df=1, P=0.045). Error bars denote standard error.

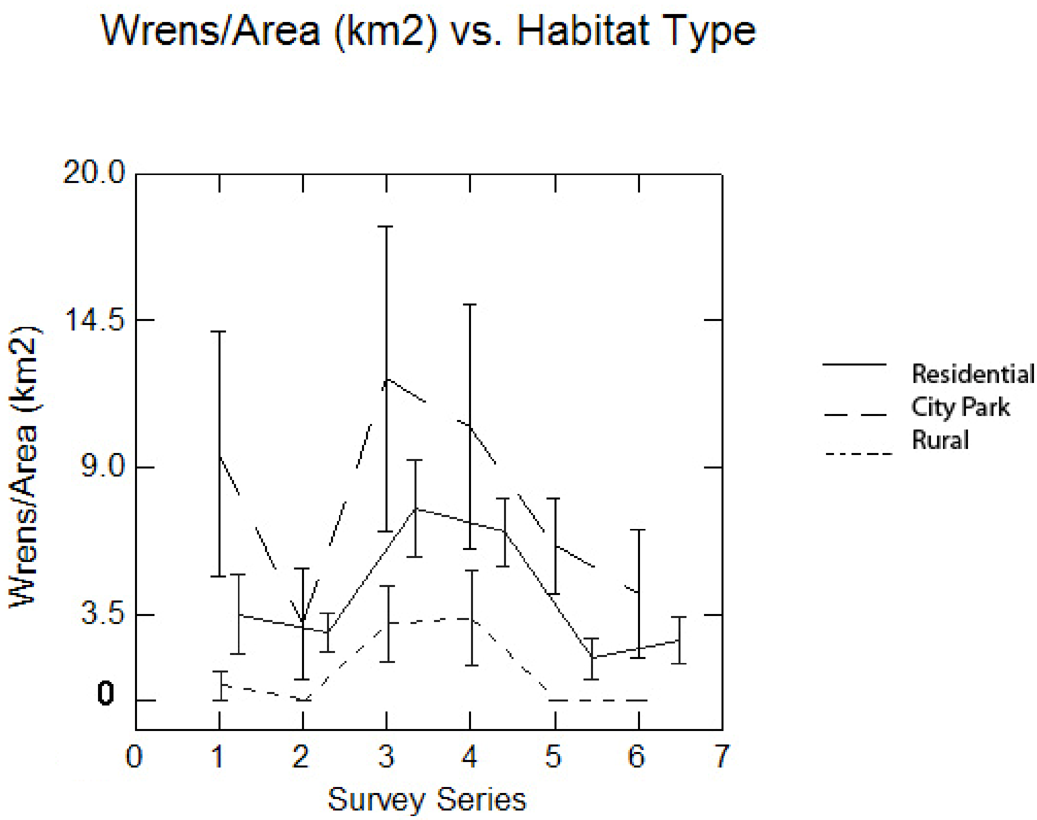

Figure 3: Mean wrens/area (km^2) for the duration of the study (January 2007-April 2008). Carolina wren densities responded similarly throughout the year, regardless of habitat (Repeated measures ANOVA F=0.865, df=10, G-G=0.547). Error bars denote standard error. The numbers on the x-axis correspond to the midpoints of each survey series (1=2/27/07, 2=6/8/07, 3=10/13/07, 4=11/26/07, 5=2/18/08, 6=4/1/08). The rural transect exhibited 0 wrens/km^2 for series 2, 5, and 6. Lines are offset to prevent error bars from overlapping.

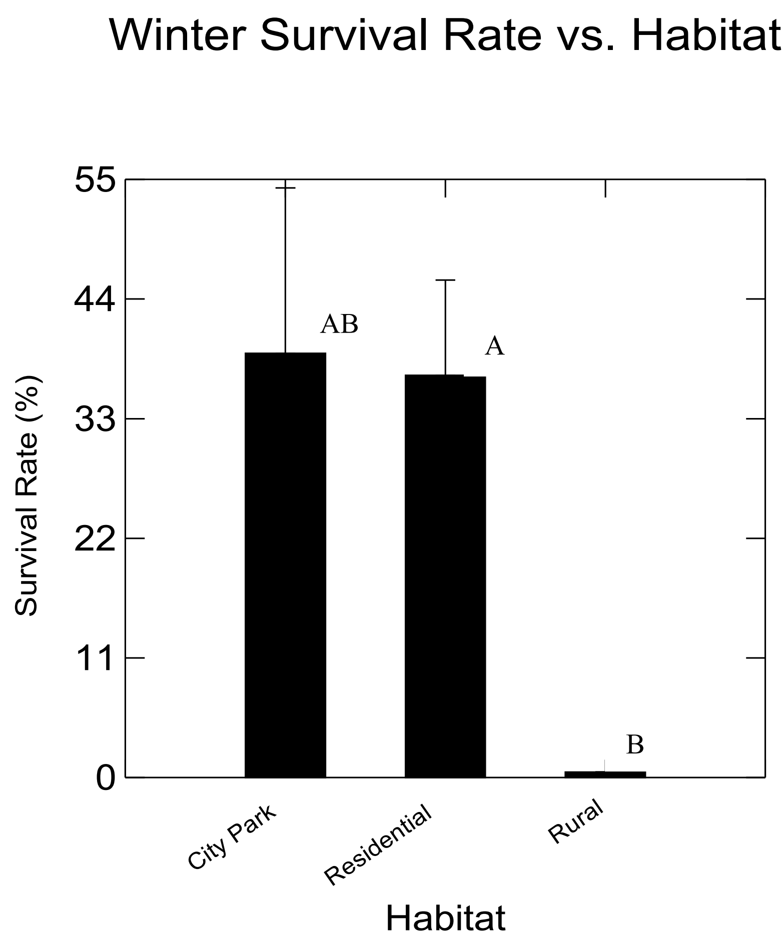

Figure 4: Mean post-winter (April 2008) survival rates of Carolina wrens for the three habitat types in Washtenaw county, Michigan. Kruskal-Wallis showed significant differences (x^2= 5.921, df=2, P=0.05). Significant differences existed between city park and rural habitats (Kruskal-Wallis x^2=3.716, df=1, P=0.05) and between residential and rural habitats (Kruskal-Wallis x^2=5.357, df=1, P=0.016). The rural habitat exhibited 0% winter survival. Error bars denote standard error.

Rural GPS Coordinates	
1	42°17'31"N 83°35'59"W
2	42°22'06"N 84°02'11"W
3	42°07'59"N 83°46'09"W
4	42°24'36"N 84°00'01"W
5	42°19'18"N 84°05'13"W

Table 1: GPS coordinates of the five rural transects surveyed during the study.

Transect Areas		
Residential	**Area (km^2)**	**Winter Survival (%)**
1	0.57	0
2	0.56	33
3	0.66	0
4	0.83	80
5	0.62	9
6	0.89	38
7	0.72	0
8	0.66	55
9	0.57	50
10	0.49	66
11	0.66	20
Mean Area (km^2)	0.66	**Mean**
City Park		37
1	0.31	25
2	0.58	66
3	0.61	44
4	0.27	0
5	0.65	0
Mean Area (km^2)	0.48	**Mean**
Rural		39
1	0.29	0
2	0.37	0
3	0.44	0
4	0.37	0
5	0.49	0
Mean Area (km^2)	0.39	**Mean**
		0

Table 2: Area and winter survival rates of 21 transects surveyed throughout the study. Residential survival rate standard error was 8.73. City Park survival rate standard error was 15.2.

Habitat Temperature Data			
	Residential (n=11)	**City Park (n=5)**	**Rural (n=5)**
Mean Daily Maximum Temp. (°C)	-2.01	-2.13	-2.61
	SD ± 0.27	SD ± 0.31	SD ± 0.29
Mean Daily Minimum Temp. (°C)	-2.33 *	-2.52	-2.99 *
	SD ± 0.25	SD ± 0.31	SD ± 0.31
Mean Temp. (°C)	-2.16	-2.34	-2.78
	SD ± 0.28	SD ± 0.31	SD ± 0.29
Proportion of Hours ≤0°C	0.690 *	0.689 ~	0.712 *~
	SD ± 0.017	SD ± 0.007	SD ± 0.006
January Mean Minimum Temp. (°C)	-3.12 *	-3.33	-3.81 *
	SD ± 0.28	SD ± 0.42	SD ± 0.32

Table 3: Temperature data collected from December 19, 2007 to April 7, 2008. ANOVA was performed on mean daily minimum temp. (°C), proportion of hours ≤0°C, and January mean minimum temp. (°C). Daily Min. (ANOVA $F_{2,18}$=9.011, P=0.002), Proportion hours ≤0°C (ANOVA $F_{2,18}$=5.591, P=0.013), Jan. min. (ANOVA $F_{2,18}$=8.028, P=0.003). Variables with similar symbols indicate significant pair-wise differences (Bonferroni df=18).

Feeder Survey Responses		
Habitat Type		Bird Feeding
Residential	Responses	% Winter
1	30	27
2	32	25
3	24	13
4	28	32
5	30	27
6	30	37
7	19	32
8	26	50
9	30	27
10	30	33
11	23	26
City Park		
1	12*	33
2	20*	25
3	14*	29
4	0	0
5	0	0
Rural		
1	0	0
2	0	0
3	0	0
4	0	0
5	0	0

Table 4: Total responses for each transect during the bird feeding survey. Responses with an * indicates that the transect did not have 30 houses bordering it.