Comparative Urban Evolution in Two Closely Related Desert Songbirds, Northern Cardinals and Pyrrhuloxia

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**Abstract**

Urbanization has reshaped ecosystems globally and has created new selective regimes to which wild animals must adapt if they are to persist in the new urban ecosystem. Urbanization presents a variety of additional novel challenges (e.g. artificial light at night, noise pollution, novel resource distributions, etc.) that may differently affect native taxa. Selection by urbanization on genes involved in behavior, cognition, and immune function has been demonstrated in several avian species. Studies of closely related sympatric species may shed new light on how organisms experience genetic change in urban settings. Here we analyzed whole genome sequences of northern cardinals (*Cardinalis cardinalis*) and pyrrhuloxia (*C. sinuatus*) from urban and rural areas of Arizona, USA to test for the presence of urban-related parallel evolution and introgression. We identified genes involved in neural function, muscle development, and immune function across both species that appear to have undergone urban selection. We demonstrate evidence of parallel urban selection on the same genes in both cardinal species and between our focal species and avian taxa in the literature. Our findings emphasize the novel dynamics of behavior, energetics, and immune challenges faced by native species in a rapidly urbanizing world.

**Introduction**

Urbanization can reshape natural selective environments and create novel challenges for wild species. Genetic variation underlying phenotypic changes associated with urbanization has been documented in several animal species, including genes that affect boldness behavior (van Dongen et al. 2015, Mueller et al. 2013), cognitive ability (Mueller et al. 2020), and immune function (Minias 2023, Pikus et al. 2021).

The effects of urbanization can be consistent within a species across different urban environments (e.g., Mueller et al. 2013, Winchell et al. 2023). For example, great tits (*Parus major*) display parallel evolution in neural and developmental genes in urban environments across the European continent (Salmón et al. 2021). Likewise, burrowing owls (*Athene cunicularia*) also show parallel evolution in genes related to cognition across many South American cities (Mueller et al. 2020). Yet despite these lines of evidence for parallelism in urban evolutionary responses, recent epigenetic research has found differences in even the fine-scale mechanisms that underlie species responses to urbanization (Caizergues et al. 2022, McNew et al. 2017). Whether selection resulting from urbanization acts on the same genes in closely related species remains an under-explored area of research.

Species that share a similar genetic background and a similar ecological niche yet differ in their persistence in an urban environment present a unique opportunity to identify potential genetic mechanisms underlying species responses to urbanization. Northern cardinals (*Cardinalis cardinalis*) and pyrrhuloxia (*Cardinalis sinuatus*) both occupy the metropolitan area of Tucson, Arizona and largely share an ecological niche, but northern cardinals occupy more highly urbanized areas than pyrrhuloxia (Jackson and McGraw unpublished data). Although northern cardinals and pyrrhuloxia are 5.1 million years divergent (CI: 4.2 - 6.0 MY; Barker et al. 2015, Hooper and Price 2017, Kumar et al. 2017), they also infrequently hybridize (Griffiths 2022), although no wild hybrids have ever been genetically confirmed, and genomic data from rural birds demonstrate no evidence of introgression (Kaiya Provost pers. comm.). Slight differences arising from the largely similar genetic backgrounds of these two species may therefore underlie the differences in urban persistence, and a comparison of the two may illuminate mechanisms associated with urban adaptation.

We analyzed whole genomes of urban and rural northern cardinals and pyrrhuloxia to identify regions that may have undergone positive selection in the urban environment. We then tested for overrepresented Gene Ontology terms and for evidence of parallel selection across taxa at the gene level. We predicted that pyrrhuloxia would show a fainter signal of selection, but that some similar genes would be under selection in both species.

**Methods**

Tissue collection, DNA sequencing, and SNP filtering:

Between 2021-2022, we collected blood samples from a total of 12 birds at residences around Tucson, Arizona spanning approximately 22 miles of the city: 6 northern cardinals and 6 pyrrhuloxia (Table 1, Figure 1). *Cardinalis* species in rural areas were difficult if not impossible to capture in part due to fieldwork limitations during the COVID-19 pandemic, so we also accessed muscle tissue samples from 12 birds (6 northern cardinals and 6 pyrrhuloxia) from the University of Washington Burke Museum and the Museum of Southwestern Biology. This produced a sample size of 6 per species per population (urban vs. rural), which is sufficient for identifying outlier regions between populations (Hahn 2019). We extracted DNA from each sample at the University of Colorado using a Qiagen DNeasy Blood & Tissue kit, and we measured DNA concentrations on a Thermofisher Qubit 3.0. Whole genome paired-end 150 base pair sequencing libraries were prepared and sequenced using the Illumina NovaSeq 6000 platform by Novogene, Sacramento, CA at approximately 5x coverage.

We trimmed raw sequence fasta files using Trimmomatic (Bolger et al. 2014) and analyzed for quality using FastQC (Andrews 2010). We used bwa mem (Li 2013) to align the trimmed sequence reads to the reference small tree finch (Camarhynchus parvulus) genome STF-HiC (1.28 GB; Genbank accession number: GCF\_901933205.1). Then we sorted the bam files using samtools (Li et al. 2009) and picard-tools (“Picard Toolkit” 2019, clipped overlapping read pairs using bam-utils (CITE), realigned around indels using GATK (3.7, CITE) and indexed the resulting using samtools and picard-tools. We used angsd to generate a list of varying sites with a minimum SNP p-value of 1e-6, minimum individual depth of 4, minimum of 20 individuals, minimum minor allele frequency of 0.05, and minimum mapping quality of 30 (review with angsd manual and A6\_snpID script). This left 2,618,696 SNPs. We additionally tested for and did not find evidence of batch effects between museum and field collected samples (Lou et al. ). After filtering, we had an average depth of coverage of 5.08 across all samples.

Population Structure Analyses

We analyzed relationships between our samples using Principal Component Analyses (PCA) and ADMIXTURE. We first used angsd to generate a bcf file which we input into plink to filter for unlinked SNPs (--indep-pairwise 50kb 1 0.5). We used pcangsd to output a covariance matrix from which we computed eigenvectors that we visualized in R and to output an ADMIXTURE plot. These revealed that two of our rural pyrrhuloxia samples may be close relatives, so we removed the individual with lower depth of coverage from all downstream analyses. We show results from the population structure analyses without that individual.

Tests for positive selection and introgression

To identify regions of the genome that have either recently undergone positive selection due to urbanization or that are associated with urban versus rural areas, we used two statistical approaches. First, we employed FST scans to compare urban populations with rural populations of the same species using 50 kb windows with a step size of 25 kb. Then, we employed RAiSD to compute μ statistics across genomes from the urban population and separately across genomes from the rural population. We considered regions that were significant within urban but not within rural populations of the same species to be regions of relevance to selection within an urban environment. RAiSD determines window sizes by number of informative sites rather than total base pair numbers, so we use windows containing 50 SNPs. For both analyses, we considered any region in the top 1% of statistics (either FST or μ) to be of interest.

To identify general selective trends, we output a list of all genes in regions of interest and tested for significant overrepresentation of Gene Ontology (GO) terms using the PANTHER classification system. We compared the lists of genes of interest to a filtered list of all genes in the reference genome. To curate our list of background genes, we filtered out any site with low mappability (< 0.95 SNP calling rate in snpable) and with less than 3x average depth across our samples or greater than 2 standard deviations above the mean depth of the sample (28.15). We also excluded any significant genes that may have been identified in these regions, to reduce errors from poor alignment. Genes excluded from the background gene list were also removed from any ultimate lists of candidate genes, as we inferred that they were in regions prone to error. We corrected for multiple testing by using a false discovery rate using the Benjamini-Hochberg FDR test with a significance level of *q* < 0.2 (CITE). Because FST and RaiSD are sensitive to different evolutionary processes, we tested for overrepresented GO terms for each species in a combined list of genes identified by both programs as well as independent lists from each statistic.

Finally, to test for significant parallel evolution in response to urbanization across avian taxa, we compared our lists of candidate genes with lists curated in two major investigations of avian urban genomic responses. One of these studies investigated urban adaptation of burrowing owls (*Athene cunicularia*) across multiple cities in Argentina and the other investigated urban adaptation of great tits (*Parus major*) across multiple European cities (Mueller et al. 2020, Salmón et al. 2021). We first tested for significant overlap between taxa and then highlight genes that show signatures of selection across multiple taxa.

**Results**

Population Structure Analyses (PCA, admixture)

All individuals first separated out species along PC1 (28.84% variation). PC2 (3.78% variation) separated northern cardinals by ecotype, with clusters associated with the Sonoran basin, montane conifer forests, and the Madrean archipelago, while pyrrhuloxia did not segregate distinctly by ecotype; neither species clustered by urbanization category (Figure 1). The ADMIXTURE analysis recovered no clusters below the species level but showed more variation within northern cardinals that suggests a genomic cline from the Madrean archipelago to the montane conifer forests to the Sonoran basin.

Overrepresented GO Terms

In northern cardinals, GO terms related to blood physiology (e.g. GO:0070527 platelet aggregation, *q* = 0.016), tissue integrity (e.g. GO:0098609 cell-cell adhesion, *q* = 0.022), muscle development (e.g. GO:0007519 skeletal muscle tissue development, *q* = 0.058), and response to external stimuli (GO: 0032102 negative regulation of response to external stimulus, *q* = 0.022) emerged as overrepresented categories in analyses of genes identified by the combination of FST and RAiSD (Figure 3). Two genes drove the signal associated with blood physiology, FGA (fibrinogen alpha chain) and FGB (fibrinogen beta chain), both of which are located in an ~15kb long segment of chromosome 4. Analyses of genes identified in just FST or RAiSD revealed similar patterns, with the addition of two GO terms that were overrepresented in the genes identified by FST (GO:1901564 organonitrogen compound metabolic process, *q* = 0.124) and in RAiSD (GO:0050878, regulation of body fluid levels, *q* = 0.013).

In pyrrhuloxia, no genes passed the FDR threshold from the combined list of FST and RAiSD outliers. In FST outliers, organic cyclic compound metabolic processes, nervous system development, tissue regeneration, and insulin-like growth factor receptor signaling pathway each emerged. Tissue regeneration was overrepresented in the outliers identified by RAiSD. Two GO terms – GO:0031099 regeneration and GO:0042246 tissue regeneration – were identified as overrepresented in both FST and RAiSD gene lists. Two candidate genes are involved in the insulin-like growth factor (IGF) receptor signaling pathway, GIGYF2 (GRB10 Interacting GYF Protein) and IGF1 (Insulin Like Growth Factor 1). We identified 15 candidate genes associated with nervous system development.

Parallel Evolution

Pairwise comparisons of species found significant evidence of overlapping genes in five of the six pairs (northern cardinals and pyrrhuloxia q=1.32x10-15, northern cardinals and burrowing owls p= 2.81x10-05, northern cardinals and great tits q=0.012, pyrrhuloxia and burrowing owls q=0.008, burrowing owls and great tits p=0.012; FDR corrected Fisher’s exact test), with only pyrrhuloxia and great tits not demonstrating significant overlap (q=0.601).

Between cardinal species, 132 genes were identified by at least one analysis in both species but no GO terms were overrepresented in the list of overlapping genes. The three genes identified by both programs in both species are CDKAL1 (CDK5 Regulatory Subunit Associated Protein 1 Like 1), COL15A1 (Collagen Type XV Alpha 1 Chain), and TGFBR1 (Transforming Growth Factor Beta Receptor 1), which are all present within the same 3.4 Mb block of chromosome 2 and which shows distinct evidence of a selective sweep in urban pyrrhuloxia (Figure 5).

No genes were identified as a candidate gene associated with urbanization in all four species, but one was identified in three of the four species (NRXN3; found in northern cardinals, burrowing owls, and great tits). 45 genes were identified in one of the two cardinal species and in one additional non-cardinal taxa. In this list of 45 genes, GO terms associated with muscle development (e.g. GO:0090257 regulation of muscle system process *q* = 0.041) and neuronal processes (e.g. GO:0007399 nervous system development, *q* < 0.001) were overrepresented.

**Discussion**

We demonstrate a polygenic response to urbanization by two cardinal species with important differences that may underlie the increase in urban occupation by northern cardinals compared to pyrrhuloxia. The urban environment appears to have selected for changes to the blood physiology, muscle development, and neural development of both species. Pyrrhuloxia displayed less evidence of a selective response to urbanization, with no significant GO-terms emerging from analyses of the combined list of genes identified across both FST and RAiSD. Northern cardinals are larger than pyrrhuloxia and therefore may have had a more favorable pre-existing muscular physiology that has allowed them to better adapt to the urban environment. The behavioral and hematological differences between these species are understudied but our results suggest that traits in these realms may predict a species’ ability to persist in developed areas, particularly in ecologies similar to the Sonoran Desert.

GO terms illustrate potential functions that selection acted upon for our candidate genes, but these are not always definitive. For example, the two genes that drove the signal associated with blood physiology in northern cardinals, FGA (fibrinogen alpha chain) and FGB (fibrinogen beta chain) influence both clotting and immune system responses. FGA is associated with immunosuppressive activities and has been shown to be downregulated in chickens resistant to Marek’s disease virus (Dong et al. 2017), and both are shown to be downregulated in response to *Riemerella anatipestifer* infection in ducks (Zhou et al. 2017). Clotting may be essential for adaptation to an urban environment, where species may interact with or even consume novel sharp objects including plastics, may be more at risk of harm from an introduced predator like a house cat (*Felis catus*), or may experience intraspecific conflicts at higher rates or with greater intensity over more concentrated resources. The signals of selection on genes involved in tissue regeneration in Pyrrhuloxia support this interpretation. Additionally, changes to blood physiology may improve the species’ responses to extended periods of dehydration. Two additionally identified GO terms support this interpretation: organonitrogen compound metabolic process and regulation of body fluid levels both suggest an adaptation to deal with low-water availability. Alternatively, avian diseases can spread more rapidly through bird feeders or interactions with poultry and released avian pets, and selection may instead act on these genes due to their immune functions. These are not mutually exclusive interpretations, as the same genotype may improve clotting, fluid retention, and immune function.

However, the evidence for selection on muscle function in northern cardinals is more straightforward. Four genes identified in northern cardinals were involved in muscle development. DMD (Dystrophin) and SGCZ (Sarcoglycan Zeta) both produce parts of the dystrophin-associated glycoprotein complex (DGC), which is a fundamental structural protein in skeletal and cardiac muscle cells and regulates insulin receptor activity in these cells with major effects on muscle development (Eid Mutlak et al. 2020). MYF5 and MYF6 (Myogenic Factor 5 and 6), essential factors in muscle tissue development, were also outlier genes. 33 additional genes were identified in various aspects of tissue integrity: cell-adhesion, junction, morphogenesis, and signaling (Supplementary Table 1). Pyrrhuloxia too showed some evidence of selection on muscle development, particularly with respect to the insulin-like growth factor (IGF) receptor signaling pathway. IGF receptors are associated with muscle development in response to acute exercise or in preparation for migration (Price et al. 2011), rapid nestling growth (Lodjak et al. 2017), more rapid moult (Lendvai et al. 2022), ovarian function (Onagbesan et al. 1999), and increased oxidative stress (Lendvai et al. 2024). IGF receptors also play a role in diabetes and this signal could emerge due to increased carbohydrates in the diets of urban birds.

Not only did we see independent evidence of selection on muscle development, but our candidate genes also overlapped with findings from burrowing owls and great tits with overrepresentation of both muscle development and neural genes. Several of these genes of note – SDK1 and PRKN for example – were not associated with any overrepresented GO terms related to neural function in our analyses of either cardinal species. This function only emerged in GO term analyses of overlapping genes identified in cardinals and either burrowing owls or great tits. This highlights the utility of comparative studies across multiple organisms for uncovering patterns in genomic data.

Three genes were identified by both RAiSD and FST in both northern cardinals and pyrrhuloxia: CDKAL1, COL15A1, and TGFBR1. These three genes are associated with muscle development in different ways. CDKAL1 is associated with obesity in multiple studies (Fall and Ingelsson 2014) and type 2 diabetes (Ragvin et al. 2010) and is overexpressed in skeletal muscle tissues in women with polycystic ovarian syndrome (Manti et al. 2020), with variants leading to misfolded insulin (Ghosh et al. 2022). COL15A1 is associated with chicken pectoral muscle disorders (Bordini et al. 2022). TGFBR1 expression is associated with corticosterone exposure in tree swallows (Tachycineta bicolor) and with cardovascular disease (Yagyu et al. 2023), asthma (Stikker et al. 2023), and various cancers in humans (Ramer et al. 2016). These diverse pathologies likely arise from TGFBR1 because it mediates inflammation and endothelial cell response to tissue injury (He et al. 2022).

Our analyses uncovered evidence of both divergent selective responses and some parallel selection between northern cardinals and pyrrhuloxia in response to urbanization. Importantly, the genes that we identified are largely associated with muscle development and neural function, both of which have emerged from studies of other avian taxa as core processes that are selected upon by urban environments. We highlight immune functions as an additional axis of important urban adaptation. Despite showing different levels of persistence in an urban environment, both cardinal taxa demonstrate selective responses on similar functional categories, although pyrrhuloxia showed a less consistent signal of selection. Comparative morphological, behavioral, and physiological studies of these taxa informed by our findings could elucidate the phenotypic effects emerging from these genetic differences. This work contributes to the growing body of literature showing the parallel responses of avian taxa to urbanization, and novelly contributes evidence of species-specific genetic nuance in evolution to human disturbance.

**Tables and Figures**

**Figure 1:** A. Sampling locations across the state of Arizona, with northern cardinals in red and pyrrhuloxia in purple. B. PCA of all genomes retained after filtering for potential close relatives (Northern cardinals: urban N=6, rural N=6; Pyrrhuloxia: urban N=6; rural N=5). C. Admixture plot ordered by species and then by ecoregion.

A map of a desert with a map of land and a map of land

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**Figure 2:** PCoA dissimilarity plots of semantic similarity for FDR-corrected overrepresented GO terms in northern cardinals for A. the full list of candidate genes identified by either FST or RAiSD analyses, B. only genes identified by FST, and C. only genes identified by RAiSD.

A diagram of a cell organ

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**Figure 3:** PCoA dissimilarity plots of semantic similarity for FDR-corrected overrepresented GO terms in pyrrhuloxia for A. genes identified by FST and B. genes identified by RAiSD. Analyses of the full list of candidate genes identified by either FST or RAiSD analyses revealed no significantly overrepresented GO terms.

A diagram of a diagram

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**Figure 4.** Evidence of parallel evolution across cardinals. A. Venn diagrams of genes identified in either cardinal species by FST or RAiSD analyses

**A diagram of different types of numbers

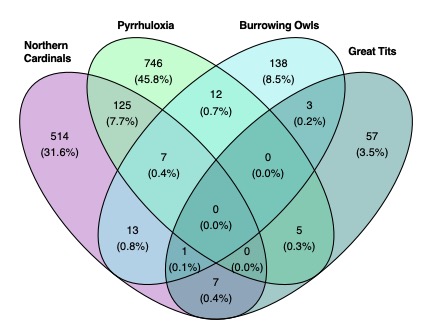
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**Figure 5.** Evidence of parallel evolution across cardinals and other avian taxa. B. Venn diagrams of genes identified in northern cardinals, pyrrhuloxia, burrowing owls, and great tits, and C. PCoA dissimilarity plots of semantic similarity for FDR-corrected overrepresented GO terms of the list of genes found to be present in one of either cardinal species and at least one of the other two species (burrowing owls or great tits). ****

**Tables**

Table 1: Sample Information.

|  |  |  |  |
| --- | --- | --- | --- |
| **Sample** | **Species** | **Population** | **Source** |
| NOCA\_003 | Northern cardinal | Urban | Field |
| NOCA\_004 | Northern cardinal | Urban | Field |
| NOCA\_006 | Northern cardinal | Urban | Field |
| NOCA\_008 | Northern cardinal | Urban | Field |
| NOCA\_012 | Northern cardinal | Urban | Field |
| NOCA\_013 | Northern cardinal | Urban | Field |
| PYRR\_003 | Pyrrhuloxia | Urban | Field |
| PYRR\_004 | Pyrrhuloxia | Urban | Field |
| PYRR\_006 | Pyrrhuloxia | Urban | Field |
| PYRR\_007 | Pyrrhuloxia | Urban | Field |
| PYRR\_009 | Pyrrhuloxia | Urban | Field |
| PYRR\_012 | Pyrrhuloxia | Urban | Field |
| UWBM\_100619 | Northern cardinal | Rural | University of Washington Burke Museum |
| UWBM\_100620 | Northern cardinal | Rural | University of Washington Burke Museum |
| UWBM\_100621 | Northern cardinal | Rural | University of Washington Burke Museum |
| UWBM\_103345 | Northern cardinal | Rural | University of Washington Burke Museum |
| UWBM\_103346 | Pyrrhuloxia | Rural | University of Washington Burke Museum |
| UWBM\_77548 | Pyrrhuloxia | Rural | University of Washington Burke Museum |
| UWBM\_77718 | Pyrrhuloxia | Rural | University of Washington Burke Museum |
| UWBM\_77780 | Pyrrhuloxia | Rural | University of Washington Burke Museum |
| UWBM\_77781 | Pyrrhuloxia | Rural | University of Washington Burke Museum |
| UWBM\_77856 | Northern cardinal | Rural | University of Washington Burke Museum |
| UWBM\_77978 | Northern cardinal | Rural | University of Washington Burke Museum |
| MSB\_25201 | Pyrrhuloxia | Rural | Museum of Southwestern Biology |

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APPENDIX D

chapter 4 Supplementary Tables and Figures

We demonstrate evidence of selection on 9 genes in two closely related songbird species. The functions of these genes include vision, lung function, muscle development, brain function, cancer, and RNA processing. Two of these genes demonstrate patterns consistent with parallel selection and affect sperm and lung efficacy and cognitive function. Four demonstrate patterns consistent with introgression from the urban population of northern cardinals into the urban population of pyrrhuloxia, two of which function in the visual system and two of which relate to muscle development. Our findings demonstrate that anthropogenic environmental change alters patterns of selection on congeneric species in similar ways and can even disrupt species boundaries and facilitate introgression.

Of the four genes that demonstrated evidence of introgression from northern cardinals into pyrrhuloxia, two are directly involved in the development of the visual system. Mutations in CH037 in humans are associated with cone-rod dystrophy and retinitis pigmentosa (Fahim et al. 2023), and RHO encodes the rhodopsin protein, which is the light-sensitive receptor protein in rod cells in the retina (Nathans 1992). CH037 was also highly differentiated between urban and rural northern cardinal populations, suggesting that this gene also experienced positive selection in the urban northern cardinal population. Several lines of evidence suggest that human activities affect the evolution of sensory systems in many fish species because eutrophication and turbidity can alter the light environment of aquatic environments. While urban environments present many novel visual challenges for species (Diamond et al. 2022), to the best of our knowledge we present the first evidence for selection on the visual system of a terrestrial vertebrate as a result of urbanization (Kelley et al. 2018, but see Bloch 2015, which presents habitat-based selection on opsin genes in a non-urban context).

The other two genes that demonstrated evidence of introgression, FXR1 and COL6A1, both affect muscle development (Mientjes et al. 2004, Pan et al. 2003). Our previous work has shown that phenotypes in urban environments are associated with increased flight maneuverability compared to rural conspecifics (Chapter 3), highlighting the importance of flight function for urban survival. A similar selective pressure could be affecting muscle development in these species. FXR1 is also involved in brain development in humans because it is associated with fragile X syndrome (Siomi et al. 1995). Sex chromosomes in birds follow a ZW configuration, and it is unknown if this gene is also associated with effects in the avian brain.

HYDIN and DLG2 are the only two genes that experienced positive selection in urban populations of both species but do not show evidence of introgression. HYDIN plays a role in both sperm function and lung function, as it affects the development of cilia and flagella (Olbrich et al. 2012). REXO1 AND CTNNA3, which were identified as genes that underwent positive selection in northern cardinals but not pyrrhuloxia, are also involved in lung function (Herrera-Luis et al. 2022, Ong et al. 2013). Urban environments could create a novel selective pressure on lung function either due to higher levels of air pollution, which has affected lung physiology in other urban species (Isaksson et al. 2009, Torres-Blas et al. 2023). Or these genes could be responding to selection for increased energetics, the latter of which aligns with our previous findings on morphologies in the city. CTNNA3 is also associated with cardiomyopathy in humans (Janssens et al. 2003), as is DCBLD2 (Alhamoudi et al. 2021) and these genes could be affected by selection for improved flight performance through their role in heart function. DLG2 is involved in brain function and also shows evidence of positive selection in urban burrowing owls (Mueller et al. 2020).

Our finding that urbanization is associated with selection on visual genes in these two species was surprising and intriguing. Because RHO specifically affects vision in dim-light environments, it suggests that nocturnal or crepuscular selection pressures (e.g. predator detection) or opportunities (e.g. foraging, singing, extra-pair mating; Kempenaers et al. 2010) may especially impact urban success of these species. Urbanization affects circadian rhythms of songbirds (Dominoni et a. 2013), and, at least in an Ohio population, urban northern cardinals fledge earlier in the day than their rural counterparts (Jones et al. 2023). Research in mammals suggests a shift toward nocturnalism among several carnivorous species in urban areas (Rtizel and Gallo 2020), which may impact nighttime selection pressures on the visual systems of prey species like songbirds. Alternatively, photoreceptors affect circadian rhythms (Prabhat et al. 2020, Senthilan et al. 2019), and this could instead represent selection allowing for the adaptation of the circadian rhythms of cardinals in the city. Some populations of great tits (*Parus major*) show selection on light-sensitive genes (Caizergues et al. 2022), but studies of several other passerine species in urban environments found no evidence of selection on visual genes (Mueller et al. 2013, Mueller et al. 2020, Salmón et al. 2021, Winchell et al. 2023). Why northern cardinals and pyrrhuloxia might experience unique selection on their visual systems in the urban environment requires further investigation. Future research into the urban behavior of passerines, and into the genotypic variation of *Cardinalis* species across other cities, will provide important context for the effects of urbanization on native wildlife.