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Transcriptomes of Nesting-Relevant Brain Regions Reflect Sex-Specific Roles During Nest Building in the Zebra Finch (*Taeniopygia guttata*)

Aalo B. Choudhary[1], Jennie E. DeVore[1], Hans A. Hofmann[2§]

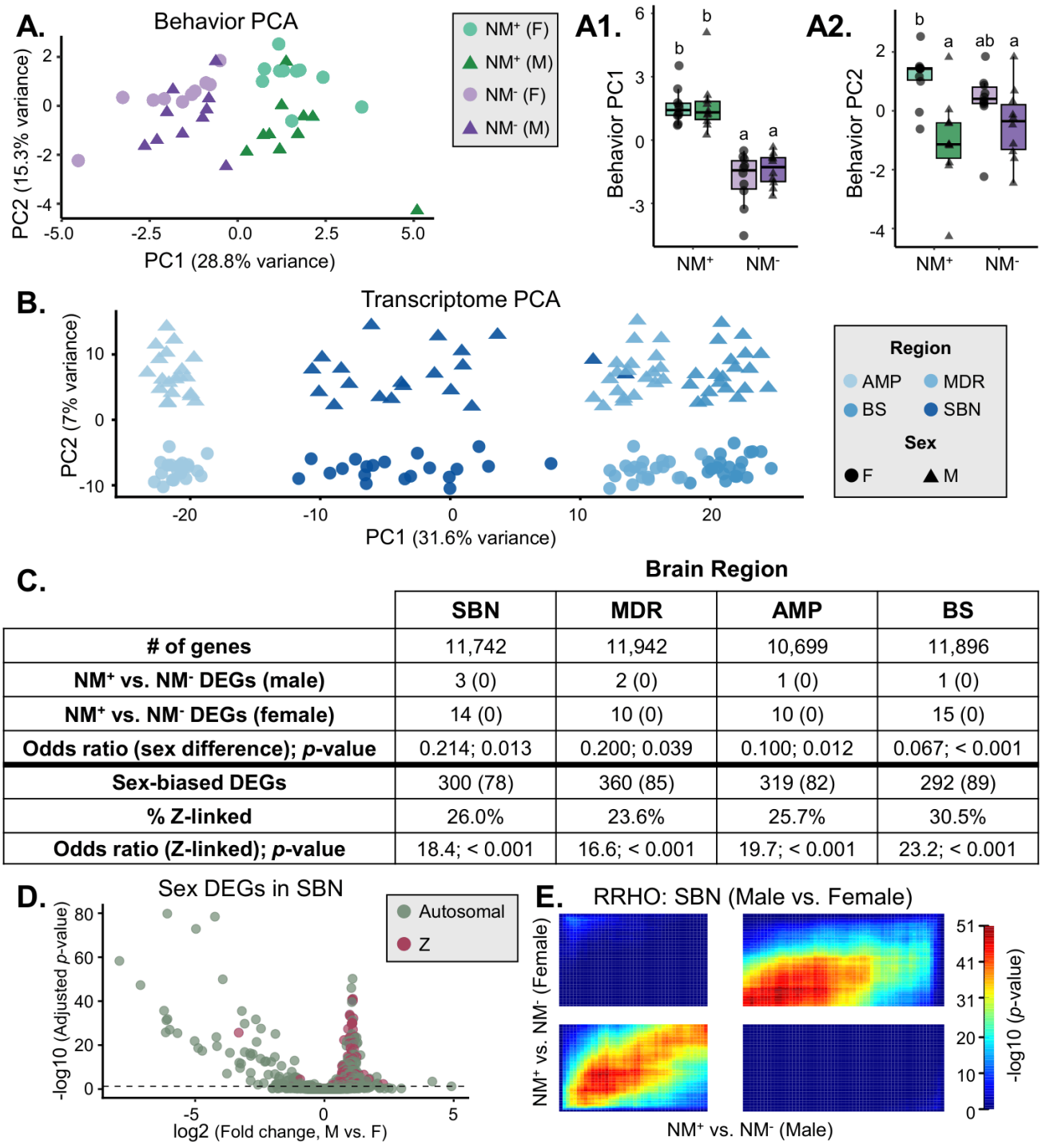
[1]Department of Integrative Biology, University of Texas at Austin, Austin, Texas, United States

[2]Department of Integrative Biology, Interdisciplinary Neuroscience Program , University of Texas at Austin, Austin, Texas, United States

[§]To whom correspondence should be addressed: hans@utexas.edu

Abstract

While nest building is common across species, its neural underpinnings are not well understood. We reanalyzed publicly available transcriptomes of nesting-relevant brain regions in zebra finch pairs and found that behavior and gene expression co-varied in a sex-dependent manner. Providing birds with nesting materials resulted in highly concordant gene expression changes in socially relevant brain regions of both sexes, whereas transcriptomic responses in brain regions associated with motor output and sensorimotor processing varied by sex, consistent with sex-specific roles in nest building. Our results underscore the importance of sex and opportunity when studying nest building behavior across species.



C.

	Brain Region			
	SBN	**MDR**	**AMP**	**BS**
# of genes	11,742	11,942	10,699	11,896
NM⁺ vs. NM⁻ DEGs (male)	3 (0)	2 (0)	1 (0)	1 (0)
NM⁺ vs. NM⁻ DEGs (female)	14 (0)	10 (0)	10 (0)	15 (0)
Odds ratio (sex difference); *p*-value	0.214; 0.013	0.200; 0.039	0.100; 0.012	0.067; < 0.001
Sex-biased DEGs	300 (78)	360 (85)	319 (82)	292 (89)
% Z-linked	26.0%	23.6%	25.7%	30.5%
Odds ratio (Z-linked); *p*-value	18.4; < 0.001	16.6; < 0.001	19.7; < 0.001	23.2; < 0.001

F.

Brain region	**DD**	**UU**	**UD**	**DU**	**Concordance**
SBN	143 (6)	121 (0)	44 (0)	14 (1)	0.74
MDR	101 (0)	438 (20)	0 (0)	17 (0)	0.97
AMP	81 (2)	75 (2)	63 (1)	101 (2)	0.49
BS	40 (1)	68 (1)	47 (0)	144 (4)	0.57

Figure 1. Neurogenomic Basis of Nest Building:

Figure 1: A) Behavioral PCA on 13 behavioral measures. Boxplots of PC1 and PC2 scores from two-way ANOVAs with treatment and sex as fixed effects, including their interaction term, assessing the effects of treatment and sex on behavior

(inserts). **B)** Transcriptomic PCA of the top 500 most variable genes. **C)** Differentially expressed genes (DEGs) by treatment (NM^+ *vs.* NM^-) and sex (male *vs.* female), with the number of Z-linked genes shown in parentheses. While a substantial number of Z-linked genes showed a sex-biased expression, none was responsive to treatment. Odds ratios and p-values were calculated using Fisher's exact test to assess enrichment of sex-biased and treatment-responsive DEGs, respectively, across brain regions. **D)** Volcano plot of sex DEGs in the SBN with chromosomal annotations from Ensembl to identify Z-linked genes and assess their contribution to sex-biased expression patterns. The vast majority of Z-linked DEGs showed higher expression in males. **E)** RRHO analysis between males and females within each brain region using genes ranked based on $\log_2$ fold-change (NM^- *vs.* NM^+) to identify concordant and discordant transcriptional responses between sexes. **F)** Concordant (DD, UU) and discordant (UD, DU) genes extracted from RRHO results (NM^+ vs. NM^-; filtered by $|LFC| > 0.5$) across the four brain regions. Note that across all regions Z-linked genes (provided in parentheses) were rare in all categories, with only a small number detected in both concordant and discordant gene sets, further demonstrating that sex chromosome-linked genes contribute minimally to treatment-responsive transcriptional variation as compared to autosomal genes. The SBN and MDR concordant gene sets, however, did notably consist of 4-5% Z-linked genes. **G)** Behavioral PCA loading vectors for the first two principal components derived from 13 quantified behavioral measures. Arrows indicate the direction and magnitude of each behavioral variable's contribution to the PCA space. **H)** Boxplots of DESeq2-normalized counts showed that two Z-linked genes, *ABPA1* (amyloid beta precursor protein binding family A member 1) and *DAB2* (Disabled homolog 2), exhibited significantly higher expression in females than males in the SBN, as well as in the other 3 regions. *ABPA1* is a neuronal adaptor and trafficking protein that binds to the amyloid precursor protein (APP) and has been implicated in synaptic vesicle trafficking in vertebrates (Borg et al., 1996; McLoughlin and Miller, 2008). The observed sex-biased expression of *ABPA1* suggests potential baseline differences in neuronal processes between males and females in zebra finches. Similarly, *DAB2* is an adaptor protein involved in clathrin-mediated endocytosis and intracellular trafficking pathways (Morris and Cooper, 2001; Traub, 2003). Its elevated expression in females may reflect sex-specific differences in cellular trafficking or signaling dynamics. Although the functions of these genes are not well characterized in avian systems, sex-biased expression of Z-linked genes is well documented in birds and is often attributed to incomplete dosage compensation (Itoh et al., 2007; Mank and Ellegren, 2009), suggesting that these patterns may contribute to intrinsic differences in neural function between males and females. **I)** Comparison of Z-linked sex-biased gene expression between treatment conditions (NM^+ vs NM^-) across brain regions. Each point represents a Z-linked gene plotted by $\log_2$ fold change (M vs F) in NM^- versus NM^+ zebrafinches. Solid black lines indicate fitted linear regressions, while dashed lines represent the 1:1 relationship. Regression statistics for each region are shown within panels. **J-L)** Rank–rank hypergeometric overlap analysis (RRHO) comparing treatment response rankings (NM^- − NM^+ $\log_2$ fold-change) between males and females for each brain region. Positive values indicate higher expression in NM^- relative to NM^+, negative values indicate higher expression in NM^+ relative to NM^-, and values near zero indicate minimal treatment effect. **M)** To determine whether the transcriptome PCA was driven primarily by Z-linked gene expression, we repeated the PCA after excluding all Z-linked genes prior to selecting the top 500 most variable genes and performing PCA. Although the proportion of variance explained by the leading principal components changed slightly following removal of Z-linked genes, the overall transcriptomic structure remained the same, indicating that the major axes of transcriptomic variation – including sex differences – cannot be explained by Z-linked gene expression.

Description

Many animals, from ants to humans, build nests (Hansell, 2005). The behavioral and cognitive mechanisms of nest building have been studied in birds and fishes (DeVore & Hofmann, 2026), but the molecular mechanisms underpinning this behavior are less studied (Hall et al., 2015). Studying transcriptional changes during such nesting behaviors can give much-needed insight into its molecular mechanisms.

A recent transcriptomic study investigated the neurogenomic basis of nest-building behavior in zebra finches (*Taeniopygia guttata*) by experimentally manipulating nesting conditions, specifically by removing the partner or nesting materials (Fang et al., 2024). These authors generated bulk transcriptomes of brain regions previously implicated in nesting behavior: the limbic-hypothalamic "social behavior network" (SBN), the anterior motor pathway (AMP), and midbrain dopaminergic regions (MDR) (Hall et al., 2014; Edwards et al., 2020); as well as the brainstem (BS) containing the principal trigeminal nucleus, which processes tactile information from the beak (Gutiérrez-Ibáñez et al., 2009). They then identified nesting-associated neural gene expression patterns enriched for neural plasticity processes and sex differences in transcriptional responses during nesting transitions. However, the study included a "No-Partner" social isolation treatment, which is known to be stressful for social animals, such as zebra finches (Limin et al., 2024), and may therefore have biased the analyses. Furthermore, the study did not take advantage of the detailed behavioral data that was collected for all experimental animals, limiting its insights into how molecular mechanisms of nest-building can influence behavior.

Here, we reanalyzed the data from Fang et al. (2024) to gain a more detailed understanding of the factors that may be influencing neural transcriptional variation. Specifically, we restricted treatment comparisons to intact pairs that were either provided with or deprived of nesting material. We then examined (1) how 13 behavioral variables responded to nest

building opportunity and how they related to the transcriptome data, (2) whether transcriptional patterns were sex-biased, with emphasis on Z-linked genes, and (3) the extent to which the transcriptomic patterns associated with nest building were concordant across the sexes. Together, our reanalysis increases our understanding of how behavioral variation and sex shape transcriptional responses during nest building.

Using Principal Components Analysis (PCA) on the 13 behavioral measures (Figure 1A), we found that PC1 (which explained 28.8% of the total variance in the data) clearly separated the animals with nesting material (NM^+) from those with no nesting materials available (NM^-), with "Nest materials used" on experimental day/sacrifice day and "Copulation" loading most strongly on this PC (Figure 1G). A two-way ANOVA revealed a significant effect of treatment on behavioral PC1 ($F_{1,36} = 90.97$, $p = 2.16 \times 10^{-11}$), with no effect of sex ($F_{1,36} = 0.54$, p = 0.467) and no Treatment × Sex interaction ($F_{1,36} = 0.36$, $p = 0.553$) (Figure 1A insert). PC2 (15.3%) separated the sexes, with two partner-directed displays ("upright fluffed singing posture" and "beak fencing") loading most strongly on this PC (Figure 1G). A two-way ANOVA revealed a significant effect of sex on behavioral PC2 ($F_{1,36} = 15.13$, $p = 4.15 \times 10^{-4}$), with no effect of treatment ($F_{1,36} = 0.07$, p = 0.791) and no Treatment × Sex interaction ($F_{1,36} = 3.14$, p = 0.085) (Figure 1A, insert).

Next, we performed a PCA on the 500 most variable genes in the four brain regions in our analysis, showing that samples clustered predominantly by brain region as expected based on the original study (Figure 1B). Regional identity accounts for 31.6% of the variance (PC1), while PC2 (7.0%) cleanly separated the samples by sex. When we examined the relationship between behavior PCs and transcriptomic PCs, we found that sex differences in behavior (Behavioral PC2) and gene expression (transcriptomic PC1) were significantly correlated in the SBN (linear model: $F_{1,38} = 11.91$, $r^2 = 0.239$, $p = 0.0014$). We also examined transcriptome PCs 3-5 for associations with the three behavioral PCs and found no significant associations.

We then identified differentially expressed genes (DEGs) between NM^+ and NM^-, with trial included as a covariate, and found few significant genes ($p_{adj} < 0.05$) (Figure 1C). However, females exhibited significantly more treatment-responsive DEGs than males across all brain regions (Fisher's exact test: SBN, $p = 0.013$; MDR, $p = 0.039$; AMP, $p = 0.012$; BS, $p = 5.17 \times 10^{-4}$). In contrast, consistent with the avian ZW sex determination system in which males are the homogametic (ZZ) sex, the vast majority of Z-linked DEGs showed higher expression in males (Figure 1D), except for two (Figure 1H). Indeed, we identified hundreds of sex-biased DEGs, of which 24–31% were located on the Z chromosome—significantly more than expected by chance (Figure 1C). Notably, 210 (58–72%) of these sex-biased DEGs were shared across brain regions, and this overlap was even greater (60 genes, 67–77%) among Z-linked DEGs, indicating highly consistent brain-wide regulation of Z-linked genes. Finally, the SBN exhibited highly concordant Z-linked sex-biased expression across treatments ($R^2 = 0.587$, $p = 1.32 \times 10^{-47}$) (Figure 1I), suggesting that these sex differences are stable and largely independent of treatment-driven transcriptional responses.

Finally, we hypothesized that brain regions involved in social decision-making, such as the SBN and MDR, would exhibit concordant transcriptomic responses to NM^- treatment across sexes, whereas regions involved in the motor control of nest building, such as the AMP, which is sexually dimorphic in zebra finches (Hall et al., 2014), would show less or no concordance. To test this, we performed rank–rank hypergeometric overlap analysis comparing treatment response rankings ($NM^- - NM^+$ $\log_2$ fold-change) between males and females for each brain region. We found strong concordance in the SBN (Figure 1E) and MDR (Figure 1F, 1J), whereas AMP and BS exhibited largely discordant expression patterns (Figure 1F, 1K, 1L).

Our reanalysis of the study by Fang et al. (2024) clearly established that in zebra finch pairs gene expression variation in nesting-relevant brain regions is largely independent of the presence of nesting materials yet highly dependent on sex, with Z-linked genes being almost exclusively male-biased due to incomplete dosage compensation. It is important to note, however, that the observed sex differences in gene expression were largely explained by the autosomal transcriptome. While SBN and MDR showed highly concordant treatment-responsive gene programs among both sexes in line with their shared roles in social decision-making (O'Connell and Hofmann, 2011, 2012), AMP and BS exhibited largely discordant expression patterns, suggesting that gene expression in brain regions generating motor output or processing beak mechanosensory input, respectively, are regulated in a more sex-specific manner. These discordant expression patterns could reflect the fact that in zebra finches nesting materials are almost exclusively collected by the male (Zann, 1996). Our interpretation is consistent with the notion that male and female zebra finches have similar physical cognitive abilities (i.e., those abilities that enable them to interact with and manipulate the physical world) despite the different roles the sexes play in nesting (Lambert et al., 2022), suggesting that behavioral divergence may be driven as much by differences in neural activity as by broad transcriptomic differences. In conclusion, our study provides a foundation for future neurotranscriptomic studies of nest building across sexes in birds (Healy et al., 2023) and beyond (DeVore & Hofmann, 2026).

Methods

1. Experimental Design and Data Source

We reanalyzed RNA-seq and behavioral data published in Fang et al. (2024). The original study included nesting control (CON), non-nesting with mate (NM), and non-nesting without mate (NP) treatment groups of 30 pairs of zebra finches across five brain regions associated with nesting behavior: the social behavior network (SBN, including the bed nucleus of the stria terminalis, medial preoptic area, anterior and ventromedial hypothalamus), midbrain dopaminergic region (MDR, including the ventral tegmental area, central grey), the anterior motor pathway (AMP, including the anterior ventral mesopallium, anterior nidopallium, anterior striatum), the brainstem (BS, including the principal trigeminal nucleus), and "Other." We restricted our reanalysis to socially paired groups (CON vs NM, relabeled to NM^+ and NM^- to indicate presence or absence of nesting material) to reduce potential confounding effects from social isolation in the NP condition. We also excluded the "Other" brain region due to ambiguity.

2. Bioinformatics Analysis

Raw paired-end RNA-seq reads were obtained from the Sequence Read Archive (SRA accession # SRP514339; BioProject: PRJNA1124911) corresponding to the original study (Fang et al., 2024) and aligned to the zebra finch reference genome (Ensembl Taeniopygia_guttata.bTaeGut1_v1, July 2025) using BWA-MEM (Li, 2013). Alignment statistics were assessed with Samtools (Danecek et al., 2021), and gene-level counts were generated using HTSeq (Anders et al., 2015) based on Ensembl gene annotations. Count data were imported into R (R Core Team, 2025) using DESeq2 (Love et al., 2014) and merged with sample metadata. Samples from the "No Partner" (NP) treatment were excluded prior to analysis. Lowly expressed genes were filtered by retaining genes with at least 10 counts in at least two samples. Counts were normalized using the DESeq2 median-of-ratios method, and variance-stabilizing transformation (VST) was applied for downstream analyses.

3. Statistical Analysis

Behavioral Analysis and PCA

Behavioral analyses were conducted using 13 supplementary behavioral variables obtained from the original dataset. Variables were standardized prior to analysis. Principal components analysis (PCA) was performed to identify major axes of behavioral variation. To assess the effects of treatment and sex on behavior, PC1 and PC2 scores were analyzed using a two-way ANOVA with treatment and sex as fixed effects, including the interaction term.

Transcriptomic PCA

Principal components analysis of transcriptomic data was performed using variance-stabilized expression values from the top 500 most variable genes. PCA was used to visualize clustering patterns by brain region, sex, and treatment condition.

Treatment Differential Expression Analysis

Differential gene expression analysis was performed using DESeq2 (Love et al., 2014). For treatment comparisons (NM^- vs NM^+), analyses were conducted separately for males and females within each brain region. The design formula included trial as a covariate to account for batch effects.

Genes with an adjusted p-value (Benjamini-Hochberg correction; Benjamini and Hochberg, 1995) < 0.05 were considered significantly differentially expressed. The number of genes tested and the number of significant DEGs were recorded for each region and sex.

Sex-Biased Differential Expression Analysis

To identify sex-biased gene expression, differential expression analysis was performed comparing males and females within each brain region. Genes with adjusted *p*-values < 0.05 were considered significant. Chromosomal annotations from Ensembl were used to identify Z-linked genes and assess their contribution to sex-biased expression patterns. We used Fisher's exact tests to determine whether Z-linked genes were overrepresented among DEGs relative to their genomic frequency.

Consistency of Sex-Biased Expression Across Treatments (Z-linked Genes)

To assess whether sex-biased gene expression of Z-linked genes was consistent across treatment conditions, differential expression analyses comparing males and females (M vs F) were performed separately within each treatment (NM^- and NM^+) and brain region using DESeq2. Genes were annotated using chromosomal information, and analyses were restricted to Z-linked genes. For each gene, $\log_2$ fold change values representing sex differences were extracted for both conditions. Concordance of sex-biased expression across treatments was evaluated by correlating $\log_2$ fold change (M vs F) values between NM^- and NM^+ across Z-linked genes. Linear regression was used to quantify the strength and significance of this relationship.

Rank-Rank Hypergeometric Overlap (RRHO) Analysis

Rank–rank hypergeometric overlap (RRHO2; Cahill et al., 2018) analysis was used to compare genome-wide treatment response patterns between males and females within each brain region. Genes were ranked based on $\log_2$ fold change

($NM^- - NM^+$), and overlap significance was assessed across ranked gene lists to identify concordant and discordant transcriptional responses between sexes. Gene sets were extracted from RRHO2 analyses corresponding to four quadrants: genes upregulated in both sexes (UU), downregulated in both sexes (DD), upregulated in males and downregulated in females (UD), and downregulated in males and upregulated in females (DU). Genes were then filtered to retain those with absolute $\log_2$ fold change > 0.5 in both sexes to focus on robust effects. Gene sets were then annotated with chromosomal information to identify Z-linked genes and counts of total along with Z-linked genes were computed for each category within each brain region. Finally, a concordance score was calculated for each region as follows:

$C = \Sigma(DD + UU) / (\Sigma(DD + UU) + \Sigma(DU + UD) + 1)$

$C \sim 1$ indicates strong concordance, $C \sim 0.5$ indicates either mixed concordance and discordance or neither, and $C \sim 0$ indicates predominantly discordant gene expression patterns.

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Extended Data

Description: Supplementary Gene Lists. Resource Type: Dataset. File: Nestbuilding_Supplement_Gene_Lists.xlsx. DOI: 10.22002/xzwpw-81x22

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