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Variation in adrenocortical stress physiology and condition metrics within a heterogeneous urban environment in the song sparrow *Melospiza melodia*

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In urban habitats, organisms face unique fitness challenges including disturbance from human activity and noise. One physiological mechanism that may be plastically or evolutionarily modified to ameliorate deleterious effects of anthropogenic disturbance is the adrenocortical stress response. Individuals in urban environments may display smaller stress responses, which may prevent pathologies associated with consistent elevation of stress hormones, and may also show differences in baseline corticosterone (CORT, the primary avian stress hormone), due to altered energetic demands or chronic stress. We examined whether stress physiology and condition metrics in male song sparrows *Melospiza melodia* vary as a function of discrete differences in anthropogenic disturbance level (activity centers and refuges) or with continuous variation in an urbanization score and noise environment. Males breeding in activity centers displayed lower maximal (acute) CORT levels than activity refuge males, and acute CORT also tended to negatively correlate with urbanization score. Baseline CORT did not differ between habitat types, and activity center males also showed no evidence of changes in body mass, hematocrit, or antioxidant capacity. Further, activity center males had higher quality feathers (indicative of higher condition at molt) than activity refuge males. We found no indication that the noise environment altered stress physiology or condition in song sparrows. Overall, results suggest that song sparrows are an urban adapter species, which are not detrimentally affected by unique selective pressures encountered in the urban environment.

Organisms evolve traits that allow maintenance of positive fitness pay-offs in a particular environment or niche (Grinnell 1917). When faced with rapid fluctuations in the environment, species persist through either rapid evolution or phenotypic plasticity. Alternatively, extirpation may result (Coppack and Partecke 2006, Partecke et al. 2006, Ghahambor et al. 2007). Current rapid rates of habitat modification by humans serve as a potent evolutionary force. In urban habitats, individuals face fitness challenges including disturbance from loud noise and human activity, pollution from chemicals and artificial light, and altered predator regimes, all of which differ from selective pressures experienced throughout most of a species' evolutionary history (Marzluff 1997, Sih et al. 2011, Fischer et al. 2012, Sol et al. 2013). Thus, in urban areas only species or individuals with a particular suite of ecological and physiological traits may persist (Yeh and Price 2004, McGlothlin and Ketterson 2008, Bonier 2012).

One physiological mechanism that may be evolutionarily or plastically modified to ameliorate deleterious effects of urban disturbance is the adrenocortical stress response (Partecke et al. 2006, Bonier et al. 2007, Bonier 2012). The adrenocortical stress response is controlled by the hypothalamus-pituitary-adrenal (HPA) axis and involves release of steroid glucocorticoids (GCs) from the adrenal cortex.

Baseline GCs help regulate glucose metabolism and energy balance, and may be elevated to support demanding life-history stages (Sapolsky et al. 2000, Romero 2002, Landys et al. 2006, Bonier et al. 2009). Thus, in urban environments, increased baseline GCs may result from increased allostatic challenge (the summation of current and predicted energetic demands) and may be adaptive. However, frequent disturbance may overwhelm internal coping mechanisms, leading to allostatic overload, chronic elevation of baseline GCs and reduced fitness (McEwen and Wingfield 2003, Wingfield 2005, Bonier et al. 2009). Indeed, elevated baseline GCs have been linked to reduced body condition and survival probability (Brown et al. 2005, Bonier et al. 2009), increased oxidative stress due to heightened metabolism (Lin et al. 2004), and cessation of reproductive activity (Silverin 1986, Wingfield and Sapolsky 2003, Ouyang et al. 2012). Activation of the acute stress response controls the vertebrate response to life-threatening situations, and has fitness benefits including facilitating escape from predators and coping with challenging weather events (Sapolsky et al. 2000, Blas et al. 2007, Breuner et al. 2008). However, frequent activation of the acute stress response may lead to termination of reproductive activity and health problems associated with elevated GCs (Wingfield et al.

1992, Wingfield and Sapolsky 2003). Indeed, high acute GCs (maximum levels after exposure to a stressor) have been correlated with lower survival rates (Romero and Wikelski 2001, MacDougall-Shackleton et al. 2009). In urban environments, many human-associated disturbances may entail little actual threat to survival. Thus, costs of mounting a large stress response may out-weigh benefits (Partecke et al. 2006, Bonier et al. 2007, Atwell et al. 2012). However, a larger stress response could also confer fitness benefits in an urban environment, for example, if an altered predation regime favors a robust survival response (Boonstra et al. 1998).

Comparisons between rural and urban populations yield some support for the idea that HPA down-regulation may promote persistence in the face of anthropogenic activity (Partecke et al. 2006, Atwell et al. 2012), while also suggesting that human disturbance may overwhelm behavioral and physiological coping mechanisms and induce chronic stress (Wasser et al. 1997, Walker et al. 2005, Bonier et al. 2007, Hayward et al. 2011). However, studies on the relationship between urbanization and GC concentrations have yielded no consistent pattern (Fokidis et al. 2009, Bonier 2012 for review), with the majority of studies actually reporting null relationships between urbanization and variation in stress physiology (Fokidis et al. 2009, Chavez-Zichinelli et al. 2010, Bókony et al. 2012). Conflicting results may be explained by the specific ecology and evolutionary history of species used in analyses, which may influence sensitivity and responses to anthropogenic disturbance (Bonier et al. 2007, Fokidis et al. 2009).

We explored how anthropogenic disturbance affects stress physiology and condition metrics within an urban population of song sparrows *Melospiza melodia*. Despite extensive and pioneering work on the effects of urbanization on stress physiology in birds, most studies to date involve broad-scale comparisons between one urban and rural or suburban population (but see Bonier 2012 for review). Heterogeneity in disturbance regime exists within urban landscapes due to presence of both activity centers, adjacent to highways or shopping centers, and activity refuges, such as parks or reserves. Thus, as on a broader scale, individuals breeding within urban environments may experience divergent selective pressures and display differences in stress physiology.

Our study had three objectives. First, we examined whether acute or baseline corticosterone (CORT, the primary avian GC) varies with urbanization level in male song sparrows. We were particularly interested in whether song sparrows in highly urbanized areas display lower acute CORT, which could facilitate maintenance of reproductive activity despite perturbation, and in whether baseline CORT is elevated in highly disturbed areas, potentially reflecting chronic stress. Second, we evaluated whether stress physiology varies with noise environment. Noise may induce chronic stress by directly disturbing individuals, altering physiological processes (Barber et al. 2009, Kight and Swaddle 2011, Francis and Barber 2013), and interfering with communication (Brumm and Slabbekoorn 2005, Leonard and Horn 2012). Indeed, noise has been associated with reduced reproductive success (Halfwerk et al. 2011, Kight et al. 2012, Strasser and Heath 2013), and elevated stress hormone levels (Hayward et al. 2011, Blickley et al. 2012, Strasser and Heath 2013) in urban birds. Third, to more comprehensively assess

whether song sparrows experience increased allostatic load in urbanized areas, we quantified a number of condition-related metrics. We used body mass as a metric of current body reserves, and feather quality as an indirect metric of condition at molt. We evaluated hematocrit levels, since chronic stress associated with disturbance may result in anemia (Fair et al. 2007, Bókony et al. 2012). Finally, we measured total antioxidant capacity (TAC). Changes in TAC may occur in urban areas due to heightened oxidative challenges and energetic demands (Isaksson et al. 2005, 2007, Cohen et al. 2007, Møller et al. 2010).

Methods

Study species and sites

We studied variation in the adrenocortical stress response in an urban population of song sparrows breeding in activity centers and refuges near the Univ. of California, Riverside (UCR). Activity center sites were located on, and in the immediate vicinity of the UCR campus and the I-215/CA-60 freeway (center: 33°58'27.23"N, 117°19'38.39"W). These birds are constantly exposed to disturbances including noise from air-conditioning units on buildings, passing traffic, and human conversation. Refuge sites included the 1150 acre Box Springs Mountains Reserve (center: 33°57'56.71"N, 117°17'7.86"W), located approximately 4 km east of the UCR campus center, and the 1550 acre Sycamore Canyon Wilderness Park (center: 33°56'14.11"N, 117°18'59.11"W), located approximately 4 km south of the UCR campus center. Although these reserves are entirely embedded within Riverside's urban matrix and show ample urban impacts on vegetation and various other attributes, birds captured within refuges are relatively buffered from anthropogenic disturbance sources. Vehicular traffic is prohibited, and recreational activity, including walking and biking, is allowed but entails light and sporadic human traffic.

We estimated the density of song sparrows breeding within the urban matrix to be approximately 3–6 males ha⁻¹, with density being similar between activity centers and refuges. This density estimate is comparable to that of the higher density site of Hill et al. (1999) in Discovery Park, Seattle, Washington. Territory size is small, approximately 0.1–0.4 ha, with birds being tightly packed into available habitat in many areas (e.g. 4 males in a 200 m long by 25 m wide habitat strip). High density of song sparrows within the Riverside urban areas suggests that these birds are successful urban breeders, such that physiological adaptations might be expected.

We focused our study on territorial breeding males, which we captured in mist nets using conspecific playback. All males were actively breeding, as assessed by the presence of a cloacal protuberance. We captured 46 males in activity centers and 25 males in activity refuges. We determined baseline CORT concentrations for all of these males, and acute CORT concentrations for 43/46 center males and 24/25 refuge males. We captured birds from 6 March through 18 April, 2011 and from 26 February through 12 April, 2012, between 07:00 and 15:00 h local time. We captured 5 males during multiple years of the study. However,

we randomly eliminated one of the duplicate observations on each of these males from the final dataset. We controlled for time, date, and year effects in statistical analyses. Upon capture, we banded each bird with an aluminum band from the United States Geological Survey and with a unique color combination.

Characterization of disturbance environment

To characterize the anthropogenic disturbance environment, we unambiguously classified activity refuges and activity centers. Refuges were distinguished by park-land designation and were separated from, although embedded within, the surrounding urban matrix. Centers were located within the urban matrix, where heavy human activity occurs. In addition, we also derived a continuous metric of anthropogenic disturbance level by taking GPS readings on territories using a Garmin ETrex 30 GPS, and then using digital photographs generated in Google Earth ver. 7.1.2.2041 to measure the distance from territories to the nearest road, major freeway, and building, and to estimate the percentage of impervious cover within a 50 m radius centered around each capture site. We then performed a principal components analysis on these 4 variables, and extracted the first principal component (PC1) for use as an urbanization score (Table 1). PC1 was negatively loaded on distance to a road, major freeway, and building, and positively loaded on percent impervious surface (Table 1). Thus, territories with higher urbanization scores (PC1) are in more urbanized areas.

We characterized the noise environment by measuring noise level in decibels (dB) on the territory of each male. We followed a protocol for measuring noise level that has been employed in studies examining effects of anthropogenic noise on bird song characteristics (Brumm 2004, Bermúdez-Cuamatzin et al. 2009). We used a Digital Instruments SL-4023SD sound level meter (range, 30–130 dB; weight, A; fast response; IEC 61672 class 2) with a windshield ball. We recorded noise levels between 06:00 and 13:00 h local

time, corresponding to the time period in which sparrows were captured, with the majority of readings taken immediately after the sparrow was captured and processed. We took measurements for 5 min, with noise levels being logged every 5 s. For one minute each, we pointed the sound level meter in each of the four cardinal directions, and straight upward. We flipped a coin to determine whether to start from north or south, and west was always followed by upwards. We took the average of all 5-s incremental measurements as a final metric of the noise environment. We extracted maximum noise, minimum noise, and the standard deviation of noise level across readings. We then reduced these variables to two orthogonal explanatory variables using principal component analysis (Table 1). PC1 had high positive loadings for average noise, maximum noise, and minimum noise level, and thus reflects the magnitude of noise level (Table 1). The second PC axis (PC2) had high positive loadings for the standard deviation of noise level and maximum noise, and thus reflects variation in noise level (Table 1).

Measuring the stress response and hematocrit

We measured the stress response using standard capture protocol (Wingfield et al. 1992), with an initial sample taken within 3 min of capture (representative of baseline CORT) and another sample taken after 30 min (representative of acute CORT). We confined birds in cloth holding bags in the interlude between sampling. We used 26-gauge needles and heparinized microcapillary tubes to withdraw small blood samples (~80 μ l) from the brachial vein. We stored blood samples on ice in the field. Plasma was separated from cell fraction via centrifugation for 12 min at 4400 g. We determined hematocrit levels immediately following centrifugation by measuring the percentage of the total blood column occupied by erythrocytes. We stored plasma at -30°C until performing CORT radioimmunoassays.

Measuring body mass and feather quality

At the time of capture, we measured body mass (± 0.1 g) using a digital scale, unflattened wingchord (± 1 mm) using a wing scale, and tarsus length (± 0.01 mm) using digital calipers. We used body mass alone as a combined metric of body reserves and size, instead of using least-square residuals or the scaled mass index (Peig and Green 2009, 2010, Bókony et al. 2012), because tarsus length and body mass were not correlated in our dataset (Spearman correlation: $r_s = 0.18$, $n = 68$, $p = 0.15$).

In addition, we scored feather wear on a scale of 0 to 4, where 0 corresponds to no wear, 1 to a trace of wear, 3 to moderate wear, and 4 to heavy wear (Ralph et al. 1993). Feather wear indicates the degree to which primary feathers (main flight feathers) are abraded away, and thus is reflective of primary feather quality. Birds in better condition at molt may grow both longer and more wear-resistant feathers (Harper 1999, Dawson et al. 2000). Further, song sparrows in our study population are resident, such that birds are present on territories, and experience similar levels of anthropogenic disturbance year-round (banded individuals have been consistently sighted on territories during the non-breeding season). We conducted a principal components analysis

Table 1. Principal components analyses on urbanization level, noise level variables, and feather quality. Entries for each variable are factor loadings.

	PC1	PC2
Urbanization PCA		
Distance from road	-0.54	
Distance from freeway	-0.50	
Distance from building	-0.54	
Percent impervious	0.41	
Eigenvalue	2.89	
Cumulative proportion of variance	0.72	
Noise level PCA		
Mean noise	0.61	0.02
Maximum noise	0.43	0.61
Minimum noise	0.61	-0.10
Standard deviation of noise level	-0.27	0.79
Eigenvalue	2.62	1.25
Cumulative proportion of variance	0.66	0.97
Feather quality PCA		
Feather wear	-0.70	
Wingchord	0.70	
Eigenvalue	1.18	
Cumulative proportion of variance	0.69	

on wingchord and feather wear, which were negatively correlated in our dataset (Spearman correlation: $r_s = -0.38$, $n = 89$, $p < 0.001$), to combine these variables into a single metric indicative of condition at molt. This metric, PC1, was positively loaded on wingchord and negatively loaded on feather wear (Table 1). Thus, higher PC1 scores reflect higher quality, more wear-resistant feathers and superior condition at molt.

Corticosterone radioimmunoassays

We conducted corticosterone assays using a MP Biomedical I¹²⁵ radioimmunoassay (RIA) kit (07-120103), which has been previously validated for use in *M. melodia* (Newman et al. 2010). We followed kit instructions with the exception that baseline plasma samples were diluted 1:100 with steroid diluent (5 μ l plasma: 495 μ l diluent), and stressed samples 1:200 (5 μ l plasma: 995 μ l diluent). We assayed all samples in duplicate, and included high and low controls provided by the kit manufacturer in each assay. We randomly distributed samples from refuge and center males between assays. Intra-assay coefficients of variation averaged 11.7% and inter-assay coefficients of variation were 8.1 and 11.0% for high and low controls, respectively.

Antioxidant assay

For a subset of males captured in 2012 ($n = 45$, 27 in activity centers and 18 in refuges), we performed an antioxidant assay to determine total antioxidant capacity (TAC) of plasma samples taken within 3 min post capture. Specifically, we used the OXY-adsorbent assay kit commercially available through Diacron International (Costantini et al. 2007), and a Spectra Max Plus 96-well plate reader capable of temperature regulation. Preparation for the assay was done on ice to avoid oxidation of samples. We diluted plasma 1:100 with distilled water (2 μ l plasma: 198 μ l water). We then generated a standard curve consisting of solutions capable of neutralizing 0, 115, 230, and 460 mM of hypochlorous acid (HOCl), a generic antioxidant. We added 200 μ l of HOCl and 5 μ l of diluted plasma (or standard) to the wells of a microplate, and performed a pre-read of the plate to control for minimal variation in sample absorbance. We incubated the plate for 5 min at 37°C, and then added 2 μ l of a chromogenic solution, mixed thoroughly and immediately read absorbance at 505 nm. We report results in terms of mM of HOCl neutralized. We randomly distributed samples from activity refuge and activity center sparrows across the 96-well plate. All samples were assayed in duplicate in a single assay. Intra-assay coefficients of variation averaged 7.15%.

Permits and ethical note

The UCR Institutional Animal Care and Use Committee approved all animal use procedures (Protocol A-20100002E), and banding and blood sampling were additionally authorized by a United States Geological Survey bird-banding sub-permit (23035-F) and a California state collecting permit (SC-11059). We followed up on a subset of male song sparrows captured in this study in the process of obtaining recordings of vocalizations. All males monitored

were present on their territory post-capture and appeared to have tolerated experimental procedures without deleterious effects. Birds were held for slightly longer than 30 min, as we immediately released all individuals after obtaining the final blood sample and weighing the bird. Other morphological measurements were taken in the interlude between blood sampling in an effort to minimize handling time.

Statistical analysis

We conducted all statistical analyses using linear models in R 2.15.2 (R Core Team). We report beta estimates (\pm SE), and additionally include effect size estimates (Cohen's d) and associated 95% confidence intervals for final models predicting CORT levels and other condition metrics from urban habitat type (Nakagawa and Cuthill 2007).

First, we used separate models to determine whether acute or baseline CORT were significantly different in activity centers than in activity refuges, and whether CORT variables were significantly related to urbanization score (PC1). We also assessed whether urbanization score could be used to predict CORT levels within activity center males alone. We log transformed acute and baseline CORT to normalize the distribution of residuals, and included time, date, and year of capture in models as covariates.

Secondly, we used linear models to assess whether body mass, hematocrit levels, total plasma antioxidant capacity, or feather quality differed between urban habitat types, with urbanization score (PC1), or with acute or baseline CORT levels. For modeling body mass, hematocrit, antioxidant capacity and feather quality, we entered habitat type or urbanization score (in separate models), and acute and baseline CORT as predictor variables. We also included interactions between habitat type or urbanization score, and CORT variables, since we were interested in whether CORT levels correlate differently with condition metrics as a function of urbanization level. We log transformed antioxidant capacity. We included time and date of capture as covariates in models predicting body mass, hematocrit and antioxidant capacity, and year of capture in models predicting body mass and hematocrit (antioxidant capacity was measured from 2012 captures only). In addition, to control for potential confounding effects of body size, we included wingchord and tarsus length in initial models predicting body mass. We applied Spearman correlations to determine whether condition metrics were correlated in our dataset.

Finally, we assessed whether noise PCs predicted CORT levels or other condition metrics either across habitat types or within activity centers alone. We applied linear models with CORT variables and other condition metrics as the dependent variable in separate models and the two sound level PCs as predictor variables.

Results

Characterizing urban habitat types

The territories of activity center males were located a mean (\pm SE) distance of 47.86 ± 7.32 m from a road, 491.63 ± 44.25 m from a major freeway, and 36.31 ± 4.40 m

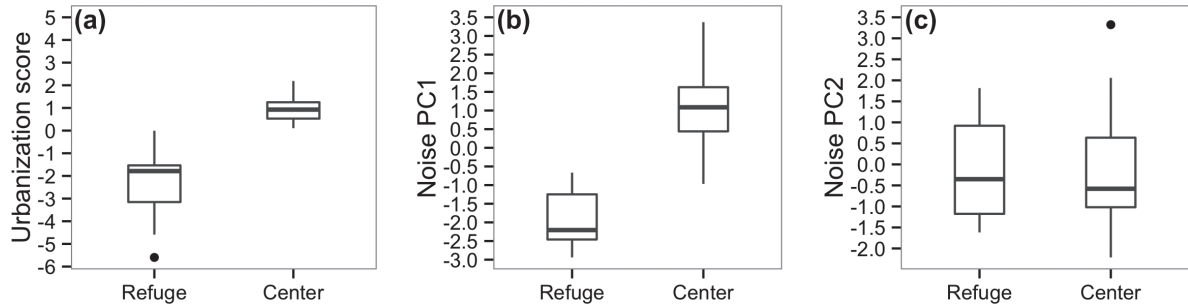


Figure 1. Boxplots showing the distribution of urbanization score (a), noise PC1 (magnitude of noise level) (b) and noise PC2 (variation in noise level) (c) between urban habitat types. Whiskers extend from the first and third quartiles to the highest value within $1.5 \times \text{IQR}$ (interquartile range).

from a building. The territories of activity refuge males were located a mean distance of 262.04 ± 38.23 m from a road, 2628.28 ± 79.18 m from a major freeway, and 261.52 ± 40.91 m from a building. Within a 50 m radius centered on the capture site of each male, a mean (\pm SE) percent of the area of 29.57 ± 3.30 consisted of impervious surfaces within activity centers, but only 1.00 ± 0.41 percent of the area within activity refuges. All urbanization metrics were significantly different when comparing between urban habitat types (t-test: $p < 0.001$ in all cases). Consequently, activity refuge territories had smaller urbanization scores (PC1) than activity centers (t-test: $t_{27} = -10.81$, $p < 0.001$; Fig. 1a). Activity refuge territories also had significantly smaller noise PC1 scores than activity center territories (t-test: $t_{64} = -14.28$, $p < 0.001$; Fig. 1b), reflecting the quieter noise environment found in refuges. Noise PC2 did not differ with habitat type (t-test: $t_{54} = 0.54$, $p = 0.59$; Fig. 1c), reflecting the fact that variation in the noise environment was similar between habitat types.

Stress response with respect to urban habitat type and urbanization score

Stress-induced (acute) CORT concentrations were significantly higher than baseline CORT concentrations (Welch

t-test: $t_{74} = 13.59$, $p < 0.001$). Activity center males had lower acute CORT than refuge males (Table 2; Fig. 2a). Baseline CORT concentrations did not differ between activity center and refuge males (Table 2; Fig. 2b). Rather, baseline CORT was higher earlier in the day (Table 2).

Acute CORT tended to be negatively related to urbanization score (LM: $F_{1,65} = 3.66$, $\beta = -0.06 \pm 0.03$, $p = 0.060$), whereas baseline CORT did not differ as a function of urbanization score (LM: $F_{1,68} = 0.15$, $\beta = -0.04 \pm 0.04$, $p = 0.70$). Urbanization score was not related to acute CORT within activity center males alone (LM: $F_{1,41} = 0.13$, $\beta = -0.05 \pm 0.14$, $p = 0.72$). We report initial full models predicting CORT levels from habitat type and urbanization score in Supplementary material Appendix 1, Table A1 and A2.

Other condition metrics with respect to habitat type and urbanization score

Male song sparrows breeding in activity centers had higher feather quality, as reflected by feather PC1 scores (Table 2). However, body mass, hematocrit and total antioxidant capacity did not differ as a function of habitat type (LM: $p > 0.10$; Table 2). When controlling for wingchord (LM: $F_{1,64} = 14.02$, $\beta = 0.21 \pm 0.06$, $p < 0.001$), body mass was

Table 2. Linear models, means, and Cohen's d for plasma CORT levels and condition metrics with respect to urban habitat type.

	N	Intercept \pm SE	$\beta \pm$ SE	R ²	F	p (> F)	Center (mean \pm SE)	Refuge (mean \pm SE)	Cohen's d (95% CI)
Acute CORT	67	4.88 \pm 0.09					113.28 \pm 7.56	143.47 \pm 12.56	
Habitat type			-0.23 \pm 0.11	0.05	4.31	0.042			-0.60 (-1.09; -0.10)
Baseline CORT	71	4.55 \pm 0.52					28.08 \pm 1.92	30.68 \pm 3.16	
Habitat type			-0.12 \pm 0.14 ^a		0.24	0.624			-0.26 (-0.73; 0.22)
Time			-0.11 \pm 0.04	0.06	6.26	0.015			
Body mass	68	5.71 \pm 3.84					20.33 \pm 0.15	20.10 \pm 0.16	
Habitat type			0.32 \pm 0.22		1.35	0.249			0.43 (-0.07; 0.92)
Time			0.12 \pm 0.07		5.56	0.021			
Year			0.58 \pm 0.26		6.84	0.011			
Wingchord			0.20 \pm 0.06	0.24	11.95	<0.001			
Hematocrit (%)	71	48.40 \pm 0.76					49.16 \pm 0.52	48.29 \pm 0.85	
Habitat type			0.86 \pm 0.95	-0.002	0.84	0.363			0.26 (-0.21; 0.73)
Feather PC1	71	-0.39 \pm 0.22					0.24 \pm 0.16	-0.40 \pm 0.22	
Habitat type			0.63 \pm 0.27	0.06	5.29	0.024			0.67 (0.19; 1.15)
TAC	45	5.72 \pm 0.04					288.51 \pm 8.92	308.35 \pm 13.39	
Habitat type			-0.06 \pm 0.05	0.012	1.56	0.216			-0.36 (-0.95; 0.23)

^aActivity center relative to activity refuge habitat.

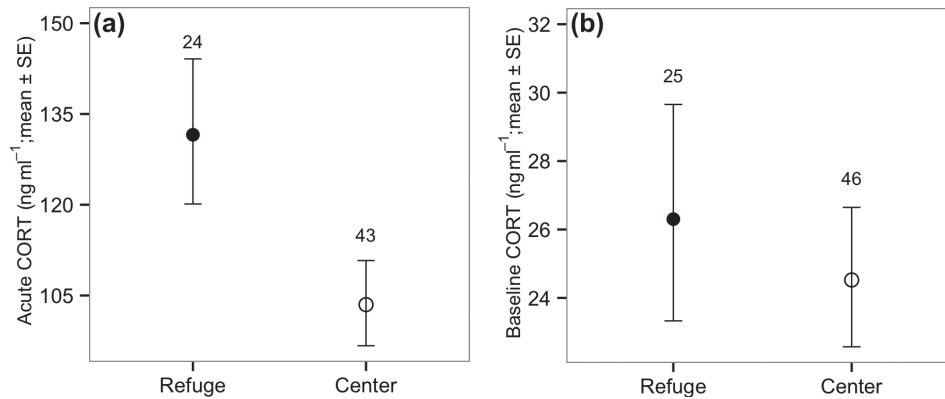


Figure 2. Acute (a) and baseline (b) CORT levels with respect to urban habitat type. Sample sizes are shown above error bars. Note differences in y-axis scales.

higher in 2012 (LM: $F_{1,64} = 4.54, \beta = 0.48 \pm 0.25, p = 0.04$) and later in the day (LM: $F_{1,64} = 4.56, \beta = 0.12 \pm 0.08, p = 0.04$). However, body mass was unrelated to date of capture and tarsus length, and no other condition metric was correlated with time, date, or year of capture ($p > 0.10$; Supplementary material Appendix 1, Table A3). Condition metrics were unrelated to CORT levels, and to the interaction between habitat type and CORT levels (LM: $p > 0.10$; Supplementary material Appendix 1, Table A3).

Urbanization score (PC1) was positively related to feather quality (LM: $F_{1,68} = 6.27, \beta = 0.15 \pm 0.07, p = 0.01$), as expected given higher feather quality detected in activity center males. Further, when characterizing anthropogenic disturbance level via urbanization score, feather quality was lower in 2012 (LM: $F_{1,68} = 4.25, \beta = -0.59 \pm 0.29, p = 0.04$). Urbanization score was not related to feather quality within activity center males alone (LM: $F_{1,41} = 0.03, \beta = 0.07 \pm 0.33, p = 0.86$). As for discrete characterization of habitat types, no other condition metric was related to urbanization score, and no interactions with CORT levels were detected (LM: $p > 0.10$ in all cases; Supplementary material Appendix 1, Table A4). Condition metrics were uncorrelated in our dataset (Spearman correlations: $p > 0.10$; Table 3).

Plasma CORT and condition metrics with respect to environmental noise

CORT variables, body mass, hematocrit, and total antioxidant capacity were unrelated to both the magnitude of noise level (noise PC1) and variation in noise level (noise PC2) (LM: $p > 0.09$ in all cases; Supplementary material Appendix 1, Table A5 and A6). Feather PC1 was positively related to noise PC1 within the entire dataset (LM: $F_{1,68} = 4.61; \beta = 0.15 \pm 0.08; p = 0.03$), with year of capture

also included in the model (LM: $F_{1,68} = 5.61; \beta = -0.66 \pm 0.28; p = 0.02$). However, noise PC1 was not related to feather quality within activity center males alone (LM: $F_{1,42} = 0.20; \beta = 0.04 \pm 0.17; p = 0.66$). Noise PC2 also tended to be positively related to feather PC1, but this effect was non-significant (LM: $p = 0.055$; Supplementary material Appendix 1, Table A6).

Discussion

Our principal finding in this study was that male song sparrows breeding on activity center territories with higher urbanization scores had lower acute CORT relative to males breeding in activity refuges. A negative relationship between acute CORT levels also tended to emerge when using urbanization score as a continuous metric of anthropogenic disturbance levels. In contrast to this study, much previous work has reported null relationships between stress physiology and urbanization levels (Fokidis et al. 2009, Chavez-Zichinelli et al. 2010, Bókony et al. 2012, Bonier 2012), and positive correlations have also been reported (Wasser et al. 1997, Walker et al. 2005, Bonier et al. 2007, Hayward et al. 2011). However, a limited number of previous studies have reported negative correlations between acute CORT levels, or the magnitude of the stress response, and urbanization and have suggested that suppression of the HPA axis may aid in adaptation to high-disturbance environments. For instance, urban populations of dark-eyed juncos *Junco hyemalis* (Atwell et al. 2012) and European blackbirds (Partecke et al. 2006) had both lower acute CORT and lower acute stress responses than rural conspecifics. Thus, lower acute CORT levels in activity center song sparrows could represent an adaptation to help cope with anthropogenic disturbance and allow for maintenance of reproductive activity.

Table 3. Spearman correlations between condition metrics.

	Hematocrit	Feather PC1	Total antioxidant capacity
Body mass	$r_s = 0.04, n = 68, p = 0.72$	$r_s = 0.10, n = 68, p = 0.42$	$r_s = 0.14, n = 43, p = 0.37$
Hematocrit	–	$r_s = 0.00, n = 71, p = 0.99$	$r_s = 0.00, n = 45, p = 0.98$
Feather PC1	–	–	$r_s = -0.12, n = 45, p = 0.45$

Due to the close proximity of activity center and refuge habitat, this adaptation would likely arise through phenotypic plasticity, rather than genetic differentiation.

However, since our results are correlational, other explanations for the differences in CORT levels observed are possible. For instance, rather than being an adaptive response to anthropogenic disturbance, lower acute CORT in activity centers could be explained by differences in breeding phenology or brood value between males breeding in the two urban habitat types. Indeed, a recent review indicates that breeding phenology and brood size often differ between birds breeding in environments with different levels of urbanization (Chamberlain et al. 2009). In many species, including song sparrows, acute elevation of CORT is suppressed during the nestling stage (Wingfield 1984, Wingfield et al. 1995). Moreover, past research on both the inter-specific and intra-specific levels has demonstrated that increased brood value is related to greater suppression of the stress response during the breeding season (Lendvai et al. 2007, Bókony et al. 2009). Thus, potential breeding-related explanations for lower acute CORT levels in activity center males include advancement of breeding in activity centers such that more individuals were in the nestling stage when captured, a more favorable breeding environment in activity centers that allowed for larger brood size, or higher nest predation rates in activity refuges that precluded many pairs in refuges from reaching the nestling stage. Unfortunately, we lack precise information about breeding stage, brood size, or nest predation rates. However, if advancement of breeding or higher brood value does explain lower acute CORT levels in activity centers, these explanations still suggest that song sparrows have adapted to the urban environment, and may actually perceive activity center habitat as more favorable than refuge habitat, despite higher disturbance levels.

Males breeding in different urban habitats showed no evidence of differences in baseline CORT concentrations. This result further supports the conclusion that song sparrows successfully cope with the challenges unique to the urban realm, either through genetic adaptation or phenotypic plasticity, such that high anthropogenic disturbance levels do not result in chronic stress or increased allostatic challenge. This result contrasts with positive correlations reported between baseline CORT and urbanization in tree sparrows *Passer montanus* (Zhang et al. 2011) and male white-crowned sparrows *Zonotrichia leucophrys* (Bonier et al. 2007), and with studies that link higher baseline CORT to tourism and logging activity (Wasser et al. 1997, Walker et al. 2005). However, past studies also report null relationships between baseline CORT and urbanization (Partecke et al. 2006, Fokidis et al. 2009, Atwell et al. 2012, Bókony et al. 2012, Bonier 2012). Discrepancy in correlations between baseline CORT and anthropogenic disturbance may relate to interspecific differences in the ability to adjust physiology and habituate to disturbance or to differences in the allostatic challenges that urbanization poses for different species (Bonier 2012). Energetic demands associated with foraging may increase in urban areas due to decreased foraging substrate and increased coverage by cement and other impervious surfaces (Zhang et al. 2011, Bonier 2012). However, Riverside is surrounded by xeric coastal sage scrub, such that urbanization

may also enhance habitat quality and ease foraging challenges (Fokidis et al. 2009).

Body mass, hematocrit, and antioxidant capacity also did not differ between habitat types, again suggesting that sparrows in activity centers are not experiencing chronic stress. Similarity in body mass suggests maintenance of comparable energetic reserves, whereas similar hematocrit levels indicate that birds are not becoming anemic due to chronic stress imposed by disturbance (Fair et al. 2007, Bókony et al. 2012). Similarity in antioxidant capacity is consistent with the interpretation that activity center sparrows do not face increased oxidative challenge, which could arise in response to urban pollution, increased foraging effort in degraded habitat, or stress related to human activity (Isaksson et al. 2005, 2007, Møller et al. 2010). In contrast to our results, great tits *Parus major* do display up-regulated antioxidant capacity in urban areas (Isaksson et al. 2007). To fully interpret the meaning of elevated antioxidant capacity one needs to directly measure oxidative damage, since high antioxidant capacity could indicate better condition rather than greater oxidative challenges (Costantini and Verhulst 2009, Monaghan et al. 2009). Unfortunately, we were unable to assess oxidative damage. Thus, activity center sparrows could face higher oxidative challenge, but be unable to increase antioxidant capacity due to poor body condition. However, contrary to this interpretation, other metrics of current condition did not differ between habitat types. Indeed, the close proximity of activity centers and refuges, and high levels of regional air pollution, may mean that sparrows breeding in both urban habitat types face substantial oxidative challenges.

Despite similarity in metrics of current condition, birds in activity centers had higher feather quality than refuge birds. This result suggests that birds in activity centers may have been in better condition at molt (Harper 1999, Dawson et al. 2000). Thus, activity center habitat may be of higher quality than refuge habitat, despite higher anthropogenic disturbance levels, and differences in condition based on habitat type may emerge only during certain life-history stages. However, as a caveat, feather wear may depend on feather age as well as quality. Thus, another possibility is that activity center males tend to molt later than refuge males, and that feather quality is actually comparable.

Noise environment was unrelated to CORT levels, suggesting that noise is not the selective agent responsible for differences in acute CORT between urban habitat types, and does not result in chronic stress and elevated baseline CORT. Rather than noise, other disturbance-related attributes of refuge and center habitat, such as differences in human foot traffic and proximity to rapidly moving vehicles, may explain lower acute CORT in activity center birds. Past studies have examined the effects of loud noise on stress physiology with varying results. Some past studies link loud noise to elevated baseline CORT (Anderson et al. 2011, Hayward et al. 2011, Blickley et al. 2012, Strasser and Heath 2013). However, other studies have reported null or even negative correlations between the noise environment and baseline CORT (Crino et al. 2013, Strasser and Heath 2013). Lack of a relationship between the stress physiology of song sparrows and noise levels may reflect the fact that this successful urban species does not perceive loud noise as a disturbance. Our metric of noise environment does capture some meaningful variation

in the noise levels experienced by song sparrows, as indicated by significantly higher noise PC1 scores in activity centers relative to in refuges (Fig. 1b). Indeed, noise from major freeways in the Riverside area is an almost constant source of loud noise during the time frame in which we captured song sparrows (06:00–13:00). Further, potential differences in noise magnitude associated with higher traffic volumes during rush hour are likely mitigated by lower traffic speeds during this period (Halfwerk et al. 2011). However, as a caveat, we recognize that our ability to detect an effect of noise on stress physiology may have been limited by the fact that our noise measurements represent ‘snap shots’ of the noise environment.

The only relationship that we detected between other condition metrics and noise environment was a positive relationship between feather PC1 (feather quality) and noise PC1 within the entire dataset, but not within activity center males alone. This relationship is unlikely to reflect a causative relationship between loud noise and feather quality. Rather, feather quality and noise PC1 likely correlate due to both being correlated with some other attribute of activity center habitat. Indeed, urbanization score also positively correlated with feather quality.

Finally, both baseline and acute CORT concentrations documented in our population of song sparrows are comparable to those reported by MacDougall-Shackleton et al. (2009), who also used the MP biomedical kit for CORT assays. The fact that these values are somewhat higher than reported by some other researchers (Wingfield 1985, Clinchy et al. 2004, Owen-Ashley and Wingfield 2006), likely derives from differences in assay technique (these other studies used direct RIA procedures, following Wingfield et al. 1992).

In conclusion, our research contributes to a growing suite of studies that examine variation in the adrenocortical stress response and other physiological condition metrics with respect to urbanization. Males breeding in activity centers had lower acute CORT, and tended to have lower stress responses than males breeding in activity refuges. Although other explanations are possible, these findings are consistent with the hypothesis that suppression of the stress response in urban areas may facilitate maintenance of health and reproductive activity. Indeed, the lack of an association between current condition metrics and urban habitat type suggests that song sparrows are not pathologically affected by human disturbance. Additionally, activity center males had higher quality feathers than refuge males, suggesting that these males were in better condition at molt than refuge males and that activity center habitat may be of higher quality for song sparrows, despite higher disturbance levels. Direct fitness measurements would be needed to fully elucidate whether human disturbance affects habitat quality from the perspective of a song sparrow. However, results suggest that song sparrows are an urban adapter species that have adjusted to the unique selective pressures encountered in the urban realm. In contrast to song sparrows, other species may be less successful at adjusting to the relatively novel selective pressures encountered in urban environments. Indeed, given the diversity of empirical relationships reported between CORT levels and urbanization, more work is needed to determine whether specific-species characteristics, such

as cognition capacity or ecology, can be linked to specific responses to anthropogenic disturbance.

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Supplementary material (Appendix JAV-00459 at <www.avianbiology.org/readers/appendix>). Appendix 1.