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Research Paper

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Natal origins of Mallards harvested in the Atlantic Flyway of North America: implications for conservation and management

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ABSTRACT. Appropriate management and conservation of migratory species requires knowledge of connectivity between natal or breeding sites and stopover or wintering sites. For game species, such as waterfowl, knowledge of source areas that produce juveniles, which are available for harvest in the autumn-winter, is of considerable interest. External markers have long been used in mark-recapture studies to identify breeding grounds of waterfowl. However, this approach is biased toward regions of marking effort and is logistically difficult in remote locations. Harvest management of Mallards (*Anas platyrhynchos*) in the U.S. portion of the Atlantic Flyway has assumed that the majority of harvested birds in the U.S. were produced there. We tested this assumption by inferring regions of natal origins of juvenile Mallards ($n = 1254$) harvested during the 2018–2019 and 2019–2020 hunting seasons in all states in the Atlantic Flyway using stable-hydrogen isotope analyses of breeding-ground grown feathers ($\delta^2\text{H}_f$). We created a species-specific feather isoscape and applied a Bayesian assignment approach to identify probable regions of origin. We determined 64% of our sample had $\delta^2\text{H}_f$ consistent with origins in Canada versus the U.S. Our data suggested all states harvested Mallards that had origins from the U.S. and Canada throughout their entire hunting season. Our results contrast with long-term breeding population estimates which suggest the majority of breeding pairs of eastern Mallards occur in the U.S. We recommend further investigation into reasons for disparities in national natal origins of harvested Mallards.

Origine des Canards colverts récoltés dans la voie de migration de l'Atlantique de l'Amérique du Nord : répercussions pour la conservation et la gestion

RÉSUMÉ. La gestion et la conservation éclairées des espèces migratrices passent par la connaissance de la connectivité entre les lieux de naissance ou sites de reproduction et les haltes migratoires ou sites d'hivernage. Pour les espèces gibier, telles que la sauvagine, la connaissance des lieux d'où proviennent les jeunes, disponibles pour la récolte en automne-hiver, est d'un intérêt considérable. Les marqueurs externes utilisés depuis longtemps dans les études de marquage-recapture servent à identifier les aires de nidification de la sauvagine. Cependant, cette approche est biaisée en faveur des régions où l'effort de marquage est important, et est difficile à mettre en œuvre dans les régions éloignées. La gestion de la chasse du Canard colvert (*Anas platyrhynchos*) dans la partie étatsunienne de la voie de migration de l'Atlantique est fondée sur la prémisse que la majorité des oiseaux récoltés aux États-Unis sont issus de ce pays. Nous avons testé cette hypothèse en inférant le lieu de naissance des jeunes Canards colverts ($n = 1254$) récoltés pendant les saisons de chasse 2018-2019 et 2019-2020 dans tous les États de la voie de migration de l'Atlantique à l'aide d'analyses des isotopes stables de l'hydrogène contenus dans les plumes ayant poussé sur les aires de nidification ($\delta^2\text{H}_f$). Nous avons créé un isopaysage de plumes spécifique à l'espèce et appliqué une approche d'attribution bayésienne pour identifier les régions probables de l'origine des jeunes. Nous avons déterminé que 64 % de notre échantillon avait des $\delta^2\text{H}_f$ correspondant à des origines canadiennes plutôt qu'étatsuniennes. Nos données ont indiqué que tous les États ont récolté des Canards colverts provenant des États-Unis et du Canada pendant toute la durée de la saison de chasse. Nos résultats contrastent avec les estimations de longue date de la population nicheuse qui laissent entendre que la majorité des couples nicheurs de Canards colverts de l'Est se trouvent aux États-Unis. Nous recommandons de poursuivre les recherches sur les raisons sous-tendant les disparités de l'origine nationale des Canards colverts récoltés.

Key Words: *Anas platyrhynchos*; deuterium; harvest management; hatch-year; stable isotope

INTRODUCTION

Migratory birds often travel long distances between breeding, stopover, and non-breeding sites during their annual cycle (Zink 2002, 2011). For migratory game species, understanding these large-scale movements between breeding grounds and harvest locations is vital to inform management decisions (Webster and

Marra 2005, Asante et al. 2017, Hobson and Wassenaar 2019). The North American Adaptive Harvest Management framework links habitat conditions and productivity on the breeding grounds to expected harvest within each major flyway to set harvest regulations for each species annually (Nichols et al. 1995, Williams and Johnson 1995, Palumbo et al. 2019). Identifying origins of

harvested populations allows managers to implement conservation effectively and manage harvest regulations.

For Mallards (*Anas platyrhynchos*), three populations have been identified for harvest management based on their affiliated breeding grounds: western, midcontinent, and eastern (U.S. Fish and Wildlife Service 2017). The eastern population of North American Mallards, which nests across southeastern Canada and the northeastern U.S., has declined by ~40% since 1997 (Sauer et al. 2014, U.S. Fish and Wildlife Service 2018). However, declines were not range wide and surveys in Canada and the U.S. detected differing population trends (U.S. Fish and Wildlife Service 2017). Estimates of Mallard abundance in the Atlantic Flyway Breeding Waterfowl Plot Survey (AFBWPS), which includes Virginia to New Hampshire, declined by ~50% during this period (U.S. Fish and Wildlife Service 2017). In contrast, Mallard population estimates from the Waterfowl Breeding Population and Habitat Survey (WBPHS), which includes eastern Canada and Maine, have been stable to slightly increasing (U.S. Fish and Wildlife Service 2017). To properly inform management strategies, it is important to identify the proportion of Mallards harvested in the Atlantic Flyway being derived from the stable Canadian population and declining U.S. breeding population.

Currently, waterfowl banding programs and subsequent harvest or recapture of banded individuals inform most of our understanding of the extent and location of wintering and breeding grounds for North American waterfowl (Crissey 1955, Anderson and Henry 1976, Munro and Kimball 1982, Zuwerink 2001, Szymanski and Dubovsky 2013). However, data limitations include labor-intensive and logistically difficult banding of juveniles prior to fledging to ensure certainty in natal origins (Crissey 1955, Szymanski et al. 2007). Sampling must occur over large spatial scales, be representative of all potential breeding areas, and be proportional to breeding-population abundance within regions to prevent potentially erroneous conclusions from analyses of band recoveries (Austin et al. 2000, Alisauskas et al. 2014, Roy et al. 2019). This design is particularly difficult to achieve for remote locations that tend to occur in the northern portions of breeding ranges (Hebert and Wassenaar 2005, Alisauskas et al. 2014, Roy et al. 2019).

One approach to address sampling limitations of banding is to use stable isotope analysis to refine identification of production locations of juvenile birds (Hebert and Wassenaar 2005). In North America the ratio of stable isotopes of hydrogen ($^2\text{H}/^1\text{H}$, depicted as $\delta^2\text{H}$) within amount-weighted annual or growing-season precipitation form predictable, strong latitudinal gradients (Bowen et al. 2005, Hobson et al. 2012, Bowen and West 2019). These patterns are passed on to consumers and can be used to infer origins, especially in metabolically inert tissues. Feathers are particularly useful in this regard because they store isotopic information assimilated during growth and periods of molt well known for waterfowl. Thus, feather $\delta^2\text{H}$ ($\delta^2\text{H}_f$) can be compared to hydrogen isotopic patterns in precipitation to infer origins where tissues were grown (Hobson et al. 2012). This approach has been used in North America to determine natal origins for various waterfowl species (Hobson et al. 2009, Ashley et al. 2010, Asante et al. 2017, Palumbo et al. 2019). By sampling juvenile birds, whose feathers were grown on the breeding grounds, this method provides a sampling framework for determining relative hatching

origins of juvenile Mallards harvested across a broad geographic area and from a greater portion of the population than other current tools allow.

From 1975 to 2019 the ratio of juvenile to adult Mallards harvested in the Atlantic Flyway declined from 1.85 to 1.18, suggesting fewer juvenile Mallards were available for harvest (Roberts 2020). Over this period, substantial land-cover change in eastern North America has occurred. Urban sprawl has expanded at the expense of open, mainly agricultural, land-cover types and forested areas (Valiela and Martinetto 2007). In fact, 32% of the U.S. portion of the Atlantic Flyway was classified as “wildland-urban interface” in 2005, a land-cover type defined by Radeloff et al. (2005) as “a reticulate mosaic of remnant natural and new residential parcels.” Less than 60% of the original wetlands in the lower Atlantic Flyway (Virginia to Florida) still exist and the quality of the remaining wetlands is declining because of nutrient loading, altered hydrology, and urban encroachment (NRCS 1995, Mitsch and Gosselink 2005). Determining where Mallards harvested in the Atlantic Flyway originate, or where production may be lacking, is crucial to inform future studies aimed at identifying potential environmental drivers of the eastern Mallard population decline.

Our goal was to use stable isotope methods to refine our understanding of the origins of hunter-harvested Mallards in the U.S. portion of the Atlantic Flyway. To meet this goal, we estimated natal origins of juvenile Mallards harvested in Atlantic Flyway states during the 2018–2019 and 2019–2020 hunting seasons. Additionally, at the state and flyway scales, we investigated if origins of juvenile Mallards varied temporally throughout the hunting season. If U.S. or Canadian Mallards were being harvested at different times throughout the hunting season, these data could be used to adjust hunting seasons and allow managers to regulate harvest for U.S.- or Canadian-produced Mallards. We hypothesized that there would be latitudinal differences in natal origins of individuals harvested throughout the hunting season. As shown by prior banding data (Heusmann 1991), we predicted that Mallards harvested early in the hunting season would originate from lower latitudes, whereas individuals harvested later in the hunting season would originate from farther north. Such a result would provide opportunity to vary harvest management seasonally to reduce take of Mallards from areas with a declining breeding population and, vice versa, liberalize bag limits and hunter harvest opportunity for Mallards from areas with stable to increasing breeding populations.

METHODS

Study area

We sampled juvenile Mallards harvested in the Atlantic Flyway (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, New York, Pennsylvania, New Jersey, Maryland, Delaware, Virginia, West Virginia, North Carolina, South Carolina, Georgia, and Florida) between October and January in the 2018–2019 and 2019–2020 hunting seasons.

Sample collection, identification, and preparation

We acquired a stratified random sample of the proximal primary flight feather from juvenile Mallards from the 2019 and 2020 U.

S. Fish and Wildlife Service Parts Collection Survey (PCS). We aimed to distribute sampling effort proportional to harvest in each state and between sex and early (before 1 December) and late (after 1 December) season when samples were available. We selected 1 December to differentiate early and late season because it is midway through the hunting season and splits our sampling periods into before and after peak Mallard migration (Notaro et al. 2016). When samples were not available for a southern state, we increased sample size in more northern states under the assumption that birds migrating southward, but potentially not reaching southern wintering areas, were available for harvest at more northern latitudes. Species, sex, and age were determined by trained USFWS identifiers at the PCS using wing characteristics (Carney 1992). To avoid detecting molt migration locations, we only sampled juvenile Mallards.

Stable hydrogen isotope analysis

Feather samples were analyzed for $\delta^2\text{H}$ at the Cornell Stable Isotope Laboratory in Ithaca, New York, USA. After washing in a 2:1 chloroform:methanol solution, feather samples were air dried under a fume hood and a subsample (0.35 mg) of vane material was loaded into silver capsules, crushed, and placed with internal lab standards into a desiccator for a minimum of three days prior to analysis. Samples were then loaded into a Zero Blank carousel under helium flow. Pyrolysis combustion on glassy carbon was at 1350°C in a Thermo Scientific Temperature Conversion Elemental Analyzer (TC/EA; Bremen, Germany) coupled via a ConFlo IV (Thermo Scientific) to a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer. Analysis of $\delta^2\text{H}$ was conducted using the comparative equilibration method of Wassenaar and Hobson (2003) with two calibrated keratin reference materials (CBS, $\delta^2\text{H} = -197\text{‰}$; KHS, $\delta^2\text{H} = -54.1\text{‰}$; SPK, $\delta^2\text{H} = -121.6\text{‰}$) corrected for linear instrumental drift. Based on within-run ($n = 5$) and across-run analyses of a third keratin standard, measurement error was approximately $\pm 3\text{‰}$ for $\delta^2\text{H}_f$. All $\delta^2\text{H}_f$ values are reported relative to the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation scale.

Assignment to origin

To estimate natal origins of harvested birds, we used likelihood-based algorithms to produce spatially explicit assignments of source areas based on analysis of feather $\delta^2\text{H}$ data (Hobson et al. 2009, Wunder 2010). We created a map (hereafter isoscape) of predicted $\delta^2\text{H}$ in feathers ($\delta^2\text{H}_p$) by applying a rescaling function derived by regressing $\delta^2\text{H}_f$ of known-origin juvenile Mallards (van Dijk et al. 2014)

$$\delta^2\text{H}_f = -27.4 + 1.28 * \delta^2\text{H}_p \quad (1)$$

against amount-weighted growing-season average precipitation $\delta^2\text{H}$ ($\delta^2\text{H}_p$) (Bowen et al. 2005). We selected this calibration equation because it is the most recently published equation available for dabbling ducks and preliminary analyses show it is the most accurate and precise calibration equation available to apply toward North American dabbling ducks (J. W. Kusack et al., *in preparation*).

The standard deviation of the residuals of this regression was set at 12.8‰ based on estimations from Clark et al. (2006, 2009). We

acquired the 2019 breeding range of Mallards from BirdLife International (<http://datazone.birdlife.org/species/requestdis>), and the spatially explicit assignments were restricted, i.e., masked, to only those areas of the continent occurring exclusively within the reported breeding range. We also considered that our Mallards originated only from the Mississippi or Atlantic Flyway because < 1% of direct recoveries of banded Mallards in the Atlantic Flyway came from outside these areas. We estimated the likelihood that individual 5 km x 5 km cells, i.e., pixels, within the isoscape represented a potential source area for a given sample by comparing the observed $\delta^2\text{H}_f$ against the isoscape-predicted $\delta^2\text{H}_p$ using a normal probability density function (Hobson et al. 2009, Palumbo et al. 2020). We then applied Bayes' Theorem to assess the posterior probability that an individual pixel within the isoscape was the putative source area of a given sample (Hobson et al. 2009, Palumbo et al. 2020). After normalizing the probabilities to sum to one, we 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 (Hobson et al. 2009, Ashley et al. 2010, Palumbo et al. 2019, 2020). We subsequently summed the results of the assignments over all individuals by addition of the surfaces. This provided a final surface of the distribution in the number of individuals assigned to each pixel. These distribution surfaces adequately reflected uncertainty because they were propagated in the Bayesian models and come from our best estimate of error of $\delta^2\text{H}_f$ between individuals at any given site.

Weighting output with band recoveries

To inform whether a source population of harvested juvenile Mallards originated from the Atlantic or Mississippi Flyway, we summarized available (1 January 1940 to 14 July 2020) band recovery data compiled by the U.S. Geological Survey Bird Banding Laboratory. We queried the database for all reported direct recoveries, i.e., a bird recovered during the first hunting season following banding, of juvenile Mallards in the Atlantic Flyway, as well as for all banding stations and number of bands placed on juvenile Mallards in the Atlantic and Mississippi Flyways. The recovery location and their corresponding banding location were displayed in a geographic information system (hereafter GIS; ArcGIS 10.8, Environmental Systems Research Institute Inc., Redlands, California, USA). For each state in the Atlantic Flyway, we selected all reported recoveries through time and used their associated banding location to assign a flyway of origin to each individual. The polygon that encompassed their associated banding coordinates was treated as the geographic area where a harvested Mallard originated. To determine banding effort, we extracted all banding stations and summed the number of bands placed on juvenile Mallards within each state's polygon. We then calculated the proportion of band recoveries derived from the Atlantic and Mississippi Flyways for each state and adjusted it for banding effort by dividing the total number of recovered, banded Mallards in each state by the total number of bands placed on Mallards that would be available for recovery. A new raster was then created for each state where the pixel values within the Atlantic and Mississippi Flyways represented those states' banding-effort informed proportion of harvest. Following the methodology outlined above, an assignment-to-origin map was created for each subset of samples that were harvested in each

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Table 1. Sample size of juvenile Mallards (*Anas platyrhynchos*) collected by state during the 2018–2019 and 2019–2020 hunting seasons across two sampling periods: early- and late-season (before or after 1 December). Sample percent and each state’s percentage of Mallard harvest for the 2018 hunting season (Raftovich et al. 2020; Harvest Percent) shown along with percentage of sample assigned to U.S. (US Origin) and Canada (Canada Origin) using $\delta^2\text{H}$ analyses of feathers. Asterix identifies states that were under-sampled relative to their harvest percent.

State	Early	Late	Total	Sample Percent	Harvest Percent	U.S. Origin (%)	Canada Origin (%)
Connecticut	21	14	35	2.79	2.17	42.86	57.14
Delaware	31	31	62	4.94	2.96	32.26	67.74
Florida	0	1	1	0.08	0.06	100.00	0.00
Georgia	3	11	14	1.12	1.12	78.57	21.43
Massachusetts*	18	12	30	2.39	2.60	50.00	50.00
Maryland*	69	77	146	11.64	13.03	33.56	66.44
Maine*	36	17	53	4.23	4.26	49.06	50.94
North Carolina*	43	64	107	8.53	18.62	57.01	42.99
New Hampshire	24	11	35	2.79	1.99	40.00	60.00
New Jersey	31	25	56	4.47	2.31	39.29	60.71
New York	214	128	342	27.27	18.08	20.18	79.82
Pennsylvania	73	64	137	10.93	9.49	45.99	54.01
Rhode Island	10	5	15	1.20	0.90	53.33	46.67
South Carolina*	22	30	52	4.15	5.05	57.69	42.31
Virginia*	40	62	102	8.13	13.68	28.43	71.57
Vermont	41	8	49	3.91	2.96	20.41	79.59
West Virginia	8	10	18	1.44	0.72	38.89	61.11
Total	684	570	1254			35.90	64.10

state. The unique states’ assignment-to-origin maps were then multiplied by the proportion of harvest raster to produce a weighted state map of Mallard origins. Finally, all individual state-map rasters were overlaid and summed to produce a final assignment-to-origin map weighted by band recovery data.

United States and Canada origins

To determine the percentage of our sample size that originated from the U.S. or Canada, we assigned each country as a bin. We assigned each individual bird to one of the country’s bins by summing the estimated probability of origins across cells occurring within these regions using a GIS zonal statistics query, and assigned individuals into the bin for which the highest cumulative likelihood was obtained (Hobson et al. 2013). We report the mean and median cumulative likelihood for all samples assigned to each country to assist with interpretation of uncertainty. Cumulative likelihood can range from 0, i.e., zero probability of origin, to 1, i.e., high probability of origin.

Temporal, sex, and state comparisons

We used linear regression models and an information theoretic approach with second-order Akaike information criterion for small sample sizes (AIC_c) to select the most parsimonious model or group of models from a set of candidate models. Any competing models were considered for inference if they were $\leq 2 \Delta AIC_c$ units of the top model and the top model parameters were not a subset of those in the competing model (Burnham and Anderson 2002, Devries et al. 2008). Competing models which did not meet these criteria were determined to contain uninformative parameters and were discarded for inference (Arnold 2010). We used the best model or group of models and associated model predictions to make inferences for $\delta^2\text{H}_f$ as a function of day of hunting season (e.g., 1 = opening day by state; Palumbo et al. 2019). We developed models to explore how $\delta^2\text{H}_f$

was influenced by day of season, sex, state of harvest, and year. We generated 19 models exploring the additive effect of all variables and interaction of state of harvest with day of hunting season. All linear regression models were created and tested using the R statistical framework (R Core Team 2018). All models were competed against an intercept-only null model. We present the top model and report 95% confidence limits for parameter estimates. We present model-predicted mean, range, 95% and 85% Confidence Limits of $\delta^2\text{H}_f$ and conducted and report pair-wise comparisons among states using Tukey-Honest Significant Difference tests at $\alpha = 0.05$.

RESULTS

We analyzed feathers from 1254 individuals distributed among all Atlantic Flyway states (Table 1). We removed Florida from our analyses of factors associated with $\delta^2\text{H}_f$ due to small sample size ($n = 1$).

We found variation in $\delta^2\text{H}_f$ was best explained by the interaction between day of hunting season and state of harvest ($w_i = 0.45$, $R^2 = 0.11$), whereas sex and year effects were not supported by the data (Table 2). The top model was 76.5 ΔAIC_c units lower than the null model. Other competing models $\leq 2 \Delta AIC_c$ units of the top model only contained uninformative parameters and were not reported (Arnold 2010). The origins of birds harvested in Georgia were significantly further south than those of birds harvested in New York, Maryland, Virginia, Vermont, and West Virginia (Table 3). Regression of $\delta^2\text{H}_f$ by day of hunting season had slopes that included or encompassed zero for all states, so we plotted the range of $\delta^2\text{H}_f$ collected during two time periods, early and late season, for ease of depicting lack of seasonal variation in $\delta^2\text{H}_f$ (Fig. 1).

The majority of our sampled Mallards harvested in the Atlantic Flyway were assigned to origins in Canada (64%) compared to

the U.S. (36%; Table 1, Fig. 2). Cumulative likelihood probability of birds assigned to Canada had $\bar{x} = 0.81$ and median = 0.84 whereas the U.S. had $\bar{x} = 0.76$ and median = 0.74. The

Table 2. Top model parameter estimates (Estimate), standard error (SE), and associated confidence limits (CLs; 85% and 95%) for variables used to model δ^2H_f in wing feathers (δ^2H_f) from juvenile Mallards (*Anas platyrhynchos*) harvested in the Atlantic Flyway during the 2018–2019 and 2019–2020 hunting seasons.

Variable	Estimate	SE	85% CLs	95% CLs
Intercept	-100.5	7.9	(-112.0,-89.1)	(-116.1,-84.9)
Day of Season	-0.2	0.1	(-0.4,0.0)	(-0.5,0.1)
Delaware	-15.4	9.9	(-29.6,-1.1)	(-34.8,4.1)
Georgia	16.6	13.9	(-3.4,36.7)	(-10.7,43.9)
Massachusetts	5.3	10.6	(-9.9,20.6)	(-15.5,26.1)
Maryland	-13.5	9.0	(-26.5,-0.5)	(-31.2,4.2)
Maine	-8.6	10.0	(-23.0,5.7)	(-28.2,10.9)
North Carolina	25.7	10.0	(11.3,40.2)	(6.1,45.4)
New Hampshire	-5.5	10.1	(-20.1,9.1)	(-25.4,14.4)
New Jersey	1.6	9.7	(-12.4,15.6)	(-17.5,20.7)
New York	-17.8	8.4	(-29.9,-5.7)	(-34.3,-1.3)
Pennsylvania	-0.7	8.7	(-13.2,11.8)	(-17.8,16.3)
Rhode Island	0.6	11.5	(-16.0,17.3)	(-22.0,23.3)
South Carolina	-8.6	9.3	(-22.0,4.8)	(-26.8,9.7)
Virginia	-9.0	9.7	(-23.0,4.9)	(-28.1,10.0)
Vermont	-16.0	9.6	(-29.9,-2.1)	(-34.9,2.9)
West Virginia	1.5	14.0	(-18.6,21.7)	(-25.9,29)
Day of Season:Delaware	0.3	0.2	(0.0,0.5)	(-0.1,0.6)
Day of Season:Georgia	0.0	0.3	(-0.5,0.4)	(-0.7,0.6)
Day of Season:Massachusetts	-0.1	0.2	(-0.3,0.2)	(-0.4,0.3)
Day of Season:Maryland	0.1	0.2	(-0.1,0.4)	(-0.2,0.4)
Day of Season:Maine	0.3	0.2	(0.0,0.5)	(-0.1,0.6)
Day of Season:North Carolina	-0.2	0.2	(-0.5,0.0)	(-0.5,0.1)
Day of Season:New Hampshire	0.1	0.2	(-0.1,0.4)	(-0.2,0.5)
Day of Season:New Jersey	0.0	0.2	(-0.3,0.2)	(-0.4,0.3)
Day of Season:New York	0.2	0.1	(0.0,0.4)	(-0.1,0.5)
Day of Season:Pennsylvania	0.1	0.2	(-0.2,0.3)	(-0.2,0.4)
Day of Season:Rhode Island	0.1	0.2	(-0.2,0.4)	(-0.3,0.5)
Day of Season:South Carolina	0.3	0.2	(0.0,0.5)	(-0.1,0.6)
Day of Season:Virginia	0.0	0.2	(-0.2,0.3)	(-0.3,0.4)
Day of Season:Vermont	0.2	0.2	(-0.1,0.5)	(-0.2,0.6)
Day of Season:West Virginia	-0.1	0.2	(-0.4,0.2)	(-0.5,0.3)

preponderance of harvested Mallards in the Atlantic Flyway had δ^2H_f consistent with natal origins in central Ontario and southern Quebec, but also possibly the Great Lakes region of U.S. and Canada (A, Fig. 2). Mallards harvested in Florida, Georgia, South Carolina, North Carolina, and Rhode Island were more likely to originate in the U.S. than Canada (Table 1), whereas all other states derived a greater percentage of Mallards from Canada than the U.S. Based on band recovery and banding-effort data, origins were primarily constrained to the Atlantic Flyway that determined that Mallards harvested in the Atlantic Flyway had δ^2H_f consistent with natal origins in southern Quebec, New Brunswick, and northern U.S. (B, Fig. 2).

DISCUSSION

Our findings that almost two-thirds of Mallards harvested in the Atlantic Flyway during our study had δ^2H_f values that traced their natal origins to Canada seems to contradict the most recently available population surveys. Surveys in 2017 estimated that the breeding-population size of eastern Mallards was 650,000 individuals with 450,000 (~70%) breeding in the northeastern United States and 200,000 (~30%) breeding in southern Quebec and Ontario (U.S. Fish and Wildlife Service 2017). There are several possible explanations for this discrepancy.

Fig. 1. δ^2H_f values of wing feathers (δ^2H_f in ‰) from juvenile Mallards (*Anas platyrhynchos*) harvested in the Atlantic Flyway during the 2018–2019 and 2019–2020 hunting seasons across two sampling periods: early- and late-season (before and after 1 December). Boxes represent the interquartile range with the median, and whiskers of box plots represent $1.5 \times$ the interquartile range. States are arranged by increasing mean δ^2H_f .

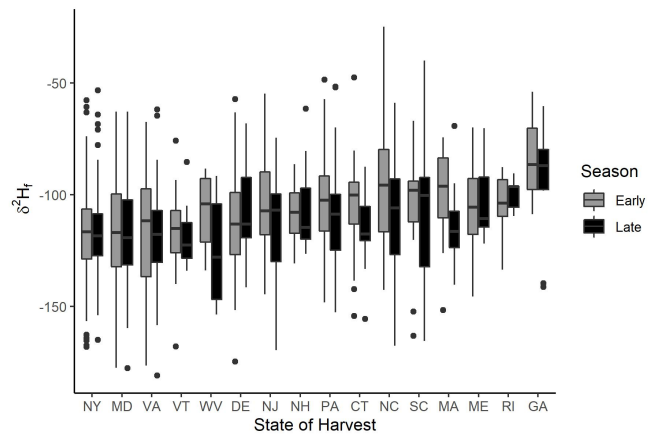
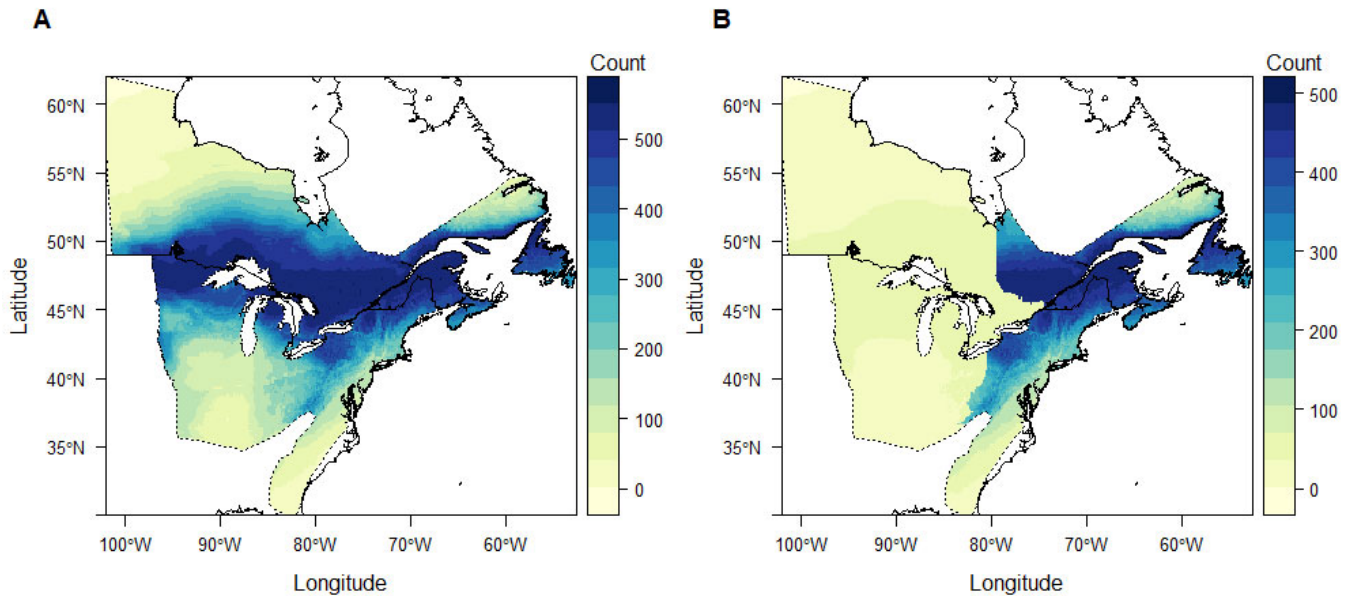


Table 3. Predicted δ^2H_f values of wing feathers (δ^2H_f mean in ‰), along with 95% confidence limits (CLs), from juvenile Mallards (*Anas platyrhynchos*) harvested in the Atlantic Flyway during the 2018–2019 and 2019–2020 hunting seasons (n = 1253) based on the top performing model. Post-hoc Tukey honesty significance test groupings (A, B) indicates that groups with the same letter are not detectably different, groups with more than one letter identify overlap between sets of groups, and different letters indicate detectably different groups. States are arranged by increasing mean δ^2H_f .

State	Mean	95% CLs	Tukey HSD Grouping
NY	-117.2	(-121.8,-113.5)	A
MD	-116.5	(-121.7,-111.4)	A
VA	-116.5	(-122.8,-110.2)	A
VT	-116.0	(-124.6,-107.4)	A
WV	-113.3	(-126.9,-99.7)	A
DE	-110.9	(-118.5,-103.3)	AB
CT	-109.1	(-119.2,-98.8)	AB
NJ	-108.1	(-115.6,-100.5)	AB
NH	-107.2	(-116.1,-98.3)	AB
PA	-107.2	(-112.2,-102.2)	AB
SC	-105.6	(-113.4,-97.8)	AB
MA	-105.3	(-115.1,-95.5)	AB
ME	-105.0	(-113.0,-97.0)	AB
RI	-103.5	(-117.2,-89.8)	AB
NC	-103.1	(-116.8,-89.3)	AB
GA	-90.8	(-105.6,-76.0)	B

First, current breeding-season survey methods and protocols in the Atlantic flyway may be underestimating the breeding population of Mallards in Canada. Count-based surveys provide an instantaneous sample for each survey stratum but breeding birds may arrive over a protracted interval. For early nesting species

Fig. 2. Maps of probable origins of juvenile Mallards (*Anas platyrhynchos*) harvested along the Atlantic Flyway during the 2018–2019 and 2019–2020 hunting season with (A) origins unconstrained by banding data and (B) origins constrained by a banding data informed weighted spatial mask. Legend numbers correspond to number of individuals assigned to each pixel (5 km x 5 km) based on a 2:1 odds ratio criterion (see Methods).



like Mallards, timing surveys with initial settling of pairs on breeding areas may lead to underestimates of the true breeding population if a percentage of pairs are still moving north (Alisauskas et al. 2014). We recommend marking and tracking a representative sample of adult female Mallards by satellite telemetry or conducting multiple breeding waterfowl surveys to determine chronology and settling dates. These methods would help determine if pre-breeding Mallards are still moving during the breeding survey period and if this causes bias in U.S. and Canada population estimates. Traditional count-based surveys such as the WBPBS also may suffer from systematic underestimation of detection probabilities. In eastern Canada, detection probabilities are based on comparisons between fixed-wing aircrafts and helicopters (Zimmerman et al. 2012). Testing the assumption that observers in helicopters see 100% of available birds would help determine if accepted values of Mallard breeding pairs in Canada are underestimated (Alisauskas et al. 2014).

A second hypothesis is that Mallard per-capita productivity could be greater in Canada than in the U.S., which would be consistent with divergent population trajectories of breeding Mallards between these countries. In the northeastern U.S., land-cover changes could contribute to breeding habitats acting as ecological traps for Mallards (Hale and Swearer 2016). Habitat that degrades over time can act as sinks for Mallards by attracting birds from source patches and decreasing overall productivity (Cowardin et al. 1995). Mallards breeding in the northeastern U.S. often select for forested wetlands during breeding season (Losito and Baldassarre 1995, Carrière and Titman 1998). In the northeastern U.S., deforestation is largely being driven by urban growth (Jeon et al. 2014). New England alone has lost 350,000 ha of forest to

urban development since 1985 (Thompson et al. 2017). Additionally, despite a no-net-loss national policy for wetlands and mandatory compensatory measures, the U.S. continues to show a net loss of wetland area and function that can exacerbate effects of breeding habitat loss (Zedler 2004, Mitsch and Gosselink 2005). Due to these changes in the U.S., breeding Mallards may have reduced nesting or fledging success. This highlights the need to conduct contemporary assessments of the quantity and quality of freshwater wetlands in the Atlantic Flyway with a focus on negative affects to Mallard productivity.

Third, introgression of game-farm genetics may be driving differences in Atlantic Flyway Mallard survival and productivity in the U.S. and Canada. Releases of game-farm Mallards in the Atlantic Flyway has resulted in the genetic swamping of the eastern Mallard population and the establishment of a stable game-farm and game-farm \times wild Mallard population (Lavretsky et al. 2020). Recent findings indicate that \sim 90% of Mallards sampled in the Atlantic Flyway had substantial ($> 10\%$) genetic input from game-farm Mallards (Lavretsky et al. 2019). This influx of artificially selected genes into the population could be potentially maladaptive and driving declines in productivity and survival (Lavretsky et al. 2020). In addition, a recent study in the Mississippi Flyway detected greater game-farm genetic introgression at southern versus northern latitudes (Schummer et al. 2023). Overall, areas of greater introgression of game-farm genetics in the northeastern U.S. are consistent with locales of Mallard population decline. We recommend further investigation into the genetics, production, and survival rates of Mallards breeding in Canada compared to the U.S. to improve our understanding of what may be driving these disparities in population trajectories.

Finally, it is important to discuss that our predictive isoscapes and use of a single measure, i.e., $\delta^2\text{H}$, can result in ambiguity in assignment (Palumbo et al. 2019). To minimize uncertainty, we utilized a Bayesian assignment approach which propagates known sources of error and in general is considered conservative (Palumbo et al. 2019). We are the first study to apply a species-specific, age-corrected calibration equation to North American dabbling ducks (van Dijk et al. 2014). Previous studies using stable-isotope analyses for dabbling ducks in North America have used a calibration equation based on known-origin Lesser Scaup (*Aythya affinis*) and relied on assumptions that differences in foraging guilds would not influence results. Van Dijk's (2014) calibration equation was created from known-origin Mallards and was corrected for age to be juvenile-specific. Finally, cumulative probability was used to assign an individual to a country of origin to minimize incorrect assignment. Despite all these efforts, we recognize that the high density of individuals whose natal origin fell close to the U.S.-Canadian border could impact our results.

Our analyses provided strong evidence that mixed harvest of migrant and locally produced Mallards occurred in all states throughout the entirety of the 2018–2019 and 2019–2020 seasons (Fig. 1). For managers, this evidence suggests hunting seasons cannot be used to target harvest of either U.S.- or Canada-produced Mallards in the Atlantic Flyway and raises questions about differences in autumn-winter migration chronology among areas where eastern Mallards are produced. Specifically, at the beginning of hunting seasons in more northern states, i.e., early October, Mallards from relatively far north in the Mallard-breeding range of Canada are harvested along with regionally produced Mallards. This suggests southward movement of Mallards from Canada prior to the beginning of the hunting season. Similarly, Palumbo et al. (2019) detected that ~70% of juvenile Mallards harvested on the Canadian side of Lake St. Clair had originated from much farther north and these northern produced Mallards were available for harvest when the Ontario, Canada, hunting season opened in late September. We suggest that states in the northern portion of the Atlantic Flyway may be banding some juvenile Mallards produced in Canada, because U. S. banding operations often continue until the end of September to meet banding quotas. There is relatively little peer-reviewed literature available on the harvest of local compared to migrant Mallards in the Atlantic Flyway. However, in the Great Lakes region, some acknowledge there may be overestimation of locally produced birds from use of banding data (Singer 2014). Southward movement of Mallards produced in Canada to the U.S. prior to the banding season would likely inflate local derivation estimates for U.S. regions receiving early migrants and be consistent with our harvest estimate of a greater abundance of Mallards being produced in Canada than the U.S. Because the current Eastern Mallard adaptive harvest management strategy relies on band-recovery data for estimating harvest rates and survival (Roberts et al. 2022) we recommend an investigation of pre-season movement of Mallards, during the banding period, i.e., July to September, to understand if pre-season movements need to be considered when interpreting these estimates and using them as inputs for population models.

Our study demonstrates that stable isotope analysis of feathers of harvested waterfowl can be applied to expand our knowledge and inform management and conservation strategies. Inference of

origins outside of the sampling region allowed us to identify that most of harvested Mallards in the Atlantic Flyway are derived from the Canadian breeding population in regions where deployment of external markers, i.e., metal leg bands, is limited and logistically difficult (Hebert and Wassenaar 2005, Alisauskas et al. 2014, Roy et al. 2019). This novel finding contradicts breeding-population surveys (U.S. Fish and Wildlife Service 2017) and the long-term belief that most of Mallards harvested in the U.S. are hatched in the U.S. Our results provide managers with information important for proper harvest management. We recommend stable-isotope techniques continue to be applied in management of North American waterfowl and encourage additional research in this area to inform population modeling, including application of integrated population models (Hobson et al. 2009, Asante et al. 2017, Palumbo et al. 2019).

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