

## Wrens on the edge: feeders predict Carolina wren *Thryothorus ludovicianus* abundance at the northern edge of their range

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The marked range shifts seen with global warming suggest that ranges are limited by temperature. Other findings, however, suggest winter survival is directly tied to food availability. We studied Carolina wrens *Thryothorus ludovicianus* at the northern edge of their range to understand the roles of temperature and food in limiting this species. We established 21 transects over 3 habitats (residential, city park, and rural) with varying degrees of human influence on temperature and food supply. The three habitat types showed variations in wren density, temperature, and feeder presence. While wren densities showed similar seasonal patterns in all habitats, significantly higher densities of birds were observed in the city park and residential habitats. Post-winter densities of Carolina wrens were predicted by the presence of bird feeders, and not by January mean minimum temperatures. Our findings suggest the winter range limits for endotherms is more directly related to food supply, and only indirectly related to temperature. Therefore supplemental feeding and other changes in food supply may modify the range shifts predicted from temperature changes alone.

The ranges of many species of animals and plants have expanded northward in the northern hemisphere during the last century, as global surface temperatures have increased by 0.6° C, with most increases occurring since 1976 (Walther et al. 2002). Among birds in Great Britain, 59 species have experienced northward range shifts, averaging 19 km, during a 20-year period (Thomas and Lennon 1999). One hundred and sixteen Finnish bird species averaged the same northerly shift in roughly half the time (Brommer 2004). Of North American birds, those with southern distributions have exhibited northward range expansions of an average of 2.35 km/yr during a 26-year stretch (Hitch and Leberg 2007).

Consistent range expansions with warming suggest that species distributions are limited by temperature. The question is how temperature determines range limits. Northern species that do not migrate must cope with thermoregulation challenges each winter, including extended periods of sub-freezing temperatures and food shortages. Using data from Christmas Bird Counts, Root (1988) noted that many bird species in the United States and Canada have northern edges of their range strongly associated with an isotherm representing the mean minimum temperature in January. She argued that this critical isotherm occurred where a ceiling on the metabolic rate of these birds prevented them from expanding their ranges northward. That is, she argued that the effect of winter temperature acted directly on survival.

In contrast, experimental evidence indicates that winter survival in some species, is directly related to food

availability. When provided with supplemental food, willow tits *Parus montanus* and song sparrows *Melospiza melodia* showed higher rates of winter survival than those on control plots without supplemental food, regardless of temperature (Smith et al. 1980, Lahti et al. 1998). Black-capped chickadees *Poecile atricapilla* on plots with supplemental food had survival rates close to double that of those found on control plots, despite frigid winter temperatures (Brittingham and Temple 1988).

We tested how temperature and food supply affect Carolina wrens *Thryothorus ludovicianus* abundance at the northern edge of their range. Low ambient winter temperatures have long been thought to limit northern Carolina wren populations (Brooks 1936) and the northern range edge for Carolina wrens correlates with January mean minimum temperatures of  $-9.4^{\circ}\text{C}$  (Root 1988, Mehlman 1997). From year to year, however, northern populations of Carolina wrens experienced a 1.1% decrease for every day with 4 cm of snow cover (Link and Sauer 2007). In southeastern Michigan, snow cover rather than temperature correlates with historical Carolina wren range expansions and contractions (Job and Bednekoff 2009). Because Carolina wrens forage on or near the ground (Haggerty and Morton 1995), snow cover can hinder their ability to locate food (Robbins et al. 1986).

In this study we utilized a gradient of human influences, including urban warmth and supplemental feeding, to understand how temperature and food supply affect the densities of Carolina wrens at the northern edge of their range. We tested for human influence by comparing the

densities of Carolina wrens in areas of great, moderate, and low human influence. We tested for direct effects of temperature by correlating temperature with post-winter density. We tested the effects of food supply by comparing post-winter density on transects with winter feeders to transects without feeders. We hypothesized that Carolina wrens take advantage of human influence at the northern edge of their range. From that, we predicted that we would see greater densities of Carolina wrens in areas of greater human influence. More specifically, we also predicted that Carolina wren post-winter densities would be greatest in areas with bird feeders.

## Methods

### Study species

Carolina wrens have undergone several northward range expansions during the twentieth century (Townsend 1909, Bent 1948, Beddall 1963, Brewer et al. 1991). An expansion into Michigan (42°N) occurred in the early 1970s, until 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 (39°N; 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 extends just beyond Lansing (Ingham County) (42.7°N; Kielb 1996, Kielb 1997, Byrne 1999, 2000, 2001, 2002, Murphy 2003, Byrne 2004, 2006, Dombroski 2007, 2008).

The biology of Carolina wrens makes them susceptible to population declines during particularly harsh winters. Carolina wrens are the only wren species east of the Mississippi River that does not migrate (Sibley 2000, Haggerty and Morton 1995), preventing them from escaping critically cold temperatures. However, pairs are known to roost together in cavities and other closely confined spaces during the non-breeding season, opportunistically taking advantage of conductive heating (Labisky and Arnett 2006). Their diet consists of 94% animal matter and 6% vegetable matter (Bent 1964), making food items difficult to locate during particularly snowy periods. They opportunistically 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), although the extent of feeder use seems not to have been quantified.

Carolina wrens pairs aggressively defend their territory year-round, with males responding strongly to conspecific songs (Haggerty and Morton 1995, Morton 1982). 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 including hardwood forests, parks, and suburbs. 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

Michigan, parks and wooded residential and suburban areas, especially those with dense undergrowth and tangles, support populations of Carolina wrens (Beissinger and Osborne 1982, Hamel et al. 1982, Brewer et al. 1991, Brewer 2001, Kaufman 1996). In Florida, urban areas (commercial and residential zones) may have the highest densities of any habitat (Rusnak and Labisky 2003).

### Study sites

Transects in three different habitat types— residential, city park, and rural – were selected in and near Ann Arbor, Washtenaw County, MI (42° 16'N 83° 43'W). Each transect included a minimum length of 0.75 km and minimum area of 0.25 km<sup>2</sup>. The residential and city park habitats were chosen with the possibility of receiving benefits from humans in the form of urban warmth and/or bird feeders. Rural areas were selected with the intent of excluding these potential benefits from those transects by choosing sites without houses.

Residential habitat included any area with one or two story houses, located at intervals no greater than 75 m 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). A total of eleven transects were selected in residential areas with an average length of 2.02 km and average area of 0.66 km<sup>2</sup>.

City parks were defined here as any parkland area free from residential/commercial development within its boundaries. The parks selected for the study were no further than 0.5 km from urban or residential areas, so they might receive heat from the urban areas. Five city park transects were selected, with three having residential areas directly bordering them on one or more sides. The average length of the city park transects was 1.82 km and the average area was 0.48 km<sup>2</sup>.

The rural habitat type was defined as any area with no housing or business structures for at least 0.5 km. All rural transects followed a hiking trail or an unpaved road, through suitable wren habitat as defined by James (1971), Dickson and Noble (1978), and Hamel et al. (1982). We excluded areas solely defined by agricultural use. Rural transects were at least 0.5 km away from human structures. Five rural transects were located around Washtenaw County with an average length of 1.37 km and area of 0.39 km<sup>2</sup>.

To determine the area of each transect and thus the area surveyed (Table 1), we measured the maximum distance a Carolina wren could be heard in each habitat type. The intensity of three Carolina wrens singing in the field was measured using an Extech model 407706 analog sound level meter. The three intensity readings were standardized as if recorded from 1m using the equation  $\Delta L (\text{intensity}) = -20 \log n1/n2$  (Miler 1982), where  $n1 = 1\text{m}$  and  $n2 =$  the distance the singing intensity was originally measured. The three measured wren intensities after standardization averaged  $92 \pm 3$  dB at 1m, which is similar to other findings (Naguib 1995). An mp3 player/external speaker was used to mimic a singing Carolina wren

Table 1. Detection distance of a Carolina wren as perceived by the researcher in each habitat type and the resulting average areas for each habitat type (km<sup>2</sup>).

Transect Area Determination		
Transect	Detection Distance (m)	Mean Area (km <sup>2</sup> ) ± SEM
Residential	198.5	0.66 ± 0.04
City Park	134	0.48 ± 0.08
Rural	140	0.39 ± 0.03

at the same intensity (92 dB at 1 m). An observer walked away from the apparatus until detection of the playback was no longer possible. Playbacks were performed on three transects, one for each habitat type, within a one hour period on the same day.

### Surveying protocol

Carolina wren density was measured throughout the 21 transects using responses to conspecific playbacks. Wrens perceive conspecific songs as intruders and will readily respond to these playbacks (Hyman 2003). A total of six randomly ordered survey series (a single survey series is the completion of all 21 transects) were completed between January 2007 and April 2008 (Table 2). All surveys were conducted between 06.00–11.00, the time of day that wrens are most active (Bibby et al. 1998, Shy and Morton 1986). Surveys were not conducted during any rain or winds exceeding 6m/s as these conditions can lead to poor detectability (Conway 2005).

Transect surveys utilized an mp3 player (Creative Zen Micro), portable speakers (Creative Travelound), and Carolina wren vocalizations (Stokes Field Guide to Birds CD 3) played at realistic volume (92 dB at 1m). Upon arrival to each transect, an initial playback was performed before walking 80m to the next playback location. This was repeated until the entire transect was covered. The presence of Carolina wrens was recorded upon detection by either sight or sound.

### Temperature measurements

All transects were outfitted with a temperature data logger–Dallas thermochron iButton (DS1921G-F5). To protect

Table 2. The dates which each of the 6 survey series were completed throughout the study.

Survey series dates		
Transect Series	Start date	End date
1	1/23/2007	4/3/2007
2	4/24/2007	7/15/2007
3	9/23/2007	11/3/2007
4	11/7/2007	12/16/2007
5	2/2/2008	3/4/2008
6	3/16/2008	4/15/2008

iButtons from precipitation and solar radiation while exposing them to air temperatures, each iButton was housed in an 80 z aluminum can that had been painted white and was ventilated with holes drilled in the sides. iButtons were attached to the inside of the cans with double-sided insulating weather stripping. All iButtons were hung on the north-facing side of trees, 0.6 m off the ground on December 18, 2007. The iButtons made hourly temperature readings from December 19, 2007 until April 7, 2008. Following Root (1988), January mean minimum temperature (° C) is reported (Job 2008).

### Bird feeder data

Carolina wrens are thought to survive prolonged periods of snow cover if they have access to bird feeding stations (Haggerty and Morton 1995). To estimate feeder availability, we surveyed homeowners along residential and city park transects about their use of bird feeders. None of the rural transects had houses nearby to provide bird feeders for resident Carolina wrens.

All houses whose property bordered the walking path of a residential transect or the boundaries of a city park were potential participants in the feeder surveys. A maximum of 30 responses were collected per transect. For transects with more than 30 houses, participating houses were selected at random. All houses that bordered the city parks were surveyed since none of the parks had more than 30 bordering houses. It should be noted that all participating houses on both residential and city park transects were located within the area covered by the Carolina wren surveys.

Surveys were conducted from June to August 2008 on weekdays from 1730 to 2000 or on weekends from 11.00 to 20.00; times that maximized the possibility of residents being home. Each participant was presented with the same two questions in order to prevent any bias in data collection: “Do you provide food to birds?” and “Did you provide food throughout this past winter?” To account for people who were not home, three total trips were made to each of these transects. The survey finished after all households responded, or after three visits.

### Statistical analyses

Carolina wren survey data, wrens/area (km<sup>2</sup>), were analyzed using repeated measures ANOVA. A log transformation of (density + 1) was used to homogenize the variances. Temperature data were analyzed using a one-way ANOVA. Because 7 transects had no feeders near them, the winter bird feeding data were treated as a binary (“yes” or “no”) variable. Post-winter densities of wrens were analyzed in an ANCOVA after confirming that there was no interactive effect between temperature and feeder presence ( $F_{(1,17)} = 0.362$ ,  $p = 0.555$ ), with feeder presence as a categorical variable and January mean minimum temperature (Root 1988) as the continuous covariate.

## Results

### Carolina wren density

Carolina wren population density differed among habitats ( $F_{2,16} = 3.855$ ,  $p = 0.043$ , Fig. 1). Densities of Carolina wrens changed through the seasons ( $F_{5,80} = 5.741$ ,  $p = 0.001$ ), and these changes followed a similar pattern in rural, residential, and city park (interaction:  $F_{10,80} = 0.865$ ,  $p = 0.547$ ) (Fig. 2). Wren populations in general were at their peak in late summer/early fall and at their lowest during and after the winter months.

### Temperature

January mean minimum temperatures were lowest in rural areas ( $-7.81 \pm 0.22^\circ \text{C}$  SEM), followed by city parks ( $-7.25 \pm 0.24^\circ \text{C}$  SEM), and residential areas ( $-6.64 \pm 0.13^\circ \text{C}$  SEM; ANOVA  $F_{2,18} = 13.825$ ,  $p < 0.001$ ). Other measures of temperature gave parallel results across habitats (Job 2008).

### Bird feeder data

None of the rural transects had houses adjoining them. Two of the city park transects had no houses near them and the other three had fewer than 30 houses. For the residential transects, five had fewer than 30 respondents, while six had 30 respondents. Of the houses surveyed on all transects,  $39 \pm 11\%$  (136 houses) provided food specifically for birds, and  $30 \pm 8\%$  (101 houses) provided food specifically for birds throughout the winter.

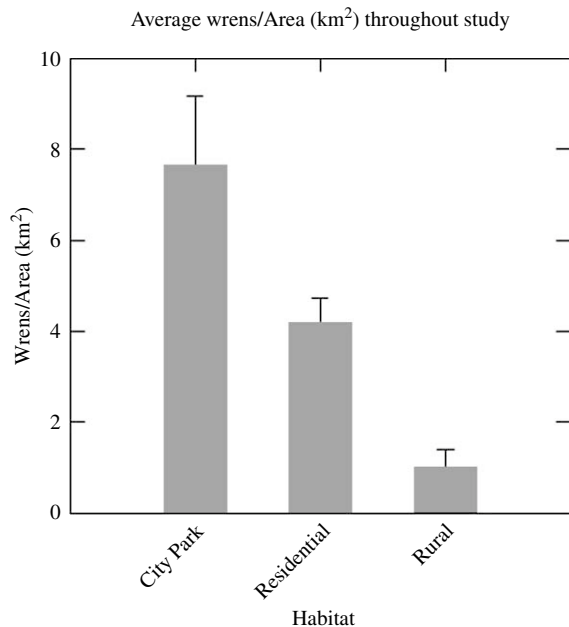


Figure 1. Mean Carolina wren densities for all three habitats throughout the entire study (January 2007–April 2008). Mean densities (wrens/km<sup>2</sup>): City Park 7.63 (SEM = 1.55, n = 30), Residential 4.19 (SEM = 0.519, n = 66), and Rural 1.01 (SEM = 0.405, n = 29).

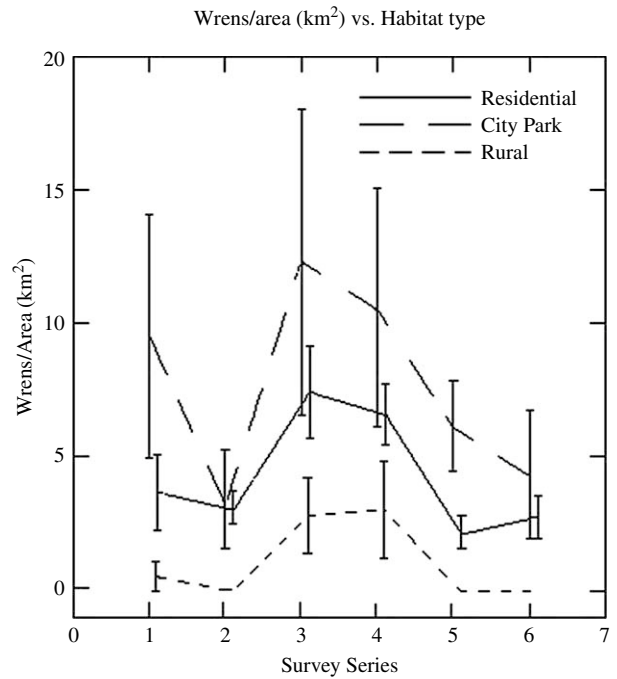


Figure 2. Mean wrens/area (km<sup>2</sup>) for the duration of the study (January 2007–April 2008). Error bars denote standard error. The numbers on the x-axis correspond to the midpoints of each survey series (1 = 2/27/07, 2 = 6/3/07, 3 = 10/13/07, 4 = 11/26/07, 5 = 2/18/08, 6 = 4/1/08). The rural transects exhibited 0 wrens/km<sup>2</sup> for series 2, 5, and 6. Lines are offset to prevent error bars from overlapping.

### Winter populations and bird feeding

At the end of winter, Carolina wrens lived in higher densities where they had access to bird feeders ( $F_{1,18} = 14.526$ ,  $p = 0.0013$ ; Fig. 3). Densities of Carolina wrens varied considerably among transects that had access to feeders but did not obviously increase in response to January mean minimum temperature ( $F_{1,18} = 0.883$ ,  $p = 0.36$ , Fig. 3).

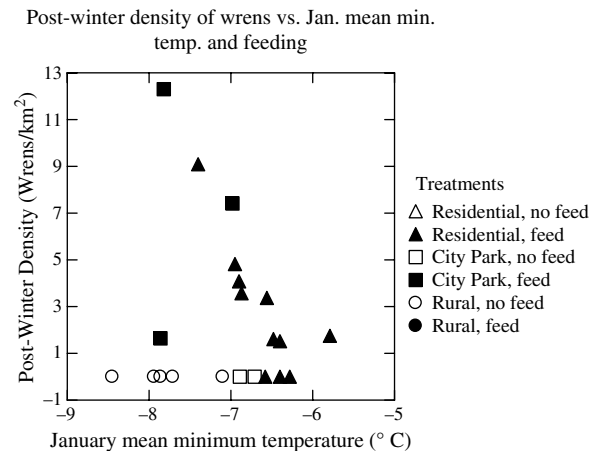


Figure 3. The effect of supplemental feeding and January mean minimum temperature ( $^\circ \text{C}$ ) on post-winter densities (wrens/km<sup>2</sup>) for all three habitat types (City park, residential, and rural). Post-winter density was found to be significantly higher in areas with access to winter feeding ( $F_{1,18} = 14.256$ ,  $p = 0.0013$ ).

## Discussion

By studying gradations of human influence, we uncovered variations in Carolina wren density, winter temperature, and supplemental feeding within a local area. City park sites averaged twice as many wrens/km<sup>2</sup> as residential sites, which averaged four times as many wrens as rural sites. Besides having more wrens on average, city parks and residential sites were substantially warmer than rural sites, likely due to their proximity to urban areas (Landsberg 1981). All of our transects had temperatures higher than Root's (1988) proposed critical January mean minimum temperature of  $-9.4^{\circ}$  C. Overall, approximately 40% of homes surveyed provided bird food during the year, and 30% provided food throughout the winter season. Transects differed in the number of houses bordering them. Because the two human influences, local temperature and supplemental feeding, varied somewhat independently, we were able to test for their separate effects on wren densities. In this study, the presence of bird feeders during the winter predicted higher densities, while temperature did not. Carolina wrens disappeared entirely over the winter from the two city park transects that had no feeders available in addition to the five rural transects, none of which had feeders available to Carolina wrens. Our results suggest that Carolina wrens were directly limited by food supply, and that bird feeders can be critical when other food supplies are interrupted.

In our study, city park habitats had higher concentrations of wrens than residential habitats. We hypothesize that this is because the city parks had habitat with dense undergrowth and tangled vegetation that Carolina wrens prefer (Beissinger and Osborne 1982, Hamel et al. 1982, Brewer et al. 1991, Brewer 2001, Kaufman 1996). In our study area, the best territories for Carolina wrens seem to combine naturalistic vegetation with access to artificial feeders.

Carolina wrens have high metabolic rates and forage in a manner that can be disrupted by snowfall and other winter weather. As one gram of insects yields approximately 5.51 kJ of metabolized energy (Kurta et al. 1989), a Carolina wren at the northern edge of its range would need to consume 14 g of insects to satisfy its daily metabolic demand of 76.2 kJ (Root 1988). Finding so much food is a substantial task during the winter, and heavy snows may eliminate entire populations of Carolina wrens (Bohlen 1989, Sauer et al. 1996). Based on body mass and body temperature from Eberhardt (1994), equations 1 and 2 from Repasky (1991), equation 7 from Root (1988), and our temperature measurements, we calculate the energy needs for our habitat types as 74.4 kJ/d in rural areas, 73.0 kJ/d in city parks, and 71.0 kJ/d in residential areas. While no study has quantified the importance of food offered at feeding stations to Carolina wrens, they certainly are known to visit feeders on occasion, especially those offering peanuts and suet (Haggerty and Morton 1995). A single peanut offers 29 kJ of energy (Fleischer 2000), and so provides over a third of a Carolina wren's daily metabolic need in one foraging event. Thus access to feeders, especially during times of heavy snow cover might tip the balance from starvation to survival for Carolina wrens near the northern edge of their range.

We expected to find a strong temperature effect on Carolina wren abundance, but found that access to food is more important. Other species of birds that winter at northern latitudes have survival rates influenced by food availability through supplemental feeding (Lack 1954, Fretwell 1972). Our study suggests that the northern expansion of Carolina wrens will follow human settlement patterns, somewhat like the expansion of house sparrows (*Passar domesticus*) and house finches (*Carpodacus mexicanus*) (Bennett 1990). Future range changes will depend on the confluence of climate change, urbanization, and supplemental feeding. This confluence will likely affect other species as well. For example, the ranges of tufted titmice *Baeolophus bicolor* and northern cardinals *Cardinalis cardinalis* have also expanded northward during the same time period as Carolina wrens (Brewer et al. 1991), and might also benefit from supplemental feeding. While generally we expect the effects of supplemental feeding to interact with natural food supplies and thermoregulatory demands, our results suggest that even small amounts of supplemental food may sometimes have large influences on birds living near their limits.

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