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Increased lead and glucocorticoid concentrations reduce reproductive success in House Sparrows along an urban gradient

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Abstract

Urbanization is increasing at a rapid pace globally. Understanding the links between environmental characteristics, phenotypes, and fitness enables researchers to predict the impact of changing landscapes on individuals and populations. Although avian reproductive output is typically lower in urban than natural areas, the underlying reasons for this discrepancy may lie at the intersection of abiotic and biotic environmental and individual differences. Recent advances in urban ecology highlight the effect of heavy metal contamination on stress physiology; as high levels of glucocorticoid hormones decrease parental investment, these hormones might be the link to decreased reproductive success in areas of high environmental pollution. In this study, we aimed to identify which abiotic stressors are linked to avian reproductive output in urban areas and whether this link is mediated by individual hormone levels. We used fine-scaled estimates ($2m^2$ spatial resolution) of nighttime light, noise, and urban density to assess their impacts on the physiological condition of adult house sparrows (*Passer domesticus*). We measured circulating levels of lead and glucocorticoid concentrations in 40 breeding pairs of free-living house sparrows and related these physiological traits to reproductive success. Using structural equation modeling, we found that increased urban density levels linked directly to increased plasma corticosterone and lead concentrations that subsequently led to decreased fledgling mass. Sparrows with increased lead concentrations in plasma also had higher corticosterone levels. Although urban areas may be attractive due to decreased natural predators and available nesting sites, they may act as ecological traps that increase physiological damage and decrease fitness. To illustrate, avian development is strongly explained by parental corticosterone levels, which vary significantly in response to urban density and lead pollution. With fine-scale ecological mapping for a species with small home ranges, we demonstrated the presence and impacts of urban stressors in a small city with high human densities.

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Keywords

corticosterone; environmental toxicology; heavy metal; light; noise; pollution; urban ecology

Introduction

Urbanization is one of the most drastic forms of habitat change. By 2050, the human population living in urban areas will increase by 2.5 billion globally, and the conversion of natural to human-modified landscapes may reach 70% (Angel et al. 2005, Nations 2019). Avian systems are especially affected by land cover change, and many species serve as bioindicators of air, water, and heavy metal pollution (Isaksson 2010, Marzluff 2017, Van Doren et al. 2017, Senzaki et al. 2020, Celik et al. 2021). Urban areas contain a multitude of characteristics that influence the composition of avian communities, such as the homogenizing effects of decreased species richness but also increased spatial heterogeneity with human-subsidized resources (Marzluff et al. 2001, Loss et al. 2013, Aronson et al. 2014). For example, shifting resources, predator presence, and noise and light pollution can have opposing effects on avian reproduction (Chamberlain et al. 2009, Senzaki et al. 2020, Grade et al. 2021). Due to these complexities, conservationists, city planners, and ecologists need better quantification of the urban environment to assess the effects of urbanization on individuals and populations (Ouyang et al. 2018).

Most urban environmental research, especially in the organismal context, examines biological phenomena in a binary, urban-versus-rural context or across classes of urban development (e.g., rural, suburban, urban; Marzluff et al. 2001, Melles et al. 2003). Studies also frequently account for urban density at spatial resolutions too coarse to accurately study the focal species. Landsat satellite imagery (30-m^2 pixel resolution; *e.g.*, National Land Cover Dataset) is one of the most commonly used datasets for quantifying degrees of urbanization. While freely available and well-accepted for identifying urban density, it is based mostly on estimates of impervious surfaces and has relatively coarse spatial and spectral resolutions for organisms with small home ranges and body sizes. Other methods include local land cover classifications using IKONOS data, regionally-flown aerial imagery, or are based on human population estimates along the urban gradient (Stout et al. 2006, Garaffa et al. 2009). These methods are mostly limited to urban derivation by aerial view and insufficiently represent other urban elements, such as soil, air, light and noise pollutants. Avian populations may be more affected by light and noise pollution than by the degree of impervious surfaces (Swaddle et al. 2015). Therefore, one aim of our study is to characterize the urban environment using multiple environmental variables and identify the variable most associated with avian phenotype and reproductive success.

Urban environments, with increases in industrial compounds, are highly prone to environmental pollution that affect the health and wellbeing of humans and wildlife (Johnson and Munshi-South 2017). For example, some heavy metal pollutants suppress immune function (Snoeijs et al. 2005), affect physiological traits (Provencher et al. 2016, Bauerová et al. 2017), alter behavior (Frederick and Jayasena 2011), and lead to reproductive dysfunction (Janssens et al. 2003, Evers et al. 2008) even when contamination is below lethal thresholds. One such compound of persistent concern is lead, with toxic levels affecting 60% of counties in the USA (Eid and Zawia 2016). Lead poisoning and toxicity is mostly studied in relation to human health, with high levels associated with physiological, neurological, and physical damage (Järup 2003, Barrett 2008, Eid and Zawia 2016). Urban birds have long been excellent bioindicators of a variety of environmental pollutants, such as lead presence (Goede and De Bruin 1986, Root 1990, Cai and Calisi 2016). Increased environmental lead levels are correlated with decreased avian reproductive success (Chatelain et al. 2021b). As industrial compounds are often endocrine disruptors (Giesy et al. 2003, Baos et al. 2006), understanding how wildlife responds to these pollutants can help explain an individual's ability to adapt to urban challenges. Currently, few studies have investigated the effects of urban metal pollution on wildlife and the underlying mechanisms that would explain those effects.

Physiological responses, *e.g.,* the stress response, act as a line of defense that organisms use to flexibly adjust phenotypes to cope with changing environmental conditions (Hau et al. 2016). Glucocorticoid hormones, specifically corticosterone in birds, are released in response to stressors, such as light, noise or heavy metal pollution (Ouyang et al. 2018). High levels of glucocorticoid hormones cause the release of gonadotropic inhibiting hormone, which directly decreases reproductive hormones (Tsutsui et al. 2010). Researchers have found differences in glucocorticoid concentrations correlate with urbanization; however, the direction of the response can vary depending on year, sex, species, and location (Chávez-Zichinelli et al. 2010, Zhang et al. 2011, Atwell et al. 2012, Foltz et al. 2015, Injaian et al. 2020). While research on the relationship between heavy metal pollutants and effects on wildlife physiology is growing, it is unclear how and which urban abiotic factors are related to individual physiology and fitness (Bauerová et al. 2017, Ganz et al. 2018). Furthermore, urban populations could be adapted to increased levels of pollutants and have altered physiological phenotypes based on evolutionary history with cities (Eeva et al. 2006, Chatelain et al. 2016, Andrew et al. 2019). Thus, a primary challenge of the field of urban ecology and physiology is to understand how phenotypic variation relates to environmental challenges and ultimately, how these factors act synergistically or antagonistically to influence organismal fitness.

We aimed to identify which urban stressors (urban density, nighttime light, noise) are linked to adult phenotype (circulating concentrations of glucocorticoids and lead levels) and avian reproductive success. We studied free-living House Sparrows, *Passer domesticus,* a human commensal that lives in a wide variety of urban, suburban, and rural agricultural habitats (Summers-Smith 1963). This species persists in the urban and suburban USA despite general songbird declines in urban areas (Marzluff et al. 2001), although recent declines have also been noted in North America (Bengali et al. 2020). They ingest small rocks and gravel to aid in digestion, in particular contaminated road particles, including lead. Because of their close association with humans, they have been proposed as a possible candidate and bioindicator of heavy metal contamination (Dmowski 1999, Swaileh and Sansur 2006). We predict that sparrows living in more urbanized areas will have more plasma lead and glucocorticoid concentrations, leading to lower reproductive output as compared to sparrows in less urbanized areas. Alternatively, sparrows adapted to urban areas could have higher concentrations of lead without showing elevated glucocorticoid levels, in which case the two biomarkers would be uncorrelated and reproductive output can be affected by either trait independently.

Materials and methods

Study System

The study area includes the urbanized landscape of Reno and Sparks, Nevada, USA (henceforth Reno-Sparks; 39.525694 N, 119.77905 W; 685 km^2; Figure 1). The urban area is transected by the Truckee River and fills the Truckee Meadows Valley. It averages 18.3 cm of precipitation and 10.5°C temperature, and experiences atmospheric inversions during winter (Center 2016). Reno-Sparks has 410,000–420,000 residents and is amid a growth period spanning 1980–2050 (Hardcastle 2010).

We conducted our study from March to August 2016. Forty nests were actively monitored from which we caught 68 individuals associated with an active nest (32 males and 36 females). We monitored nest boxes ($n = 5$) and natural cavity nests ($n = 35$) of house sparrows regularly to determine the date of hatch (day 0). Nesting in natural or human provided nest boxes did not affect physiological and fitness measurements ($p > 0.05$). We captured parents with a mist net or automatic spring trap at the nest box when young were 8–10 days old (type of trap and age of young did not affect corticosterone levels or was related to any environmental variable, $p > 0.5$) between 8:00–12:00. We collected a blood sample from the adults (210 μL) from the brachial vein within 3 minutes of capture and released birds after measuring their mass (0.1 g) and tarsus (0.01 mm), which we used to calculate body condition, as a scaled mass index (Peig and Green 2009). Blood was stored on ice until centrifuged (800 g, 10 min) within 4 hours. We removed the plasma and stored at −80°C until further analyses. At day 16, we weighed all young within a nest (0.1 g) to determine mass at fledge.

Hormone and lead measurements—Lead concentrations were measured in the field using a LeadCare® II portable anodic stripping voltammetry (ASV) device. Fresh blood (<50 μL) from hematocrit tubes was placed on the sensor and a reading was obtained within 3 minutes. We used enzyme-linked immunosorbent assay kits (Enzo Life Sciences, Farmingdale, NY, USA) to measure corticosterone levels (Davies et al. 2017). To validate this assay for use with house sparrow plasma in our lab, we first removed endogenous hormones by incubating plasma for 20 minutes in a solution of 1% charcoal and 0.1% dextran. We then added corticosterone standard from the assay kit so that the concentration of corticosterone in each stripped sample was equal to 500 pg/mL. We assayed stripped and spiked samples at three dilutions (1:20, 1:30, and 1:40) with steroid displacement reagent (SDR; 0.5% and 1% of plasma volume). We determined that house sparrow plasma should be diluted 1:40 with 0.5% SDR. We randomly assigned 5 μL of each sample across three plates. To calculate coefficients of variation (CV), we included three pooled house sparrow plasma samples on each plate in triplicate. The intra-plate CV was 6.4% and the inter-plate CV was 7.8%.

Urban environment variables—We modeled urban density for the Reno-Sparks area by combining four equally weighted metrics at the building level: the number of residents, number of employees, building-footprint area, and building-height estimates (number of floors) (Washoe County Assessor 2014; Truckee Meadows Regional Planning Agency; White et al. 2018). This model allowed us to incorporate where humans spend the majority of their time and the built environment volumetrically. We used the kernel density function to model urban density in a 2-m^2 rasterized surface (White et al. 2018). The resulting urban density values were rescaled from 0–1. We modeled noise for the area based on decibel levels recorded at 64 locations during May–June 2016 using an Extech 407730 Digital Sound Level Meter. The meter used A-weight and fast response settings (Fang and Ling 2003). The decibel level was recorded every 10 minutes between 6:30–8:30 h and 9:00–11:00 h at each sampling site on a random weekday and weekend day during the nesting season between mid-April and early June. We then averaged the two periods and created an interpolated, continuous noise surface (range: 29–79.97 dB). Noise sampling locations were distributed throughout the urban gradient and were based on nest locations used in other urban-avian guild research (White et al. 2020). We also acquired nighttime light emittance for each nest site captured by the Visible Infrared Imaging Radiometer Suite satellite dataset (750 m resolution). We note that this resolution is coarse relative to the range of our study species; however, it is reasonable considering the distribution of our sparrow capture sites along the nighttime light emittance spectrum. Our approach to modeling urban density, noise, and nighttime light emittance resulted in all continuous variables for ease and robustness of statistical analyses. All environmental variables were geoprocessed in ArcGIS 10.7 (ESRI 2016).

Statistical measurements—We used structural equation modeling (SEM), represented as a path analysis (*lavaan package in R)* to determine if 1) environmental variables (*nighttime light, noise, and urban density*) influenced lead and corticosterone concentrations in individual adult birds, 2) whether lead concentrations within adult birds influenced plasma corticosterone levels, and 3) whether corticosterone and lead concentrations would influence average fledgling mass within nests. Path analyses are designed to test how inter-correlated variables may be causally related to each other, allowing us to test which environmental variables can explain individual phenotypic differences that ultimately lead to effects on reproduction. We initially included body condition in paths along with physiological measurements but analyses showed that paths without body condition were all better fit, so we removed it from subsequent paths. Additionally, adult body mass did not vary by urbanization degree in this study ($p = 0.55$). The model included covariance structures for (i) nighttime light emittance, noise, urban density, and lead concentrations, (ii) corticosterone and lead concentrations, and (iii) average fledgling mass. All variables included in the path analysis were standardized. To assess model fit, we compared all ecologically relevant model paths and used the comparative fit index (CFI) and standardized room mean square residual index (SRMR) to correct for small sample size ($n = 68$) and parsimony. We provide standardized path coefficients (*i.e.,* partial regression parameters) to describe relationships between variables. All statistical analyses were performed in R 3.2.1 (R Core team 2016).

Results

We present a final model that most accurately describes our *a priori* hypotheses with the best fit ($\chi 2$ = 24.5, df = 3, CFI = 0.907, SRMR = 0.048, and AIC = 381.6; Figure 2). Our model satisfies previous cutoffs of both the standardized root mean squared residual and comparative fit indexes, which are relatively independent from sample size and yields better performance when studied with smaller sample sizes (Schermelleh-Engel et al. 2003, Chen 2007, Cangur and Ercan 2015). Parameter estimates showed that urban density had a direct positive effect on corticosterone (path coefficient: 0.42) and lead concentrations (path coefficient: 0.57; Figures 2 and 3). Noise also had a direct positive effect on lead concentrations (path coefficient: 0.31) while night light had a direct negative effect (although to a lesser degree than urban density; path coefficient: −0.15). The strongest relationship within the path analysis was seen as a direct positive effect of lead concentrations on plasma corticosterone levels (path coefficient: 0.60; Figures 2 and 3). Additionally, fledgling mass was directly negatively affected by corticosterone levels (path coefficient: −0.48) and to a lesser extent, by lead levels (path coefficient: −0.20; Figures 2 and 3).

Discussion

Using a novel method to characterize the urban environment, we showed that urban density correlates with lead and corticosterone concentrations in a free-living songbird while noise and light pollution have weak effects. We also observed a positive relationship between lead concentrations and plasma corticosterone in adult birds. Our results demonstrate a direct, positive link between urban environmental factors with physiological traits in adult birds, leading to decreased fledgling mass of nestlings in more urban regions of the Reno-Sparks area. Urban-driven alternation of avian reproductive outputs in this study are therefore partially mediated by corticosterone levels.

Heavy metal toxicity is a relatively newly identified health threat and because industrial compounds are often endocrine disruptors (Norris 2000), assessing the correlation between these compounds and endocrine function is vital. Although lead levels have decreased 99% between 1980 and 2017 in the US due to a ban on lead-based products in construction, lead remains a significant environmental threat (Washoe County Health District 2020). Lead paint is still widely found in buildings and atmospheric particulate lead can increase by a hundred fold after building demolition (Datko-Williams et al. 2014). We show that birds in central urban areas of Reno-Sparks (high urban density) have plasma lead levels above 10 ug/dL, which is of health concern (National Toxicology Program 2012). Reno-Sparks also experiences intense atmospheric inversions in the winter and spring leading to further pollutant accumulation in the urbanized basin. With increases in human population, industrial activity, urban development projects, and vehicular traffic in Reno-Sparks, pollutants may be increasing, which may affect water and soil concentrations of heavy metal compounds (Gyawali et al. 2009, Lin et al. 2017). Assessing how lead particles enter the soil, water, insects, and/or plant products that birds ingest is the next step to minimizing health impacts.

We used a novel method to measure urban density at a continuous scale and found strong relationships with physiological traits and other urban stressors. Our urban density model paves the way for experimental studies to investigate relationships between the urban environmental elements and local biophysiology. We found a positive association between urban density and corticosterone levels. Studies have found varying relationships between urbanization and corticosterone levels (Bonier et al. 2007, Sepp et al. 2017) that are likely due to differences in the urban environment, species, or time of study. Using a fine-scale representation of urban density, we show that at an individual nest level, adult house sparrows are affected by human presence. Urbanized areas are associated with decreased natural food availability and quality which can affect wildlife physiology and fitness (Seress et al. 2018, Baldan and Ouyang 2020). Other challenges in cities include increased light, noise, and heavy metal pollution, all of which is correlated to building density and human foot-print. Therefore, environmental factors correlated to urban density may strengthen the association between urban density and corticosterone levels. As cities continue to grow and rural areas urbanize, finding the environmental sources of impact will be critical for mitigating physiological damage.

The strongest path association in our study is a positive link between plasma levels of lead and corticosterone. While there is discrepancy in the effects of lead on corticosterone levels, with some studies reporting no effect of lead on glucocorticoid levels (Eeva et al. 2005, Snoeijs et al. 2005, Eeva et al. 2014, Provencher et al. 2016, Chatelain et al. 2018, Ganz et al. 2018), a study, similar to ours, shows a clear link between plasma lead levels in an urban-adapted songbird and baseline corticosterone concentrations (Meillère et al. 2016). The contrasting results may be due to differences in methodology of lead measurements (*e.g.*, fecal, feather, tissue, or plasma) as well as discrepancies in dose-dependent effects of lead in experimental studies. Additionally, responses to heavy metal contamination may be taxon-specific and dependent on species' history in urbanized environments. As urban areas vary in environmental concentrations and compositions of heavy metals (Chatelain et al. 2021a), physiological responses are likely to vary across urban areas, which are already heterogeneous in habitat composition. For example, plasma lead concentrations are positively associated with stress-induced corticosterone levels of white storks (*Ciconia ciconia*), with authors suggesting that lead contamination working in tandem with other anthropogenic stressors are more detrimental than either stressor alone (Baos et al. 2006). We note that the higher baseline corticosterone levels of urban sparrows at our study sites could be related to other urban environmental factors instead of environmental pollutants; however, our path analysis shows that the strongest predictor of circulating corticosterone levels is circulating lead levels. Disentangling these associations is critical in urban habitats where birds are faced with different urban stressors that may escalate lead's effects on fitness.

In this study, we show that birds with high levels of lead and corticosterone in their plasma had offspring with lower mass. Past studies in European songbirds also show that higher levels of heavy metal pollutants lead to lower reproductive success and reduced offspring body condition (Janssens et al. 2003, Fritsch et al. 2019, Chatelain et al. 2021b). Higher mass at fledgling is a good indication of whether the young are likely to survive and recruit back into the population (Ringsby et al. 2009). Increased parental corticosterone levels are related to decreases in feeding rates (Lendvai et al. 2007, Ouyang et al. 2013), which may be one reason parents with higher corticosterone levels have offspring with lower mass. If increases in lead concentrations also affect learning and memory in birds as they do in humans (Järup 2003), birds exposed to higher levels of lead pollution may also exhibit a reduced foraging success, indirectly causing lower nestling mass. However, further research into the connection between lead and avian cognition is needed to better understand the effects of heavy metal pollution on wild bird populations.

Urban habitats have been proposed to act as ecological traps for wildlife, as these areas seem enticing because of decreased natural predators and competition for nesting sites (Schlaepfer et al. 2002, Suvorov and Svobodová 2013, Demeyrier et al. 2016). However, these areas can be detrimental to recruitment or offspring growth, possibly exacerbated through settlement by younger age classes or less experienced individuals (Martin et al. 2014), and could lead to species extinction (Battin 2004). We show that urban areas may be an evolutionary trap with increased pollutants that lead to physiological change and lower fitness for offspring. In a recent study, there is evidence that Australian house sparrows are locally adapting at the genetic level to lead contamination in populations surrounding mining communities (Andrew et al. 2019). Given enough evolutionary time with strong selection, avian populations may be able to adapt to heavy metal trace elements commonly found in cities. However, this evidence is rare with most studies reporting deleterious effects from lead contamination (Janssens et al. 2003, Roux and Marra 2007). Our study, which finds a strong association between environmental pollutants with corticosterone, suggests that adaptation to urbanization may not yet be evident. As natural and rural lands increasingly become modified by human activities, conservation biologists and urban planners should consider the effect of ecological traps for urban wildlife.

We combine ecological sensing and physiological responses across an urban density gradient to show well-defined associations between the urban environment, the physiological phenotype, and its downstream effects on offspring fitness. Whether these phenotypes are a result of directional selection or adaptation in urban environments remains a key question in evolutionary physiology. We show that parsing out the factors that contribute to the corticosterone phenotype is feasible at a fine scale with detailed measurements of the environment. Continuous sampling in gradient analysis is a powerful method by which we can relate individual physiology and environmental conditions and significantly helps to identify the environmental factors that explain urban-driven effects on wildlife. Though large cities (>1 million people) have been shown to negatively impact ecosystem health and function (Garaffa et al. 2009), we demonstrate that similar impacts of the urban environment occur in smaller cities with high human densities.

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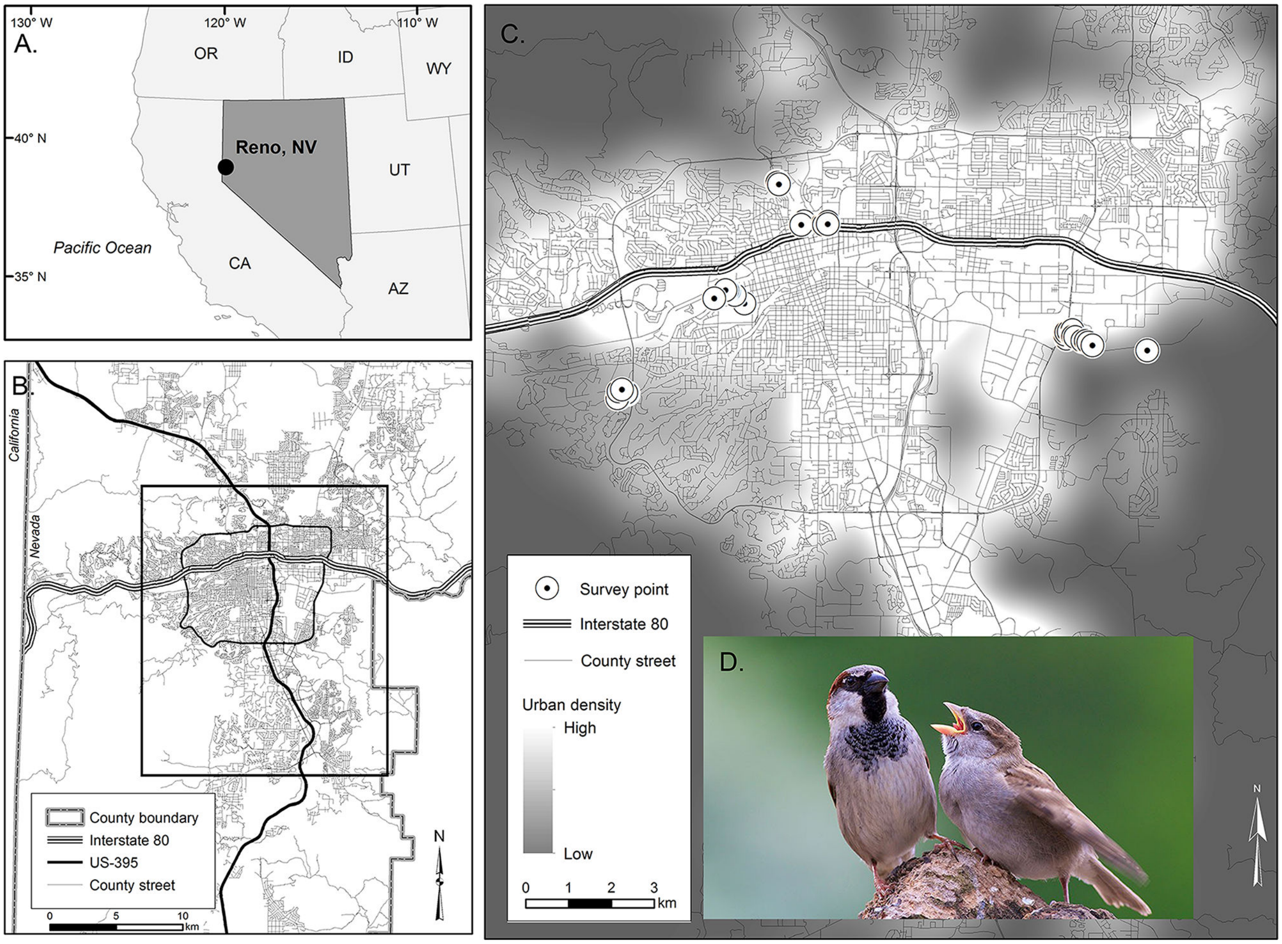

Figure 1.

(A) Location of Reno, NV, USA (B) Map of Reno and Sparks including major roads and highways (C) Surveyed house sparrow nests shown in dotted white circles (n = 40) atop the urban density landscape (D) Adult male house sparrow with juvenile, photo credit Z. Darius

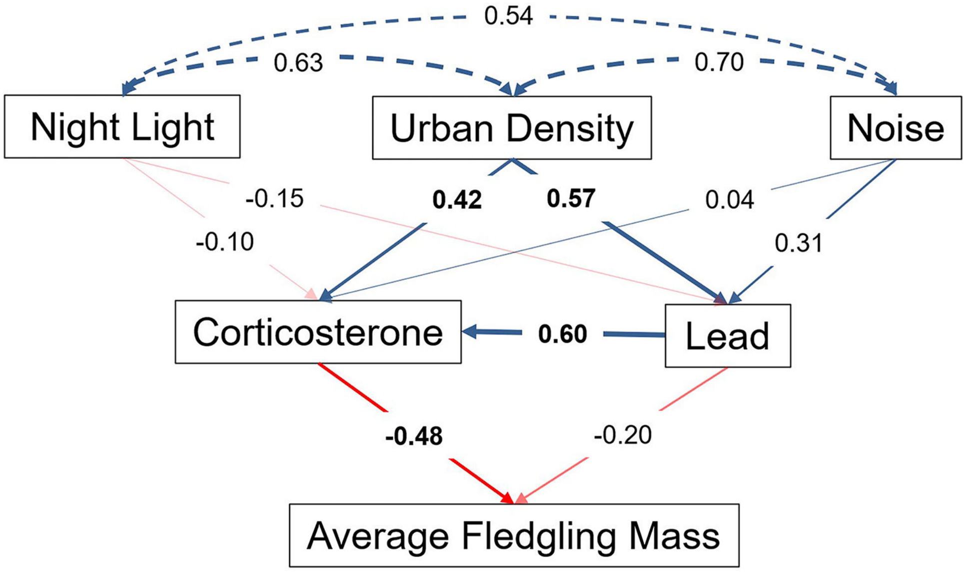

Figure 2.

Path diagram of the relations between environmental variables (nighttime light, noise, and urban density), adult physiological variables (corticosterone and lead concentrations in blood), and fitness (fledgling mass). Width and transparency of the path lines are proportional to the strengths of the relationships (indicated by standardized path coefficients). Blue, dotted lines indicate a positive effect and red, straight lines indicate a negative effect.

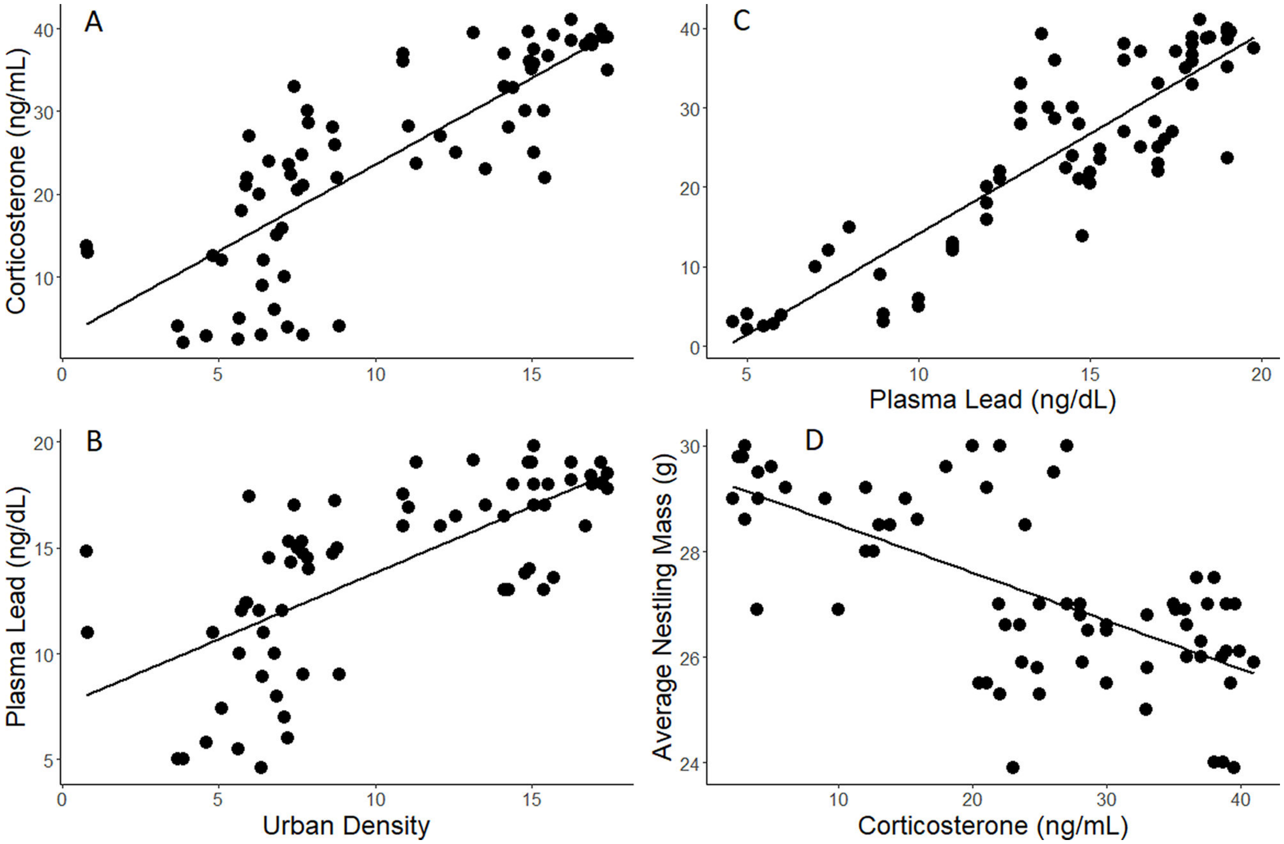

Figure 3.

Plasma concentrations of corticosterone (A) and lead (B) in adult house sparrows are positively related to urban density. Plasma corticosterone concentrations are positively correlated with lead levels (C). Lastly, average nestling mass is negatively affected by adult corticosterone levels (D).