

Are urbanization and brood parasitism associated with differences in telomere lengths in song sparrows?

Abstract

Urbanization reflects a major form of environmental change impacting wild birds globally. Whereas urban habitats may provide increased availability of water, some food items, and reduced predation levels compared to rural, they can also present novel stressors including increased light at night, ambient noise, and reduced nutrient availability. Urbanization can also alter levels of brood parasitism, with some host species experiencing elevated levels of brood parasitism in urban areas compared to rural areas. Though the demographic and behavioral consequences of urbanization and brood parasitism have received considerable attention, their consequences for cellular-level processes are less understood. Telomeres provide an opportunity to understand the cellular consequences of different environments as they are a well-established metric of biological state that can be associated with residual lifespan, disease risk, and behaviour, and are known to be sensitive to environmental conditions. Here we examine the relationships between urbanization, brood parasitism, and blood telomere lengths in adult and nestling song sparrows (*Melospiza melodia*). Song sparrows are a North American songbird found in both urban and rural habitats that experience high rates of brood parasitism by brown-headed cowbirds (*Molothrus ater*) in the urban, but not the rural, sites in our study system. Among adults and nestlings from non-parasitized nests, we found no differences in relative telomere lengths between urban and rural habitats. However, among urban nestlings, the presence of a brood parasite in the nest was

associated with significantly shorter relative telomere lengths compared to when a brood parasite was absent. Our results suggest a novel, indirect, impact of urbanization on nestling songbirds through the physiological impacts of brood parasitism.

Introduction

Human-induced rapid environmental change is a threat to biodiversity and is substantially impacting songbirds (Vitousek et al. 1997, Crick 2004, Both et al. 2006). The impacts of one form of anthropogenic change, urbanization, have been especially well-studied (Isaksson 2018, Marzluff 2001). Ecological studies resolving the aspects of urbanization that impact wildlife, including songbirds, have demonstrated that ambient noise, light at night, frequent human disturbance, temperature changes, and shifts in predation intensity and prey availability collectively generate novel ecological pressures in urban habitats (Isaksson 2018, Marzluff 2001). Though urbanization has been linked with local extinctions, many songbird species successfully persist in urban habitats (Blair 1996, Marzluff 2001, McKinney 2002, Both et al. 2006, Bonier et al. 2007, Shochat et al. 2010, Sih et al. 2010, Sol et al. 2013, Wong and Candolin 2015). Whereas some animals can thrive under urban conditions (Blair 1996, McKinney 2006), there is an underlying assumption that inhabiting urban habitats is costly for most individuals (Birnie-Gauvin et al. 2016, Murray et al. 2019). Indeed, some urban-dwelling birds exhibit poor body condition (Capilla-Lasheras et al. 2017, Murray et al. 2019) and reduced reproductive success (Chatelain et al. 2021) compared to rural conspecifics. However, there are also cases where birds inhabiting urban environments exhibit better body condition (Auman et al. 2008, Minias 2016), higher reproductive success (Lane et

al. 2023) and increased survival (Møller 2009, Phillips et al. 2018) compared to rural birds of the same species. One approach to resolving the contradictory findings among rural-urban comparisons is to examine cellular and physiological mechanisms driving condition and fitness outcomes and which may also generate variation in these outcomes (Isaksson 2015, Ouyang et al. 2018).

In addition to effects at the species level, urbanization can impact community structure, with one potentially important effect being an alteration in rates of brood parasitism (Burhans & Thompson 2006, Møller et al. 2016, Zhang et al. 2023). Avian obligate brood parasitism is a life-history strategy in which brood parasites lay their egg(s) in the nest of another species, the host, which then provides parental care for the young (Payne 1977, Rothstein, 1990). Although there are only a handful of known avian brood parasites, consisting of only ~1% of birds globally, (Payne 1977, Davies 2000), many bird species - global estimates suggest more than 14% - can serve as hosts (Kennerley et al. 2002). Cowbirds (genus: *Molothrus*) alone are known to parasitize the nests of over 144 species of songbirds (Friedmann and Kiff 1985). Brood parasitism can negatively impact both the host parents and offspring, though the magnitude of impact varies among species (Payne 1977, Pollock et al. 2021). Urbanization can substantially alter interactions between brood parasites and their hosts, though in some systems urbanization is associated with reduced rates of brood parasitism (Rodewald et al. 2013, Buxton et al. 2018), and in others it is associated with increased rates of brood parasitism (Burhans and Thompson 2006, Tewksbury et al. 2006, Rodewald 2009, Padilla and Sutherland 2022). The most common brood parasite in North America is the brown-headed cowbird (*Molothrus ater*; hereafter “cowbirds”; Peer et al. 2013), a native

species of songbird that has historically used human-disturbed habitats (i.e., farmlands; Chace et al. 2005) and is now successfully inhabiting urban environments (Rodewald 2009, Padilla and Sutherland 2022). Cowbird offspring compete with host offspring for resources provided by host parents (Rothstein 1975, Lichtenstein and Sealy 1998, Kilner et al. 2004, Moskát et al. 2017), often resulting in reduced host nestling hatch rate, growth rate, and survival (Lorenzana and Sealy 1999, Hauber 2003, Hoover 2003, Scharf et al. 2021). Though the negative effects of brood parasitism on host nestlings are well-documented, the physiological mechanisms mediating these effects are less clear (but see Ibáñez-Álamo et al. 2018, Scarf et al. 2021).

One approach to understanding the impacts of urbanization on songbirds experiencing multifaceted ecological changes is to examine physiological and molecular responses. These measures have the potential to reveal both pathological effects of living in urban habitats and provide insight into the adaptive mechanisms underpinning responses that facilitate urban living (Isaksson 2015). Previous work has shown associations between urbanization and altered levels of hormones, oxidative stress, hematological parameters, and immune function (Bonier 2012, Isaksson 2015, Isaksson 2018, Goodchild et al. 2022, Bonier 2023). Additionally, there is increasing interest in the impacts of urbanization on telomeres - tandem repeats of DNA and a shelterin protein complex at the end of chromosomes (Shay and Wright 2019, Salmón and Burraco 2022). Functionally, telomeres protect the ends of linear chromosomes and are also involved in various cellular-signaling processes, including cellular senescence (Casagrande and Hau 2019, Shay and Wright 2019). Telomeres are relevant to aging, cancer, and disease, and variation in telomere lengths (i.e., the number of tandem

repeats) and their dynamics (i.e., within-individual changes in telomere lengths) relate to differences in lifespan within (Wilbourn et al. 2018, Schneider et al. 2022) and between species (Dantzer and Fletcher 2015, Sudyka et al. 2016, Tricola et al. 2018, Wirthlin et al. 2018). Within species, telomeres can also correlate with life-history strategies, behavior, and individual quality (Bateson and Nettle 2018, Young 2018, Angelier et al. 2019, Giraudeau et al. 2019, Sudyka 2019, Tobler et al. 2021, Vernasco and Watts 2022). Thus, telomeres can provide an integrative measure of somatic state (Monaghan 2010, Boonekamp et al. 2013, Bateson et al. 2015). Importantly, telomeres and their dynamics can be impacted by environmental factors (Angelier et al. 2018), including anthropogenic disturbances (Salmón and Burraco 2022). At the time of writing, the relationships between urbanization and telomere lengths has been examined in only two avian species, European blackbirds (*Turdus merula*) and great tits (*Parus major*) (Salmón et al. 2016, Biard et al. 2017, Salmón et al. 2017, Ibáñez-Álamo et al. 2018). Further, the relationship between brood parasitism and host telomere lengths in adults and offspring has not been described.

Here, we examined whether blood telomere lengths differed between song sparrows (*Melospiza melodia*) living in replicate urban and rural study sites, and further, whether brood parasitism is a specific means by which telomeres may be impacted in urban habitats. Song sparrows, a common songbird native to North America, are an excellent model to study physiological responses to urbanization because they successfully breed in both rural and urban habitats. Adult song sparrows in our urban and rural study sites show consistent behavioral differences (Hyman et al. 2004, Evans et al. 2010, Davies and Sewall 2016, Davies et al. 2018, Fossett and Hyman 2021) and

urban birds have higher reproductive success (Lane et al. 2023). However, hormone concentrations, oxidative stress, and hematological measures do not reliably differ across habitats (Foltz et al. 2015, Lane et al. 2021, Goodchild et al. 2022), nor is there detectable genetic differentiation between birds at our rural and urban sites (Brewer et al. 2020). Song sparrows are a common host for brown-headed cowbirds (Hauber and Russo 2000), and at our study sites brood parasitism occurs at high rates in urban habitats but is very rare in rural habitats (Lane et al. 2023). Specifically, across 5 years of nest monitoring 44% of urban nests were parasitized (n=84/191) compared to only 8% of rural nests (n=10/125) (Lane et al. 2023). Here, we sought to examine the associations among telomere lengths, urbanization, and brood parasitism. To do this, we compared telomere lengths between adult birds in rural and urban habitats. For nestling birds, we evaluated the effects of urbanization apart from brood parasitism by comparing telomere lengths from urban and rural birds belonging to non-parasitized nests. To evaluate the effects of brood parasitism, specifically, we compared telomere lengths from urban nestlings belonging to parasitized or non-parasitized nests. Additionally, this dataset afforded us the opportunity to examine age- and sex-related differences in telomere lengths and age-specific associations between telomere lengths and urbanization.

Methods

Adult capture

Adult song sparrows were captured from February to October in 2019 – 2022 at 6 established urban and rural sites (n = 3 each) in Southwestern Virginia, USA that are

at the ends of an urban-rural gradient (Figure S1, Davies et al. 2016, Davies et al. 2018). Birds were captured through blanket mist netting, targeting males on their territories using simulated territorial intrusions (Hyman et al. 2004), and capturing females as they returned to or left active nest sites. After capture, a small blood sample was taken via brachial venipuncture with a 26-gauge needle, and blood was collected with heparinized 70 μ L capillary tubes. Whole blood was stored on ice in the field. Red blood cells were then separated from plasma within 6 hours and stored in 100% ethanol at -80°C until being shipped to Washington State University (WSU) on dry ice. At WSU, samples were stored at -20°C until DNA extraction. Across 4 years, 64 urban (21 females and 43 males) and 58 rural (23 females and 35 males) adult song sparrows were sampled.

Nest searching and nestling sampling

Song sparrow nests were located and monitored at the same sites and in the same four breeding seasons described above. Nests were found in the morning (0500 to 1100) during peak parental behavior, from early March to late July through behavioral observations of adults and systematic searching of known territories and nesting substrates (Martin & Geupel 1993). Complete clutches were inspected for brown-headed cowbirds eggs using previously established methods to distinguish host eggs from those of brown-headed cowbirds (Smith & Arcese 1994). If a nest was found after hatch, visual identification and morphometrics were used to identify cowbird nestlings (Pyle 1997). Blood samples were collected from nestlings at an advanced day of development (day 5-11 post-hatch) and samples were stored using the methods

described above. Across 4 years 90 urban nestlings (51 from 28 parasitized nests and 39 from 21 non-parasitized nests) and 34 rural nestlings from 14 non-parasitized nests were sampled.

Measurement of relative telomere lengths

The Gentra Puregene Blood Kit (Qiagen) and the modified extraction protocol described in Vernasco et al. (2021) were used to extract DNA from whole blood. This extraction approach results in high molecular weight DNA that is suitable for telomere measurement by real-time quantitative PCR (qPCR; Eastwood et al. 2018, Vernasco et al. 2021). A NanoDrop ND-1000 was used to assess DNA purity and concentration (mean DNA concentration \pm SD = 288 ± 145.5 ng/ μ L, range of DNA concentrations = 7.73-778.76 ng/ μ L, mean 260/280 ratio \pm SD = 1.87 ± 0.06 , mean 260/230 ratio \pm SD = 2.19 ± 0.22). Extracted DNA was stored at -20°C and relative telomere lengths were quantified using qPCR following Criscuolo et al. (2009) and Eastwood et al. (2018). This qPCR approach measures an individual's relative telomere length by comparing the number of telomere-repeats to the number of copy numbers of a single-copy gene. Glyceraldehyde-3-phosphate dehydrogenase (GAPDH) was used as the single-copy gene. Samples were analyzed on a CFX Duet Real-Time PCR System (Bio-Rad) on 96 well plates and with 15 μ L reaction volumes. Reactions included 7.5 μ L of SsoAdvanced™ Universal SYBR® Green Supermix, 3.6 μ L of DNase-free water, 0.15 μ L of forward and reverse 100nM telomere or single-copy control gene primers (Sigma-Aldrich), and 3.6 μ L of template DNA (4.5 ng of DNA per reaction). Separate plates were used for telomere and GAPDH primers. A “golden sample” was made up by

185 combining DNA from 3 different adult song sparrows that were not a part of the current
186 study and included on each plate for use as the inter-plate control. Telomere primer
187 sequences were Tel1b 5' - CGG TTT GTT TGG GTT TGG GTT TGG GTT TGG GTT
188 TGG GTT - 3' and Tel2b 5' - GGC TTG CCT TAC CCT TAC CCT TAC CCT TAC CCT
189 TAC CCT - 3' (Criscuolo et al. 2009). The GAPDH primers were developed from the
190 song sparrow reference genome (NCBI GCA_022749695.1) using the primer design
191 tool in Geneious v10.2.3 (Kearse et al. 2012; Forward: 5' - TCA TCC CTC CTT AGG
192 CGT GA - 3', Reverse: 5' - GCC TTC TCC ATG GTG GTG AA - 3'). Melt curve
193 analyses identified a single peak in the qPCR products of both primer sets. Reaction
194 conditions for telomere primers were as follows: 95°C for 10 min, followed by 40 cycles
195 of 1 min at 95°C, and 1 min at 58°C. GAPDH reaction conditions were identical except
196 for the annealing and extension temperature was set to 60°C. Samples were randomly
197 assigned across seven plates. Three randomly selected samples were also included on
198 all seven plates to estimate inter-assay repeatability. Two no template controls were
199 included in each plate and all samples, standards, and controls were run in duplicate.
200 Cycle quantification (Cq) values and individual well qPCR efficiencies for samples were
201 calculated using LINREGPCR version 11 (Ruijter et al. 2009; mean \pm SD: Cq-GAPDH =
202 23.75 ± 0.51 , Cq-telomere = 8.86 ± 0.44 , Efficiency-GAPDH = 1.95 ± 0.02 , Efficiency-
203 telomere = 2.07 ± 0.05). Samples were excluded if duplicates Cq values differed by
204 more than > 0.5 (Eastwood et al. 2018), though no samples required exclusion using
205 this criterion. Relative telomere lengths were calculated following equation one in Pfaffl
206 (2001) and values from the sample replicates were then averaged. Technical
207 repeatability and 95% confidence intervals (CIs) were calculated using the rptR package

within R Statistical Software (Stoffel et al. 2017). Duplicate measurements of relative telomere length values were used to estimate technical repeatability and samples measured on more than one plate were used to estimate inter-plate repeatability (Kärkkäinen et al. 2021). Technical repeatability was estimated to be 0.97 (95% CIs [0.955, 0.973], $p < 0.001$) and inter-plate repeatability was estimated to be 0.85 (95% CIs [0.82, 0.88], $p < 0.001$).

Statistical analysis

Statistical analyses were conducted using R Statistical Software (R Core Team 2022 v. 4.2.2). All telomere data were analyzed using linear mixed-effects models (LMM). All LMM's were fit using the package "lme4" (Bates 2010, Bates et al. 2014). We tested the fixed effects in the LMMs using the lmerTest (Kuznetsova et al. 2017) package, which estimates degrees of freedom (df) with the Satterthwaite approximation. Backward stepwise variable selection was performed such that only fixed effects or interactions between variables with a p-value of 0.2 or lower were included in the final model (Wang et al. 2007) except for the variables of interest derived from our hypotheses, which were always retained. All final models were examined using the *check_model()* function within the "performance" package to check the assumptions of LMMs (Lüdtke et al. 2021). In all models, relative telomere length (rTL) was the response variable and qPCR plate number was included as a random effect to control for variance among plates. All models also included year as a random effect to control for non-independence of rTLs collected within years.

The effects of age on rTL were analyzed using a model with habitat type and age (adult/nestling) as categorical fixed effects with an interaction indicated. In this model, the unique nest ID was included as a random effect to control for non-independence among nestlings from the same nest. As the interaction between habitat type and age was not significant ($p\text{-value} = > 0.2$) in this model, the interaction was not included in the final model.

The effect of habitat type on adult rTL was examined using an initial model that included habitat type and genetic sex as categorical fixed effects with an interaction indicated. In this model, the interaction between habitat type and sex was > 0.2 and the interaction was dropped from the final model.

Two separate models were used to examine the effects of urbanization and brood parasitism on nesting rTL, using subsets of the data, to isolate the effects of each factor on nestling rTL. To examine the effect of habitat type on nestling rTL, only data from nests that hadn't been parasitized by brown-headed cowbirds were included in a model with habitat type as a fixed effect. A model that included brood parasitism as a fixed effect was used to examine the effect of brood parasitism on nestling rTL using data from parasitized and non-parasitized, urban nests. Nests from rural sites, which experience very low levels of brood parasitism, were excluded. The two nestling models included nest ID as a random effect and the initial models also included brood size and nestling age as fixed-effects covariates to control for potentially influential sources of variation in rTL. In the model examining the relationship between habitat type and nestling rTL, habitat type, nestling age, and brood size were all included as fixed effects in the final model. In the final model examining the effect of brood parasitism on nestling

rTL, only brood parasitism was retained as a fixed effect. See supplemental materials for a full summary of models and results.

Results

There was no difference in rTL between adult urban and rural song sparrows of either sex (Habitat: $\beta_{\text{Urban}} = 0.01 \pm 0.03$, $t_{116.33}=0.42$, $p = 0.67$; Sex: $\beta_{\text{Male}} = 0.0004 \pm 0.03$, $t_{116.33}=0.01$, $p = 0.67$; Figure 1). However, there was a significant difference between adult and nestling rTL across both habitat types, with nestlings having longer rTLs compared to adults (Age: $\beta_{\text{Nestling}} = 0.09 \pm 0.03$, $t_{168.21}= 2.78$, $p = 0.006$; Figure 2).

We failed to detect a significant difference between urban and rural nestling rTL (Habitat: $\beta_{\text{Urban}} = 0.11 \pm 0.06$, $t_{18.89}=1.71$, $p = 0.10$; Figure 3). However, older nestlings had significantly longer rTLs (Nestling age: $\beta = 0.05 \pm 0.02$, $t_{29.92}= 2.50$, $p = 0.02$) and rTL was positively associated with brood size (though only in this model; Brood size: $\beta = 0.07 \pm 0.03$, $t_{24.76}= 2.08$, $p = 0.048$). Finally, among urban nestlings, brood parasitism had a significant, negative effect on rTLs, with nestlings from parasitized nests having shorter telomeres compared to those from non-parasitized nests on average (Brood parasitism: $\beta_{\text{Parasitized}} = -0.14 \pm 0.06$, $t_{28.06}= -2.25$, $p = 0.03$; Figure 4).

Discussion

Although urban habitats are often presumed to present challenges for birds, here we found no evidence for an association between urbanization and rTLs - an indicator of somatic state - in adults or in nestlings when we controlled for brood parasitism. Among adult song sparrows, rTLs did not differ between rural and urban habitats (Fig.

1). Further, even during early development when animals are expected to be particularly vulnerable to adverse conditions (Nowicki et al. 2002, Monaghan 2008, Chaby 2016), nestlings from non-parasitized nests in urban habitats had similar rTLs to their non-parasitized rural counterparts (Fig. 3). However, urban habitats may impact nestling rTLs indirectly as we found that among urban nestlings, those from parasitized nests had shorter rTLs compared to those from non-parasitized nests (Fig. 4). This could reflect an indirect effect of urban living in several species because brood parasitism can be more prevalent in urban habitats for many host species (Burhans and Thompson 2006, Tewksbury et al. 2006, Rodewald 2009, Padilla and Sutherland 2022, Lane et al. 2023). Among adult birds, we found no sex differences in rTLs, which is consistent with previous studies (Barrett & Richardson 2011, Remot et al. 2020). We did find that rTLs varied with age in two ways. First, nestlings had longer telomeres compared to adults, a pattern common, though not ubiquitous, among birds and many other vertebrates (Tricola et al. 2018, Remot et al. 2022). Second, rTLs increased with nestling age among birds 5-11 days post-hatch. A lengthening of telomeres early in life, before a later decline, has been reported in other vertebrates (Ujvari & Madsen 2009, Anchelin et al 2011, Ujvari et al. 2017), though this is not a common pattern (Remot et al. 2022). Viewed together, these results provide new evidence describing the extent to which the multi-faceted environmental changes associated with urbanization are associated with variation in telomere lengths in a songbird that persists in both urban and rural habitats.

Anthropogenic disturbances (e.g., chemical pollution and noise), many of which are associated with urbanization, generally show negative correlations with telomere lengths in a variety of species (Salmón and Burraco 2022). Yet, prior intraspecific

comparisons of telomeric traits in urban and non-urban bird populations report mixed results. In European blackbirds, both yearling and older birds from urban environments have shorter telomeres compared to forest-dwelling conspecifics (Ibáñez-Álamo et al. 2018). In contrast, studies on one population of great tits show that urban habitats are associated with shorter nestling telomeres and longer adult telomeres, a pattern mediated by the selective disappearance of fledglings with short telomeres (Salmón et al. 2016, Salmón et al. 2017). However, a study on another population of urban and rural nestling great tits found no differences in telomere lengths, despite phenotypic differences (Biard et al. 2017). Thus, among adults, urban habitats may be associated with shorter telomere lengths, longer telomere lengths, or no differences. Among younger birds, telomere lengths are either shorter or do not differ between urban and rural habitats. These differences in findings may not be surprising given that both the effects of urbanization and telomere dynamics often differ with species' life histories and can also vary geographically (Callaghan et al. 2019, Burraco et al. 2021, Salmón and Burraco 2022, Neate-Clegg et al. 2023). Future studies comparing urban and rural populations should therefore prioritize (1) working with replicate urban and rural sites across broader spatial scales to test for parallel differences in telomere lengths (e.g., Campbell-Staton et al. 2020) and (2) examining the contributions of interspecific life history variation.

Our finding that adult urban and rural birds did not differ in rTLs is consistent with prior studies on song sparrows showing that adult birds in urban and rural areas have similar body condition and physiological and cellular markers of health (Fokidis et al. 2009, Bókony et al. 2012, Ibáñez-Álamo et al. 2012, Ibáñez-Álamo et al. 2020,

Goodchild et al., 2022). Collectively, these studies suggest that adult birds at our urban study sites are not negatively impacted by urban environmental conditions. It is important to recognize that our urban sites reflect habitat typical of suburban areas, not highly urbanized city centers, which could present more substantial challenges to birds. Nonetheless, previous studies on urban animals have shown that despite the presence of stimuli shown to be stressors (e.g., artificial light at night, ambient noise), urban habitats can also present benefits such as improved access to food and water, respite from nest predation (Fischer et al., 2012, Seress and Liker, 2015), and maintained green space for foraging and breeding territories (McKinney 2002, McKinney 2008, Chamberlain et al. 2009, Reynolds et al. 2019). Our study provides further evidence that for some species, the benefits of some urban habitats may outweigh the potential costs.

Although we did not find any differences between urban and rural nestling rTLs, we did find that nestlings from parasitized nests within urban habitats had shorter rTLs compared to those from non-parasitized nests. Our results are consistent with prior studies demonstrating the negative effects of brood parasites on host nestling condition, physiology, and survival (Lorenzana and Sealy 1999, Hoover 2003, Scharf et al. 2021), including in this study system (Lane et al. 2023), though in some cases such negative effects are not observed (Vernasco et al. 2018, Jones et al. 2023). The observed relationship between brood parasitism and telomere lengths we report here could arise because of direct impacts of brood parasites on the growth and physiology of host young. Alternatively, this relationship could arise indirectly if parental telomere lengths are heritable, as has been shown in other vertebrates (Chik et al 2022) and are

associated with vulnerability to brood parasitism such that parents with shorter telomeres are more likely to be parasitized. Further work will be necessary to distinguish between these potential underlying causes. By demonstrating an association between brood parasitism and telomere lengths, our results suggest a previously unrecognized correlation between brood parasitism and a measure of somatic state. Disentangling the causal nature of this relationship, whether it persists into adulthood, and whether it impacts fitness will require further study. Whereas many studies have highlighted how urbanization can impact animals through the direct effects of abiotic factors in the urban environment, this study also highlights the potential for the effects of urbanization to occur through indirect processes such as shifts in community dynamics.

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