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RESEARCH ARTICLE

Geographic origins and genetics of eastern and Great Lakes mallards

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Abstract

Eastern and Great Lakes populations of mallards (*Anas platyrhynchos*) have experienced a significant decline in recent years. These subpopulations are increasingly wild × game-farm mallard hybrids because of widespread releases of game-farm individuals. Concurrent with an increasing prevalence of releases, a near 50% decline in mallard populations in the United States occurred, while abundances remained stable in Canada. We aimed to refine our understanding of the metapopulation dynamics of eastern North American and Great Lakes mallards to provide information useful in population and harvest management. We used stable isotope and genetic techniques during pre-hunting season (July–September) banding to determine if banding location was representative of hatch or molt origin of mallards and if wild mallards captured and banded had more northern origins than wild × game-farm hybrids. Mallards are expected to be largely of local origin during the pre-hunting season, but nearly 50% of our sample had an origin north of their banding site, suggesting substantial movements during the banding period. We detected a similar percentage of wild × game-farm hybrid prevalence for the eastern mallard population (~89%), but a substantial increase in the Great Lakes region (~75%) compared to prior studies. However, we did not detect strong evidence for geographic or temporal variation in isotopic values (i.e., origins) of wild and hybrid mallards, which suggests that genotypes of mallards occurred together throughout the sampling period. Our results

suggest that banding location of mallards in eastern North America does not equate to breeding ground origin or genotype (wild or hybrid), and we recommend investigation of other methods to understand if vital metrics differ among regions and genotypes. The movement we inferred during the banding season could potentially violate important assumptions that birds do not move among banding units and confound population vital rates estimated using banding returns. Thus, we recommend that current integrated population models consider eastern mallards as a single population because their movement throughout the banding period makes assessment at smaller geographic units invalid.

KEYWORDS

Anas platyrhynchos, Atlantic Flyway, hydrogen, Mississippi Flyway, stable isotope

Migration is defined as the movement of animals from one geographic area to another in search of food resources, reproductive needs, or better conditions (Dingle and Drake 2007). Among organisms, birds readily adopt the practice of seasonal migration, as over half of the estimated 10,000 bird species worldwide are considered migratory (Berthold 2001). Long-term banding programs of waterfowl in North America provide a basis for understanding connections between breeding areas, migration corridors, and wintering areas (Bellrose 1980), as well as information on vital rates used in population modeling (Anderson et al. 2018).

Three primary populations of breeding mallards (*Anas platyrhynchos*) have been identified using banding data according to their breeding ground affiliations: western, mid-continent, and eastern (U.S. Fish and Wildlife Service [USFWS] 2020). The Great Lakes population is considered part of the mid-continent population but is also monitored separately (USFWS 2022). The eastern breeding population of mallards has declined by about 40% since the 1990s, when the eastern waterfowl population survey was initiated (USFWS 2020). In the Great Lakes region, the mallard population declined by 19% over the same period (Schummer et al. 2023). However, the decline has not been population-wide. Mallard breeding pair abundance has been stable in eastern Canada but is declining in the northeastern United States (USFWS 2020). Although there is extensive research on the demographics of mid-continent and western mallards, there are substantial gaps in knowledge for the eastern population.

Mallards were not common in the Atlantic Flyway until about the 1940s (Allen 1909, Eaton 1910, Heusmann 1991). Two hypotheses are proposed for how mallards became common in eastern North America: 1) expansion of mid-continent mallards eastward (Johnsgard 1961, Johnsgard, DiSilvestro 1976) and 2) large-scale releases of game-farm mallards used to augment wild populations and provide additional hunting opportunity (Huntington 1910, Hepp et al. 1988). Although the decline of eastern mallards is not well understood, one proposed mechanism for the decline of eastern mallards is the introgression of game-farm mallards into portions of the eastern breeding range of mallards (Lavretsky et al. 2019, 2020). The eastern mallard and Great Lakes population comprises wild North American mallards, released game-farm mallards, and varying degrees of wild × game-farm mallard hybrids (Lavretsky et al. 2019, 2020; Schummer et al. 2023). Given that wild and game-farm mallards are known to significantly differ in various vital rates such as survival (Soutiere 1989, Söderquist et al. 2021), these differences may confound population estimates when using a single, range-wide population model for eastern mallards or mid-continent mallards.

Data from the eastern breeding population of mallards suggest that most mallards harvested in the eastern United States are banded there and, to a lesser extent, in Canada. However, the natal origins of ducks are uncertain unless they are banded prior to fledging (Crissey 1955). Furthermore, some areas where mallards nest in Canada are difficult to access, which may geographically bias banding effort and harvest derivation estimates (Hobson et al. 2009*b*).

Among the important assumptions when banding data are used for harvest derivations and in population modeling is that populations do not move between survey units (Munro and Kimball 1982). Mallards are considered a facultative migrant and are generally thought to be a late migrant relative to most other waterfowl (Schummer et al. 2010, Baldassare 2014, Van Den Elsen 2016). Krementz et al. (2012) report the mean fall migration start date of mallards in the mid-continent to be 23 October (range = 17 September–7 December). However, other research suggests the possibility of movement of mallards prior to the hunting season. Palumbo et al. (2019) detected that a substantial portion of mallards harvested on the Canadian side of Lake St. Clair, Ontario, at the beginning of the hunting season in September originated from locales farther north. Additional research on the origins of harvested juvenile mallards in the Atlantic Flyway suggests that 64% of birds harvested in the United States originated from Canada (Kucia et al. 2023); this pattern was consistent even at the beginning of the hunting season. The studies above highlight the need to reevaluate the assumption that banding during the pre-hunting season (July–September) represents locally produced mallards.

Measuring naturally occurring stable isotopes is useful in determining the source areas (natal or molting origins) of unmarked eastern mallards and could help refine our knowledge about harvest derivation (Wassenaar 2019). Stable hydrogen isotope measurements in feathers (δ^2H_f) may be used to estimate spatial origins of individuals banded during the pre-hunting season banding period (pre-season, Asante et al. 2017). Stable isotope analysis uses isotopic patterns or isoscapes that depict natural gradients that vary from north to south over broad landscape scales (Hobson et al. 2009*a*, Ashley et al. 2010, Guillemain et al 2014). Feathers are metabolically inert after they are formed, so δ^2H measurements of feathers reflect where they were grown. Juvenile waterfowl grow their flight feathers at their natal locations, and adults undergo a complete wing molt that renders them flightless. As a result, δ^2H measurement of feathers can represent a juvenile's natal location and where adults molted during summer (Kusack et al. 2023*a*).

Overall, the goals of this study were to validate the assumptions used for analysis of banding during the pre-season and determine the extent of game-farm mallard hybridization in the sample. Our first objective was to determine what percentage of mallards banded during the pre-season originated nearby or did not migrate from north or south of their banding location. Given recent information in Palumbo et al. (2019) and Kucia et al. (2023) that banded and harvested mallards were from areas farther north of their expected locations, we expected that some proportion of captured mallards would originate away from banding locations during the pre-season. Our second objective was to investigate the relationships of sex, age, and date of banding on the origin of banded individuals. We predicted that over the banding period (July–September), δ^2H_f of captured mallards would become increasingly representative of natal and molt origins from farther north, as a result of movement of mallards during the banding season. We also predicted that adult males would differ in δ^2H_f from adult females or juveniles because molt migration is common in adult males (Bellrose 1980). Our final objective was to determine the levels of hybridization and the relationship between mallard genotype and δ^2H_f. We predicted that mallards with a more northern δ^2H_f value and banding location would have a greater percentage of wild mallard ancestry than those with southern δ^2H_f values. We predicted this because the majority of game-farm mallard releases have occurred along the mid-Atlantic coast and not Canada (Heusmann 1991), so we expected greater proportions of wild ancestry mallards at more northern latitudes.

STUDY AREA

We distributed our sampling effort spatially and temporally across the upper portions of the Atlantic and Mississippi flyways in the United States, including Maine, New Hampshire, Vermont, Massachusetts, Connecticut, New York, Pennsylvania, Ohio, Michigan, Illinois, Indiana, and Wisconsin, and the provinces of Quebec and Ontario, Canada,

July–September 2019–2021. These regions experience seasonality and a range of climates including harsh winters with appreciable amounts of snow and warm, humid summers. Types of geography range widely but include coastal wetlands, inland forested areas, and several rivers and bays in the Atlantic flyway, and relatively flat terrain such as prairies, seasonal wetlands, and the Mississippi River system in the upper Mississippi flyway.

METHODS

Sample collection

We asked state and provincial waterfowl banders to collect 40 feather and 20 blood samples from each state and province each year, pairing feathers and blood samples (Table S1). We aimed for an equal number of samples before and after 15 August, and by age (juvenile and adult) and sex cohorts. Banders collected a 1-cm sample of the distal end of the P1 feather (i.e., the primary feather adjacent to the secondaries) for stable isotope analysis. The Cornell Stable Isotope Laboratory processed the feather samples for δ^2H. The genetic samples consisted of approximately 0.01 ml (8–10 drops) of blood stored in DNA buffer, which was held at −80°C and processed at the Population and Evolutionary Genetics Lab at the University of Texas, El Paso.

Stable hydrogen isotope analysis and assignment to origin

Technicians washed samples in a 2:1 chloroform:methanol solution, air dried samples in a fumehood, loaded a subsample (0.35 mg) of vane material into silver capsules, crushed subsamples, and placed them with internal lab standards into a desiccator for a minimum of 3 days. They then loaded samples into a Zero Blank carousel (Costech Analytical Technologies, Valencia, CA, USA) under helium flow. Pyrolysis combustion on glassy carbon took place at 1,350°C in a Thermo Scientific Temperature Conversion Elemental Analyzer (Thermo Scientific, Bremen, Germany) coupled via a Conflo IV (Thermo Scientific) to a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer. The laboratory conducted analysis of δ^2H using the comparative equilibration method of Wassenaar and Hobson (2003) with 3 calibrated keratin reference materials (CBS, δ^2H = −197‰; KHS, δ^2H = −54.1‰; SPK, δ^2H = −121.6‰) corrected for linear instrumental drift. Based on within-run and across-run analyses of a third keratin standard, measurement error was approximately ± 3‰ for δ^2H_f. All δ^2H_f values are reported relative to the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW-SLAP) scale.

We used likelihood-based algorithms to produce spatially explicit assignments of source areas based on analysis of δ^2H_f data (Hobson et al. 2009*b*, Wunder 2010). We created an isoscape for predicted δ^2H_f by applying a rescaling function derived by regressing δ^2H_f of known origin mallards against amount-weighted growing season precipitation δ^2H (Van Dijk et al. 2014). We selected this calibration equation because it is the most recently published equation for dabbling ducks and analysis shows it is the most accurate and precise calibration equation to apply to North American dabbling ducks (Kusack et al. 2023*a*). We set the standard deviation of the residuals at 12.8‰ based on estimations from Clark et al. (2006, 2009). We delineated the breeding range of mallards from range maps (BirdLife International and Handbook of the Birds of the World 2019), and spatially explicit assignments were limited to their breeding range. We calculated the likelihood that individual cells (i.e., pixels) within the derived δ^2H_f isoscape represented a potential source area for a given sample by comparing the measured δ^2H_f with the isoscape-predicted δ^2H_f using a normal probability density function (Hobson et al. 2009*b*, Palumbo et al. 2020). We then applied the Bayes' Theorem to assess the posterior probability that an individual pixel within the isoscape was the putative area of a given sample (Hobson et al. 2009*b*, Palumbo et al. 2020). We normalized the probabilities of all pixel origins to one. We then assigned individuals to source areas within the isoscape by selecting the raster cells that were consistent with the upper 67% of estimated probabilities of origin for each individual and coded those as

one and all others as zero, consistent with 2:1 odds (Palumbo et al. 2019, 2020). Subsequently, we summed results of the assignments over all individuals by adding the surfaces, providing a final surface of the distribution of the number of individuals assigned to each pixel (Hobson et al. 2009*b*, Palumbo et al. 2020). The surfaces adequately reflected uncertainty because they were propagated in the Bayesian model and came from the best estimate of error of δ^2H_f between individuals at any given site.

We determined whether individuals originated within a region (originating near the banding region) or outside the region (migrating into the banding region) using likelihood-based assignments. First, we calculated the expected value (δ^2H_b) for each banding station by applying the rescaling function using the mallard calibration equation ($\delta^2H_f = -27.4 + [1.28 \times \delta^2H_p]$; Van Dijk et al. 2014). We then compared the observed δ^2H_f to the δ^2H_b at the sight of capture using a normal probability density function (mean = δ^2H_b) and the expected variation using the distribution of residuals (SD = 12.8‰ from the Clark et al. [2006, 2009] rescaling function). If the observed δ^2H_f occurred within ±12.8‰ of δ^2H_{fd} (expected δ^2H_f), we classified the duck as within region (i.e., was produced in the area if juvenile or molted in the area if adult) based on a 2:1 odds ratio. We classified mallards outside the δ^2H_{fd} range for the banding station as outside (north or south) of the region. We further described individuals that were classified as originating north of the banding station based on how many standard deviations away from the banding station to highlight the distance from the banding station, Only latitudinal (i.e., north or south) classification is possible because of the underlying precipitation isoscape for North America, which generally follows a north-south gradient in eastern Canada and the United States.

Genetic analysis

We extracted genomic DNA from 558 blood samples using a DNeasy Blood and Tissue kit following the manufacturer's protocol (Qiagen, Valencia, CA, USA). The DNA quality was based on the presence of a high molecular weight band visualized using gel electrophoresis and with a 1% agarose gel, and quantified using a Qubit 3 Fluorometer (Invitrogen, Carlsbad, CA) to ensure a minimum concentration of 20 ng/μL.

We prepared double-digest restriction-site associated DNA sequencing (ddRAD Seq) libraries following Lavretsky et al. (2015), and with fragment size selection protocols as outlined in Hernández et al. (2021). We first digested approximately 0.2 ng of genomic DNA with 10 U each of SbfI and EcoRI restriction enzymes, followed by ligating adapters containing sequences compatible with TruSeq reagents (Illumina, San Diego, CA) and barcodes for de-multiplexing. We then conducted double-sided size selection based on a 0.8X solution of AMPure XP beads (Beckman Coulter, Brea, CA) that included a 0.55X and 0.25X solution for right- and left-sided selection. The protocol repeatedly targets an average fragment length of 350 base pairs (bp). We then amplified size-selected DNA through polymerase chain reaction (PCR) with Phusion High-Fidelity DNA Polymerase (Thermo Scientific), and with amplified products once again cleaned using a 1.8X solution of AMPure XP magnetic beads (Beckman Coulter). We quantified library concentrations across samples using a Qubit dsDNA BR Assay Kit (Invitrogen) following the manufacturer's protocols and then pooled samples in equimolar amounts. We sent multiplexed libraries for high-throughput sequencing using 150 bp, single-end chemistry on an Illumina HiSeq X at Novogenetics LTD (Sacramento, CA).

Next, we demultiplexed raw Illumina sequences based on perfect barcodes using the ddRADparser.py script of the BU ddRAD-seq pipeline (DaCosta and Sorenson 2014). We included previously published ddRAD-seq raw sequence data generated using the same protocols in alignments and subsequent analyses, serving as reference wild mallards (Lavretsky et al. 2019), game-farm mallards, and Khaki Campbell mallards (Lavretsky et al. 2020). Khaki Campbells are a common domestic breed of mallard that are not typically released for game purposes, and thus, serve as an outgroup breed of domestic mallards that wild populations could potentially interbreed with (Lavretsky et al. 2020). We trimmed all sequences for any base pair falling below a quality Phred score of 30 or discarded sequences if the average Phred score of the entire length fell below 30 using trimmomatic

(Bolger et al. 2014). We aligned remaining reads to a chromosomal-level reference wild mallard genome (Lavretsky et al. 2023) using the Burrows Wheeler Aligner version 07.15 (Li and Durbin 2011). We then sorted and indexed samples in Samtools version 1.7 (Bolger et al. 2014) and combined them using the mpileup function with parameters that included the retention of anomalous read pairs (-A), and retention of base pairs (-Q 30) and average sequences (-q 30) with a minimum quality Phred score of 30. All steps through mpileup were automated using a custom in-house Python script (Python scripts available at https://github.com/jonmohl/PopGen; Lavretsky et al. 2020). Next, we filtered variant call format (VCF) files for any base pair missing >5% of samples that also included a minimum base-pair depth of 5X (i.e., 10X per genotype) and quality per base Phred scores of ≥30 using VCFtools version 0.1.15 (Danecek et al. 2011). We used only autosomal loci in population genetics analyses.

Prior to analyses, we used PLINK version 1.90 (Purcell et al. 2007) to ensure that singletons (i.e., minimum allele frequency = 0.00142) and any single-nucleotide polymorphism (SNP) missing >5% of data across samples were excluded in each dataset. We further pruned for independence among SNPs by conducting pair-wise linkage disequilibrium (LD) tests across ddRAD-seq autosomal SNPs (--indep-pairwise 2 1 0.5) in which we tested for LD between every 2 base pairs with moving a window of one base pair so that 1 of 2 linked SNPs are then randomly excluded if we obtained an LD correlation factor (r^2) > 0.5.

We conducted all population genetics analyses without *a priori* information on population or species identity. First, we visualized population structure across all samples by running the PCA function in PLINK to perform a principal component analysis (PCA). Next, we estimated maximum likelihood individual population assignments in the program ADMIXTURE version 1.3 (Alexander et al. 2009, Alexander and Lange 2011), with datasets formatted for the ADMIXTURE analyses using PLINK, and following steps outlined in Alexander et al. (2012). We ran ADMIXTURE analyses with a 10-fold cross-validation and 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 to ensure that hybridization is not with alternative domestic mallards. Although we expected to find the optimum *K* population models to be 3 and 2 for datasets with and without Khaki Campbells, respectively, we evaluated *K* populations 1 through 5 to ensure we are not missing additional structure. Optimum population models were based on the lowest cross-validation errors. Moreover, we calculated standard deviations 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. Finally, we used assignment probabilities to categorize samples as pure wild and across 3 filial hybrid classes (i.e., F1-F3), as well as hybrids of unknown generational age (FX) as described in Lavretsky et al. (2019; also see Schummer et al. 2023). We considered individuals with point ancestries (+SD) that overlap 95% wild as wild, 50% wild as F1 hybrid, 75% wild as F2 hybrid, 88% wild as F3 hybrid, and with all others that fall in between these assignment ancestries as FX.

Statistical analyses

We analyzed samples from the Atlantic and Mississippi flyways separately. For each state and province, we described data as percentages of mallards originating near the banding site (within banding region) and those originating elsewhere (north or south of banding region), and percentages of each hybrid class (e.g., pure wild, F1 game-farm × wild, F2, hybrid swarm). Additionally, we noted how many standard deviations away from the banding region samples were if they were classified as outside of the banding region.

To model relationships between δ^2H_f and selected parameters, we used linear regression models and an information-theoretic approach with second-order Akaike's information criterion for small sample sizes (AIC_c) to select the most parsimonious model or group of models from a set of candidate models (Table 1; Burnham and Anderson 2002). We used the best model or group of models using the criteria described in Burnham and Anderson

TABLE 1 Model selection results for 7 candidate models explaining stable hydrogen isotope measurements (δ^2H_f) in mallard wing feathers sampled during the pre-hunting season banding period from 2019–2021 for mallards from the Atlantic and Mississippi flyways. For each model, we present the number of parameters (*K*), corrected Akaike's Information Criterion (AIC_c), and Akaike weight (w_i).

Flyway	Model structure	*K*	AIC_c	ΔAIC_c	w_i
Atlantic	Ordinal date × latitude group + sex + age + year	11	7,969.1	0.0	0.6
	Ordinal date × latitude group + year	9	7,969.9	0.9	0.4
	Ordinal date + year	5	8,158.1	189.0	0
	Sex + year	5	8,159.1	190.0	0
	Age + year	5	8,161.2	192.1	0
	Age × sex + year	7	8,162.2	193.1	0
	Null	2	8,163.3	194.2	0
Mississippi	Ordinal date × latitude group + sex + age + year	10	2,482.9	0.0	0.6
	Ordinal date × latitude group + year	8	2,483.8	0.9	0.4
	Ordinal date + year	4	2,492.6	9.8	0
	Age + year	4	2,495.2	12.4	0
	Age × sex + year	6	2,496.0	13.1	0
	Sex + year	4	2,500.0	17.1	0
	Null	2	2,512.7	29.8	0

(2002) and associated model predictions to make inferences for δ^2H_f as a function of ordinal day of banding season (i.e., 7 July = 1), age, sex, and latitude group. For the latitude group, we divided the latitudes at which birds were sampled into 3 relatively equal geographic sections (north: >42°, mid: 40–42°, south: <40°) to determine if there were patterns that depended on latitudinal group. We chose a categorical variable for latitude to provide potential management units that could theoretically be under different types of mallard harvest and population management. Additionally, we were interested in whether trends changed across latitudes. The model sets included single-variable (3 models) and 2-variable interactions (2 models), along with an intercept-only model and a global model. We included age and sex as an interactive model to determine variation among age and sex classes. We also assessed interactive models including ordinal date and latitude group to determine if there were different patterns of δ^2H_f over time at different latitudes. We included year as a fixed parameter in all models to account for variation among years of sampling. We present the top models and report 95% confidence limits for parameter estimates. We also made inferences for δ^2H_f as a function of genetic category. We grouped all hybrid categories because of small sample sizes. We conducted analysis of variance (ANOVA; $\alpha = 0.05$) tests to determine differences in δ^2H_f between hybrid and wild mallards. We implemented all linear regression models in R version 4.3.1 (R Core Team 2021).

RESULTS

Stable hydrogen isotope analysis

We sampled 919 mallard feathers from the Atlantic Flyway and 292 from the Mississippi Flyway. For the Atlantic Flyway, there was model uncertainty during model selection, with 2 models receiving all the weight. The model

containing the interaction of ordinal date and latitude grouping and additive effects of age and sex was the highest ranked model (w_i = 0.60), with the interaction model of ordinal date and latitude group following (w_i = 0.40; Table 1). Parameter estimates were similar for ordinal date and latitude groups for each model (Table S2). For each latitude group, the mean estimated δ^2H_f value became more negative with increasing latitude, indicating more northern origins were associated with northern banding locations (Table S3; Figure 1). The northern latitude group had a significant change over the banding period with a slope of −0.52‰ per day or 44.2‰ throughout the banding period, suggesting an increasingly northern origin of birds through the banding period at the most northern latitude group. Sex was determined to be important for explaining variation of δ^2H_f, with estimates for males 2.4‰ less than for females, suggesting a more northern origin. Age was included in models, but confidence limits crossed zero, making the age parameter a relatively ambiguous predictor (Table S3).

We determined that 47% of Atlantic Flyway ducks originated within the region of capture, 45% were classified as immigrants from north of the banding station (i.e., >12.8‰ north of the banding station), and 8% were classified as immigrants originating south of the banding station (i.e., >12.8‰ south of the banding station; Table 2). Of the ducks classified as originating north of the banding station, 55% were between 1–2 standard deviations north

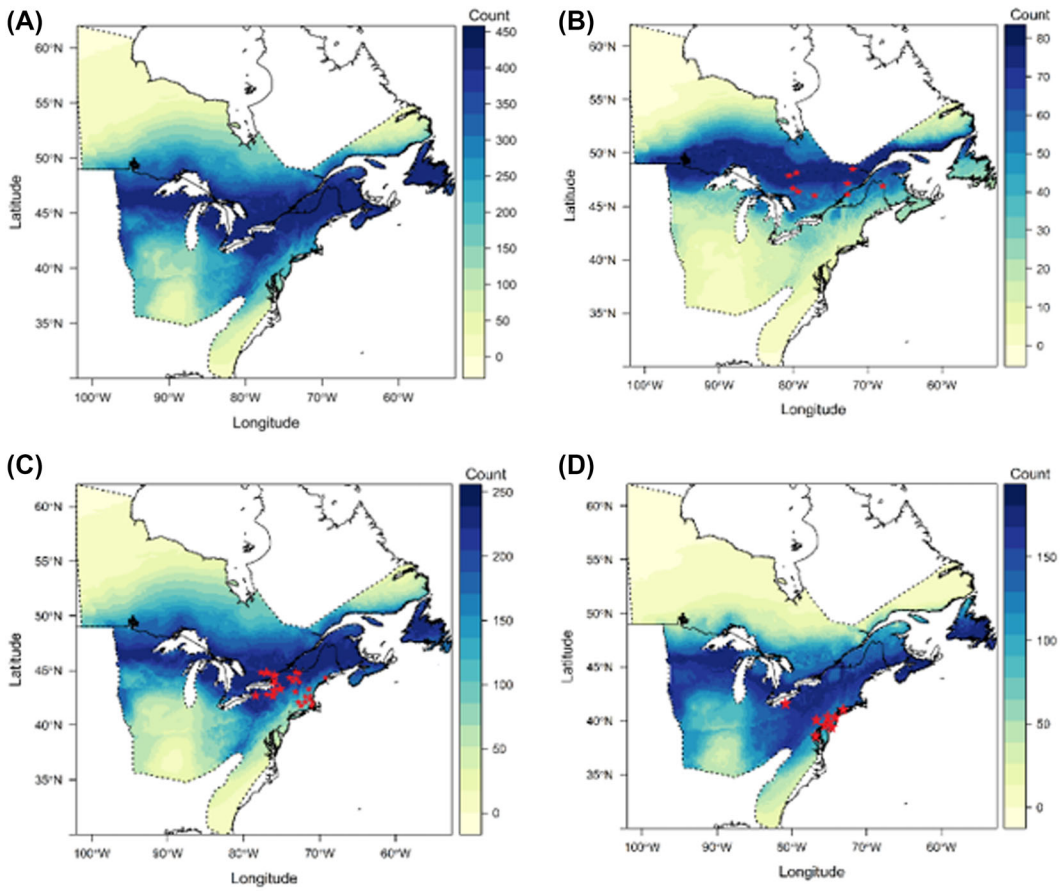

FIGURE 1 Probable origins for mallard samples taken during the pre-hunting season banding period in the Atlantic Flyway from 2019–2021, indicating the origins are near or slightly north of the banding stations. Banding stations are indicated by red stars. Numbers associated with the colors refer to the number of individuals assigned to each pixel at a 2:1 odds ratio. We present separate maps for A) all samples, B) northern banding stations, C) mid banding stations, and D) southern banding stations.

TABLE 2 Assignment of mallards sampled during the pre-hunting season banding period from 2019–2021 in the Atlantic and Mississippi flyways to the region they were banded (within region) or areas north or south of the banding region, based on a threshold approach with stable hydrogen isotope measurements of feathers (δH^2f); we include the total number of individuals sampled (*N*), the number assigned to each origin (*n*), and summary of the number of standard deviations (1 SD = 12.8‰) for individuals assigned to areas north of the banding region.

Flyway	Latitude group	*N*	Within region *n* (%)	North *n* (%)	1-2 SD north *n* (%)	>2 SD north *n* (%)	South *n* (%)
Atlantic	North	125	64 (51%)	49 (39%)	31 (63%)	18 (37%)	12 (10%)
	Mid	441	189 (41%)	250 (54%)	119 (48%)	133 (53%)	25 (5%)
	South	330	177 (54%)	112 (34%)	76 (60%)	37 (33%)	41 (12%)
	Total	919	430 (47%)	411 (45%)	226 (55%)	188 (46%)	78 (8%)
Mississippi	North	18	5 (28%)	12 (67%)	9 (75%)	3 (25%)	1 (6%)
	Mid	190	95 (50%)	80 (42%)	49 (61%)	36 (45%)	15 (8%)
	South	84	27 (32%)	50 (60%)	24 (48%)	26 (52%)	7 (8%)
	Total	292	127 (43%)	142 (49%)	82 (58%)	60 (42%)	23 (8%)

(in ‰) of the mean for the banding region (Table 2). Collectively, ducks classified as within region or within 1–2 standard deviations accounted for 71% of the Atlantic Flyway samples.

For Mississippi Flyway mallards, there was also uncertainty in the model selection process, with 2 models receiving all the weight. As found for the Atlantic Flyway, the model containing the interaction of ordinal date and latitude grouping and additive effects of age and sex was the highest ranked model ($w_i = 0.61$), with the model containing interaction of ordinal date and latitude group ranking second ($w_i = 0.38$; Table 1). Parameter estimates were similar for ordinal date and latitude groups for each model (Table S3). Estimated δ^2H_f value became more negative with increasing latitude group, indicating more northern origins were associated with northern banding stations (Table S4; Figure 2). For the southern latitude group, δ^2H_f increased throughout the banding period, indicating more southern origins as the banding season progressed. However, there were fewer samples early and late in the season for the southern latitude group. Sex and age were uninformative predictors for the Mississippi Flyway, based on 95% confidence intervals overlapping 0.

Approximately 43% of Mississippi Flyway samples were classified as within-region samples, 49% were classified as originating north of the banding station, and 8% originating south of the banding station (Table 2). Of the samples considered as originating north of the banding station, 58% were between 1–2 standard deviations north of the banding region (Table 2). Collectively, birds classified as within region or within 1–2 standard deviations accounted for 72% of the Mississippi Flyway samples.

Genetic analysis

We achieved sufficient DNA quality and quantity required to construct ddRAD-seq libraries for 561 samples that included 386 samples for the Atlantic Flyway and 175 samples for the Mississippi Flyway. A total of 106,189 base pairs, resulting in 30,573 SNPs across autosomal loci, met our criteria for sequencing coverage and missing data, with an average depth of 168 reads/locus and depth range of 41–260 reads across samples.

Population structure analyses were based on 29,706 (of 30,573) independent bi-allelic SNPs. Plotting the first 2 components of the PCA clearly differentiated between feral Khaki Campbell (i.e., park ducks), game-farm, and wild

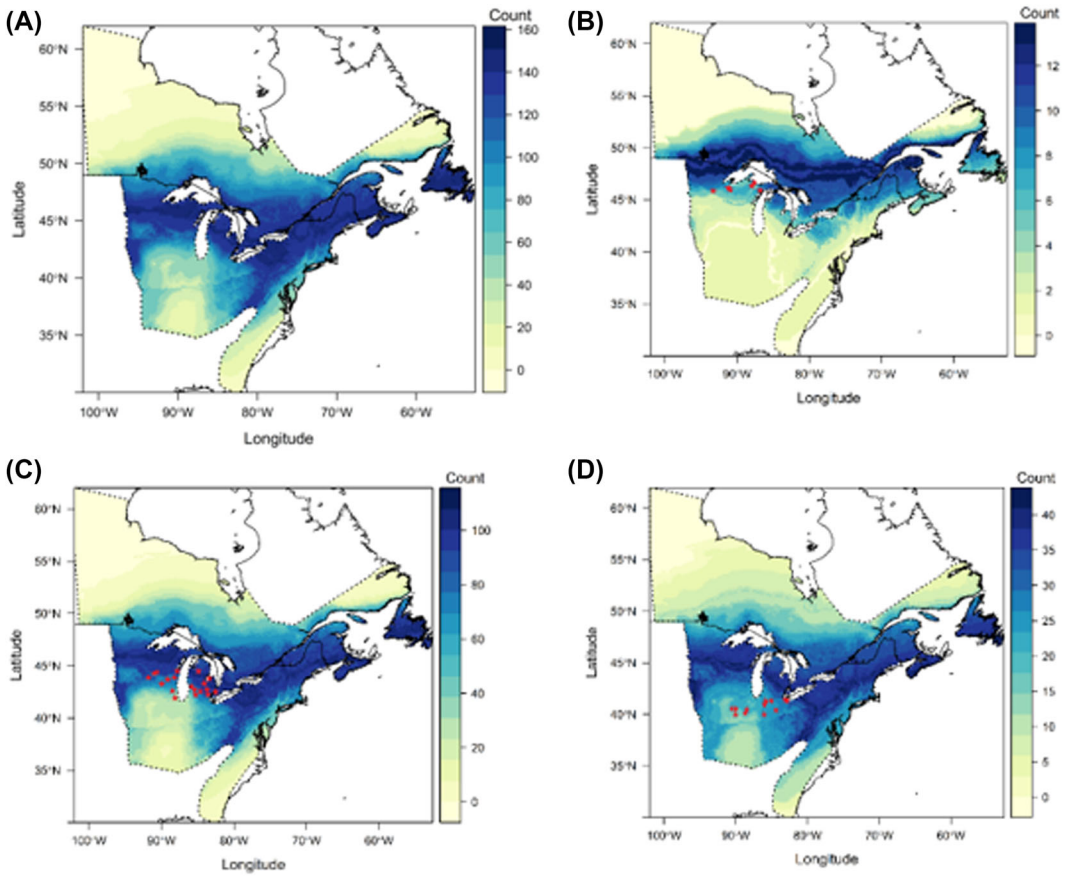

FIGURE 2 Probable origins for mallard samples taken during the pre-hunting season banding period in the Mississippi Flyway from 2020–2021, indicating the origins are nearby or slightly north of the banding stations. Banding stations are represented by red stars. Numbers associated with the colors refer to the number of individuals assigned to each pixel at a 2:1 odds ratio. We present separate maps for A) all samples, B) northern banding stations, C) mid banding stations, and D) southern banding stations.

mallards (Figure 3A). Given the general absence of any park ducks or park-duck hybrids, we ran ADMIXTURE excluding Khaki Campbell mallards. Calculating individual assignment probabilities under the *K* population of 2, the ADMIXTURE analysis successfully assigned all reference samples to their respective genetic group, with samples collected in this study showing a continuum of ancestry ranging from wild to feral (Figure 3B).

Generally, proportions of samples identified as wild x game-farm mallard hybrids were greatest in coastal Atlantic Flyway states and decreased further west into the upper Mississippi Flyway (Figure 4). For Atlantic Flyway samples, we categorized 9.5% (37 of 386) of samples as wild mallard, with the remaining roughly 90% of samples assigned among hybrid categories: 1% (3 of 386) of samples as F1 wild × game-farm hybrid, 3% (12 of 386) as F2 – wild backcrosses, 7.5% (29 of 386) as F3 – wild backcrosses, 1% (4 of 312) as unknown generation game-farm backcrosses (FX – game-farm), and 78% (301 of 386) as unknown generation wild backcrosses (FX – wild mallard; Figure 5). For Mississippi Flyway samples, 26% (46 of 175) of samples were wild mallards, with the remaining 84% of samples within specific hybrid categories: 2% (4 of 175) of samples as F1 wild × game-farm hybrids, 3% (6 of 175) as F2 – wild backcrosses, 1% (1 of 175) of samples as F2 – game-farm backcrosses, 9% (15 of 175) as F3 – wild backcrosses, 3% (6 of 175) of samples as FX – game-farm backcrosses, and 55% (97 of 175) as FX – wild backcrosses (Figure 5).

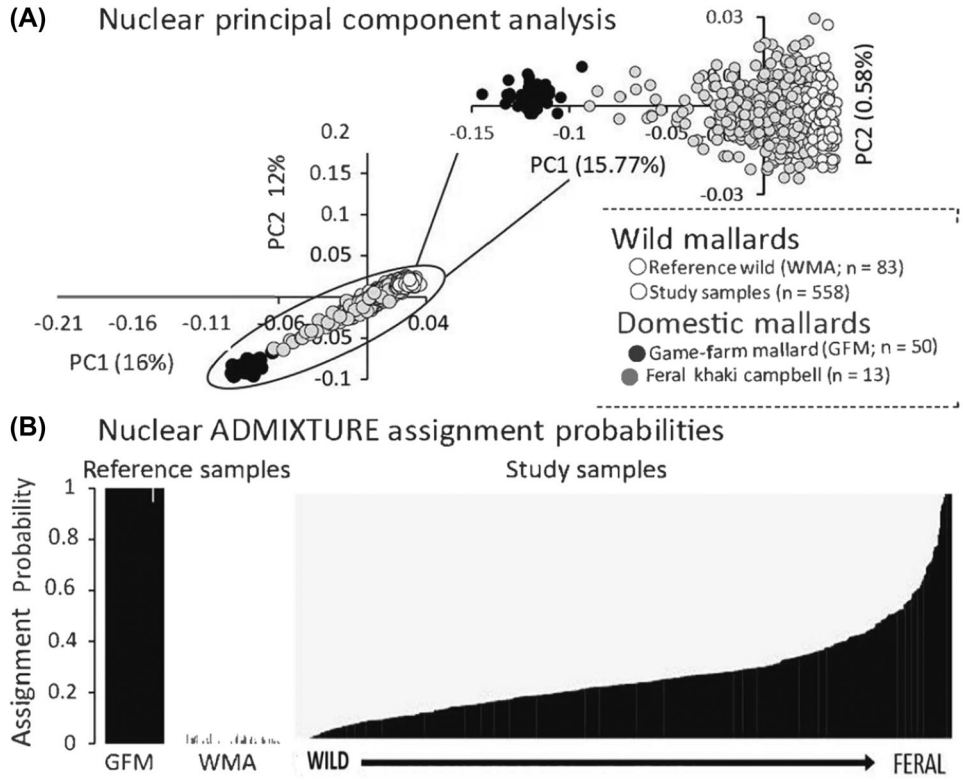

FIGURE 3 A) The principal components (PCs) from our principal component analysis across wild mallards and game-farm mallards and wild × game-farm hybrids and feral Khaki Campbell mallards from reference samples and study samples obtained from the Atlantic and Mississippi flyways from 2019–2021. We also provide B) individual assignment probabilities as estimated in the program ADMIXTURE (Alexander et al. 2009).

Combining stable isotope and genetic analysis

We had corresponding δ^2H_f and genetic data for 312 Atlantic Flyway samples and 167 Mississippi Flyway samples. Generally, wild mallards had a slightly more northern δ^2H_f compared to hybrid mallards, but we did not find strong evidence for a relationship in the Atlantic ($P = 0.10$) or Mississippi flyways ($P = 0.08$). In the Atlantic Flyway, wild mallards had an estimated marginal mean δ^2H_f of −107.0 (−114.0, −101.0), whereas hybrid mallards had a δ^2H_f of −101.0 (−104.0, −99.0). In the Mississippi Flyway, wild mallards had an estimated marginal mean δ^2H_f of −103.7 (−109.0, −98.3), and hybrid mallards had a δ^2H_f of −98.1 (−101.0, −94.9). We did find that FX – game-farm hybrids were only detected at southern and mid latitudes (Figure 6). In the Mississippi Flyway, there were increasing percentages of wild mallards as banding regions decreased in latitude (Figure 6).

DISCUSSION

Determining origin of mallards during the pre-hunting season

An important, but rarely tested, assumption of duck banding during the pre-season is that marked individuals originate near the banding station (Munro and Kimball 1982). Violation of this assumption can lead to biased

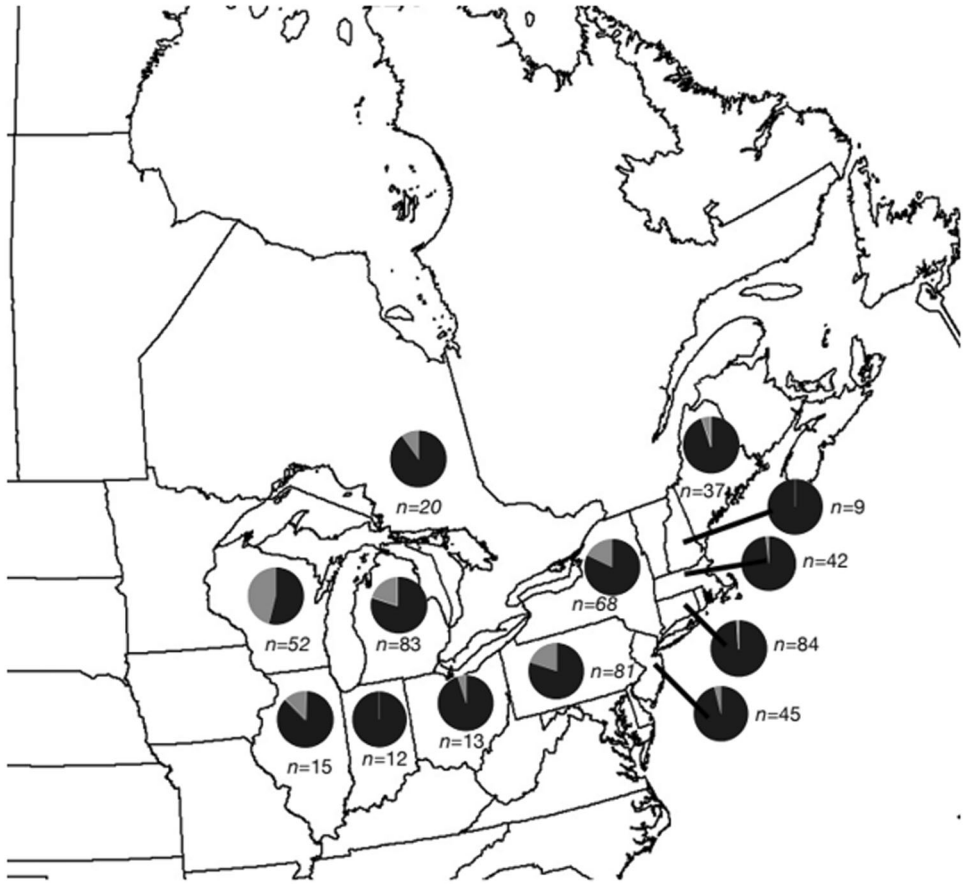

FIGURE 4 The proportions of wild (gray), and game-farm × wild hybrids with at least 10% game-farm assignment probabilities (black) for each state and province in the sampling area for mallards in the Atlantic and Mississippi flyways, 2019–2021. Sample sizes for each state are noted.

population and vital rate estimates because ducks may be counted or included in survival analysis in one population when they may in fact be from another. Our analysis of isotopic signatures of mallards detected that δ^2H_f values varied predictably by latitude and showed that only about 50% of sampled mallards had δ^2H_f values consistent with their banding region (≤12.8‰ north or south of their banding station or 1 SD), while the remainder had δ^2H_f values predominantly farther north from their respective banding region. This may be an indication that mallards in the pre-season do not originate near their banding locations, which has the potential to violate assumptions used for banding data analysis. Our result of no differences in δ^2H_f between age groups contrasts with earlier observations that detected age-specific differences in post-breeding period movement of mallards (Boyd 1961). The Atlantic Flyway contained an influence of sex (with males having a more northerly δ^2H_f); however, the difference (about 3‰) was within 1 standard deviation (12.8‰). The small difference in δ^2H_f between sexes was likely due to some male mallards moving to specific molting sites that are often far from the breeding grounds (Munro 1949, Bellrose, Kortright 1976); however, their movements appear restricted to places with a similar expected δ^2H_f value of their breeding grounds (Gollop 1960, Gilmer et al. 1977). Nevertheless, these results are generally consistent with earlier findings for 5 species of ducks for which there were no differences in post-breeding movement patterns between age and sex classes (Asante et al. 2017), indicating that all age and sex classes are following similar movement patterns.

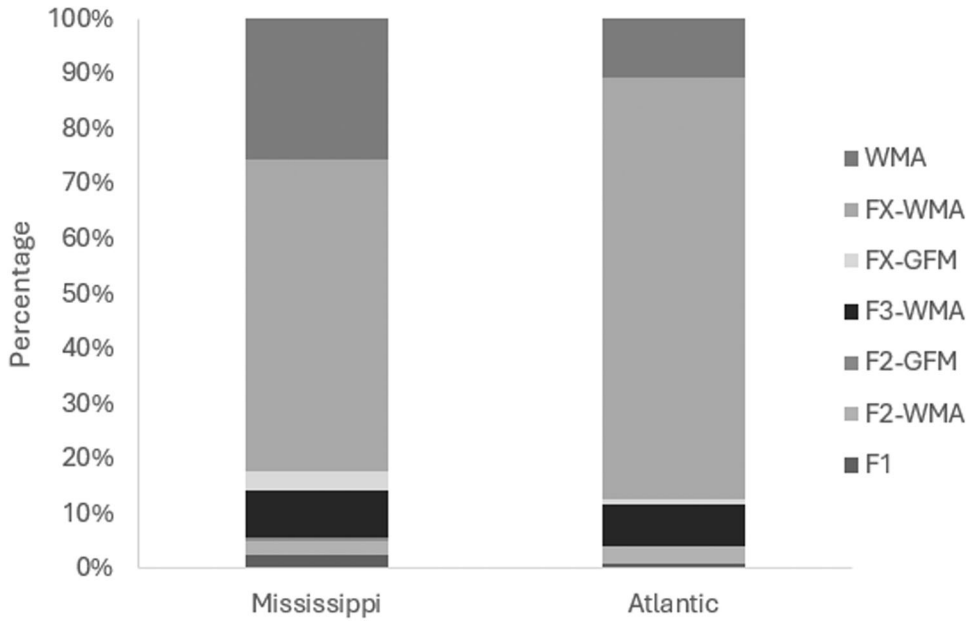

FIGURE 5 Genetic hybrid assignment proportions compared between the Atlantic and Mississippi flyways for mallards sampled during the pre-hunting season banding period from 2019–2021. Assignments include wild mallards (WMA), unknown generation wild backcrosses (FX-WMA), unknown generation game-farm backcrosses (FX-GWM), F3-wild backcrosses (F3-WMA), F2 game-farm backcrosses (F2-GFM), F2 wild backcrosses (F2-WMA), and F1 hybrids.

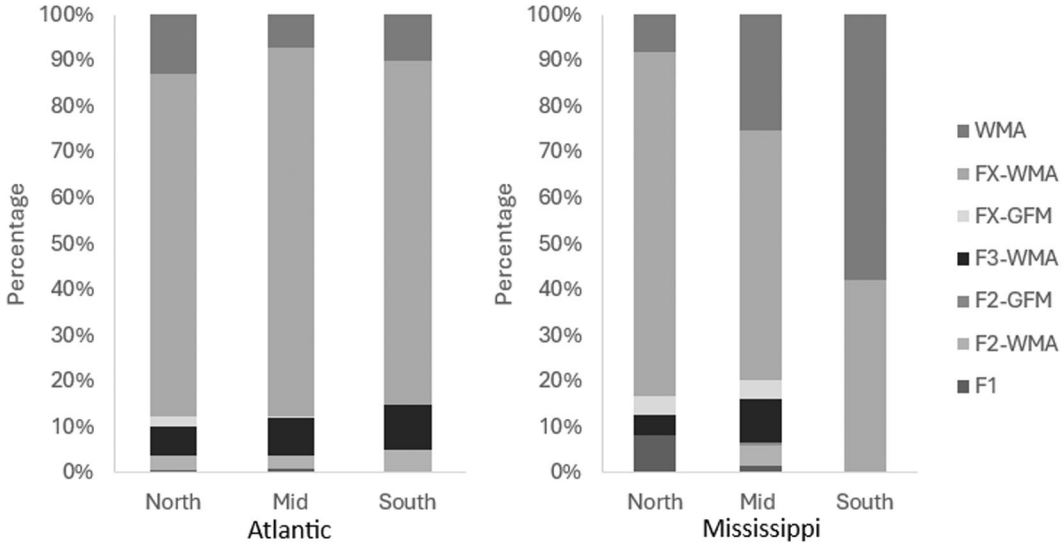

FIGURE 6 Genetic hybrid assignment proportions for the Atlantic and upper Mississippi flyways, grouped by latitude of sampling (north: >42°, mid: 40–42°, and south: <40°) for mallards sampled during the pre-hunting season banding period from 2019–2021. Assignments include wild mallards (WMA), unknown generation wild backcrosses (FX-WMA), unknown generation game-farm backcrosses (FX-GWM), F3-wild backcrosses (F3-WMA), F2 game-farm backcrosses (F2-GFM), F2 wild backcrosses (F2-WMA), and F1 hybrids.

Mallard movement during the pre-season banding period could include the onset of autumn migration (Krementz et al. 2012), molt migration of adult males (Boyd 1961) and females (Boyd 1961, Yarris et al. 1994), or post-fledging dispersal of hatch-year birds (Kirby et al. 1989). Most samples had δ^2H_f values expected from more northerly locations than their respective banding regions (45% of Atlantic Flyway and 49% of Mississippi Flyway samples). Of these, 55% and 58% for the Atlantic and Mississippi flyways, respectively, were roughly estimated to be coming from 240–560 km (1-2 SD) away from their banding site. Such movement is not unexpected, as juvenile mallards have been known to make relatively large movements (145 km) out of natal marshes, and some may even move farther (Kirby et al. 1989). We found that 45% and 42% of immigrants originating from north of banding stations in the Atlantic and Mississippi flyways, respectively, had δ^2H_f values consistent with origins even farther away from their banding location (>2 SD); these distances are more consistent with migratory behavior than local movement (Schummer et al. 2010, Baldassarre et al. 2014, Van Den Elsen 2016). These trends were found throughout pre-season banding months at the mid- and southern-latitude regions, suggesting mallard immigration occurred throughout the banding period. However, δ^2H_f values became more negative throughout the banding period in the most northern latitude group in the Atlantic Flyway, suggesting an influx of migrants from the north during the banding period. Together, these results are consistent with substantial numbers of mallards moving during the pre-season banding period, and potentially violating assumptions used for estimating demographic rates from banding data.

Although we initially expected to find δ^2H_f values consistent with immigration in later pre-season months, δ^2H_f patterns were consistent with northern immigrants throughout the banding period in the Atlantic Flyway, except mallards sampled at northern latitudes. We also found 8% of mallards in both flyways having δ^2H_f values consistent with locations south of their banding locations. Telemetry studies of mallards have observed relatively large movements in late summer (Davis 2018). We suggest that a portion of post-fledging mallards and post-breeding adult females make initial movements to acquire nutrients for migration and survival during the non-breeding period. Together, the lack of temporal variation in δ^2H_f and the roughly 50% of banded mallards originating outside of their respective banding region suggest that substantial movement away from breeding areas is occurring throughout pre-season banding months and may indeed be common (Palumbo et al. 2019). These post-breeding period movements are occurring well outside the timing of typical weather cues associated with autumn migration (Schummer et al. 2010). Regardless of why these birds move so early, movement behavior of mallards is likely misrepresented based on pre-season banding data. Harvest derivation is typically calculated as the percentage of individuals recovered by state or province from various banding regions after controlling for differences in reporting rate (Cristina et al. 2017, Arnold et al. 2020). We recommend that harvest derivation based on banded mallards include percentages of individuals by banding location and not natal origins because of the substantial movement we detected during the pre-season banding period.

Our results also demonstrate the opportunity that stable isotope analyses provide to estimate the geographic origins of mallards and other waterfowl. Our results enabled us to increase our understanding about movement of individual mallards from relatively inaccessible breeding areas (e.g., boreal forest) to locales where they are banded (Kusack et al. 2023*b*); without stable isotope analysis, the origins of these mallards would be unknown.

The abundance of mallards we inferred to move during late summer and early autumn during the banding season and out of their breeding or molting areas suggests that a greater understanding of staging behavior and nutrient needs is important. Habitat management for dabbling ducks during the non-breeding period typically focuses on providing carbohydrate-rich foods, but mallards in our study began movements before plant senescence and seeds and tubers were readily available (Schummer et al. 2012). Early in autumn migration, emergent marshes are attractive to dabbling ducks, possibly because they continue to provide diverse food resources, including protein-rich invertebrates for growth (juvenile) and recovery (adult females; Farley et al. 2022). Additional information may be needed on initial movements of mallards away from breeding period locales because most current habitat management for non-breeding waterfowl does not focus on this period of the annual life cycle.

Whether the movements we detected violate the assumption that mallards do not move among survey units will depend on how populations are designated. Currently, Atlantic Flyway mallards are considered a single population in harvest management (Roberts et al. 2023); thus, estimated distances moved by most mallards in our study do not appear to strongly violate the assumption that mallards banded in the pre-season do not move among survey units (Munro and Kimball 1982). However, if managers wished to differentiate the 2 survey areas, further discussion of distance thresholds that would constitute a violation of this assumption would be needed. Eastern mallards have 2 survey areas with different population trajectories, and currently, these 2 survey estimates are combined to obtain a single eastern mallard estimate for management purposes. Mallards surveyed in eastern Canada and Maine have a stable and slightly increasing trend, whereas mallards surveyed in the eastern United States have a significant declining trend (USFWS 2020). If these 2 surveyed areas have different vital rates, movement of northern birds into the southern range during the banding period confounds the capacity to detect declines in survival and reproduction by mallards breeding in the United States. Currently, no research or model has shown differences in vital metrics between mallards banded in Canada and the United States (Anthony Roberts, USFWS, personal communication). Our results suggest that detecting differences in vital rates may be difficult because a portion of the mallards that originate in Canada appear to be banded and designated as mallards originating in the United States. Developing methods to differentiate between mallards originating in Canada and the United States in operational banding would help further investigate differences in vital rates among these regions. One possibility is to apply a buffer zone around the boundary of the 2 survey areas, decreasing the chances that a mallard that moved is counted as having an origin in the United States, which may have different vital rates. However, this would eliminate a substantial portion of the mallard population in the Great Lakes region of the United States, which is an area of relatively greater density of breeding mallards in the United States portion of their range.

Hybridization levels and relationship to origin

Eastern mallard populations are known to have significant amounts of introgression with genes from game-farm birds (Lavretsky et al. 2019). Pairing molecular and isotopic data, we found that wild mallards tended to have slightly more northern δ^2H_f values than hybrids. This, though, was not statistically significant, suggesting that mallard genotypes cannot be differentiated spatially. When examined at the state scale, proportions of samples with game-farm introgression were greatest (>95%) in the coastal states of the northern Atlantic Flyway, where there are high levels of urban land cover. The ratio of mallards with substantial game-farm introgression (>10% in game-farm assignment probabilities) was the same in the Atlantic Flyway as reported for mallards a decade ago, indicating that much of the Atlantic Flyway may indeed be at the cusp of forming a wild × game-farm mallard hybrid swarm (Lavretsky et al. 2019, 2020). Conversely, in the Great Lakes region, we detected a greater percentage of hybrid mallards in the surveyed area (i.e., 58%) as compared to reported rates for the upper Mississippi Flyway a decade ago (40%; Lavretsky et al. 2019). The westward spread of game-farm mallard ancestry from the Atlantic Flyway (Lavretsky and Sedinger 2023) or possibly increasing numbers of game-farm mallards being directly released in the surveyed area of the Mississippi Flyway seems to be driving this result. Increased levels of hybridization are only seen in the upper Mississippi Flyway, whereas mallards harvested in the southern part of the flyway area remain essentially pure wild mallards (~96% wild; Davis et al. 2022). Additional stable isotope and transmitter studies will help to determine the level of movement between flyways that can help establish rates of gene flow from birds originating in the Atlantic Flyway into the Mississippi Flyway. Nevertheless, without strong evidence for an association between molecular and geographical origins, we conclude that game-farm genetic ancestry is not restricted to areas of release and appears to be moving west, and that geographic location cannot be used as a proxy for genotype when developing population models. There is growing concern about the implications of game-farm mallard introgression in wild populations and the subsequent introduction of maladaptive traits. Further

research on the consequences of game-farm mallard genes is necessary. As genetic analysis is relatively costly, additional tools that enable direct designation of mallard genotype using morphological characteristics at the time of banding would be useful so that managers can begin to test for differences in survival and movements among them throughout North America.

MANAGEMENT IMPLICATIONS

Isotopic analysis of feathers from waterfowl is a useful technique to infer the origins of unmarked individuals. We conclude that roughly 50% of mallards banded during the pre-season originate from the banding location, and while most can be considered within the same survey unit, a significant percentage come from outside the survey area. Given that >95% of mallards are indeed originating within the eastern survey area, the movement we detected does not violate population model assumptions when considering the entire eastern mallard population as a single unit. However, more fine-scale research is needed to understand post-breeding movements of eastern mallards because it may influence how we interpret banding data and conserve and manage habitats for this declining population of mallards. Further, we recommend that harvest derivation based on banded mallards include percentages of individuals by banding location and not natal origins because of the substantial movement we detected during the pre-season banding period. Continued monitoring will be needed to determine the cause for increasing game-farm mallard genotypes in both flyways. Additionally, research on the implications of game-farm mallard genes in the wild population is needed.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animals were handled in accordance with State University of New York, Environmental Science and Forestry animal care protocol 191201 and United States Geological Survey banding permit 23928.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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