CHAPTER 4

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

**Authors**

Danny Jackson1, Sabrina McNew1, Scott Taylor2, Kevin McGraw3,

1. University of Arizona
2. University of Colorado Boulder
3. Michigan State University

\*Corresponding author. Email: dannyjackson@arizona.edu

**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.

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 (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. 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 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. Finally, we highlight specific genes that may underlye 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 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 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 4.57 across all samples.

Population Structure Analyses

We analyzed relationships between our samples using Principal Component Analyses (PCA). 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.

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 genome 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. 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. We corrected for multiple testing by using a false discovery rate using the Benajimini-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.

While GO terms can provide insight into selective events that have impacted multiple genes within single biological processes, individual genes can have large phenotypic effects. To investigate individual genes that are potentially associated with urbanization, we reduced candidate GO terms to those with p < 0.05 without a correction for multiple testing and manually identified any categories associated with predicted responses to urbanization: physiological response to heat, limited water availability, light stimulus, digestion, immune function, or carotenoid metabolism. We reduced these GO terms to just that were not caught in our enriched GO term analysis, and filtered our list of candidate genes to those associated with these GO terms. We conservatively reduced this list to only genes that contain a SNP that is fixed in the urban population, that expresses some variability in our rural samples, and that have functional differences between individuals identified by snpEff (Cingolani 2012).

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 (sp) across multiple cities in Argentina and the other investigated urban adaptation of Great Tits (*Parus major*) across multiple European cities. 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, montaine conifer forests, and the Madrean archipelago, while pyrrhuloxia did not segregate 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 an elevational genomic cline from the Madrean archipelago to the montaine conifer forests to the Sonoran basin.

Overrepresented GO Terms

In northern cardinals, GO terms related to blood physiology, tissue integrity, and muscle development emerged as overrepresented categories in analyses of genes identified by FST, RAiSD, and the combination of the two (Figure 3). Two GO terms that were overrepresented in the genes identified by RAiSD -- organonitrogen compound metabolic process and regulation of body fluid levels – suggest an adaptation to deal with low-water availability.

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.

Outlier Genes of Interest

In the manual analysis of candidate genes in northern cardinals, genes related to coagulation, immune function, muscle development, nitrogen processing and tissue structure emerged. All of these were previously identified in the analysis of overrepresented GO terms.

In pyrrhuloxia, genes related to tissue structure, circadian rhythm, insulin, immune function, muscle development, and neuronal development emerged. Of these, circadian rhythm and neuronal development were not picked up in the analyses of overrepresented GO terms. Six candidate genes associated with circadian rhythm are CRY1 (Cryptochrome Circadian Regulator 1), FSHB (Follicle Stimulating Hormone Subunit Beta), ID4 (Inhibitor Of DNA Binding 4), MTA1 (Metastasis Associated 1), and RHO (Rhodopsin). Of these, only Rhodopsin was fixed in the urban samples but variable in the rural samples and contained a missense mutation with medium or high effect.

Parallel Evolution

Pairwise comparisons of species found significant evidence of overlapping genes in five of the six pairs (northern cardinals and pyrrhuloxia p=1.32x10-15, northern cardinals and burrowing owls p= 2.81x10-05, northern cardinals and great tits p=0.012, pyrrhuloxia and burrowing owls p=0.008, pyrrhuloxia and great tits p=0.601, burrowing owls and great tits p=0.012; FDR corrected Fisher’s exact test).

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).

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.

**Discussion**

**Northern cardinal GO terms**

Two genes drove the signal associated with blood physiology, FGA (fibrinogen alpha chain) and FGB (fibrinogen beta chain). In addition to clotting, both genes influence 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).

Four genes 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 GO terms**

Two candidate genes were involved insulin-like growth factor (IGF) receptor signaling pathway, GIGYF2 and IGF1. IGFs 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).

Our analyses identified 15 candidate genes in pyrrhuloxia associated with nervous system development.

Neural genes:

RUNX2 involved in Marek’s disease.

PRKN, GPM6A, and SDK1 were 3/6 genes of note in an urbanization burrowing owl study. Note that panther didn’t identify SDK1 as neural associated, and PRKN isn’t in the GO short list but is an outlier gene. Bring it up in the manual section.

<https://onlinelibrary.wiley.com/doi/full/10.1111/mec.15451>

Genes involved in epigenetic regulation were overrepresented in all analyses across both species except for the combined list of outliers from FST and RAiSD in pyrrhuloxia. Two GO terms – GO:0008033 tRNA processing and GO:0006399 tRNA metabolic process – were identified in RAiSD analyses of both species.

**Parallel evolution**

Overlap between species:

(The three genes identified by both programs in both species)

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 is associated in humans with cardovascular disease (Yagyu et al. 2023), asthma (Stikker et al. 2023), and with 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).

**Tables and Figures**

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

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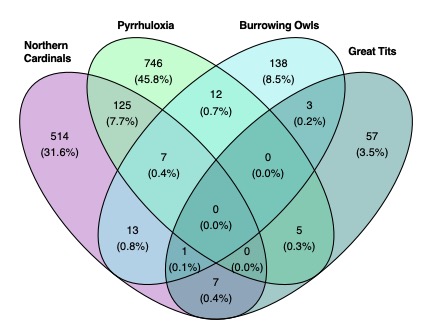
A diagram of a cell organ

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**Figures**

**Tables**

Table 1: Sample Information.

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| --- | --- | --- | --- |
| **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.

**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.

A screenshot of a map

Description automatically generated

**A**

A map with a location on it

Description automatically generated

**B**

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.

A close-up of a label

Description automatically generated

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)

A graph with red dots and black dots

Description automatically generated

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.

A diagram of a diagram of a number of colored rectangular objects

Description automatically generated with medium confidence

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.

A screenshot of a computer screen

Description automatically generated

**Tables**

Table S1: Regions of Interest

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| NOCA\_Urban | NOCA\_Rural | PYRR\_Urban | PYRR\_Rural | FST | TajimasD | NucleotideDiversity | SweeD | OmegaPlus | Scaffold | TrueMin | TrueMax | SearchMin | SearchMax | Genes |
| X | X | X | X | X |  |  |  |  | 1005221 | 2174717 | 2174761 | 2124717 | 2224761 | Plekhf2,Ch037 |
| X | X |  |  | X |  |  |  |  | 1008768 | 38618 | 38684 | 0 | 88684 |  |
| X | X |  |  | X |  |  |  |  | 1009024 | 271029 | 371029 | 221029 | 421029 | Ctnna3\_0, Lrrtm3 |
| X | X |  |  | X |  |  |  |  | 1011506 | 97212 | 97217 | 47212 | 147217 | Mrps5 |
| X | X |  |  | X |  |  |  |  | 1018132 | 45204 | 45210 | 0 | 95210 |  |
| X | X |  |  | X |  |  |  |  | 1019412 | 27631 | 27631 | 0 | 77631 |  |
|  |  | X | X | X |  |  |  |  | 1006626 | 142206 | 142346 | 92206 | 192346 | Ift122,Rho |
|  |  | X | X | X |  |  |  |  | 1008328 | 194860 | 194882 | 144860 | 244882 | Tmcc1 |
|  |  | X | X | X |  |  |  |  | 1008382 | 691075 | 791075 | 641075 | 841075 | Fxr1\_0,Fxr1\_1 |
|  |  | X | X | X |  |  |  |  | 1020886 | 118926 | 119094 | 68926 | 169094 | Pcbp3\_0,Col6a1 |
|  |  | X | X | X |  |  |  |  | 1021115 | 168762 | 238957 | 118762 | 288957 | Chga,Itpk1 |
| X |  | X |  |  | X |  |  |  | 1009321 | 580000 | 600000 | 530000 | 650000 | Dlg2 |
| X |  |  |  |  | X |  |  |  | 1016584 | 0 | 20000 | -50000 | 70000 | Rexo1 |
|  | X |  |  |  | X |  |  |  | 1007098 | 0 | 20000 | -50000 | 70000 | Mtco2\_0,Kcna6 |
|  | X |  |  |  | X |  |  |  | 1011537 | 0 | 20000 | -50000 | 70000 | Tp73,Tp73as1,Ccdc27,Lrrc47,Cep104,Dffb |
|  | X |  |  |  | X |  |  |  | 1019264 | 160000 | 180000 | 110000 | 230000 | Slc26a5 |
|  | X |  |  |  | X |  |  |  | 1026539 | 0 | 20000 | -50000 | 70000 |  |
|  |  | X |  |  | X |  |  |  | 1000233 | 0 | 20000 | -50000 | 70000 |  |
|  |  | X |  |  | X |  |  |  | 1001023 | 0 | 20000 | -50000 | 70000 |  |
|  |  | X |  |  | X |  |  |  | 1002912 | 20000 | 40000 | -30000 | 90000 | Dcbld2 |
|  |  |  | X |  | X |  |  |  | 1001302 | 0 | 20000 | -50000 | 70000 |  |
|  |  |  | X |  | X |  |  |  | 1007741 | 620000 | 640000 | 570000 | 690000 | Rad21 |
|  |  |  | X |  | X |  |  |  | 1010057 | 0 | 20000 | -50000 | 70000 |  |
|  |  |  | X |  | X |  |  |  | 1010419 | 20000 | 40000 | -30000 | 90000 |  |
|  |  |  | X |  | X |  |  |  | 1010703 | 0 | 20000 | -50000 | 70000 |  |
|  |  |  | X |  | X |  |  |  | 1019758 | 0 | 20000 | -50000 | 70000 |  |
|  |  |  | X |  | X |  |  |  | 1019804 | 280000 | 300000 | 230000 | 350000 | Kcnq3,Oc90,Efr3a |
| X | X | X | X |  |  | X |  |  | 1006187 | 20000 | 40000 | -30000 | 90000 | Hydin\_0 |
| X |  | X |  |  |  |  | X |  | 1006187 | 198 | 5561 | -49802 | 55561 | Hydin\_0 |
|  | X |  |  |  |  |  | X |  | 1023961 | 1073 | 2405 | -48927 | 52405 |  |
|  |  |  | X |  |  |  | X |  | 1022801 | 5198 | 5593 | -44802 | 55593 |  |
| X |  |  |  |  |  |  |  | X | 1013494 | 364 | 442 | -49636 | 50442 |  |
|  | X |  |  |  |  |  |  | X | 1017116 | 2124 | 2139 | -47876 | 52139 |  |
|  | X |  |  |  |  |  |  | X | 1023961 | 4638 | 12327 | -45362 | 62327 |  |
|  |  | X |  |  |  |  |  | X | 1008477 | 966 | 1218 | -49034 | 51218 |  |
|  |  |  | X |  |  |  |  | X | 1015323 | 152 | 1532 | -49848 | 51532 |  |