Understanding the behavioral and physiological consequences of life in the city: A comparison of urban and rural chipping sparrows

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Introduction

Land consumption has grown in conjunction with the growing human population. More and more landscapes are changing from their previous unaltered state into human dominated ecosystems as the human population increases (Vitousek et al. 1997). Urbanization causes immense changes to available resources and climate. The high thermal capacity of concrete and other manmade surfaces retain heat, making surface temperatures at urban sites warmer than their unaltered counterparts; this is known as the Urban Heat Island effect. The severity of these temperature differences increases with growing populations (Zhang et al. 2010).

Urbanization also has dramatic effects on species diversity and species abundance, with relatively few species dominating urban landscapes (Marzluff 2001). These differences have been observed, yet there is little known about what makes one species better suited for urban living over other species. “Urban adapters” successfully live in urban environments despite differences in predation, climatic conditions and resources. “Urban avoiders” are unable to withstand the divergence between urban and natural ecosystems, and are rarely found within urban boundaries. “Urban exploiters” survive better in urban environments, and are usually outcompeted in natural landscapes. Understanding the individual-level responses of species of urban adapters, urban avoiders and urban exploiters is critical if we are to understand the ecological mechanisms of community changes in human-altered ecosystems (Shochat et al. 2006, Kark et al. 2007).

One hypothesis poses that urban adapters may survive city life because individuals of such species exhibit flexibility in the way they respond behaviorally as well as

physiologically to urban stresses. Under adverse conditions, many organisms exhibit a stress response, in which high concentrations of glucocorticoid steroid hormones are secreted by the adrenal glands (Wingfield and Ramenofsky 1999). These hormones inhibit the use of glucose by non-essential tissues, mobilize fat stores and increase the availability of energy, and alter behavior, each of which helps organisms deal in the short-term with acute stress (Sapolsky et al. 2000). If elevated for extended periods however, organisms may suffer from impaired reproduction as well as impaired immune and brain functions (Sapolsky 1992). For urban adapters, it may be that individuals are able to adjust their stress response to avoid the high costs of a prolonged elevation of glucocorticoids, whereas urban avoiders are unable to alter their stress response over the long term and urban living becomes too costly (Schoech et al. 2004, Partecke et al. 2006).

We studied the chipping sparrow, *Spizella passerina*, in rural and urban environments to ascertain behavioral and physiological differences between populations. Chipping sparrows breed in both urban and rural environments (Middleton 1998), which suggest they may be adequate urban adaptors, and therefore not threatened by increasing urbanization. However, several recent studies on other urban adapters have shown that individuals in urban populations are generally smaller and in poorer condition than birds in natural habitats (Ruiz et al. 2002, Partecke et al. 2005, Liker et al. 2008), suggesting that urban living may be costly even for urban adaptors.

Birds living in urban environments alter their behavior to sing at a higher pitch and more frequently than birds in native habitats (Slabekoorn and Peet 2003), which may compensate for the increased ambient noise present in urban landscapes. Urban birds

also tend to reproduce sooner than rural birds primarily due to differences in environmental conditions (Partecke et al. 2004), such as higher temperatures. Urban birds also face a lower frequency of predation than birds in rural environments (Ryder et al. 2010), which may help explain expansion into urban sites. These findings suggest that living in urban environments is accompanied by significant alterations in behavior and physiology even in urban adapters.

We tested the hypothesis that chipping sparrows living in urban and rural sites differ in behavior, physiology and timing of reproduction (e.g. Partecke et al. 2005). We compared male arrival dates, song characteristics, body condition and stress hormones between our urban and rural sites.

Methods

Study sites: We studied chipping sparrow populations at two sites. Our urban site was the main campus of Western Michigan University, which is 95% urban. Western Michigan University is located in Kalamazoo, Michigan at approximately 42° 17' 30" N / 85° 35' 14" W. The rural site was Pierce Cedar Creek Institute, which is less than 5% urban and located in Hastings, Michigan at approximately 42° 38' 45" N / 85° 17' 27" W.

Environmental conditions. - To compare the environmental conditions at the rural site and the urban site over the entire breeding season, we summarized data on temperature (minimum, mean and maximum, in °C), which were available from Pierce Cedar Creek Institute and for Kalamazoo from weather underground (www.wunderground.com).

Banding- Beginning in early April 2010, we surveyed both sites for singing males to determine the date of arrival of males. The locations of singing males were revisited every 1-3 d to determine pairing status (i.e. whether male is unpaired or paired). Once sparrows were identified at these sites, we set up 3-4 mist nets in the morning (before 1100) around singing locations to capture breeding them. Birds were processed as follows: (1) Blood collection: See below. (2) Banding: Each bird received a numbered aluminum band plus a unique combination of three colored leg bands. These bands allowed individual identification and therefore monitoring known individuals over the course of their breeding season. (3) Body measurements and condition: Several morphological traits were measured: wing chord, tarsus length, (all to the nearest mm with calipers or rulers) and mass (to the nearest 0.1 g with a Pesola 60-g scale). We assessed body condition by regressing tarsus length versus body mass and using residuals as a standardized body mass. Separate regressions were run for each sex. Chipping sparrows are monochromatic, but sexes were distinguishable during breeding by the presence of cloacal protuberances on males and brood patches on females (Middleton 1998).

Blood Collection- We immediately removed captured birds from nets and took a 40 µl blood sample by puncturing the alar vein with a sterile, single-use 26-guage needle and collecting the blood in microcapillary tubes. Time was recorded from the moment the bird was captured in the mist net to the time it took to get the initial blood sample to assess whether duration of handling influenced corticosterone levels, as corticosterone levels rapidly rise after three minutes of application of stressor (Romero and Romero 2005). From this initial sample, we measured baseline (non-stressed)

corticosterone in all birds. Two stress series were performed, which consists of collecting an initial blood sample and then placing birds in a bag for 30 minutes (Wingfield et al. 1995). All blood samples were transferred to labeled Eppendorf tubes, which were placed on ice in a cooler until we returned from the field to the lab.

A small (10 µl) portion of the blood sample was smeared on microscopre slides and air dried in the field. We examined the number of leucocytes, or white blood cells (lymphocytes, monocytes, heterophils, eosinophils, basophils), and from these data calculated the heterophil/lymphocyte (H/L) ratio, which provides an independent measure of body condition (Ochs and Dawson 2008, Quillfeldt et al. 2008). We produced two blood smears per individual per sampling date and prepared them according to Campbell (1988). Briefly, smears were fixed in methanol, allowed to air dry, and then stained using Diff-Quick. The proportion of different types of leukocytes was obtained from examination of a total of 100 leucocytes.

Upon returning from the field, we separated red blood cells and plasma by centrifuging for 5-6 min blood samples in a portable microcentrifuge. The plasma portion of the sample was drawn off using Hamilton syringes and stored in a newly labeled Eppendorf tube. Both plasma and cell portions were frozen until analyzed.

Sound Observations- We used Marantz PMD660 solid-state recorder and Sennheiser ME-66 microphone to record male chipping sparrow song for up to 30 minutes. Ambient noise was quantified using American Recorder SPL-8810 sound pressure level meter. On other occasions, we observed males and quantified the number of songs produced in 15-minute periods. In the lab, we used the program

RavenPro 1.3 to analyze recorded songs from each individual sampled, by taking 10 random songs from each male we had recorded and measuring the duration of each song and the maximum and minimum frequencies (kHz).

Reproductive Success. – We monitored nests from clutch initiation through to fledging or nest failure (due to depredation or abandonment), and recorded number of eggs laid, hatch dates, total number of eggs hatched, date fledged, and total number of fledglings. We calculated the proportion of pairs that fledged young at both sites.

Hormone assays. - Corticosterone concentrations were measured using direct radioimmunoassays (RIA) using established methodologies (Wingfield and Farner 1975, see Gill et al. 2007, 2008). Prior to RIA, steroids were extracted from plasma with 2 ml ether, dried under nitrogen stream, and resuspended in PGSB buffer. All samples had concentrations above the minimum detection limit of 0.65 ng/ml. Intra-assay variability of standards (four standards per assay) and samples was 4.7 and 2.2%, respectively. Water blanks were included in the assay procedure to assess assay quality.

Results

Environmental conditions- The mean daily high temperature was higher in the urban environment than the rural site ($Z=5.716$, $P<0.001$; Figure 1). The mean daily low temperature was lower at the rural environment than the urban site ($Z=6.892$, $P<0.001$; Figure 2).

Arrival dates - Males arrived first and more rapidly at the urban than rural site (Figure 3).

Body condition - Male mass did not differ between sites (mean±s.e.: urban=12.0±0.947g versus rural= 12.25±0.524g; Z=.163, P=.870). However, urban sparrows appear to be in poorer condition based on blood smears, as the mean heterophil-lymphocyte ratios for urban sparrows tended to be higher that for rural sparrows (Z=1.786, P=0.074; Figure 4).

Sound Observations- The urban site was noisier (mean±s.e.=58.286±4.094 dB), than the rural site (41.6±0.83 dB). The mean maximum frequencies of chipping sparrow song were 8634.25 and 8438.92 at the urban site and the rural site respectively (P=1.00). Low frequencies at the urban site and the rural site were 3790.12 and 3514.55 respectively (Z=-1.262, P=.245)(Table 1). The mean total song duration at each location was 2.60s at the urban site and 2.45s at the rural site (Z=-.387, P=.699). Males sang a mean of 76.27±51.73 songs per 15 minutes at the urban site and 55.45±39.53 songs per 15 minutes at the rural site (Z=1.183, P=0.237).

Reproductive Success- The very first clutch was initiated more than one week earlier in the urban (April 28) than rural population (May 6). The mean date of clutch initiation was also earlier for urban (May 10±2.89 days, n=11) than rural birds (May 17±2.78 days, n=7; t=2.33, P=0.03). Of the monitored pairs, 28.6% rural pairs (n=7) fledged offspring compared with 70.6% urban pairs n=12, χ^2=3.60, P=0.07).

Hormone assays- Corticosterone levels increase with increasing duration of handling (Figure 5). Two stress series were completed on urban birds, both of which showed a robust stress response to a standardized stressor (Figure 6). Due to small sample sizes, we did not analyze the data, but there appears to be a trend toward lower

corticosterone concentrations in females than males, and urban versus rural birds (Figure 7).

Discussion

As expected from urban heat island models (e.g. Zhang et al. 2010), average daily high and low temperatures were higher at the urban than rural site. Male chipping sparrows arrived earlier at the urban site than rural site, which may possibly be a response to warmer temperatures in the urban environment. With more males established earlier in the season, the urban birds started breeding before the rural birds, with first clutches initiated a week earlier on average. An earlier onset of breeding may be responsible for the higher reproductive success exhibited by urban birds, as earlier clutch initiation typically leads to more fledglings (Grüebler and Naef-Daenzer 2010). The urban birds fledged more offspring than the rural birds, suggesting there was less predation at the urban site. Although urban birds had higher apparent reproductive success, leukocyte data revealed that they were in poorer condition than the rural birds, and it may be that survival, but not reproductive, costs to living in urban environments exist.

Differences in song were expected. The higher ambient noise at the urban site may have resulted in urban birds singing at higher frequencies than the rural birds to avoid masking by noise. This response has been documented in other bird species (Slabekoorn and Peet 2003), and increased song length at the urban site may also be due to the higher ambient noise. you need to explain this more. Why would urban birds sing longer songs?

Using the heterophil lymphocyte ratio as a stress indicator we found that there may be a trend in which the urban birds are more stressed than the rural birds (Figure 4). Corticosterone concentrations between sites showed an opposite trend, with the urban birds showing lower baseline corticosterone levels (Figure 7). More research efforts, namely larger sampling sizes, need to be done to clarify these findings.

We found evidence for few differences between birds inhabiting rural versus urban environments. Urban birds began breeding earlier, but other behaviors and indicators of stress did not differ significantly between the two sites. The few differences between urban and rural birds may be consistent with the species being classified an "urban adapter." Urban adapters are species that can adapt to urban habitats but also utilize natural resources (Shochat et al. 2006). Based on our findings, chipping sparrows may not be threatened by increasing urbanization; however, more research is needed to clarify contradictory results before firm conclusions may be reached.

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Table 1. Characteristics of chipping sparrow songs recorded at urban and rural sites. Data are given as mean±s.e.

	Site	
Song characteristic	Urban	Rural
Low frequency (Hz)	3790.115	3388.546
High frequency (Hz)	8634.245	8366.669
Song length (s)	2.60075	2.36926
Song rate (#/15 min)	76.27±51.73	55.45±39.53

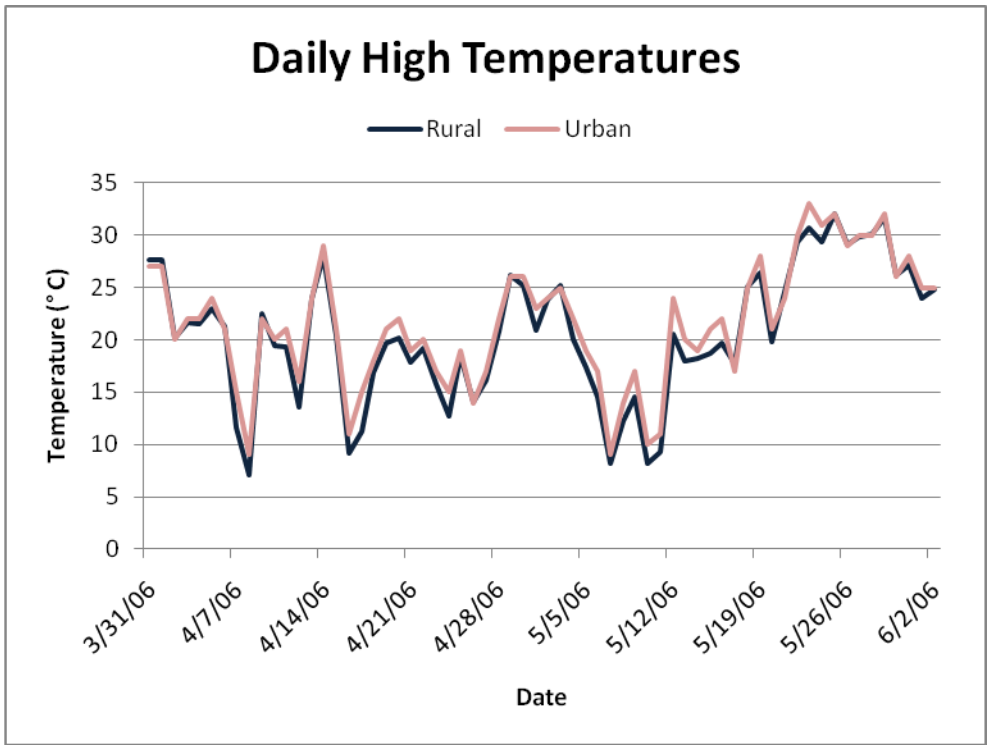

Figure 1. Daily high temperatures from both urban and rural sites in Michigan.

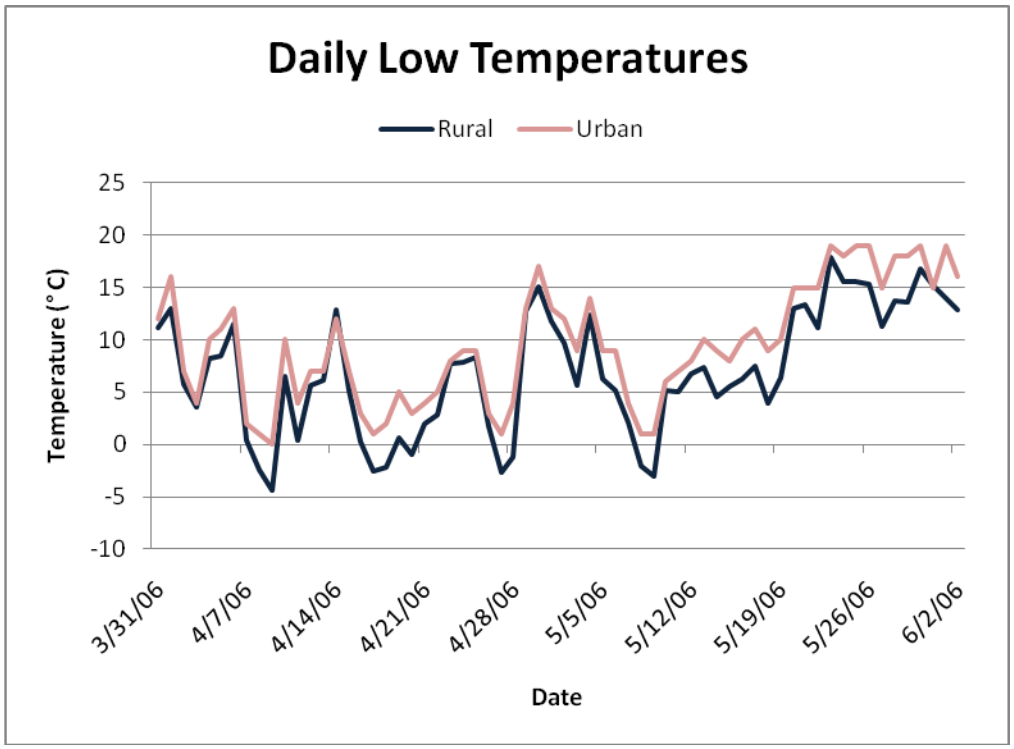

Figure 2. Daily overnight low temperatures for rural and urban sites in Michigan.

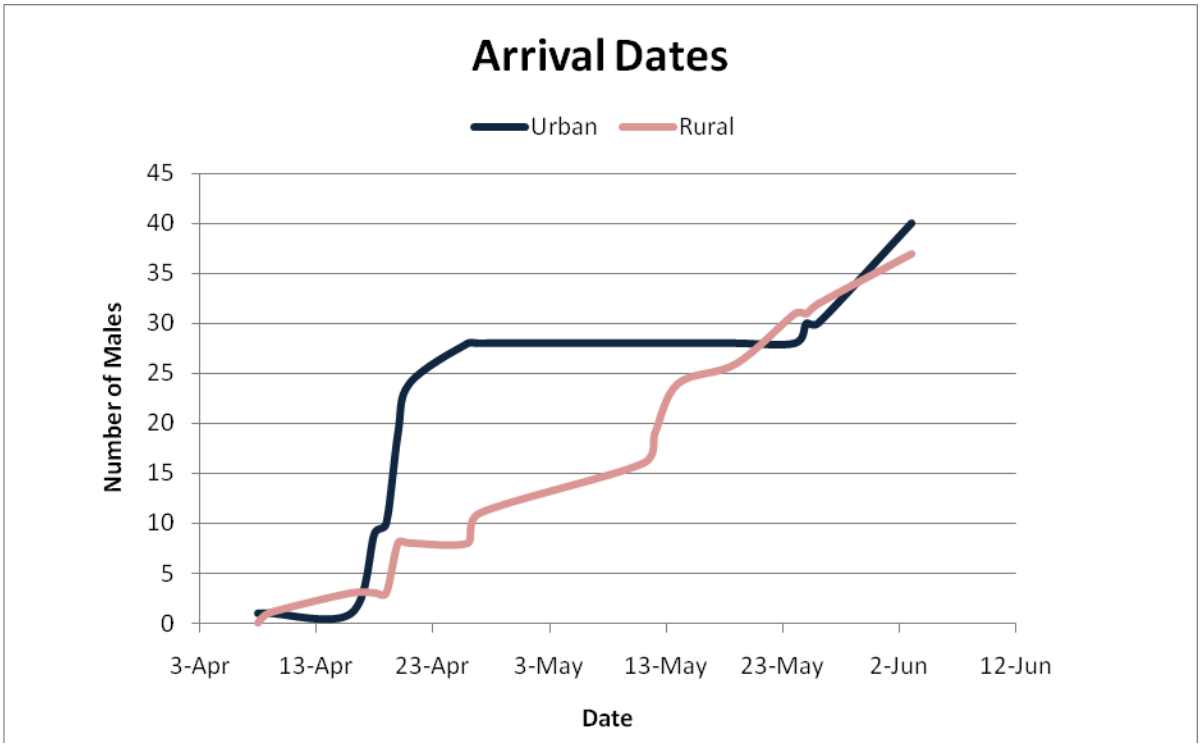

Figure 3. Arrival dates for male chipping sparrows to urban and rural sites in Michigan.

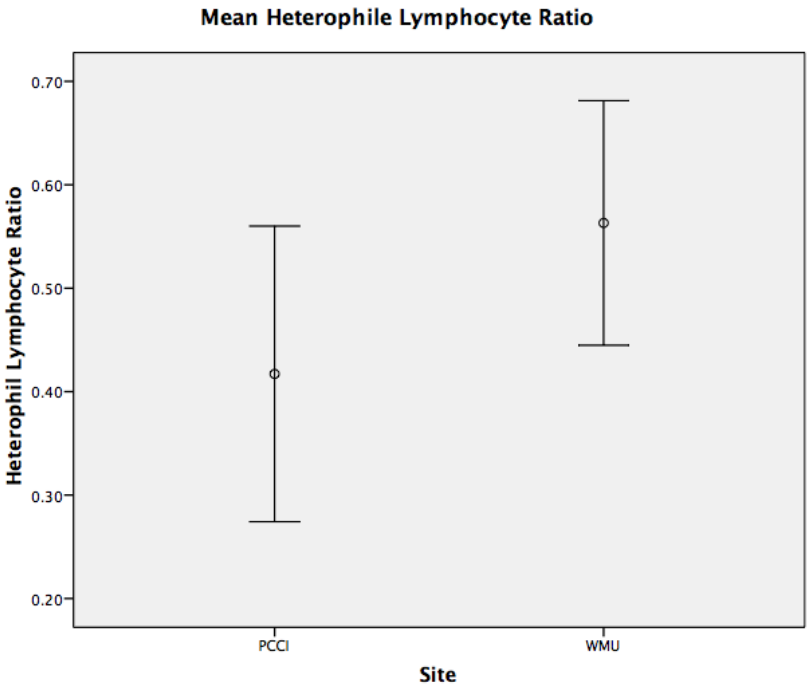

Figure 4. Mean heterophil:lymphocyte ratio for chipping sparrows at urban and rural sites in Michigan.

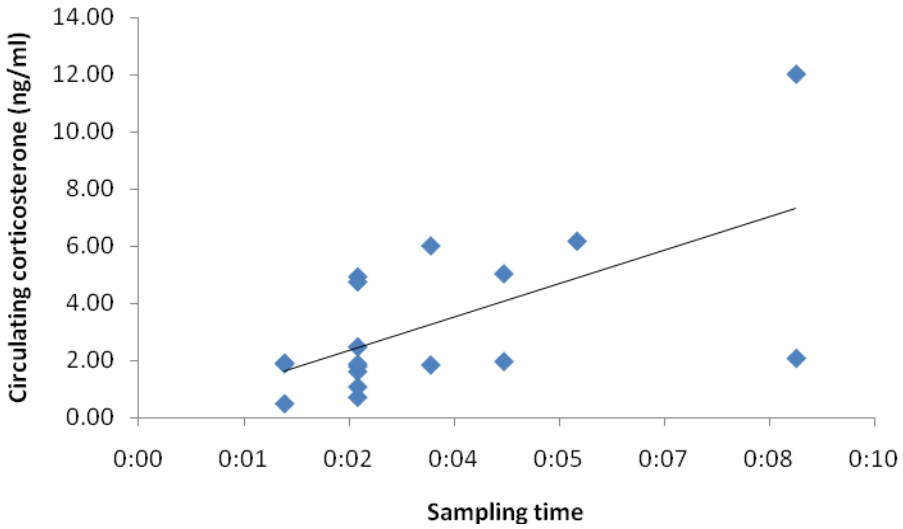

Figure 5. The relationship between sampling time (min between capture and bleeding) and concentrations of circulating cortisosterone (ng/ml) in male and female chipping sparrows (n=18). Increased sampling time influenced corticosterone levels. Only individuals sampled within 5 min of capture were analyzed and presented in Figure 7.

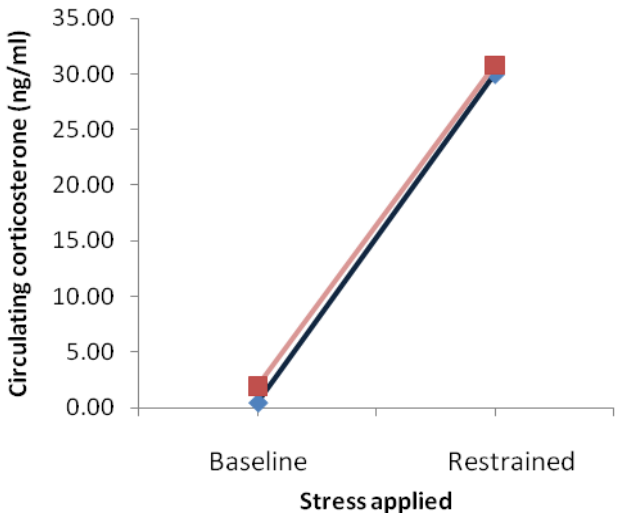

Figure 6. Stress response in two male chipping sparrows sampled at the urban site. Both males showed a robust stress response.

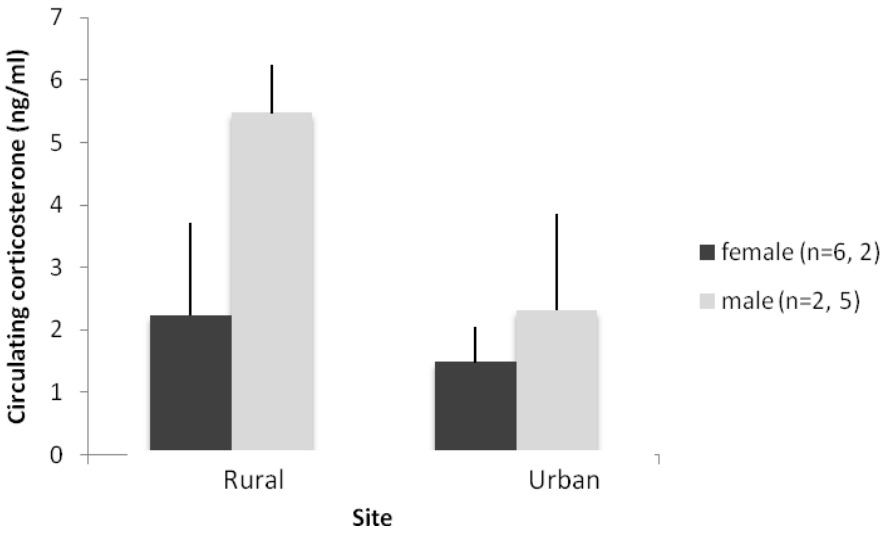

Figure 7. The concentration of circulating corticosterone (ng/ml) in male and female chipping sparrows sampled at rural and urban sites. Small sample sizes preclude analyses, but data suggest that males may have higher corticosterone levels than females at both sites and that urban birds may have lower corticosterone concentrations than rural birds.