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RESEARCH ARTICLE

Low levels of hybridization between domestic and wild Mallards wintering in the lower Mississippi Flyway

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ABSTRACT

The Mallard (*Anas platyrhynchos*) duck is a ubiquitous and socio-economically important game bird in North America. Despite their generally abundant midcontinent population, Mallards in eastern North America are declining, which may be partially explained by extensive hybridization with human-released domestically derived game-farm Mallards. We investigated the genetic composition of Mallards in the middle and lower Mississippi flyway, key wintering regions for the species. We found that nearly 30% of wild Mallards carried mitochondrial (mtDNA) haplotypes derived from domestic Mallards present in North America, indicating that the individuals had female game-farm Mallard lineage in their past; however, nuclear results identified only 4% of the same sample set as putative hybrids. Recovering 30% of samples with Old World (OW) A mtDNA haplotypes is concordant with general trends across the Mississippi flyway and this percentage was stable across Mallards we sampled a decade apart. The capture and perpetuation of OW A mtDNA haplotypes are likely due to female breeding structure, whereas reversal of the nuclear signal back to wild ancestry is due to sequential backcrossing and lower and/or declining admixture with game-farm Mallards. Future studies of wild ancestry of Mississippi flyway Mallards will benefit from coupling molecular and spatial technology across flyways, seasons, and years to search for potential transitions of Mallard populations with different genetic ancestry, and whether the genetic ancestry is somehow linked to an individual's natal and subsequent breeding location.

Keywords: Anas platyrhynchos, conservation, ddRAD-seq, domestication, genetics, hybridization, Mallard

LAY SUMMARY

- Mallard ducks are common worldwide but are declining in the Atlantic flyway of eastern North America, a decline that may be influenced by widespread hybridization between genetically wild Mallards and domestic game-farm birds that are released for hunting.
- We used hunter-harvested birds to investigate possible westward expansion and hybridization rates in the lower Mississippi flyway.
- Despite recovering 30% of samples possessing game-farm Mallard-derived mitochondrial DNA, only 4% were identified as hybrids across thousands of nuclear loci.
- Prevalence of game-farm Mallard-derived mitochondrial haplotypes were consistent in Mallards sampled a decade apart, suggesting mitochondrial introgression can be captured and persist within lineages far longer than nuclear DNA.
- Whereas the prevalence of wild × game-farm Mallard hybrids remains significantly less in the lower Mississippi relative to the Atlantic flyway, continued genetic monitoring and development of management strategies to abate future hybridization will be required.

Bajos niveles de hibridación entre individuos domésticos y silvestres de *Anas platyrhynchos* que invernan en la ruta migratoria inferior del Mississippi

RESUMEN

Anas platyrhynchos es un ave de caza ubicua y socio-económicamente importante en América del Norte. A pesar de su población generalmente abundante en el centro del continente, la especie está disminuyendo en el este de América

del Norte, lo que puede explicarse en parte por la hibridación extensiva con individuos de *A. platyrhynchos* liberados de granjas de caza de origen doméstico. Investigamos la composición genética de *A. platyrhynchos* en la ruta migratoria media e inferior del Mississippi, regiones clave de invernada para la especie. Descubrimos que casi el 30% de los individuos silvestres de *A. platyrhynchos* portaban haplotipos mitocondriales derivados de los individuos domésticos presentes en América del Norte, indicando que los individuos tenían un linaje femenino de individuos de granja en el pasado; sin embargo, los resultados nucleares identificaron solo un 4% del mismo conjunto de muestras como híbridos putativos. La recuperación del 30% de las muestras con haplotipos de ADNmt A del Viejo Mundo (VM) concuerda con las tendencias generales a lo largo de la ruta migratoria del Mississippi y este porcentaje se mantuvo estable en los individuos de *A. platyrhynchos* que muestreamos con una década de diferencia. La captura y perpetuación de los haplotipos de ADNmt A VM probablemente se debe a la estructura reproductiva de las hembras, mientras que la reversión de la señal nuclear hacia la ascendencia silvestre se debe al retro-cruzamiento secuencial y a una mezcla menor o en declive con individuos de *A. platyrhynchos* provenientes de las granjas de caza. Los estudios futuros sobre la ascendencia silvestre de los individuos de *A. platyrhynchos* de la ruta migratoria del Mississippi se beneficiarán de la unión de la tecnología molecular con la espacial a través de las rutas migratorias, las estaciones y los años para buscar transiciones potenciales de poblaciones de *A. platyrhynchos* con diferente ascendencia genética, y para determinar si la ascendencia genética está de alguna manera vinculada al lugar de nacimiento y subsecuente lugar de cría de un individuo.

Palabras clave: *Anas platyrhynchos*, conservación, ddRAD-seq, domesticación, genética, hibridación

INTRODUCTION

The Mallard (*Anas platyrhynchos*) duck is ubiquitous worldwide. Wild Mallards have been an important food source dating back to ancient peoples (Jensen et al. 2019) and were domesticated in Eurasia > 2,000 years ago (Boessneck et al. 1979, Larson and Fuller 2014). Human interest in the species explains continued efforts to hunt, observe, conserve, domesticate, relocate, and integrate these birds into societies and environments around the world. While these human-facilitated efforts have expanded Mallard numbers globally, they have also exacerbated hybridization with other duck species (Söderquist et al. 2017, Makino et al. 2018, Lavretsky et al. 2020). In North America, waterfowl biologists experimented with rearing and releasing wild-strain Mallards (Foley 1954, Bailey 1979, Gatti 1981); however, domesticated lineages derived from the old world have been used predominately in Mallard introductions and restorations, primarily in eastern North America (Rhymer et al. 1994, Rhymer and Simberloff 1996, Brown et al. 2019, Wells et al. 2019).

Domesticated animals often differ substantially from wild conspecifics genetically, morphologically, and ecologically (Ankney et al. 1986; Söderquist et al. 2017, 2021), and may have lower survival in the wild (e.g., <5%; Söderquist et al. 2021; 21–42%, respectively, Gunnarsson et al. 2008). Moreover, Champagnon et al. (2010) reported domesticated and domesticated × wild hybrids had 10% lesser lamellar density, suggesting they may have lower feeding efficiency on small seeds and invertebrates. Thus, extensive interbreeding between captive-reared and wild Mallards and subsequent gene flow of domestic-derived traits that are putatively maladaptive in the wild is hypothesized to partially explain currently declining wild Mallard populations in Europe (Champagnon et al. 2012, Söderquist et al. 2017) and eastern North America (Lavretsky et al. 2019, 2020).

In North America, the Mallard's geographical range has steadily expanded eastward outside their ancestral range of regions west of the Mississippi River since the 1900s (Heusmann 1974, Osborne et al. 2010, Lavretsky et al. 2020; Figure 1A). In addition to their range expansions being influenced by the conversion of eastern forests to agricultural and other open lands (Hanson et al. 1949, Heusmann 1974), extensive releases of hundreds of thousands of captive-bred Mallards along the eastern seaboard have occurred since the 1920s (Heusmann 1974, USFWS 2013, Lavretsky et al. 2020). This history of captive-release programs has been linked to marked changes in the ancestry of wild Mallards, with wild and captive-reared Mallard ancestry now readily found across North America (Lavretsky et al. 2019, 2020). In fact, the interbreeding between captive-reared and wild Mallards explains the presence of two divergent mitochondrial (mtDNA) lineages—Old World (OW; Eurasian Origin) A and New World (NW; North American Origin) B—now readily found across North American Mallards (Lavretsky et al. 2020). Though several evolutionary hypotheses could explain the presence of both haplotypes in North America (Ankney et al. 1986, Avise et al. 1990, Lavretsky et al. 2014a), recent molecular analyses confirmed that OW A haplotypes in North America were largely introduced through interbreeding between wild and captive-reared Mallards (Lavretsky et al. 2020). In fact, the frequency of interbreeding between released captive-bred and wild Mallards has resulted in the Atlantic flyway Mallard population coming to be considered a feral × wild Mallard hybrid swarm (Lavretsky et al. 2019, 2020). By 2010, ~8% of Mallards sampled throughout the Atlantic flyway were identified to be of wild ancestry compared to ~40% of those from the Mississippi flyway, whereas >90% of Mallards sampled west of the Mississippi River were wild descent (Figure 1A). Essentially, the proportion of Mallard populations consisting of individuals of wild ancestry

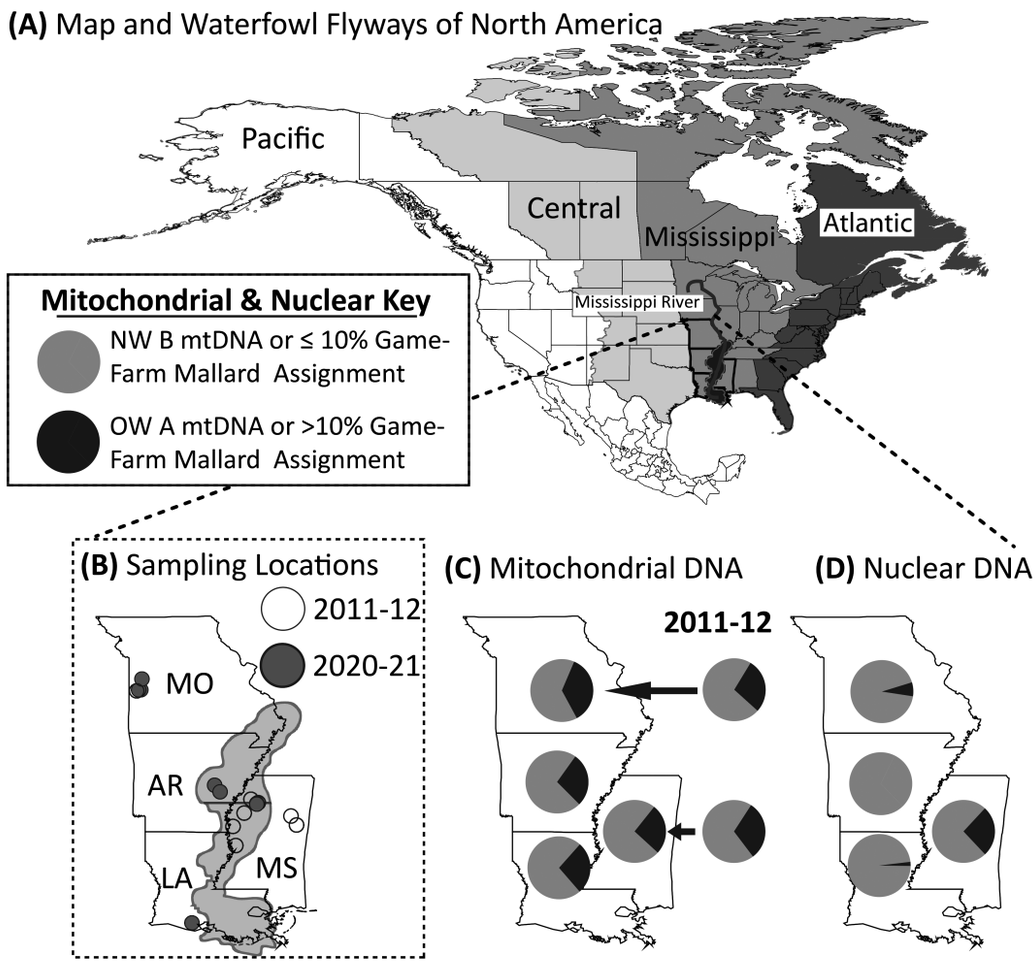

FIGURE 1. (**A**) Map of North America with the four Waterfowl flyways and the Mississippi River denoted and colored. The Mississippi Alluvial Valley is also highlighted on the map. (**B**) States and sampling locations are plotted spatially—Missouri (MO), Arkansas (AR), Mississippi (MS), and Louisiana (LA)—and temporally (i.e. 2011–2012 vs. 2020–2021 sampling years). (**C**) Proportion of samples possessing New World (NW) B vs. Old World (OW) A haplotypes by state for the 2020–2021 season shown inside and the 2011–2012 proportions for Missouri and Mississippi outside the state lines. (**D**) Proportion of samples collected in the 2020–2021 season and identified as pure wild or hybrid based on nuclear ddRAD-seq data are denoted for each state.

increases geographically westward and is closely associated with regions where captive-bred Mallards are not being released in numbers comparable to the Atlantic flyway (i.e. 210,000 captive-bred Mallards annually released in the Atlantic flyway; USFWS 2013).

Study System

The Mississippi flyway is one of the four primary flyways for migratory birds in North America (Lincoln 1935, Bellrose 1980, Davis et al. 2014, Herbert et al. 2021; Figure 1A). The Mississippi Alluvial Valley (MAV; Figure 1A) extends from southern Illinois through the terminus of the Mississippi River in Louisiana and is considered the ancestral wintering grounds for North American mid-continent Mallards (Bellrose 1980, Nichols et al. 1983, Reinecke et al. 1989, Baldassarre 2014). Despite the significant transformation of wetlands in this region, it remains one of the most important wintering areas for nonbreeding Mallards and other waterfowl in North America (Nichols et al. 1983, Davis et al. 2011, Pearse et al. 2012, Baldassarre 2014, North American Waterfowl Management Plan 2018). Mallards form pair bonds on wintering and migrational grounds, and males follow their mate to their breeding habitat of choice (Rhodes et al. 1995); thus, each winter individuals from different breeding habitats have the opportunity to intermix and reassort (Greenwood 1980, Anderson et al. 1992). As a result, several waterfowl breeding reference areas, including southern Saskatchewan, Manitoba, the Missouri River Basin, and other areas may contribute Mallards to the wintering population of the species using the MAV (Munro and Kimball 1982, Nichols and Hines 1987). However, how birds from specific regions (i.e.

prairie, prairie-parkland, and Great Lakes regions) and flyways distribute themselves spatially and temporally among wintering areas in the Mississippi flyway, especially with redistributions of wintering ducks occurring in relation to climate warming remains unknown (Meehan et al. 2021). Indeed, the largest exchange of Mallards has been reported to occur in the Mississippi flyway between midcontinent Mallards and those of the adjacent eastern flyway (Alisauskas et al. 2014). Taken in combination with the genetic swamping of eastern Mallards by game-farm ancestry, the Mississippi flyway supports wintering Mallards from different breeding regions that are now comprised of genetically distinct populations (Lavretsky et al. 2019). In fact, the mixing of these groups could explain partially the ~40% of Mallards from the northern Mississippi flyway (Great Lakes Region) carrying substantial captive-bred Mallard ancestry (Lavretsky et al. 2019). Importantly, wild and captive-reared Mallards have been shown to migrate at different rates and distances (Söderquist 2013, Heusmann 2017). Thus, it is possible that birds of different heritage can distribute across flyway space in distinct manners, although this remains unknown.

Here, we focus on the genetic ancestry of Mallards wintering in the central (west-central Missouri [MO]) and southern portions of the Mississippi flyway (Arkansas [AR], Mississippi [MS], Louisiana [LA]; Figure 1B). We used mtDNA and thousands of nuclear sequences of several hundred Mallard samples and comparable reference wild and domestic Mallards to test for the occurrence of captive-bred Mallard ancestry in mallards harvested in the aforementioned four states. In addition to describing current ancestry, we compared the genetic integrity of wintering populations sampled a decade apart (i.e. winters 2011–2012 vs. 2020–2021) to determine the stability of wild and captive-bred Mallard ancestry through time. Given that Mallard exchange between the Mississippi and Atlantic flyways appears to occur in the Great Lakes and northern Mississippi flyway regions (e.g., Minnesota, Wisconsin, and Iowa; Otis 2004), Mallards wintering in the central and lower Mississippi flyway (e.g., Arkansas, Mississippi, and Louisiana) may originate from the Central flyway or more northern areas of Canada, both of which have lower levels of introgression of captive-bred ancestry (Lavretsky et al. 2019). Thus, we expected to find stable and largely wild Mallard ancestry within the southern region.

METHODS

Sample Collection and DNA Extraction

A total of 369 and 130 Mallards were sampled from hunter-killed birds during autumn–winters of 2011–2012 and 2020–2021, respectively. Specifically, samples from the 2011–2012 hunting season were collected in west-central Missouri and Mississippi, while we expanded geographical sampling for the 2020–2021 hunting season to also include Arkansas and Louisiana (Figure 1A). In the end, we either conducted temporal comparisons between states sampled between decades (i.e. west-central Missouri and Mississippi) or among states within the same time period, and we acknowledge that sample sizes are unequal between the two types of analyses.

DNA was extracted for all 499 samples using a DNeasy Tissue Kit (Qiagen, Valencia California, USA), following the manufacturer's protocols. We ensured DNA quality based on the presence of high molecular weight bands visualized using gel electrophoresis with a 1% agarose gel, and quantified using a Qubit 3 Fluorometer (Invitrogen, Carlsbad, California, USA) having a minimum concentration of 20 ng/μL.

Mitochondrial DNA Sequencing and Analyses

We used primers *L78* and *H774* to polymerase chain reaction (PCR) to amplify and sequence ~625 base pairs (bp) of the mitochondrial control region (Sorenson and Fleischer 1996, Sorenson et al. 1999), following PCR reaction concentrations and thermocycler conditions described in Lavretsky et al. (2014b). The PCR products were visualized via agarose electrophoresis and then purified using either the QIAquick PCR Purification kit (Qiagen) or ExoSAP-IT (ThermoFisher). Clean PCR products were then sent for Sanger sequencing using the *L78* primer on a 3130XL Genetic Analyzer at either the Core Laboratories of Arizona State University School of Life Sciences or the University of Texas at El Paso, Border Biomedical Research Center's Genomic Analysis Core Facility. Sequences were aligned and edited using Sequencher 4.8 (Gene Codes) and all sequences were subsequently submitted to GenBank (see Supplementary Material Table S1 for accession numbers). We note that mtDNA control region sequences for reference wild and domestic mallards from previous studies were included in the analyses (Lavretsky et al. 2014a, 2014b, 2019, 2020).

Relationships among mtDNA haplotypes were assessed through a median-joining network constructed with POPART (Leigh and Bryant 2015). Given that mtDNA haplotypes can be permanently captured through maternal inheritance, we were particularly interested in individuals possessing OW A mtDNA haplotypes as this is a proxy to determine individuals in which their lineage at some point included a female captive-bred Mallard (Lavretsky et al. 2020). This was especially informative for early 2011–2012 Mallard samples for which we were unable to assess nuclear variation (see below). Consequently, in addition to visualizing haplotype relationships, we examined OW A vs. NW B haplotype ratios across space (i.e. four states) and time (2011–2012 vs. 2020–2021).

Nuclear DNA ddRADseq Library Preparation, Sequencing, and Bioinformatics

For the 2020–2021 Mallard samples, we followed procedures presented by Lavretsky et al. (2015), but with fragment size selection following Hernandez et al. (2021) to create multiplexed double digest restriction-site associated DNA (ddRAD-seq) fragment libraries. Briefly, we enzymatically fragmented genomic DNA using *SbfI* and *EcoRI* restriction enzymes and ligated Illumina TruSeq compatible barcodes that permitted future de-multiplexing. We pooled libraries in equimolar concentrations, and 150 bp, single-end (SE) sequencing was completed on an Illumina HiSeq X at Novogenetics LTD (Sacramento, California, USA). Illumina reads were deposited in NCBI's Sequence Read Archive (SRA; http://www.ncbi.nlm.nih.gov/sra; see Supplementary Material Table S1 for SRA data).

We used the *ddRADparser.py* script of the BU ddRAD-seq pipeline (DaCosta and Sorenson 2014) to de-multiplex raw Illumina reads based on perfect barcode/index matches. As with mtDNA, previously published ddRAD raw sequence data generated using the same protocols were included in alignments and subsequent analyses, serving as reference wild Mallard (Lavretsky et al. 2019) and domestic Mallards (Lavretsky et al. 2020). Note that known game-farm Mallards and Khaki Campbells were included as known domestic lineages, with the latter one serving as a genetic signature of a "park" duck, another potential source of hybridization with wild Mallards (also see Lavretsky et al. 2020). All sequences were first trimmed or discarded for poor quality using trimmomatic (Bolger et al. 2014), and then the remaining quality reads aligned to a reference Mallard genome (Huang et al. 2013) using the Burrows Wheeler Aligner 07.15 (bwa; Li and Durbin 2011). Next, samples were sorted and indexed in Samtools 1.6 (Li et al., 2009) and combined using the *mpileup* function with the following parameters "-c -A -Q 30 -q 30." All steps through *mpileup* were automated using a custom in-house Python script (Python scripts available at https://github.com/jonmohl/PopGen). Next, we used VCFtools 0.115 (Danecek et al. 2011) to further filter variant call format files for any base pair missing >5% of samples, which also required a minimum base-pair sequencing depth coverage of 5X (i.e. 10X per genotype) and quality per base PHRED scores of ≥30 to be retained.

Though only autosomal loci were used in subsequent population structure analyses, the alignment of ddRAD-seq loci to our reference genome also provided positions across sex chromosomes, allowing us to use differences in expected sequencing depth to demarcate sex across samples. In short, the heterogametic sex (i.e. female; ZW) is expected to have half the sequencing depth across both sex-chromosomes as compared with autosome-linked loci, whereas the homogametic sex (i.e. males; ZZ) shows the same sequencing depth at Z-sex chromosome and autosome linked loci and no W-linked loci (also see Lavretsky et al. 2015).

Nuclear Analyses

To evaluate nuclear population structure, we used only the autosomal ddRAD-seq bi-allelic single nucleotide polymorphisms (SNPs). Prior to analyses, we used PLINK 0.70 (Purcell et al. 2007) to ensure that singletons (i.e. minimum allele frequency [maf] = 0.0038) and any SNP missing >5% of data across samples were excluded in each dataset. Additionally, we identified independent SNPs by conducting pair-wise linkage disequilibrium (LD) tests across ddRAD-seq autosomal SNPs (--indep-pairwise 2 1 0.5) in which one of two linked SNPs are randomly excluded if we obtained an LD correlation factor (r^2) >0.5. We conducted all analyses without a priori information on population or species identity.

First, we used the principal component analysis (PCA) function in PLINK to perform a PCA. Next, we used ADMIXTURE 1.3 (Alexander et al. 2009, Alexander and Lange 2011) to attain maximum likelihood estimates of population assignments for each individual, with datasets formatted for the ADMIXTURE analyses using PLINK, and following steps outlined in Alexander et al. (2012). We ran each ADMIXTURE analysis with 10-fold cross-validation, incorporating a quasi-Newton algorithm to accelerate convergence (Zhou et al. 2011). Each analysis used a block relaxation algorithm for point estimation and terminated once the change in the log-likelihood of the point estimations increased by <0.0001. We ran separate ADMIXTURE analyses that included all possible samples and another excluding Khaki Campbell mallards. Each analysis was run for K populations of 1 through 5, and with 100 iterations per each value of K. The optimum K in each analysis was based on the average of cross-validation errors across the iterations per K value; however, we examined additional values of K to test for further structural resolution across analyses. We used the R package PopHelper (Francis 2016) to convert ADMIXTURE outputs into CLUMPP input files at each K value, and to determine the robustness of assignments of individuals to populations at each K value with the program CLUMPP 1.1 (Jakobsson and Rosenberg 2007). In CLUMPP, we employed the Large Greedy algorithm and 1,000 random permutations. Final admixture proportions for each K value and per sample assignment probabilities (Q estimates; the log-likelihood of group assignment) were based on CLUMPP analyses of all 100 replicates per K value. In addition to the above replicates, standard deviations were calculated under the optimum K population value based on 1,000 bootstraps as implemented in the ADMIXTURE program. Doing so permitted us to evaluate how sensitive our assignment probabilities were given our SNP dataset.

RESULTS

Sequencing and Data Output

We attained 587 overlapping base pairs of the mtDNA control region across 645 novel and reference Mallards in both decades (Supplementary Material Table S1). For 130 (of 133) of the 2020–2021 and reference Mallard samples, we recovered 2,524 ddRAD-seq autosomal loci (657,507 bp and 19,740 bi-allelic SNPs) that met our criteria for sequencing coverage and missing data (see specifics in Supplementary Material Table S1). We had an average depth of 107 sequences/locus and a depth range of 27–163 sequences across samples. In addition, plotting sequencing depth ratios between autosomal and recovered W- and Z-sex chromosome linked ddRAD-seq loci correctly assigned sex across 2020–2021 Mallard samples (Supplementary Material Figure S1); only female Mallards were sampled in the 2011–2012 season and used as a control for sex identification in the analysis.

Mitochondrial DNA

The mtDNA haplotype network recovered known OW A and NW B haplogroups that included 55 and 209 total haplotypes, respectively (Figure 2A). Of 132 samples collected in 2020–2021, 95 (72%) and 37 (28%) carried NW B and OW A haplotypes, respectively. Generally, we found a 70:30 ratio of NW B vs. OW A haplotypes despite sampling efforts being a decade apart in Mississippi and Missouri (Figure 1C). Generally, the 70:30 ratio recovered across analyzed states was concordant with results for the wild Mallard reference set here (Figure 2C), and those previously reported for the Mississippi flyway more generally (Lavretsky et al. 2019). As expected, haplotypes of the reference game-farm and Park Mallards were all within the OW A haplogroup (Figure 2A and C).

Nuclear DNA

Population structure analyses were based on 19,727 independent bi-allelic SNP dataset with samples collected across Missouri, Arkansas, Mississippi, and Louisiana. First, plotting the first two components of the PCA differentiated and recovered near equidistant relationships between wild, game-farm, and feral Khaki Campbell Mallards (Figure 2B). Nearly all 2020–2021 samples from the Mississippi flyway overlapped samples serving as our reference wild Mallards in the PCA. This pattern was further supported in the ADMIXTURE analysis of all samples where an optimum K population of three was recovered distinguishing between Khaki Campbell, game-farm, and wild mallards (Supplementary Material Figure S2). However, unlike previous analyses that showed clearer assignment probabilities between the two domestic forms (Lavretsky et al. 2020, 2021), our Khaki Campbell Mallards showed split ancestry between their unique cluster and game-farm mallards. Given that none of the wild sampled Mallards showed clustering toward Khaki Campbell Mallards in the PCA (Figure 2A), we used assignment probabilities attained from ADMIXTURE analyses excluding them (Figure 2C). Finally, overlapping game-farm ancestry and their respective standard deviations attained from 1,000 bootstrap replicates provided highly correlated ($r^2 > 0.99$) values to our original assignments and an average deviation of ~1.5%, providing confidence in our ancestry assessments based on the SNP dataset. In the end, we recovered only five (4%) samples possessing substantial (i.e. >10%; Lavretsky et al. 2020) game-farm Mallard ancestry, with one individual recovered in Louisiana and four in Mississippi (Figures 1C and 2C). Finally, only one of these nuclear hybrids possessed an OW A haplotype (Figure 2C, Supplementary Material Table S1).

DISCUSSION

Genetics of wild North American Mallards continue to be influenced by releases of game-farm Mallards since the 20th century (Lavretsky et al. 2020). At the flyway level, Lavretsky et al. (2019) reported nearly 40% of sampled Mallards possessed substantial game-farm Mallard ancestry. In contrast, we discovered that 96% of 130 Mallards collected in Missouri, Arkansas, Mississippi, and Louisiana had pure North American wild ancestry (Figures 1 and 2). Moreover, we did not identify any sample that represented feral game-farm Mallards or early hybrids (i.e. F1 and F2), as has been reported previously (Lavretsky et al. 2019, 2020, 2021, Lawson et al. 2021). Our results contrast with other North American areas where the releases of game-farm Mallards have significantly impacted the genetic composition of those Mallards (e.g., Atlantic flyway). In short, recovering ~30% of samples with OW A mtDNA haplotypes today is concordant with more general trends of the Mississippi flyway sampled a decade ago by Lavretsky et al. (2019), as well as those states temporally sampled here (Figure 1C). Thus, we suggest the retention of OW A mtDNA haplotypes may be due to mitochondrial capture and perpetuation of these lineages among breeding females, whereas backcrossing and lower or declining admixture with game-farm Mallards reversed the nuclear signal back to wild ancestry in many of these lineages.

Mallards sampled from more northern reaches of the Mississippi flyway and into the Great Lakes Region have greater proportions of Mallards with game-farm ancestry (Lavretsky et al. 2019). This is supported by existing banding and telemetry data (Green and Krementz 2008, Krementz et al. 2012, Alisauskas et al. 2014) that show an exchange between Mallards breeding in the Mississippi and Atlantic flyways during migration and winter. So,

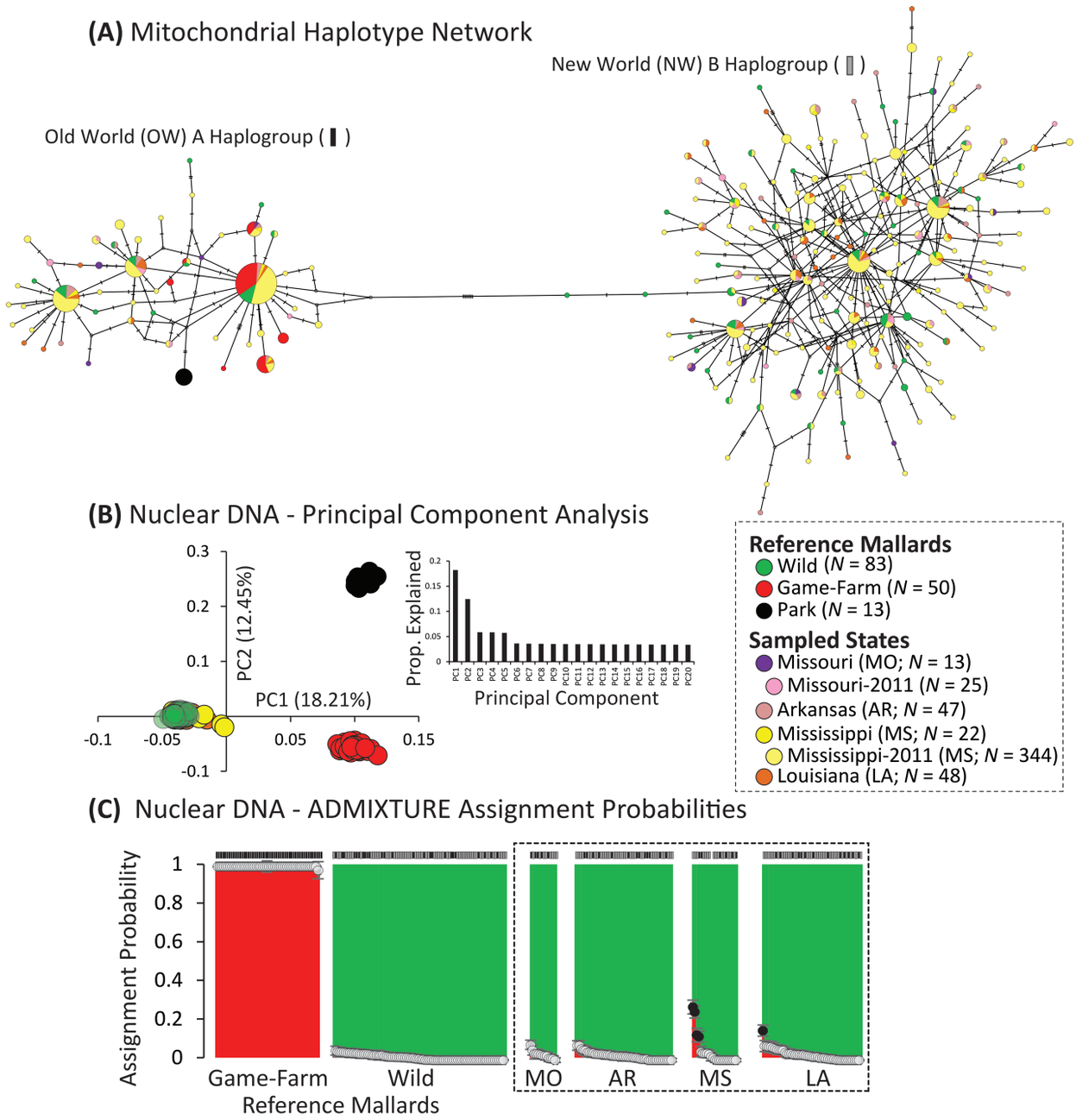

FIGURE 2. (**A**) A haplotype network reconstructed from 587 base pairs of the mitochondrial control region (mtDNA) for sampled North American reference populations of wild and domestic mallards, as well as samples from Missouri (MO), Arkansas (AR), Mississippi (MS), and Louisiana (LA). Sampled groups are color coded or indicated on the network, including respective sample sizes, as well as whether samples were collected in the 2011–2012 (MO and MS samples indented in the key) and 2020–2021 seasons. Circles in the network denote different haplotypes with circle size proportionate to the number of samples represented within the haplotype, and the number of mutations separating two haplotypes equal the number of hash marks. (**B**) Plot of the first two principal components for the PCA of nuclear ddRAD-seq data from reference wild and domestic mallards, as well as samples from MO, AR, MS, and LA. Inset includes the proportion of variation explained by each principal component. (**C**) Nuclear ddRAD-seq data based ADMIXTURE assignment probabilities for *K* populations of two for reference game-farm and wild mallards, as well as those samples collected in the study. In addition, assignment probability to the game-farm mallard genetic cluster and respective standard-errors are overlaid across samples, and with the five putative hybrids denoted by black circles. Finally, bars above ADMIXTURE assignment probabilities denote whether the sample harbored OW A (black) or NW B (grey) haplotypes.

whereas breeding Mallards from both flyways are known to winter in the northern parts of the Mississippi flyway (e.g., Minnesota, Wisconsin, and Iowa; Otis 2004, Meehan et al. 2021), Mallards originating from the prairie pothole and parkland regions of the Central flyway are overwintering in the middle and southern regions of the Mississippi flyway (e.g., Arkansas, Mississippi, and Louisiana; Otis 2004, Krementz et al. 2012). These populations are largely distinct genetic stocks, with those of the Central flyway being predominantly wild, unlike the feral and feral × wild hybrids in the Atlantic flyway (Lavretsky et al. 2019). We note that understanding whether the five putative nuclear hybrids resulting in elevated hybrid prevalence in Mississippi and Louisiana (Figure 1D) is biologically relevant will require regular sampling efforts to monitor these dynamics over time.

Additionally, we posit that the genetic patterns we recovered also may be explained by spatio-temporal dynamics related to the location of Mallards with variable ancestry across autumn–winter months. For example, while the general lack of hybrids in the lower Mississippi flyway may be due to Mallards of mixed ancestry being infrequently present in the mid- and lower Mississippi flyway, there may be a turn-over of Mallards of varying genetic ancestry occurring differentially over space and time during autumn–winter. Coupling molecular and GPS spatial technology may help elucidate the potential reason(s) for the apparent unique levels of wild ancestry of Mallards within the southern parts of the Mississippi flyway. Moreover, this combined approach may reveal whether genetic ancestry influences subsequent breeding locations.

Historical Perspective and Potential Mechanisms Maintaining Wild Mallard Ancestry

Although only 4% of contemporary Mallards had game-farm Mallard ancestry at nuclear loci, ~30% possessed OW mtDNA haplotypes (Figure 1C and D). In fact, we found no change in the ratios of OW and NW mtDNA haplotypes that we sampled in the 10-year span for birds collected in Mississippi and Missouri (Figure 1C). This stability suggests Mallards wintering in the sampled region at some point in time experienced introgression by game-farm or game-farm × wild Mallard hybrids. However, if socio-behavioral and mating interactions were lingering between wild and feral Mallards, we would expect to see increasing OW A Mallard presence in our sampling region through time, but this was not the case (Lavretsky et al. 2019). Furthermore, if only male game-farm Mallards were introducing the domestic ancestry, then we should have detected their influence on the nuclear variation of the population irrespective of the mtDNA lineage (i.e. game-farm exclusive mtDNA haplotypes), but this also was not the case. Thus, we conclude that the lower Mississippi flyway was at some point impacted by game-farm Mallards, similarly to the rest of the flyway (Lavretsky et al. 2019) but has since experienced a decrease in game-farm mallard introgression.

By examining both mtDNA and nuclear DNA, we obtained a more complete understanding of current and historical hybridization. Previous work has demonstrated that backcrossing only three or four generations into the same parental population can cause complete genetic replacement of nuclear DNA (Lavretsky et al. 2016, 2019). Conversely, given the life history and breeding philopatry of female ducks and female progeny (Rohwer and Anderson 1988, Anderson et al. 1992), mtDNA can be captured within these maternal lineages and perpetuated for much longer than nuclear DNA. While possessing an OW A haplotype suggests that an individual had a female game-farm Mallard in their historical past, deciphering current genetic integrity requires nuclear evidence. Additionally, understanding recombination events across full genomes will be required to better establish the true generation each putative hybrid represents as the number of recombination events is expected to be proportional to the number of backcrossing events since the original hybridization event (Janzen et al. 2018, Lavretsky et al. 2019).

Conclusions

Despite increasing presence and possible threat of hybridization between game-farm and wild Mallards (Lavretsky et al. 2019, 2020, 2021, Lawson et al. 2021), our results of the genetic ancestry of Mallards sampled from the middle and lower Mississippi flyway region contrast with the general trend of increased levels of game-farm × wild Mallard hybridization in much of the Atlantic flyway and the northern region of the Mississippi flyway. We hypothesize that the probability of recovering individuals of mixed ancestry may be explained by geography, temporal differences in the migratory phenology by wild vs. mixed ancestry Mallards, redistributions of wintering Mallards with climate warming (Meehan et al. 2021), and various sociobiological factors. This scenario seems consistent with previous telemetry and band-recovery studies showing how midcontinent Mallards are often recovered in the middle to lower Mississippi flyway region, whereas Atlantic flyway Mallards tend to be recovered in more northern parts of the Mississippi flyway (Bellrose 1980, Otis 2004). Thus, future research will especially benefit from understanding how each of the adjacent flyways that hold populations of significantly different genetic Mallard ancestry influence Mallard population composition and dynamics within the Mississippi and other flyways.

Finally, contrasting evidence of hybridization provided by mitochondrial and nuclear DNA exposes the potential

biases in making inferences when using only one of these marker types. In fact, we conclude that the retention of OW A mtDNA haplotypes among nuclear wild individuals (Figure 2C, Supplementary Material Table S1) may be due to mitochondrial capture and perpetuation of these lineages among breeding females, whereas backcrossing and lower or declining admixture with game-farm Mallards reversed the nuclear signal back to wild ancestry in many of these lineages. Thus, future research should be cognizant of the potential for backcrossing but also how the differential inheritance among markers and the biology of their organisms may create discordances. Together, the conservation and management of wild Mallard populations clearly require an enhanced understanding of the biological consequences of gene flow from domestic ducks into the wild Mallard gene pool, including the consideration by wildlife biologists of how wild populations experience high frequency of hybridization with domestic conspecifics should be managed and regulated (Gering et al. 2019, Hirashiki et al. 2021, Tanaka et al. 2021).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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Author contributions: J.B.D., D.C.O., R.M.K., and P.L. conceived the idea and designed the experiment. J.B.D., R.M.K., and K.M.R. collected specimens. D.C.O. and P.L. collected molecular data. P.L. analyzed data. J.B.D., D.C.O., R.M.K., K.M.R., and P.L. equally contributed to the writing of the manuscript.

Data availability: Analyses reported in this article can be reproduced using the data provided by Davis et al. (2022). Raw Illumina data in SRA and mtDNA Sanger Sequence accession numbers are provided across samples in Supplementary Material Table S1.

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