

## CHAPTER 4

# URBAN-RELATED INTROGRESSION AND PARALLEL EVOLUTION IN TWO CLOSELY RELATED DESERT SONGBIRDS

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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. Urban selection on genes involved in behavior, cognition, and immune function has been demonstrated in several avian species, but urbanization presents a variety of additional novel challenges (e.g. artificial light at night, noise pollution, novel resource distributions, etc.) that may differently shape gene flow and architecture. 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 9 genes that appear to have undergone urban selection. 2 of the genes experienced parallel selection, and 4 show evidence of introgression from urban northern cardinals into urban pyrrhuloxia. Our findings emphasize the role of introgression in

evolutionary responses to rapid environmental change, and identify light at night, energetic challenges, and pollution as driving stressors for urban adaptation.

## **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). Although the effects of urbanization can be consistent within a species across different urban environments (e.g., Mueller et al. 2013, Mueller et al. 2020, Salmón et al. 2021, Winchell et al. 2023), recent 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 unexplored area of research.

Urbanization can also disrupt species boundaries and facilitate gene flow (i.e., introgression) between species (Chafin et al. 2019, Grabenstein et al. 2022), either by increasing the rate of hybridization or by decreasing selection against hybrids (Grabenstein and Taylor 2018). If both species experience novel selection on the same traits in an urban environment, selection may act on one species while the other is unable to adapt, or both species might experience parallel selection on the same genomic regions (e.g. Winchell et al. 2023). If positive selection acts on an allele in only one species and hybridization occurs, selection has the potential to facilitate introgression (e.g., Jones et al. 2018).

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 (Chapter 2). Both species demonstrate phenotypic responses to urbanization for traits involved in color signaling, heat tolerance, food handling, and flight maneuverability (Chapter 3). 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. Two captive birds produced a viable hybrid offspring at the Sonoran Desert Museum (Griffiths 2022), and several sightings of hybrid individuals on eBird contain compelling photographic evidence, although no wild hybrids have ever been genetically confirmed, and genomic data from rural birds demonstrate no evidence of introgression (Kaiya Provost pers. comm.).

We compared whole genomes of northern cardinals and pyrrhuloxia to identify regions that are highly differentiated between urban and rural populations of each species and that may have undergone positive selection in the urban environment. We compared candidate regions between the species and identified regions that either underwent positive selection in both species or that likely introgressed between the species in the urban environment. To test between parallel selection and introgression, we conducted phylogenetic analyses of these candidate regions. Finally, we identified the functions of each candidate gene and compared functions within and between species to propose putative mechanisms underlying species responses to urbanization.

## **Methods**

### **Tissue collection, DNA sequencing, and SNP filtering:**

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 S1). *Cardinalis* species in rural areas were difficult if not impossible to capture without destructive methods, 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 4X coverage.

We trimmed raw sequence fasta files using Trimmomatic (Bolger et al. 2014) and analyzed for quality using FastQC (Andrews 2010). We aligned the trimmed sequence reads to the reference northern cardinal genome generated by the Birds 10,000 Genomes (B10K) Project genome (Feng et al. 2020; Assembly ASM1339721v1, GenBank ID GCA\_013397215.1, 39,279 scaffolds, 72,526 contigs, N50 = 451.3 kb, L50= 559) using bwa mem (Li 2013). Then we sorted and indexed the resulting bam files using samtools (Li et al. 2009) and picard-tools (“Picard Toolkit” 2019), and called SNPs using BCFtools (Narasimhan et al. 2016). We filtered the resulting VCF using BCFtools to filter out SNPs with a quality of 100 or lower, and VCFtools to filter out SNPs with a read depth of less than 2. This left 52,334 SNPs with an average read depth of 8.83 per sample (minimum of 6.73, maximum of 17.63). Finally, we used Plink (Purcell 2007) to filter out SNPs with a genotype quality score of less than 0.25, a minor allele frequency

of less than 0.1, and to prune linked SNPs using a window size of 50kb, a step size of 5 SNPs, and an  $r^2$  threshold of 0.5. This left 32,437 SNPs, which we used in all analyses.

### Phylogenetic and Population Structure Analyses

We analyzed relationships between our samples using Randomized Accelerated Maximum Likelihood analyses (RAxML; Stamatakis 2014) and Principal Component Analyses (PCA). For RAxML, we converted the VCF to a Phylip file (Ortiz 2019) and ran RAxML under the GTRCAT model with 1000 random seeded bootstrap replicates using a Felsenstein ascertainment bias correction to account for the absence of non-variant sites. We visualized the tree in FigTree (Rambaut 2018) and we present the best tree with bootstrap support values. We conducted PCAs on the VCF in R using gdsfmt and SNPRelate (Zheng et al. 2012) on all samples and then separately on each species. We used the program STRUCTURE with 20,000 repetitions with clusters ( $K$ ) of 2-6. We used VCFtools (Danecek et al. 2011) to calculate  $F_{ST}$  values between the two species, between urban and rural populations of each species, between urban populations of the two species, and between rural populations of the two species.

### 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 six statistical approaches. First, we employed two approaches ( $F_{ST}$  scans and bayescan) that compare urban populations with rural populations of the same species. The other four approaches compute statistics within populations (i.e. on both urban and rural populations separately): nucleotide diversity  $\theta\pi$  (Korunes and Samuk 2021, Nei and Li 1979), Tajima's  $D$  (Korneliussen et al. 2013,

Tajima 1989), SweeD (Pavlidis et al. 2013), which detects recent selective sweeps based on allele frequencies, and OmegaPlus (Alachiotis et al. 2012), which detects recent selective sweeps based on linkage disequilibrium. 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. We explored 50 kb upstream and downstream of relevant regions to identify candidate genes, and we used snpEff to identify which of these genes have functional differences between individuals (Cingolani 2012).

We identified 9 genes (see below) within regions of interest that had functional mutations between urban and rural populations of one or both species. All of these were identified by either comparative analysis of urban and rural populations or by analysis of a single urban population. None of the analyses of rural populations resulted in the identification of any genes of interest with functional mutations. The remaining genes may have experienced positive selection on regulatory regions rather than on functional mutations. To test for the presence of parallel selection and introgression, we conservatively restricted our analyses to only the subset of genes that had evidence of functional mutations. We first filtered the VCF to contain only sites within each gene and then analyzed each gene using PCA and, when possible, RAxML. RAxML requires more stringent filtering for missing data, and it could only be performed on 5 genes.

## **Results**

### **Phylogenetic and Population Structure Analyses (RAxML, PCA, STRUCTURE)**

In the RAxML analysis, each species formed a clade, but urban birds did not form a monophyletic clade in either species (Figure S2). In the PCA, the analysis that included all individuals first separated out species along PC1 (23.03% variation) but did not uncover any

population structure along PC2 (4.05% variation; Figure S3). In the PCA of all northern cardinals, PC1 mostly separated urban samples from rural samples (9.91% variation) and PC2 spread rural samples but kept urban samples clustered together (9.45% variation). In the PCA of all pyrrhuloxia, PC1 separated urban birds from rural birds (23.03% variation) and PC2 mostly kept all urban and all rural birds clustered but spread one rural bird from the others. STRUCTURE recovered no clusters below the species level (Figures S3, S4).

We identified 162 fixed SNPs between the two species (genome-wide Weir and Cockerham weighted  $F_{ST} = 0.151$ ), 9 fixed SNPs between urban and rural northern cardinals (Weir and Cockerham weighted  $F_{ST}$  of 0.006), and 0 fixed sites between urban and rural pyrrhuloxia (Weir and Cockerham weighted  $F_{ST}$  of 0.004). We identified 501 fixed sites between the rural samples of the two species (genome-wide Weir and Cockerham weighted  $F_{ST} = 0.152$ ) and 347 fixed sites between the urban samples of the two species (genome-wide Weir and Cockerham weighted  $F_{ST} = 0.148$ ).

### Tests for Selection and Differentiation

We identified 34 genomic regions of interest, containing 31 total genes. Of these regions,  $F_{ST}$  scans identified 11, Tajima's D identified 15, nucleotide diversity identified 1, SweeD identified 3, and OmegaPlus identified 5. Two regions were identified by multiple programs: one by both nucleotide diversity and SweeD, and another by both SweeD and OmegaPlus. Only 3 regions were identified in both the urban northern cardinal population and the urban pyrrhuloxia population, containing 4 genes. snpEff found functional mutations in 3 of these genes (Table 2).

$F_{ST}$  analyses between urban and rural populations of northern cardinals found an additional 3 regions of interest. Of these, snpEff only identified functional mutations in 1 gene



(Table 2).  $F_{ST}$  analyses between urban and rural populations of pyrrhuloxia found an additional 8 regions of interest, which contained 8 genes. Of these, snpEff identified functional mutations in 3 genes (Table 2).

Tajima's D found 1 additional region of interest in urban northern cardinals which contained a single gene, and 9 additional regions of interest in rural northern cardinals which contained 9 genes. Of these, snpEff only identified functional mutations in the gene identified in the urban population (Table 2). Tajima's D also found 1 additional region of interest in urban pyrrhuloxia, which contained a single gene, and 4 additional regions of interest in rural pyrrhuloxia, which contained the genes 4 genes. Of these, snpEff again only identified functional mutations in the gene identified in the urban population (Table 2).

In total, we found 3 genes in both species with functional mutations that demonstrate evidence of either positive selection in an urban environment or differentiation between urban and rural populations: CH037, HYDIN, and DLG2 (Table 2). We found 4 genes in just pyrrhuloxia: COL6A1, DCBLD2, RHO, and FXR1. And we found 2 genes in just northern cardinals: REXO1 and CTNNA3. Both HYDIN and CH037 function in the development of cilia and flagella, but while CH037 affects retinal development (Fahim et al. 2023), HYDIN affects lung function and sperm motility (Olbrich et al. 2012). Like CH037, RHO also affects the visual system (Nathans 1992). Both DLG2 and FXR1 influence brain functions (Branch et al 2022, Siomi et al. 1995), although FXR1 also influences muscle function (Mientjes et al. 2004). COL6A1 also affects muscle development (Pan 2003), and both CTNNA3 and DCBLD2 affect the heart muscle (Alhamoudi et al. 2021, Janssens et al. 2003). Finally, REXO1 affects RNA processing and can affect lung function (Herrera-Luis et al. 2022).

Of the 9 genes of interest, 4 displayed trends associated with introgression from urban northern cardinals into urban pyrrhuloxia: CH037, RHO, FXR1, and COL6A1 (Figure 2) and 5 did not (Figure S5). All 4 introgressed genes were identified in  $F_{ST}$  scans between urban and rural pyrrhuloxia (Figure 1). The RAxML analyses of RHO and COL6A1 found a clade containing all urban and rural northern cardinal samples as well as urban pyrrhuloxia samples, and a second clade containing just rural pyrrhuloxia samples (Figure 2). The PCA of all CH037 and RHO clustered urban samples together and separated rural samples of both species, and the PCA of COL6A1 clustered all northern cardinals together with a nearby cluster of urban pyrrhuloxia and a distant cluster of rural pyrrhuloxia (Figure 2).

## **Discussion**

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 al. 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 (Ritzel 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.

## **Figures**

**Figure 1: Weighted Weir and Cockerham  $F_{ST}$  Values of SNPs Comparing Urban and Rural Samples Within Species.**

Plot A (top plot):  $F_{ST}$  Scan of Urban vs. Rural Northern Cardinals. Plot B (bottom plot):  $F_{ST}$  Scan of Urban vs. Rural Pyrrhuloxia. Genes within significant regions that snpEff identified as having functional mutations are annotated.

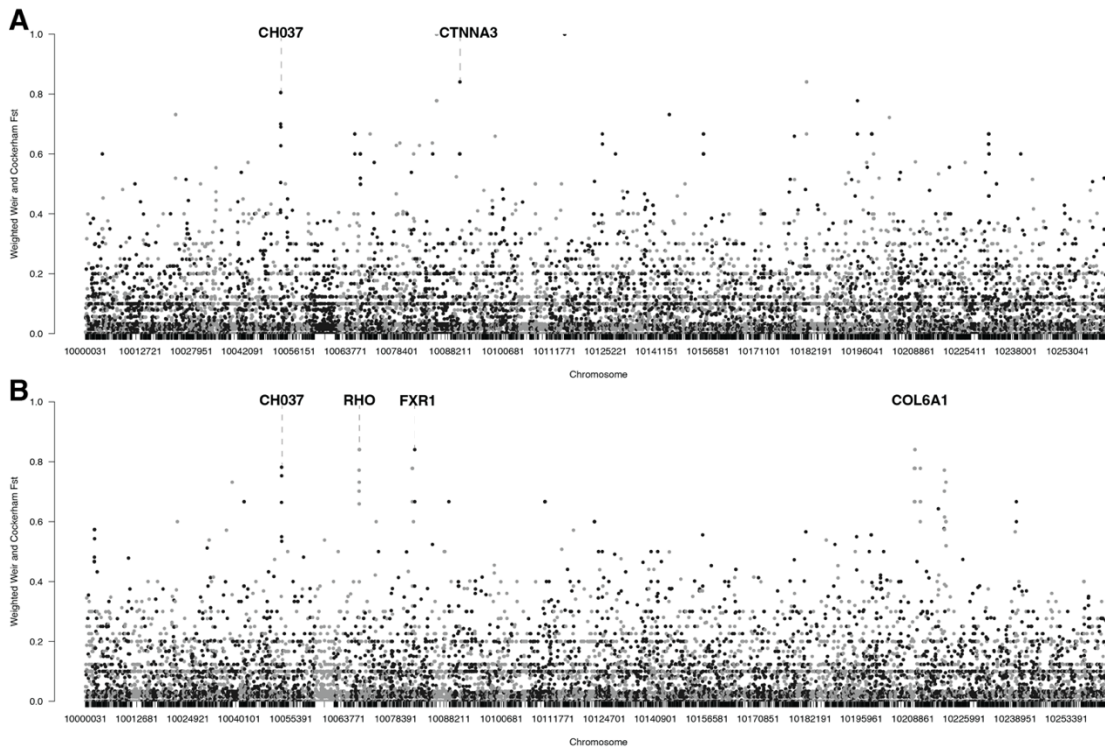
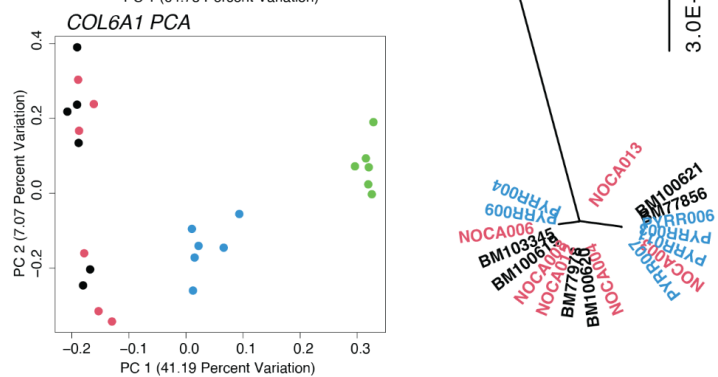
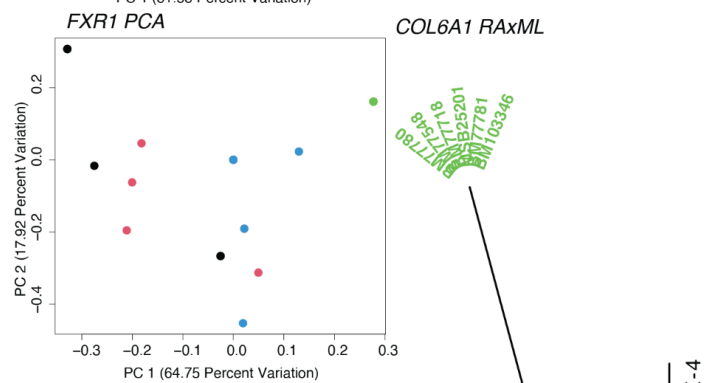
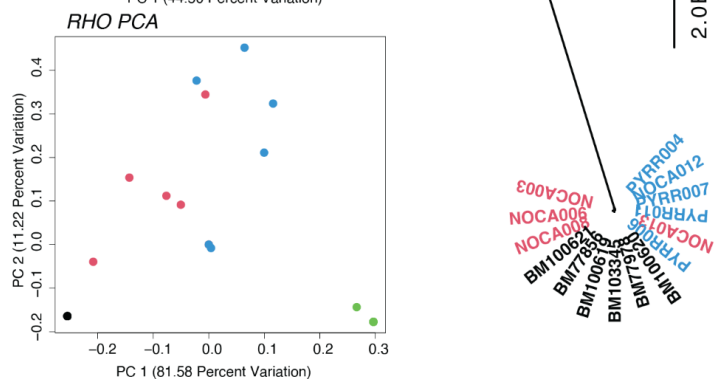
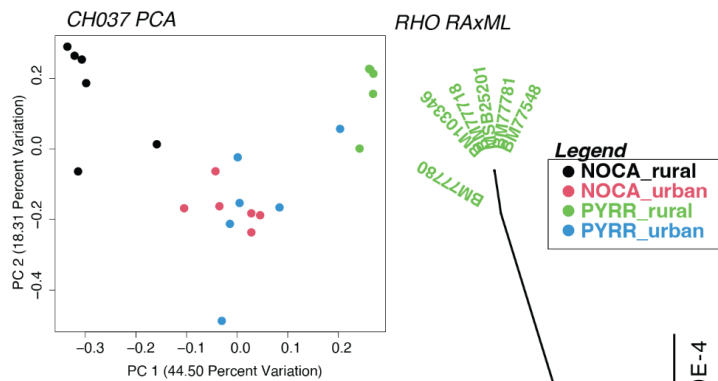


Figure 2: Phylogenetic Analysis of Introgressed Genes.

PCA plots (left) of CH037, RHO, FXR1, and COL6A1 show patterns of clustering between urban samples. Unrooted RAxML trees (right) of RHO and COL6A1 show that urban pyrrhuloxia samples are more closely related to all northern cardinal samples than to rural pyrrhuloxia samples at these genes.





## **Tables**

**Table 1: Sample Information.**

| <b><u>Sample</u></b> | <b><u>Species</u></b> | <b><u>Population</u></b> | <b><u>Source</u></b>                  |
|----------------------|-----------------------|--------------------------|---------------------------------------|
| 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        |

**Table 2: Genes of Interest**

| <b>Gene name</b>                            | <b><u>Program(s)<br/>that identified<br/>the gene</u></b> | <b><u>Species</u></b>              | <b><u>Function</u></b>  |
|---|---|------------------------------------|---|
| HYDIN                                       | OmegaPlus and SweeD                                       | Northern cardinals and pyrrhuloxia | Axonemal central pair apparatus protein. Cilia and flagella development. Especially important for sperm function and lung function.                 |
| DLG2  | Tajima's D  | Northern cardinals and pyrrhuloxia | Discs large MAGUK scaffold protein 2. Cognitive function and neuronal development.  |
| CH037 (synonym of <a href="#">CFAP418</a> ) | F <sub>ST</sub>   | Northern cardinals and pyrrhuloxia | Cilia and flagella associated protein 418. Vision, associated with retinal <a href="#">dystrophy</a> . Can affect both cones and rods.              |
| FXR1  | F <sub>ST</sub>   | Pyrrhuloxia                        | FMR1 autosomal homolog 1. Brain function (fragile X syndrome), <a href="#">muscle development</a> , and cancer                                      |
| REXO1                                       | Tajima's D  | Northern cardinals                 | RNA exonuclease 1 homolog. RNA polymerase II transcription, cervical cancer cell proliferation and progression. Putatively involved in asthma.      |
| RHO   | F <sub>ST</sub>   | Pyrrhuloxia                        | Rhodopsin. Night vision   |
| CTNNA3                                      | F <sub>ST</sub>   | Northern cardinals                 | Catenin alpha 3. Cell-to-cell adhesions. Cardiac myopathy, <a href="#">growth</a> , <a href="#">testicular development</a> , <a href="#">asthma</a> |
| COL6A1                                      | F <sub>ST</sub>   | Pyrrhuloxia                        | Collagen type VI alpha 1 chain. Muscle development  |
| DCBLD2                                      | Tajima's D  | Pyrrhuloxia                        | Discoidin, CUB and LCCL domain containing 2. Cancer (reduces metastatic properties of cancer cells)   |

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## APPENDIX D

### CHAPTER 4 SUPPLEMENTARY TABLES AND FIGURES



## **Figures**

**Figure S1: Maps of sampling locations by species and urban category. Map A (top):**

Northern cardinal sampling locations. **Map B (bottom):** Pyrrhuloxia sampling locations. Rural birds represented by a red-orange pin and urban birds represented by a dark green pin.

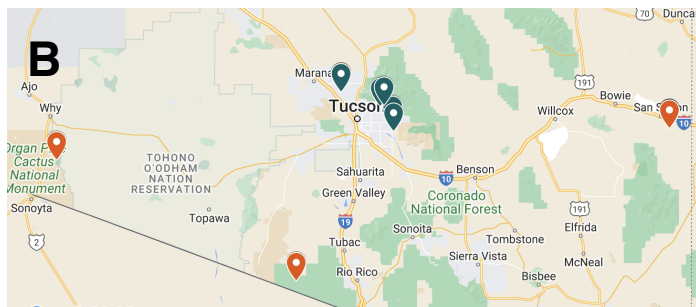
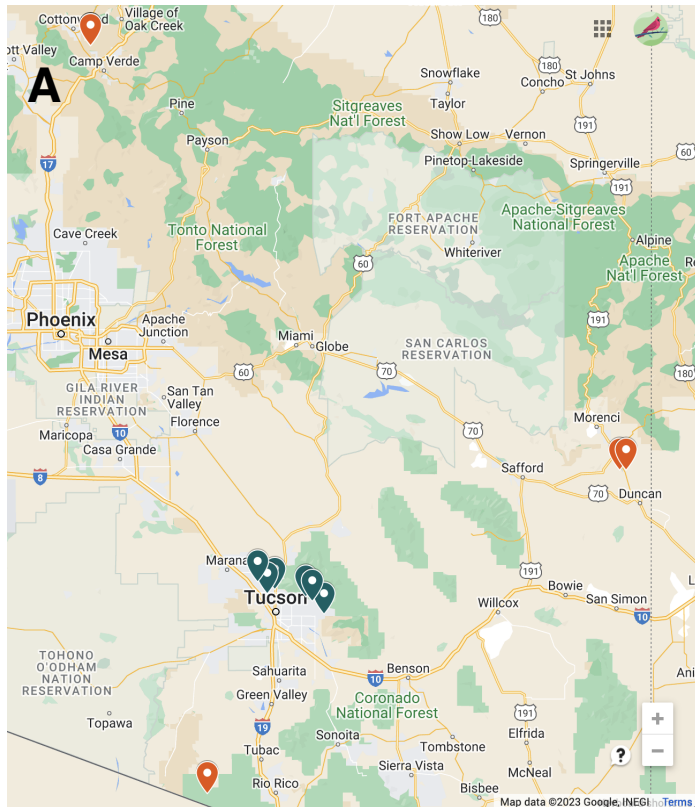


Figure S2: Unrooted RAxML best tree of all samples using 32,437 genome-spanning SNPs.

All northern cardinal samples cluster on the left and all pyrrhuloxia samples cluster on the right, with no clades forming of urban or rural samples.

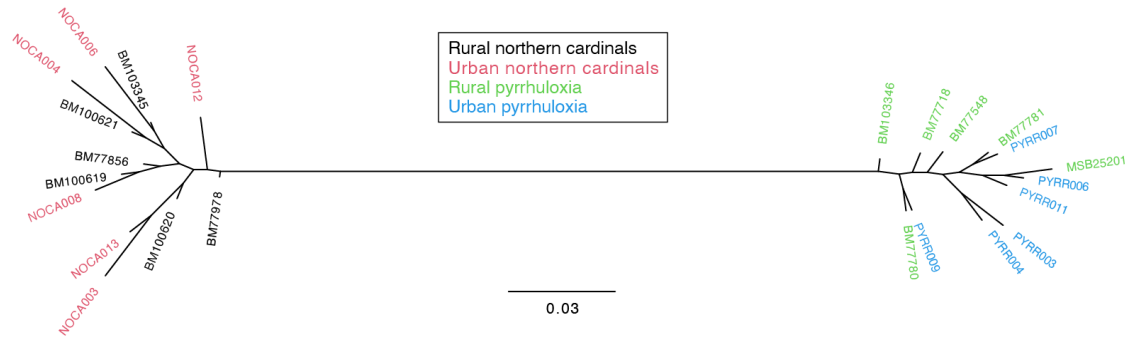


Figure S3: Principal Component Analyses.

**Plot A (Left):** PCA of all samples. PC 1 separates the two species (23.03% variation), but PC2 does not separate urban samples from rural samples. **Plot B (Center):** PCA of just northern cardinal samples. PC 1 mostly separates urban samples from rural samples (9.91% variation). **Plot C (Right):** PCA of just pyrrhuloxia samples. PC 1 separates urban samples from rural samples (23.03% variation)

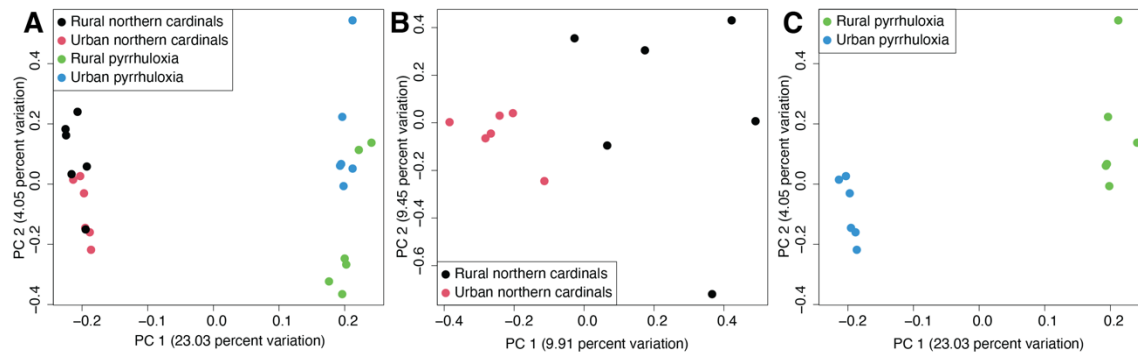


Figure S4: STRUCTURE plots ( $K$  1-6).

All analyses regardless of the value used for  $K$  found separation by species but not by urban versus rural.

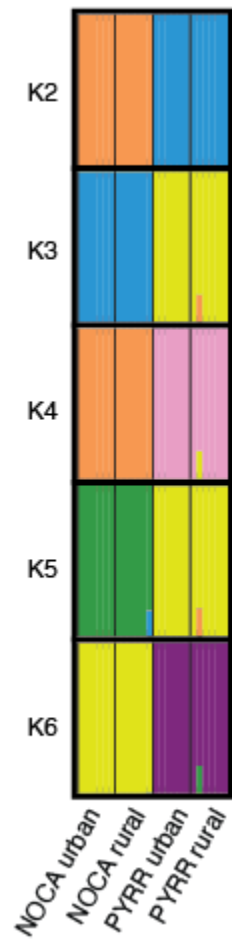
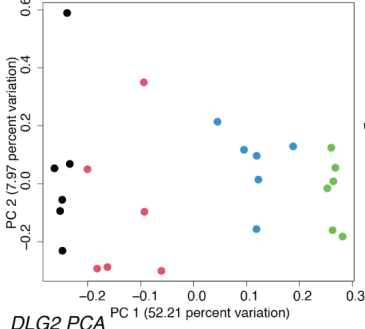


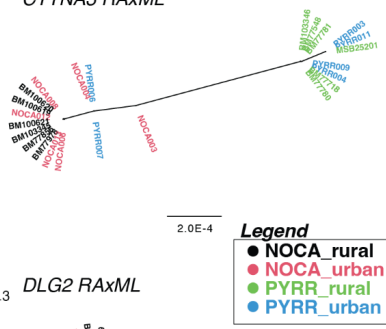
Figure S5: Gene Specific RAxML and PCA of genes that do not display patterns of introgression.

In all PCAs, PC1 separates the two species, and urban samples do not cluster. In all RAxML trees, either species cluster or no discernible pattern is apparent. CTNNA3 is the only outlier, as both the PCA and RAxML analysis are slightly consistent with some introgression, but could also be explained by convergent evolution in genotype.

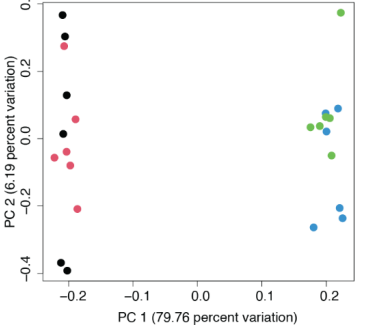
CTTNA3 PCA



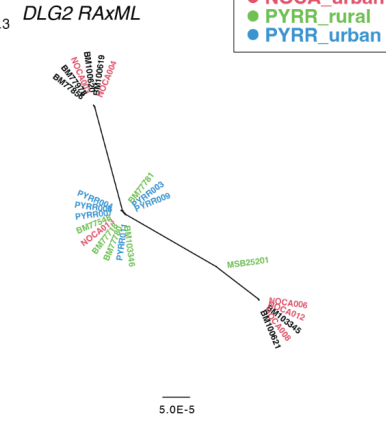
CTTNA3 RAxML



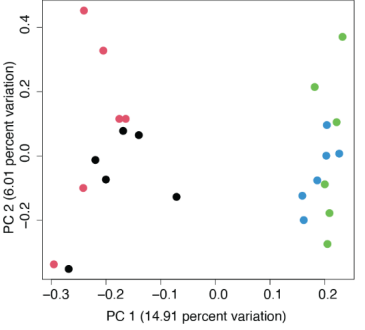
DLG2 PCA



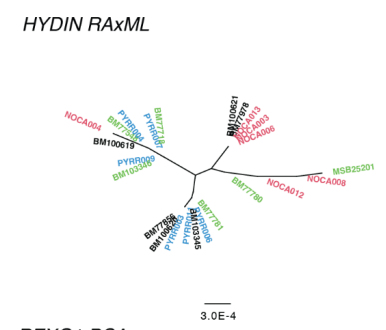
DLG2 RAxML



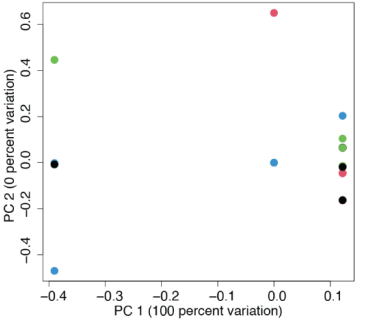
HYDIN PCA



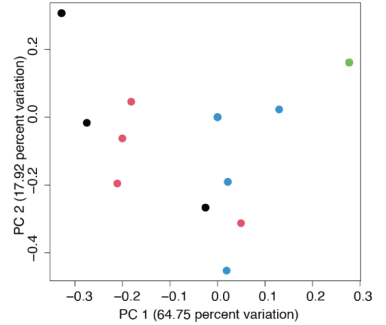
HYDIN RAxML



DCBLD2 PCA



REXO1 PCA



## Tables

Table S1: Regions of Interest

| NOC<br>A_U<br>rban | NO<br>CA_<br>Rural | PYR<br>R_U<br>rban | PYR<br>R_R<br>ural | FST | Taji<br>mas<br>D | Nucleot<br>ideDive<br>rsity | Swe<br>eD | Ome<br>gaPl<br>us | Scaf<br>fold | True<br>Min | True<br>Max | Sear<br>chM<br>in | Sear<br>chM<br>ax | Genes  |
|--------------------|--------------------|--------------------|--------------------|-----|------------------|-----------------------------|-----------|-------------------|--------------|-------------|-------------|-------------------|-------------------|--|
| X                  | X                  | X                  | X                  | X   |                  |                             |           |                   | 1005<br>221  | 2174<br>717 | 2174<br>761 | 2124<br>717       | 2224<br>761       | Plekhhf2,Ch037                                 |
| X                  | X                  |                    |                    | X   |                  |                             |           |                   | 1008<br>768  | 3861<br>8   | 3868<br>4   | 0                 | 8868<br>4         |  |
| X                  | X                  |                    |                    | X   |                  |                             |           |                   | 1009<br>024  | 2710<br>29  | 3710<br>29  | 2210<br>29        | 4210<br>29        | Ctnna3_0, Lrrtm3                               |
| X                  | X                  |                    |                    | X   |                  |                             |           |                   | 1011<br>506  | 9721<br>2   | 9721<br>7   | 4721<br>2         | 1472<br>17        | Mrps5  |
| X                  | X                  |                    |                    | X   |                  |                             |           |                   | 1018<br>132  | 4520<br>4   | 4521<br>0   | 0                 | 9521<br>0         |  |
| X                  | X                  |                    |                    | X   |                  |                             |           |                   | 1019<br>412  | 2763<br>1   | 2763<br>1   | 0                 | 7763<br>1         |  |
|                    |                    | X                  | X                  | X   |                  |                             |           |                   | 1006<br>626  | 1422<br>06  | 1423<br>46  | 9220<br>6         | 1923<br>46        | Ift122,Rho                                     |
|                    |                    | X                  | X                  | X   |                  |                             |           |                   | 1008<br>328  | 1948<br>60  | 1948<br>82  | 1448<br>60        | 2448<br>82        | Tmcc1  |
|                    |                    | X                  | X                  | X   |                  |                             |           |                   | 1008<br>382  | 6910<br>75  | 7910<br>75  | 6410<br>75        | 8410<br>75        | Fxr1_0,Fxr1_1                                  |
|                    |                    | X                  | X                  | X   |                  |                             |           |                   | 1020<br>886  | 1189<br>26  | 1190<br>94  | 6892<br>6         | 1690<br>94        | Pcbp3_0,Col6a1                                 |
|                    |                    | X                  | X                  | X   |                  |                             |           |                   | 1021<br>115  | 1687<br>62  | 2389<br>57  | 1187<br>62        | 2889<br>57        | Chga,Itpk1                                     |
| X                  |                    | X                  |                    |     | X                |                             |           |                   | 1009<br>321  | 5800<br>00  | 6000<br>00  | 5300<br>00        | 6500<br>00        | Dlg2   |
| X                  |                    |                    |                    |     | X                |                             |           |                   | 1016<br>584  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         | Rexo1  |
|                    | X                  |                    |                    |     | X                |                             |           |                   | 1007<br>098  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         | Mtco2_0,Kcna6                                  |
|                    | X                  |                    |                    |     | X                |                             |           |                   | 1011<br>537  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         | Tp73,Tp73as1,Cc<br>dc27,Lrrc47,Cep1<br>04,Dffb |
|                    | X                  |                    |                    |     | X                |                             |           |                   | 1019<br>264  | 1600<br>00  | 1800<br>00  | 1100<br>00        | 2300<br>00        | Slc26a5  |
|                    | X                  |                    |                    |     | X                |                             |           |                   | 1026<br>539  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         |  |
|                    |                    | X                  |                    |     | X                |                             |           |                   | 1000<br>233  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         |  |
|                    |                    | X                  |                    |     | X                |                             |           |                   | 1001<br>023  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         |  |
|                    |                    | X                  |                    |     | X                |                             |           |                   | 1002<br>912  | 2000<br>0   | 4000<br>0   | -<br>3000<br>0    | 9000<br>0         | Dcbld2   |
|                    |                    |                    | X                  |     | X                |                             |           |                   | 1001<br>302  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         |  |
|                    |                    |                    | X                  |     | X                |                             |           |                   | 1007<br>741  | 6200<br>00  | 6400<br>00  | 5700<br>00        | 6900<br>00        | Rad21  |
|                    |                    |                    | X                  |     | X                |                             |           |                   | 1010<br>057  | 0           | 2000<br>0   | -<br>5000<br>0    | 7000<br>0         |  |
|                    |                    |                    | X                  |     | X                |                             |           |                   | 1010<br>419  | 2000<br>0   | 4000<br>0   | -<br>3000<br>0    | 9000<br>0         |  |

|   |   |   |   |  |   |   |   |   |             |            |            |                |            |                      |
|---|---|---|---|--|---|---|---|---|-------------|------------|------------|----------------|------------|----------------------|
|   |   |   | X |  | X |   |   |   | 1010<br>703 | 0          | 2000<br>0  | -<br>5000<br>0 | 7000<br>0  |                      |
|   |   |   | X |  | X |   |   |   | 1019<br>758 | 0          | 2000<br>0  | -<br>5000<br>0 | 7000<br>0  |                      |
|   |   |   | X |  | X |   |   |   | 1019<br>804 | 2800<br>00 | 3000<br>00 | 2300<br>00     | 3500<br>00 | Kcnq3,Oc90,Efr3<br>a |
| X | X | X | X |  |   | X |   |   | 1006<br>187 | 2000<br>0  | 4000<br>0  | -<br>3000<br>0 | 9000<br>0  | Hydin_0              |
| X |   | X |   |  |   |   | X |   | 1006<br>187 | 198        | 5561       | -<br>4980<br>2 | 5556<br>1  | Hydin_0              |
|   | X |   |   |  |   |   | X |   | 1023<br>961 | 1073       | 2405       | -<br>4892<br>7 | 5240<br>5  |                      |
|   |   |   | X |  |   |   | X |   | 1022<br>801 | 5198       | 5593       | -<br>4480<br>2 | 5559<br>3  |                      |
| X |   |   |   |  |   |   |   | X | 1013<br>494 | 364        | 442        | -<br>4963<br>6 | 5044<br>2  |                      |
|   | X |   |   |  |   |   |   | X | 1017<br>116 | 2124       | 2139       | -<br>4787<br>6 | 5213<br>9  |                      |
|   | X |   |   |  |   |   |   | X | 1023<br>961 | 4638       | 1232<br>7  | -<br>4536<br>2 | 6232<br>7  |                      |
|   |   | X |   |  |   |   |   | X | 1008<br>477 | 966        | 1218       | -<br>4903<br>4 | 5121<br>8  |                      |
|   |   |   | X |  |   |   |   | X | 1015<br>323 | 152        | 1532       | -<br>4984<br>8 | 5153<br>2  |                      |