



RESEARCH ARTICLE

Tracing origins of waterfowl using the Saskatchewan River Delta: Incorporating stable isotope approaches in continent-wide waterfowl management and conservation

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ABSTRACT

Understanding the catchment areas of key stopover sites for migratory birds is important for their management and conservation. The Saskatchewan River Delta (SRD) in central Canada is North America's largest inland delta and an important spring and fall stopover site for migratory waterfowl, but there is little information on the origins of waterfowl that use the SRD. We used stable isotope analyses of hydrogen ($\delta^2\text{H}$) and sulfur ($\delta^{34}\text{S}$) in feathers of hunter-killed waterfowl on the SRD to infer natal or molt origins of 5 duck species, using spatially explicit assignment to a $\delta^2\text{H}$ feather isoscape developed for waterfowl in North America. Initial classification with $\delta^2\text{H}$ estimated that 50% were migrants from the north and 10% were assigned to regions south of the SRD, leaving only 39% of the sample with origins in the SRD. Using thresholds in feather $\delta^{34}\text{S}$ values associated with prairie and forest biomes, we further reassigned 64% of SRD birds as having originated from nearby agricultural and forested areas that have similar $\delta^2\text{H}$ values as the delta. Together, these results suggest that >80% of all waterfowl sampled were recent arrivals that were using the SRD as a stopover site. This demonstrates that stable isotope analyses of hunter-killed birds can be used to monitor changes in origins and recruitment into the fall waterfowl population of key stopover sites.

Keywords: American Wigeon, Blue-winged Teal, deuterium, Green-winged Teal, Mallard, migration, Northern Pintail, stable isotopes, sulfur-34, wetlands

Retracer la provenance de la sauvagine utilisant le delta de la rivière Saskatchewan : incorporer des approches d'isotopes stables dans la gestion et la conservation de la sauvagine à l'échelle du continent

RÉSUMÉ

La compréhension des bassins versants des haltes migratoires clés pour les oiseaux migrateurs est importante pour leur gestion et leur conservation. Le delta de la rivière Saskatchewan (DRS), situé au centre du Canada, est le plus grand delta continental de l'Amérique du Nord et constitue une importante halte migratoire au printemps et à l'automne pour la sauvagine migratrice. Il existe cependant peu d'information sur la provenance de la sauvagine qui utilise le DRS. Afin d'inférer les origines natales ou de mue de cinq espèces de canards, nous avons effectué des analyses d'isotopes stables de l'hydrogène ($\delta^2\text{H}$) et du soufre ($\delta^{34}\text{S}$) sur des plumes de canards tués par des chasseurs dans le DRS, en utilisant une localisation spatialement explicite d'un isoscape $\delta^2\text{H}$ de plume développée pour la sauvagine en Amérique du Nord. La classification initiale avec $\delta^2\text{H}$ a estimé que 50 % étaient des migrants provenant du nord et 10 % étaient assignés à des régions au sud du DRS, ce qui laissait seulement 39 % de l'échantillon provenant du DRS. À l'aide de seuils dans les valeurs de $\delta^{34}\text{S}$ des plumes associées aux biomes de la prairie et de la forêt, nous avons ensuite reclassé 64 % des oiseaux du DRS comme provenant de zones agricoles et forestières avoisinantes ayant des valeurs de $\delta^2\text{H}$ similaires à celle du delta. Mis ensemble, cela suggère que > 80 % de toute la sauvagine échantillonnée était récemment arrivée et utilisait le DRS comme halte migratoire. Ceci démontre que les analyses d'isotopes stables d'oiseaux tués par les chasseurs peuvent être utilisées pour suivre les changements dans la provenance de la sauvagine et le recrutement dans la population automnale sur les haltes migratoires clés.

Mots-clés: *Anas acuta*, *A. americana*, *A. crecca*, *A. discors*, *A. platyrhynchos*, deutérium, isotopes stables, migration, milieux humides, soufre 34

INTRODUCTION

Establishing connections between breeding, stopover, and wintering sites used by populations of migratory birds is important for their conservation and management (Webster et al. 2002, Szymanski et al. 2007, Hobson et al. 2009, Nelson et al. 2015). For harvested species, connectivity information also facilitates decisions about the allocation of harvest quotas by identifying key production areas and factors potentially influencing recruitment (Alisauskas et al. 1998, Webster and Marra 2005, Boere and Stroud 2006) as well as identifying movements of pathogens and contaminants (Gunnarsson et al. 2012). Combined with breeding population estimates, such information for harvested species allows a more refined assessment of the impact and sustainability of the hunt.

Approximately 50 million waterfowl breed in northern regions of North America and migrate to overwintering sites in the south, including Mexico, the Caribbean, Central America, and South America (Bellrose 1976, U.S. Fish and Wildlife Service [USFWS] 2015). The Central Flyway accounts for roughly half of the North American migratory waterfowl population, with ~12.3 million waterfowl breeding in Canadian portions of this flyway and another 12.2 million breeding in the north-central United States in 2013 (USFWS 2015).

Waterfowl movements in North America have been described primarily through extensive banding programs (Lavretsky et al. 2014, Buhnerkempe et al. 2016). Such programs have been an invaluable resource for waterfowl management but, like all extrinsic markers, suffer from limitations. For example, data are limited to the banded cohort and so are biased toward the region of initial sampling (Hobson and Norris 2008, Korner-Nievergelt et al. 2010). This can be a serious issue for birds that occupy large geographic regions. For many species, sampling young-of-the-year can be difficult, and so inferring which areas are the most or least productive can be almost impossible at continental scales. Miniaturization of satellite transmitters and geolocators has extended remote monitoring to small songbirds, but cost and logistics still limit the use of these technologies, especially when tags need to be recovered in remote places (Dieter and Anderson 2009, Bridge et al. 2011, Brown et al. 2017, Kramer et al. 2017).

The use of intrinsic assays such as molecular markers or naturally occurring stable isotope ratios offers a way to augment more conventional means of tracking migrant wildlife (Hobson and Wassenaar 2008). Stable hydrogen isotope ($^2\text{H}/^1\text{H}$, measured as $\delta^2\text{H}$) measurement of animal tissues is a powerful tool for inferring origins of migrants because this isotope undergoes predictable changes in food webs across continents. This approach has been used successfully in describing origins of several waterfowl

populations in North America (Hebert and Wassenaar 2005a, Yerkes et al. 2008, Hobson et al. 2009, Ashley et al. 2010; see also Hobson et al. 2006).

The Saskatchewan River Delta (SRD), North America's largest inland delta (~10,000 km²), has long been recognized as an important breeding and stopover location for waterfowl within the Central and Mississippi flyways (Bellrose 1976, Schmutz 2001, Baschuk et al. 2012). Over the past century, water flow through the delta has been modified by climate change, construction of dams, and extractions for irrigation (Schindler and Donahue 2006, Gober and Wheeler 2014). As a result, the Saskatchewan River has reduced summer peak floods and smaller total wetland area (Sagin et al. 2015). In light of these developments and the paucity of information on the origins of waterfowl that use the SRD, we used stable isotope approaches to infer origins of hunter-killed ducks during the fall harvests of 2013 and 2014. Our objective was to provide fundamental baseline information on the structure of the fall harvest by differentiating between locally produced (or molted) birds and those derived from breeding populations away from the SRD. We anticipated that most migrants would be from the north, but we had no *a priori* expectations on the composition of populations and how they might differ among species and age–sex classes. Our ultimate goal was to demonstrate the utility of the stable isotope approach as a monitoring tool to track changes in the use of the SRD by waterfowl, particularly in anticipation of major anthropogenic changes expected for waterfowl habitat throughout their range (Johnson et al. 2005). We also wanted to emphasize stable isotopes as a monitoring and research tool in the broader context of managing and conserving waterfowl in North America.

METHODS

The SRD lies at the Saskatchewan–Manitoba border in the Boreal Plain, a transition zone between prairie and the forests of the Boreal Shield. Sampling for waterfowl was conducted at 5 shallow lakes and river backwaters (Grassy Point, Muskeg Lake, Dumbell Lake, Bens Lake, and Big Eddy) in the upper SRD (53.9°N, 102.9°W; Figure 1) in the fall seasons of 2013 (September 5–October 22) and 2014 (September 17–October 10). In 2013, there was extensive flooding in the SRD, with greater spring and summer river discharge compared to the long-term recorded average (spring peak discharge = 1,690 m³ s⁻¹; summer peak discharge = 3,640 m³ s⁻¹; compared to average spring and summer values of 650 m³ s⁻¹ and 870 m³ s⁻¹, respectively; Water Survey of Canada gauge station 05KD003). There was similar spring flooding but reduced summer flooding in 2014 (spring peak discharge = 1,750 m³ s⁻¹; summer peak discharge = 1,730 m³ s⁻¹). At the time of sample collection, the backwaters and lakes were open water with vegetation interspersed at the periphery.

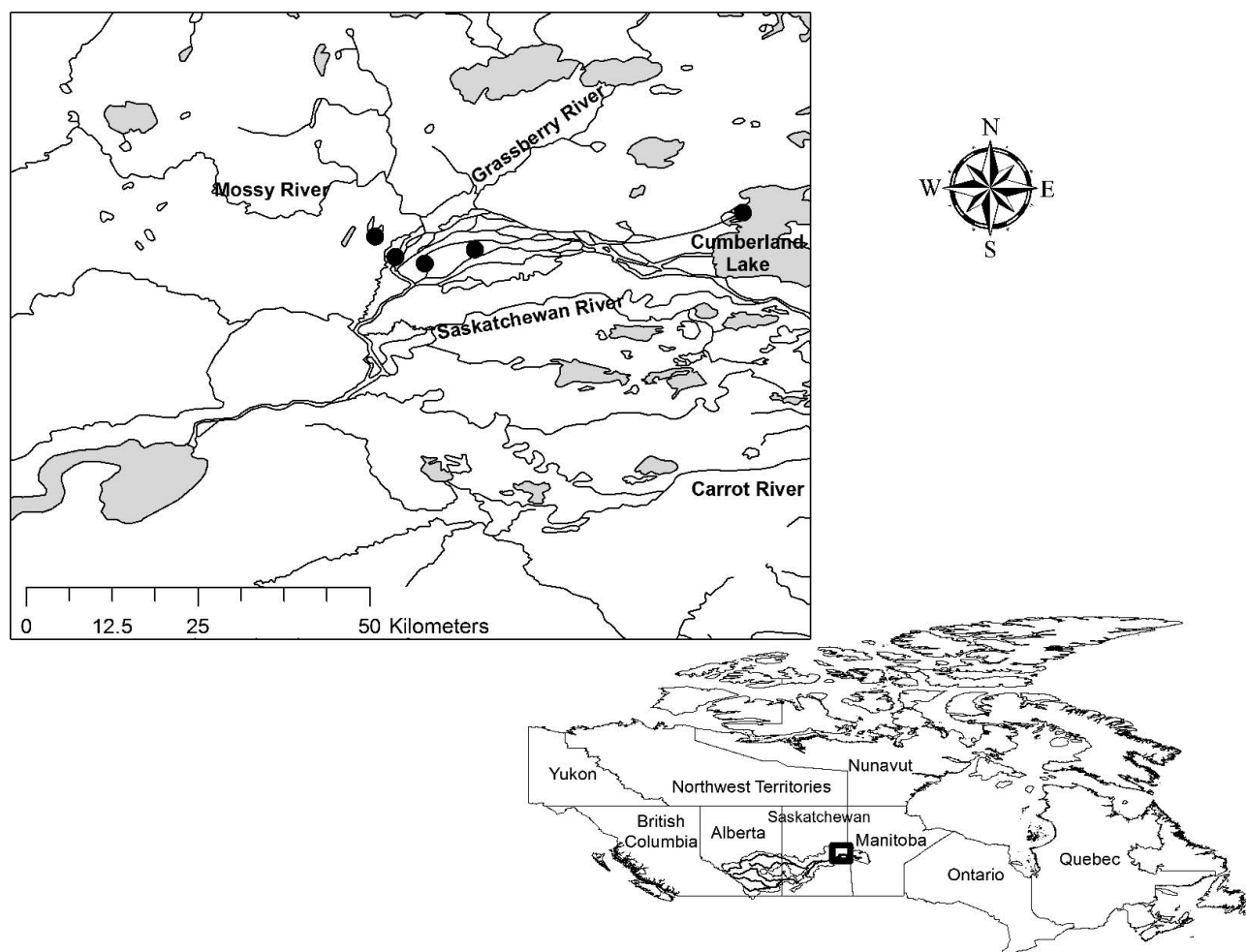


FIGURE 1. Sampling locations (solid circles) where waterfowl were collected by hunters in the Saskatchewan River Delta, Canada, in autumn 2013 and 2014.

Aquatic macrophytes such as sedges (*Carex* spp.), reed grass (*Phragmites australis*), and cattails (*Typha* spp.) dominated the emergent zone vegetation.

Wing and Water Collection

A total of 236 hunter-killed birds were sampled, comprising Mallard (*Anas platyrhynchos*, $n = 93$), Northern Pintail (*A. acuta*, $n = 36$), American Wigeon (*A. americana*, $n = 20$), Green-winged Teal (*A. crecca*, $n = 35$), and Blue-winged Teal (*A. discors*, $n = 52$). With the exception of Mallard, all species were collected in both years, with the majority of collections occurring in 2013 (202 of 236 birds). Wing samples from each bird were kept on ice in the field, frozen, and transported to the aquatic food webs laboratory at the Toxicology Centre, University of Saskatchewan (Table 1).

To compare with modeled amount-weighted mean annual $\delta^2\text{H}$ in precipitation ($\delta^2\text{H}_p$) for our study site, surface water samples ($n = 7$) were collected at various SRD locations in August 2013, including 3 of the sites

where birds were later harvested. These water samples were kept at room temperature, with no head space, in closed vials until they were analyzed for $\delta^2\text{H}$.

Wing Preparation and Identification

Wings were allowed to thaw and then were sexed and aged using a wing identification manual (Carney 1992) with assistance from a trained technician at the Canadian Wildlife Service, Saskatoon, Saskatchewan, Canada. The first primary feather (P1) from each wing was cleaned of surface oils and dirt using a 2:1 chloroform:methanol solution by soaking for 24 hr and drying under a fume hood for 48 hr. Feather vane material was then clipped from the distal portion of the feather vane and weighed into silver cups (~ 0.35 mg) for stable isotope analysis.

Stable Hydrogen Isotope Analysis

Both water and feather samples were analyzed for $\delta^2\text{H}$ at the National Hydrology Research Center of Environment

TABLE 1. Hunter-collected ducks sampled on the Saskatchewan River Delta, Canada, for stable isotope analysis, 2013 and 2014.

Species	Adult males	Adult females	Hatch-year males	Hatch-year females
American Wigeon	3	8	2	7
Mallard	17	15	25	36
Blue-winged Teal	14	15	9	14
Northern Pintail	5	9	10	12
Green-winged Teal	5	12	7	11
Total	59	44	53	80

Canada in Saskatoon. Water $\delta^2\text{H}$ values were measured with an LGR DLT-100 OA-ICOS liquid water isotope analyzer coupled to a LC-PAL autosampler with a measurement precision of $\pm 1\text{‰}$. Feather samples were loaded into silver capsules and placed with standards into a zero blank carousel under helium flow. Pyrolysis combustion was at $1,350^\circ\text{C}$ in a Hekatek furnace, and gases were separated using a Eurovector Elemental Analyzer (Milan, Italy) interfaced with an Elementar Isoprime (Isoprime, Manchester, UK) Continuous Flow Isotope Mass Spectrometer (CFIRMS). Analysis of $\delta^2\text{H}$ was conducted using the comparative equilibration method of Wassenaar and Hobson (2003) with 3 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 analyses ($n = 5$ each) of the keratin standards, measurement error was approximately $\pm 2\text{‰}$ for hydrogen isotopes in feather ($\delta^2\text{H}_f$). All $\delta^2\text{H}$ values are reported in relation to the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP) scale.

Statistical Analyses

All statistical analyses were conducted in SPSS 22.0 (IBM, Armonk, New York, USA). First, ordinary least squares regression was used to test for the effects of timing of collection on $\delta^2\text{H}_f$, and analysis of variance (ANOVA) was used to test for a year effect. The year effect was tested using only 4 of the 5 species because Mallards were not collected in 2014. An ANOVA was then used to evaluate whether observed $\delta^2\text{H}_f$ differed according to age (adult or juvenile), sex (male or female), and species; this model included all 2-way interactions. A Tukey's post hoc test was used to make comparisons of marginal means for each species. Differences were considered significant at $\alpha = 0.05$.

Assignment to Origin

Previous studies have used estimates of the amount-weighted mean annual or growing-season precipitation $\delta^2\text{H}$ ($\delta^2\text{H}_p$) to estimate expected $\delta^2\text{H}_f$ at a given location using an appropriate calibration algorithm (Bowen et al. 2005, Hobson 2008). However, waterfowl habitat in the SRD was clearly dominated by flows from the Saskatch-

ewan River (Sagin et al. 2015), with $\sim 75\%$ of the flow originating from the Rocky Mountains in Alberta, where $\delta^2\text{H}_p$ tends to be more negative than local precipitation. For example, queries in the Online Isotopes in Precipitation Calculator (Bowen and Revenaugh 2003) for locations west of the cities of Calgary and Edmonton (-114.78°W , 52.19°N to -116.66°W , 52.21°N ; elevations of 1,000–2,200 m) yielded values ranging from -179‰ to -126‰ ($n = 10$), lower than predicted values for precipitation at the SRD (approximately -120‰). Evaporation of this water during transit along the basin further complicates the choice of $\delta^2\text{H}_p$. Thus, we used summer-collected surface water samples from the SRD (mean $= -126\text{‰}$, SD $= 13\text{‰}$, range: -140‰ to -100‰ , $n = 7$) as a best estimate of water available for feather growth in local birds. This approach was further supported by average winter water isotope values from wetlands in the same region (mean $= -125\text{‰}$, SD $= 10.6\text{‰}$, range: -145‰ to -112‰ , $n = 26$ sites; MacKinnon et al. 2016).

Prior to assigning birds to their molt origins, we first assigned birds as locals vs. migrants using likelihood-based assignments. We first calculated the expected feather value for birds molting on the delta ($\delta^2\text{H}_{fd}$) by applying a rescaling function derived by regressing $\delta^2\text{H}_f$ of known-origin Lesser Scaup (*Aythya affinis*) against $\delta^2\text{H}_p$ (Clark et al. 2006, 2009). Specifically, we rescaled our measured summer mean surface water value (-126‰) using the equation $\delta^2\text{H}_f = -30.4 + 0.93 \cdot \delta^2\text{H}_p$, resulting in a predicted mean $\delta^2\text{H}_{fd}$ of -148.1‰ . Following Van Wilgenburg et al. (2012), we then compared the observed $\delta^2\text{H}_f$ values for unknown-origin birds against the predicted mean $\delta^2\text{H}_f$ using a normal probability density function to assess the likelihood that the unknown-origin sample had grown its feather on the delta, given expected variation in $\delta^2\text{H}_f$ between individuals growing their feathers at the same location. We estimated expected variation using the distribution of residuals (SD $= 12.8\text{‰}$) from the Clark et al. (2006, 2009) rescaling function. If $\delta^2\text{H}_f$ fell within $\pm 12.8\text{‰}$ around the expected $\delta^2\text{H}_f$ for the SRD ($\delta^2\text{H}_{fd}$), they were classified as local birds, based on a 2:1 odds ratio. We examined the sensitivity of our analyses by repeating this approach using a 3:1 odds ratio corresponding to $\delta^2\text{H}_f$ falling within $\pm 14.1\text{‰}$ (i.e. $1.15 \cdot 12.8$) of $\delta^2\text{H}_{fd}$ (Chabot et al. 2012, Van Wilgenburg et al. 2012, Wunder 2012). Birds not falling within the expected range for the SRD were classified as "northern" birds if $\delta^2\text{H}_f$ was less than $\delta^2\text{H}_{fd} - 12.8\text{‰}$ (at 2:1 odds) or as "southern" birds if $\delta^2\text{H}_f$ was greater than $\delta^2\text{H}_{fd} + 12.8\text{‰}$.

To further elucidate the origins of birds classified as southern or northern, we used likelihood-based assignment algorithms to conduct spatially explicit assignments to origin, based on joint analysis of $\delta^2\text{H}$ and band recovery data (Hobson et al. 2009, Wunder 2010, Van Wilgenburg and Hobson 2011). We first created a map (hereafter

TABLE 2. Prior probabilities (determined from hunter recoveries of banded birds) that the 5 study species originated from a specific flyway, given that they were harvested in the Central Flyway.

	Green-winged Teal		American Wigeon		Blue-winged Teal		Mallard		Northern Pintail	
	<i>n</i>	Prior	<i>n</i>	Prior	<i>n</i>	Prior	<i>n</i>	Prior	<i>n</i>	Prior
Atlantic Flyway	1	<0.01	1	<0.01	4	<0.01	0	<0.01	6	<0.01
Central Flyway	340	0.89	509	0.91	1,833	0.91	819	0.74	3,208	0.94
Mississippi Flyway	8	0.02	4	0.01	159	0.08	180	0.16	32	0.01
Pacific Flyway	34	0.09	47	0.08	17	0.01	108	0.10	179	0.05

“isoscape”) of predicted $\delta^2\text{H}$ in feathers ($\delta^2\text{H}_f$) by applying the aforementioned rescaling function of Clark et al. (2006, 2009) to rescale the precipitation amount-weighted growing-season $\delta^2\text{H}$ in the precipitation map ($\delta^2\text{H}_p$) of Bowen et al. (2005) into equivalent feather values. Finally, we used a spatial “mask” operation to limit the isoscape to only those areas of the continent falling exclusively within the species’ breeding range, based on a digital breeding-range map (Ridgely et al. 2007).

Following Hobson et al. (2009), we used band recovery data to calculate prior probabilities that a hunter-killed bird shot within the Central Flyway originated from the Atlantic, Mississippi, Central, or Pacific flyway. We first obtained band recovery data from the Bird Banding Lab of the U.S. Geological Survey (<https://www.pwrc.usgs.gov/BBL/index.cfm>) for all 5 of our study species that were banded and subsequently recovered between 2004 and 2014. From these data, we selected only records involving hunter-recovered birds, and we further screened the data so that only birds banded during the breeding months of May, June, and July were retained. We overlaid the banding location and recovery locations on a geospatial layer delineating the flyway boundaries (see Hobson et al. 2009) and associated each banding and recovery location with the flyway in which it occurred. Finally, we used cross-tabulation to calculate the frequencies at which a species was banded in a given flyway and subsequently recovered elsewhere. Based on these frequencies, we parameterized a set of prior probabilities (Table 2) to be used in our assignment model (below).

Following isoscape creation and band recovery analysis, we estimated the likelihood that individual cells (i.e. pixels) within the isoscape represented a potential origin for a given sample by comparing the observed $\delta^2\text{H}_f$ against the isoscape-predicted $\delta^2\text{H}_f$ using a normal probability density function (Hobson et al. 2009). Following Hobson et al. (2009), we then applied Bayes’ theorem to assess the posterior probability that an individual pixel within the isoscape was the putative origin of a given sample, conditional on the prior probability that it originated from the flyway in which the pixel in question occurred, based on the band recovery analyses (above). After normalizing

the probabilities to sum to 1, we assigned individuals to likely origins 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 1 and all others as 0. In addition, we examined sensitivity to the choice of odds ratio by repeating the assignments by selecting the upper 75% of estimated “probabilities of origin” for each individual and coding those as 1, and all others as 0, consistent with 3:1 odds. We subsequently summed the results of the assignments over all individuals by addition of the surfaces (Hobson et al. 2009, Van Wilgenburg and Hobson 2011).

While our classification using $\delta^2\text{H}_f$ allowed assignment of birds to local vs. northern or southern migrant categories, there is overlap in $\delta^2\text{H}_p$ between source water in the SRD and precipitation over a large portion of the prairies. Therefore, to further segregate birds that had been assigned to the SRD into prairie and forest biomes, we also analyzed feathers from a subset of 75 birds with the highest (least negative) $\delta^2\text{H}_f$ values for stable sulfur isotopes ($^{34}\text{S}/^{32}\text{S}$ or $\delta^{34}\text{S}$). That analysis was motivated by spatial structure for feather $\delta^{34}\text{S}$ values over a large region of the Canadian prairies (Hebert and Wassenaar 2005b). Based on their findings, we expected birds that molted in prairie wetlands to have $\delta^{34}\text{S}$ values less than -6‰ . This threshold was further evaluated by analyzing $\delta^{34}\text{S}$ values in invertebrate and fish samples collected from SRD wetlands in August 2013. Since there is little or no discrimination of $\delta^{34}\text{S}$ in food webs (McCutchan et al. 2003), we assumed that local birds would have the same $\delta^{34}\text{S}$ value as invertebrates and fishes collected there. Feather, invertebrate, and fish samples were weighed (~ 3.5 mg) into tin capsules for analysis by CFIRMS and calibrated using secondary organic isotopic reference materials (BWB; $\delta^{34}\text{S} = 17.5\text{‰}$, $n = 5$, and CFS; $\delta^{34}\text{S} = -3.8\text{‰}$, $n = 5$). The instrument used was a Thermo Finnigan Delta V stable isotope ratio mass spectrometer coupled to a Costech model 4010 elemental analyzer via an open split. Results were expressed as isotopic ratios (units per mil \pm SD, in relation to the Canyon Diablo Troilite standard). Based on within-run analyses of standards, measurement error was estimated to be approximately $\pm 0.3\text{‰}$ for $\delta^{34}\text{S}$.

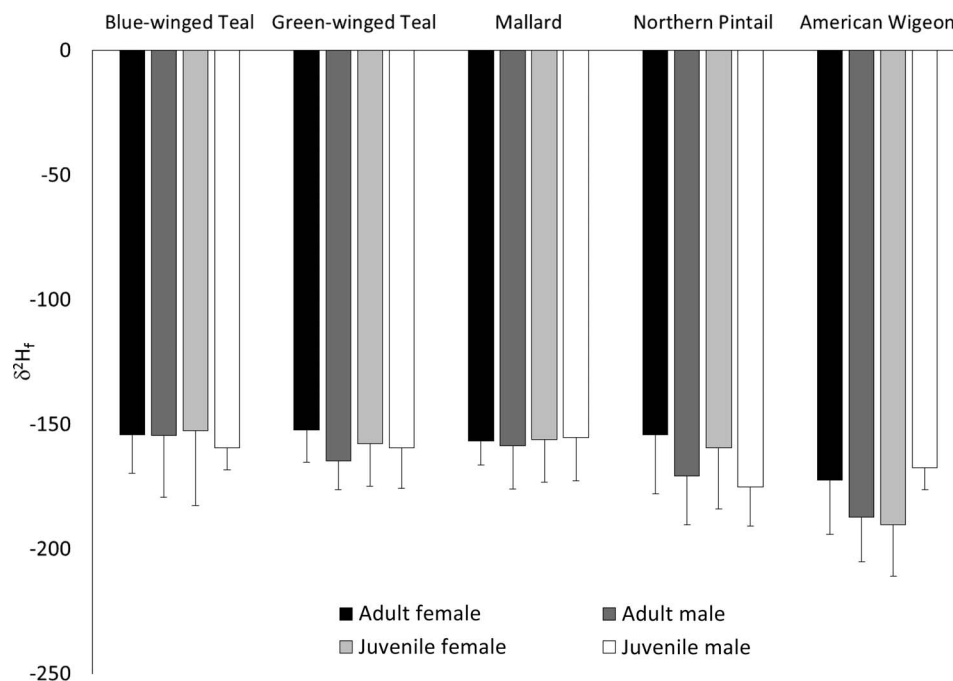
TABLE 3. Assignment of 5 species of waterfowl killed by hunters in the Saskatchewan River Delta, Canada, to the delta or areas north and south of the delta, based on a threshold approach with $\delta^2\text{H}$ (N = total number of individuals sampled; n = number assigned to each origin).

Species	N	Delta n (%)	Northern n (%)	Southern n (%)
2:1 odds				
American Wigeon	20	1 (5%)	18 (90%)	1 (5%)
Mallard	93	41 (44%)	41 (44%)	11 (12%)
Blue-winged Teal	52	25 (48%)	21 (40%)	6 (12%)
Northern Pintail	36	10 (28%)	23 (64%)	3 (8%)
Green-winged Teal	35	16 (46%)	16 (46%)	3 (9%)
3:1 odds				
American Wigeon	20	2 (10%)	17 (85%)	1 (5%)
Mallard	93	53 (57%)	31 (33%)	9 (10%)
Blue-winged Teal	52	30 (58%)	17 (33%)	5 (10%)
Northern Pintail	36	11 (31%)	22 (61%)	3 (8%)
Green-winged Teal	35	17 (49%)	16 (46%)	2 (6%)

RESULTS

Feather $\delta^2\text{H}$ values ranged widely, from -230‰ to -60‰ , but 75% of the samples ($N = 236$) had values between -180‰ and -140‰ . There was no significant variation with respect to collection date ($r^2 < 0.05$, $P > 0.05$) in 2013 or 2014 (Appendix Figure 6), and there was no difference between collection years ($F_{1,135} = 0.499$, $P = 0.51$). Therefore, data were grouped into a single analysis for sex, age, and species effects. No interactions were significant ($P > 0.05$), and neither sex ($F_{1,235} = 2.326$, $P =$

0.13) nor age ($F_{1,235} = 0.212$, $P = 0.93$) had significant effects on observed $\delta^2\text{H}_f$, but there were significant differences among species ($F_{4,235} = 5.867$, $P < 0.001$) (Figure 2). American Wigeon had the lowest $\delta^2\text{H}_f$ mean ($-180.5 \pm 20.9\text{‰}$), lower than those of all other species ($P \leq 0.001$ for all pairwise comparisons). Northern Pintail ($-164.0 \pm 22.4\text{‰}$) had the next-lowest $\delta^2\text{H}_f$ values, but these did not differ significantly from Mallards ($-156.5 \pm 16.1\text{‰}$), Blue-winged Teal ($-154.8 \pm 21.7\text{‰}$), or Green-winged Teal ($-157.3 \pm 14.8\text{‰}$) after a Bonferroni adjustment for multiple comparisons ($\alpha/10$, $P < 0.005$).

**FIGURE 2.** Stable hydrogen isotope ratios ($\delta^2\text{H}$ mean \pm SD) in feathers of 5 species of waterfowl shot in the Saskatchewan River Delta, Canada, in autumn 2013 and 2014.

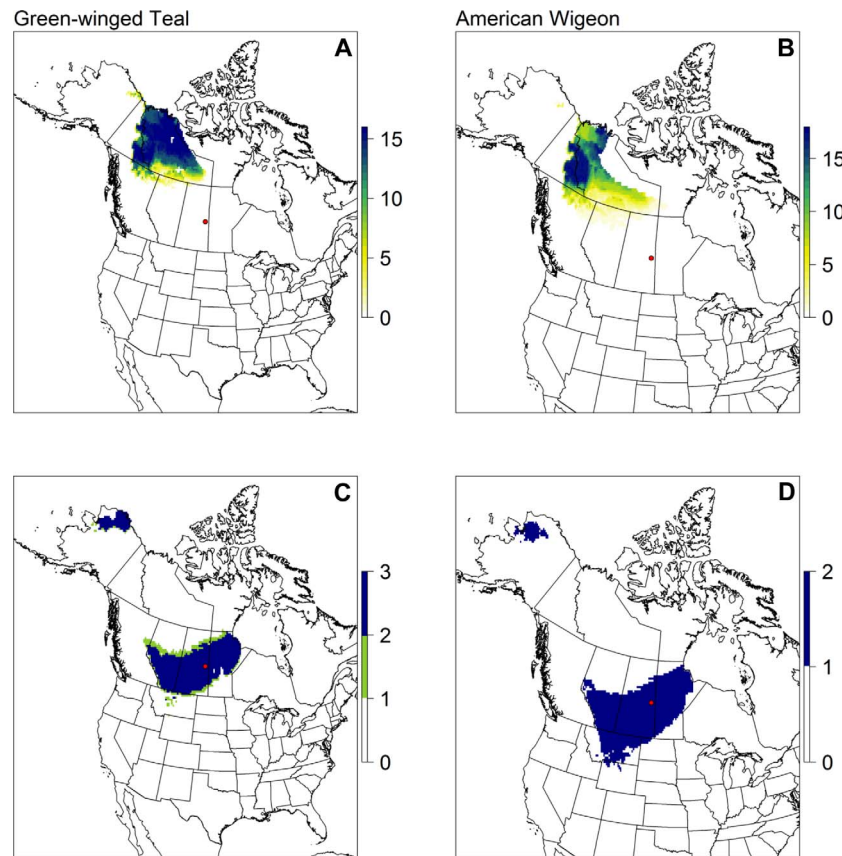


FIGURE 3. Spatially explicit assignment probabilities for Green-winged Teal and American Wigeon assigned to areas north of the Saskatchewan River Delta, Canada (**A, B**), and to the delta or southern areas (**C, D**). Numbers associated with the colors refer to the number of individuals in the sample assigned to each pixel at a 2:1 odds ratio.

Assignments to Origin

Applying the rescaling function resulted in predicted $\delta^2\text{H}_f$ values for birds growing their feathers in the SRD ranging between -161‰ and -135‰ at 2:1 odds, and between -163‰ and -133‰ at 3:1 odds. In total, 93 birds were classified as having grown their feathers in the delta (Table 3), representing $\sim 39\%$ of the total when assessed at 2:1 odds. Only 24 birds (10%) were classified as having come from south of the delta; 119 birds (50%) were classified as having come from north of the delta. The proportion of local birds was $\sim 8.5\%$ higher when assessed using 3:1 odds, with a total of 113 birds classified as having grown their feathers in the delta (Table 3).

Using our spatially explicit assignment approach, source areas for northern birds differed slightly among species (Figures 3–5). Of the 16 Green-winged Teal assigned as having come from north of the SRD, all were primarily consistent with origins north of 60° latitude from eastern Yukon to the Nunavut border and north to the Arctic Ocean (Figure 3). Three Green-winged Teal assigned as having come from “south” of the SRD were consistent with much of the prairie pothole region of

western Canada, northern boreal regions of Manitoba, and southern boreal regions of Alberta and Saskatchewan; however, our assignment algorithm could not rule out portions of northwest Alaska as a potential origin for Green-winged Teal (Figure 3). Northern-origin American Wigeon ($n = 18$) were largely consistent with areas surrounding the Mackenzie Mountains along the Yukon–Northwest Territories border, or with areas along the northern reaches of the Mackenzie River (Figure 3). Only one American Wigeon was assigned an origin “south” of the SRD, its likely origins including much of the prairie pothole and boreal regions of Manitoba and Saskatchewan (Figure 3).

Origins of 21 Blue-winged Teal that were assigned as northern migrants were primarily consistent with origins north of 60° latitude from eastern Yukon to the central Northwest Territories north of Great Slave Lake (Figure 4). Of the 6 Blue-winged Teal that were assigned as migrants from south of the SRD, the majority ($n = 5$) were assigned to prairie pothole and southern boreal regions immediately south of or surrounding the SRD, while 1 individual (a juvenile female with a $\delta^2\text{H}_f$ value of -60.5‰) was

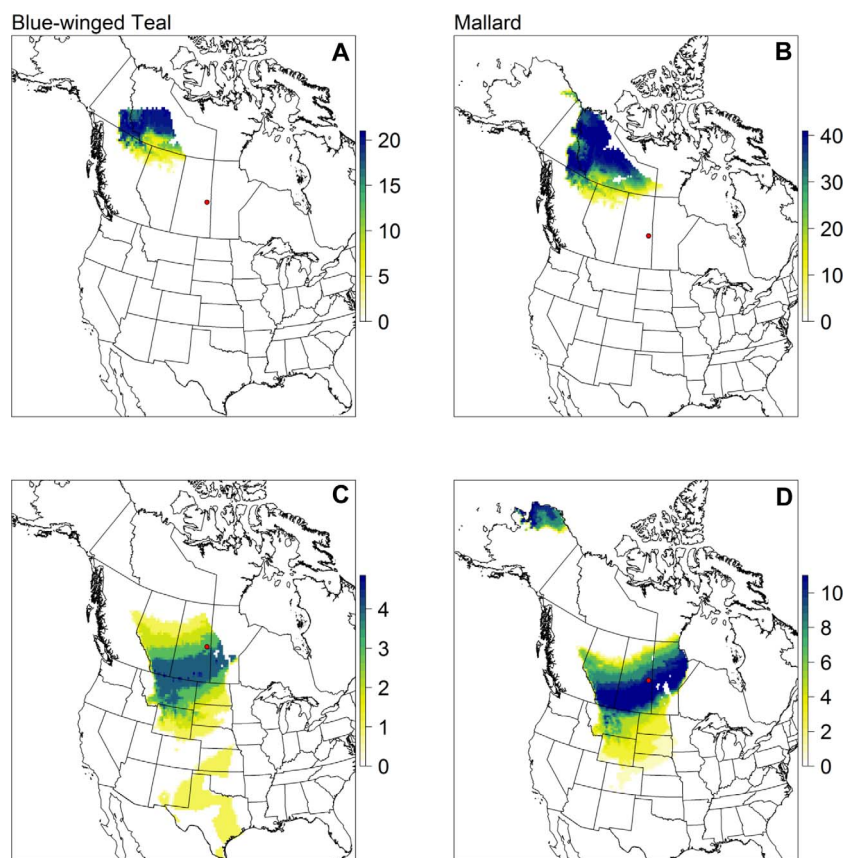


FIGURE 4. Spatially explicit assignment probabilities for Blue-winged Teal and Mallards assigned to areas north of the Saskatchewan River Delta, Canada (A, B), and to the delta or southern areas (C, D). Numbers associated with the colors refer to the number of individuals in the sample assigned to each pixel at a 2:1 odds ratio.

consistent with southern portions of the breeding range near the Texas Panhandle (Figure 4). Of the 41 Mallards assigned as northern migrants, all were primarily consistent with origins north of 60° latitude from eastern Yukon to a few hundred kilometers west of the Nunavut border and north to the Arctic Ocean (Figure 4). Of the 11 Mallards assigned as having come from “south” of the SRD, the majority were consistent with the prairie pothole and southern boreal regions immediately south of or surrounding the SRD; however, our assignment algorithm could not rule out portions of northwest Alaska as a potential origin for these individuals (Figure 4).

The majority of the 21 Northern Pintails that were identified as northern migrants had likely origins in a region surrounding Great Bear Lake from the Yukon–Northwest Territories border eastward to western Nunavut; only a few individuals were consistent with areas south of Great Slave Lake (Figure 5). Like other species, the 3 Northern Pintails assigned to origins south of the SRD were largely consistent with the prairie pothole and southern boreal regions immediately south of or sur-

rounding the SRD but could not be distinguished from potential origins in northwestern Alaska on the basis of our assignment algorithm (Figure 5).

Results for the 75 delta birds analyzed for $\delta^{34}\text{S}$ ranged from -18‰ to 10‰ (mean = $-3.2 \pm 5.9\text{‰}$). Though this mean value was similar to our values for delta invertebrates ($\delta^{34}\text{S}$: $-3.2 \pm 1.8\text{‰}$, range: -5.8‰ to -1.2‰ , $n = 5$) and fishes ($\delta^{34}\text{S}$: $-1.9 \pm 0.8\text{‰}$, range: -3.2‰ to 0.8‰ , $n = 28$), the broad range of feather $\delta^{34}\text{S}$ values meant that very few presumed delta birds had values that matched local prey. In total, 49 of 75 birds that were analyzed had feather $\delta^{34}\text{S}$ values outside the range of delta fishes or invertebrates. A reassignment of these birds based on $\delta^{34}\text{S}$ reclassified 37% of that cohort as originating from prairie ($\delta^{34}\text{S}_f < -6\text{‰}$), 27% classified as coming from forested areas ($\delta^{34}\text{S}_f > 1\text{‰}$) that typically occur north of the delta, and only 36% within the expected range for delta birds (-6‰ to 1‰). All subsequent assignments reported for each species take into consideration both $\delta^2\text{H}$ and $\delta^{34}\text{S}$.

Considering both $\delta^2\text{H}$ and $\delta^{34}\text{S}$ when reassigning origins of birds for each species, only 45 of 236 birds (19%) had

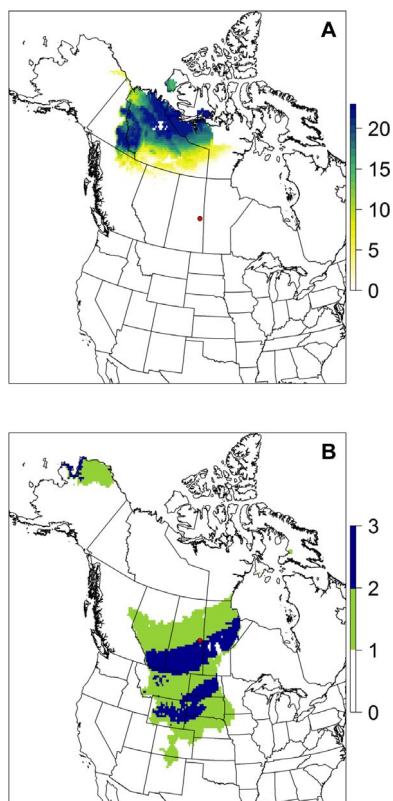


FIGURE 5. Spatially explicit assignment probabilities for Northern Pintails assigned to areas north of the Saskatchewan River Delta, Canada (**A**), and to the delta or southern areas (**B**). Numbers associated with the colors refer to the number of individuals in the sample assigned to each pixel at a 2:1 odds ratio.

isotopic values consistent with a delta origin. At the species level, 28% of Mallards ($n = 26$) were classified as prairie or southern birds, 52% ($n = 48$) were assigned to the north or forest, and 20% ($n = 19$) were assigned to delta origins. Blue-winged Teal had almost equal numbers classified as southern–prairie (29%, $n = 15$) and northern–forest (48%, $n = 25$), and 23% ($n = 12$) assigned to the delta; and Green-winged Teal had 23 birds (66%) classified as northern–forest, 5 birds (14%) classified as southern–prairie, and only 7 of 35 birds (20%) assigned to the delta. Most (95%) American Wigeon were reassigned to the north, with only 5% assigned to each of southern–prairie origins and the delta. Northern Pintails also exhibited a similar trend, with the majority (25 of 36 birds, 69%) classified as northern–forest. Only 5 birds (14%) were classified as southern–prairie birds, and only 6 birds were assigned to the delta (17%).

DISCUSSION

By measuring $\delta^2\text{H}_f$ and $\delta^{34}\text{S}_f$ values in feathers of hunter-killed birds, our results confirm the importance of the SRD

as a stopover site for migratory ducks during fall migration. The assignment of birds to various origins on the basis of isotope data complements existing knowledge from band recovery data and the literature. Sulfur isotope data proved to be a useful tool in further delineation of birds into prairie and forest regions, respectively, and the dual isotope approach improved assignment (Hebert and Wassenaar 2005a, 2005b).

The lack of variation in $\delta^2\text{H}_f$ according to age and sex suggests a lack of differential migration between sexes and ages. This is in agreement with Guillemain et al. (2009a, 2009b) and with Legagneux et al. (2012) for Green-winged Teal in Europe. However, our observations contrast with studies done by Moisan et al. (1967) and Jahn and Hunt (1964), who showed inter-individual variation in migration in Green-winged Teal and Blue-winged Teal. Individual American Wigeon and Northern Pintails have also demonstrated this behavior (Sowls 1955, Jahn and Hunt 1964), as have Mallards (Boyd 1961). Our observations do not support the hypothesis that males travel to specific sites far from the breeding grounds to molt (Munro 1949, Bellrose 1976), as this would have produced variation in $\delta^2\text{H}_f$ between males and females. While males and females could still be moving to different places with similar isotopic values after breeding, these movements are likely relatively restricted, with adult males molting at locations within the same isotopic range of the females and juveniles (but see Gollop 1960, Gilner et al. 1977). The nonsignificant differences between sexes could also be a result of the relatively small sample sizes. More sampling is clearly required to fully resolve details of postbreeding movements within species.

It is important to acknowledge that assignment based on spatially explicit and threshold approaches using stable isotopes have sources of error associated with estimation of true isotopic relationships between local waters driving food webs in any given year and the incorporation of those values into bird tissues (Hobson 2008). For this reason, we employed both a threshold approach and spatial, probabilistic assignment. Spatial interpolation error can also arise when data from points are interpolated over a given geographic area using precipitation models (Wunder and Norris 2008). To account for this error, we used $\delta^2\text{H}$ of river water in the years of study to better anchor values for the SRD relevant to waterfowl diet and then calibrated the existing feather isoscape using known-origin samples (Clark et al. 2006). Other sources of error include possible differences in isotopic discrimination factors between environmental waters and feathers of adults and juveniles grown at the same location (Langin et al. 2007, Coulton et al. 2010) as well as a large overall range in values within sites for known-origin birds (Clark et al. 2006). However, we accounted for expected within-site variation in $\delta^2\text{H}_f$ values by using the standard deviation of the residuals to

develop the thresholds and to propagate error in the spatially explicit assignments (Hobson 2008, Wunder and Norris 2008).

The assignment of a large proportion of birds to the north suggests that the few band recoveries taken in the SRD from northern areas (only 4 of 625 total recoveries in the USGS banding database) reflect a lack of banding effort in those areas (Slattery 2008), rather than limited production. Prairie wetland abundance is positively correlated with the amount of waterfowl produced (Johnson et al. 2005). The relatively few birds that were produced or molted in the SRD, despite the vast habitat available, may be attributed to extensive flooding in summer 2013; nests and molting individuals were likely displaced as water levels were abnormally high (C. K. Asante personal observation). Rapid rises in water levels during nesting are known to cause nest failure in waterfowl (Greenwood et al. 1995), as has been observed in the Peace–Athabasca Delta (Timoney 2013).

Our results suggest that birds flock into the SRD from the boreal forest and large wetland complexes such as the Peace–Athabasca Delta (theoretical $\delta^2\text{H}_p$ range for that area: -130‰ to -139‰ , expected $\delta^2\text{H}_f \approx -169\text{‰}$ to -145‰) during fall migration, and most of these birds are produced or have molted in the north. Our assignment surfaces showed that the majority of individuals of all species originated in the Northwest Territories, primarily north of Great Slave Lake or perhaps along the Mackenzie Mountains and/or the Mackenzie River (Figures 3–5). This is supported by $\delta^{34}\text{S}$ data for feathers that further classified many supposed SRD birds as coming from forested areas, as suggested by previous studies (Hebert and Wassenaar 2005a, 2005b). An additional challenge with hydrogen isotopes is that in North America, there are similarities in $\delta^2\text{H}_p$ between southwest and central Canada, northern Quebec–Labrador, and Alaska (Bowen et al. 2005), such that incorrect assignment can occur if birds cross flyways. Band recovery data suggest that a small proportion of birds that were banded in Alaska have been recovered in the SRD and the prairies (18 recoveries over the past 50 yr), which was reflected in our prior probabilities in the spatial assignment.

The presence of prairie birds and southern birds in the SRD with $\delta^{34}\text{S}$ less than -6‰ may reflect the movement of waterfowl from temporary pond habitats that desiccate or otherwise decline in resources seasonally (Stephens et al. 2007, Johnson et al. 2010). The large number of birds assigned to the prairies indicated that these birds were either produced or molted there, likely because annual precipitation was above average in the Canadian prairies in both years, leading to a higher-than-average number of ponds in the region (USFWS 2015).

Mallards are the most abundant waterfowl species in North America and also have the largest breeding range

(Bellrose 1976). Moreover, harvest regulations for this species in North America are based largely on the midcontinent population model. Assignment for this species was consistent with knowledge of its breeding range, and $\delta^2\text{H}_f$ of southern birds ($\delta^2\text{H}_f > -134\text{‰}$) was consistent with the results of Szymanski et al. (2007), who reported values between -120‰ and -80‰ for flightless Mallards in North Dakota. Most of the birds in the SRD that were later classified as “prairie” were Mallards. The isotopic monitoring of natal origin for Mallard, as demonstrated here, seems particularly relevant to the management of this species and the delineation of birds derived from the prairie and boreal biomes.

Assignment regions were largely consistent with known breeding ranges of the 5 waterfowl species. However, Green-winged Teal had a similar proportion of birds assigned to the north as Blue-winged Teal, despite slight differences in their breeding ranges (Bellrose 1976). Blue-winged Teal largely breed and molt in southern areas such as the prairie pothole region (Klett et al. 1988, Barker et al. 2014), so further isotopic sampling of this species may be warranted. The overwhelming assignment of American Wigeon and Northern Pintail to northern geographic areas is consistent with these species’ range maps (Bellrose 1976); notably, for Northern Pintail, there have been isotope studies connecting the species to breeding areas as far north as Alaska (Yerkes et al. 2008). It is also important to note that $>60\%$ of the North American population of American Wigeon breed in the boreal forest of Canada (USFWS 2015) and that Northern Pintails have one of the most northern migrations (Bellrose 1976). Studies of the latter species based on $\delta^2\text{H}$ and $\delta^{34}\text{S}$ showed that the isotopes provided reliable estimates of origins of individuals at broad spatial scales, and that individuals breeding in the north are underestimated because regular surveys in the central Canadian Arctic may miss many areas that Northern Pintails use in some years (Hebert and Wassenaar 2005a, 2005b). The Northern Pintail is of conservation significance because of a reduction in populations (Miller and Duncan 1999, USFWS 2015). Increases in wetland density have not resulted in increased populations, which suggests that other factors, like wetland and upland habitat quality, may be involved (Podrutzny et al. 2002).

Because waterfowl survey and banding efforts are limited in northern Canada, the potential of northern habitats to contribute to waterfowl populations is poorly documented. Our research confirms that isotopic tools can be used to document regions of actual production and recruitment of waterfowl that occupy vast and largely inaccessible regions of the continent (Hobson et al. 2009). Such information would be invaluable as a means of informing predictive models (e.g., Barker et al. 2014). Unfortunately, despite the obvious contributions to

management that can be made by adopting a significant isotopic assessment of waterfowl origins in North America on an annual basis, there is little evidence to date that such an initiative is forthcoming. With expected rapid changes to waterfowl habitat in prairie and boreal biomes, isotopic monitoring as demonstrated here should be fully adopted in the SRD and in other key wintering and stopover sites (Webb et al. 2010) whose value as critical habitat is likely to increase (Johnson et al. 2005).

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Ethics statement: Only salvaged tissue samples from hunters were used.

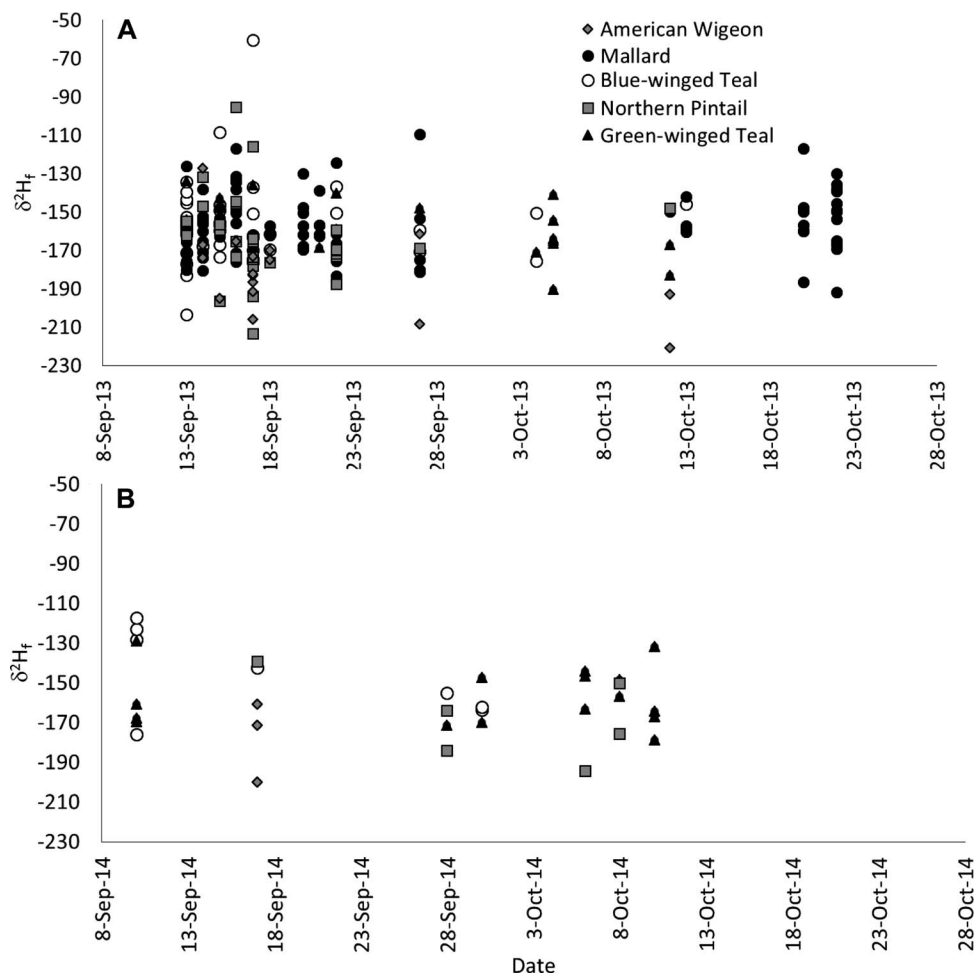
Author contributions: T.D.J. and K.A.H. conceived the idea and study design, C.K.A. collected and processed samples, C.K.A. and S.L.V. analyzed the data, and C.K.A. wrote the paper with considerable editorial input from S.L.V., T.D.J., and K.A.H.

LITERATURE CITED

- Alisauskas, R. T., E. E. Klaas, K. A. Hobson, and C. D. Ankney (1998). Stable-carbon isotopes support use of adventitious color to discern winter origins of Lesser Snow Geese. *Journal of Field Ornithology* 69:262–268.
- Ashley, P., K. A. Hobson, S. L. Van Wilgenburg, N. North, and S. A. Petrie (2010). Linking Canadian harvested juvenile American Black Ducks to their natal areas using stable isotope (δD , $\delta^{13}C$, and $\delta^{15}N$) methods. *Avian Conservation and Ecology* 5: 7.
- Barker, N. K. S., S. G. Cumming, and M. Darveau (2014). Models to predict the distribution and abundance of breeding ducks in Canada. *Avian Conservation and Ecology* 9:7.
- Baschuk, M. S., N. Koper, D. A. Wrubleski, and G. Goldsborough (2012). Effects of water depth, cover and food resources on habitat use of marsh birds and waterfowl in boreal wetlands of Manitoba, Canada. *Waterbirds* 35:44–55.
- Bellrose, F. C. (1976). *Ducks, Geese and Swans of North America*, second edition. Stackpole Books, Harrisburg, PA, USA.
- Boere, G. C., and D. A. Stroud (2006). The flyway concept: What it is and what it isn't. In *Waterbirds around the World* (G. C. Boere, C. A. Galbraith, and D. A. Stroud, Editors). Stationery Office, Edinburgh, UK. pp. 40–47.
- Bowen, G. J., and J. Revenaugh (2003). Interpolating the isotopic composition of modern meteoric precipitation. *Water Resources Research* 39:1299.
- Bowen, G. J., L. I. Wassenaar, and K. A. Hobson (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* 143:337–348.
- Boyd, H. (1961). The flightless period of the Mallard in England. *Wildfowl* 12:140–143.
- Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, W. D. Robinson, and M. Wikelski (2011). Technology on the move: Recent and forthcoming innovations for tracking migratory birds. *BioScience* 61:689–698.
- Brown, S., C. Gratto-Trevor, R. Porter, E. L. Weiser, D. Mizrahi, R. Bentzen, M. Boldenow, R. Clay, S. Freeman, M.-A. Giroux, E. Kwon, et al. (2017). Migratory connectivity of Semipalmated Sandpipers and implications for conservation. *The Condor: Ornithological Advances* 119:000–000.
- Buhnerkempe, M. G., C. T. Webb, A. A. Merton, J. E. Buhnerkempe, G. H. Givens, R. S. Miller, and J. A. Hoeting (2016). Identification of migratory bird flyways in North America using community detection on biological networks. *Ecological Applications* 26:740–751.
- Carney, S. M. (1992). *Species, Age and Sex Identification of Ducks Using Wing Plumage*. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA.
- Chabot, A. A., K. A. Hobson, S. L. Van Wilgenburg, G. J. McQuat, and S. C. Loughheed (2012). Advances in linking wintering migrant birds to their breeding-ground origins using combined analyses of genetic and stable isotope markers. *PLoS ONE* 7:e43627.
- Clark, R. G., K. A. Hobson, and L. I. Wassenaar (2006). Geographic variation in the isotopic (δD , $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) composition of feathers and claws from Lesser Scaup and Northern Pintail: Implications for studies of migratory connectivity. *Canadian Journal of Zoology* 84:1395–1401.
- Clark, R. G., K. A. Hobson, and L. I. Wassenaar (2009). Corrigendum—Geographic variation in the isotopic (δD , $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) composition of feathers and claws from Lesser Scaup and Northern Pintail: Implications for studies of migratory connectivity. *Canadian Journal of Zoology* 87:553–554.
- Coulton, D. W., R. G. Clark, and C. E. Hebert (2010). Determining natal origins of birds using stable isotopes ($\delta^{34}S$, δD , $\delta^{15}N$, $\delta^{13}C$): Model validation and spatial resolution for mid-continent Mallards. *Waterbirds* 33:10–21.
- Dieter, C. D., and B. J. Anderson (2009). Reproductive success and brood movements of giant Canada Geese in eastern South Dakota. *The American Midland Naturalist* 162:373–381.
- Gilner, D. S., R. E. Kirby, I. J. Ball, and J. H. Reichmann (1977). Post-breeding activities of Mallards and Wood Ducks in north-central Minnesota. *The Journal of Wildlife Management* 41: 345–359.
- Gober, P., and H. S. Wheeler (2014). Socio-hydrology and the science-policy interface: A case study of the Saskatchewan River basin. *Hydrology and Earth System Sciences* 18:1413–1422.
- Gollop, J. B. (1960). Mallard goes north after nesting. *Blue Jay* 18: 77.
- Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer (1995). Factors associated with duck nest success in the prairie pothole region of Canada. *Wildlife Monographs* 128.
- Guillemain, M., R. Hearn, R. King, M. Gauthier-Clerc, G. Simon, and A. Caizergues (2009a). Comparing migration of teal from two main wintering areas of Western Europe: A long-term

- study from Essex, England, and Camargue, France. *Ringling & Migration* 24:273–276.
- Guillemain, M., R. Hearn, R. King, M. Gauthier-Clerc, G. Simon, and A. Caizergues (2009b). Differential migration of the sexes cannot be explained by the body size hypothesis in teal. *Journal of Ornithology* 150:685–689.
- Gunnarsson, G., L.-M. Neus, K. A. Hobson, S. L. Van Wilgenburg, J. Elmlberg, B. Olsen, R. A. M. Fouchier, and J. Waldenström (2012). Disease dynamics and bird migration—linking Mallards *Anas platyrhynchos* and subtype diversity of the influenza A virus in time and space. *PLoS ONE* 4:e35679.
- Hebert, C. E., and L. I. Wassenaar (2005a). Feather stable isotopes in western North American waterfowl: Spatial patterns, underlying factors, and management applications. *Wildlife Society Bulletin* 33:92–102.
- Hebert, C. E., and L. I. Wassenaar (2005b). Stable isotopes provide evidence for poor Northern Pintail production on the Canadian prairies. *The Journal of Wildlife Management* 69: 101–109.
- Hobson, K. A. (2008). Applying isotopic methods to tracking animal migration. In *Tracking Animal Migration with Stable Isotopes* (K. A. Hobson and L. I. Wassenaar, Editors). Elsevier, New York, NY, USA.
- Hobson, K. A., and D. R. Norris (2008). Animal migration: A context for using new techniques and approaches. In *Tracking Animal Migration with Stable Isotopes* (K. A. Hobson and L. I. Wassenaar, Editors). Elsevier, New York, NY, USA.
- Hobson, K. A., S. Van Wilgenburg, L. I. Wassenaar, H. Hands, W. P. Johnson, M. O'Meilia, and P. Taylor (2006). Using stable hydrogen isotope analysis of feathers to delineate origins of harvested Sandhill Cranes in the Central Flyway of North America. *Waterbirds* 29:137–147.
- Hobson, K. A., and L. I. Wassenaar (2008). *Tracking Animal Migration with Stable Isotopes*. Elsevier, New York, NY, USA.
- Hobson, K. A., M. B. Wunder, S. L. Van Wilgenburg, R. G. Clark, and L. I. Wassenaar (2009). A method for investigating population declines of migratory birds using stable isotopes: Origins of harvested Lesser Scaup in North America. *PLoS ONE* 4:e7915.
- Jahn, L. R., and R. A. Hunt (1964). Duck and coot ecology and management in Wisconsin. *Wisconsin State Conservation Department Technical Bulletin* 33.
- Johnson, W. C., B. V. Millett, T. Gilmanov, R. A. Voldseth, G. R. Guntenspergen, and D. E. Naugle (2005). Vulnerability of northern prairie wetlands to climate change. *BioScience* 55: 863–872.
- Johnson, W. C., B. Werner, G. R. Guntenspergen, R. A. Voldseth, B. Millett, D. E. Naugle, M. Tulbure, R. W. H. Carroll, J. Tracy, and C. Olawsky (2010). Prairie wetland complexes as landscape functional units in a changing climate. *BioScience* 60:128–140.
- Klett, A. T., T. L. Shaffer, and D. H. Johnson (1988). Duck nest success in the prairie pothole region. *The Journal of Wildlife Management* 52:431–440.
- Korner-Nievergelt, F., A. Sauter, P. W. Atkinson, J. Guélat, W. Kania, M. Kéry, U. Köppen, R. A. Robinson, M. Schaub, K. Thorup, H. Van Der Jeugd, and A. J. Van Noordwijk (2010). Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. *Journal of Avian Biology* 41:8–17.
- Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood, D. J. McNeil, J. L. Larkin, and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. *The Condor: Ornithological Advances* 119:108–121.
- Langin, K. M., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe (2007). Hydrogen isotopic variation in migratory bird tissues of known origin: Implications for geographic assignment. *Oecologia* 152:449–457.
- Lavretsky, P., J. H. Miller, V. Bahn, and J. L. Peters (2014). Exploring fall migratory patterns of American Black Ducks using eight decades of band-recovery data. *The Journal of Wildlife Management* 78:997–1004.
- Legagneux, P., R. G. Clark, M. Guillemain, C. Eraud, M. Théry, and V. Bretagnolle (2012). Large-scale geographic variation in iridescent structural ornaments of a long-distance migratory bird. *Journal of Avian Biology* 43:355–361.
- MacKinnon, B. D., J. Sagin, H. M. Baulch, K.-E. Lindenschmidt, and T. D. Jardine (2016). Influence of hydrological connectivity on winter limnology in floodplain lakes of the Saskatchewan River Delta, Saskatchewan. *Canadian Journal of Fisheries and Aquatic Sciences* 73:140–152.
- McCutchan, J. H., Jr., W. M. Lewis, Jr., C. Kendall, and C. C. McGrath (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390.
- Miller, M. R., and D. C. Duncan (1999). The Northern Pintail in North America: Status and conservation needs of a struggling population. *Wildlife Society Bulletin* 27:788–800.
- Moisan, G., R. I. Smith, and R. K. Martinson (1967). The Green-winged Teal: Its distribution, migration, and population dynamics. U.S. Department of the Interior, Fish and Wildlife Service, Special Science Report 100.
- Munro, J. A. (1949). Studies of waterfowl in British Columbia: Baldpate. *Canadian Journal of Research* 27:289–307.
- Nelson, D. M., M. Braham, T. A. Miller, A. E. Duerr, J. Cooper, M. Lanzone, J. Lemaitre, and T. Katzner (2015). Stable hydrogen isotopes identify leapfrog migration, degree of connectivity, and summer distribution of Golden Eagles in eastern North America. *The Condor: Ornithological Advances* 117:414–429.
- Podrutzny, K. M., J. H. Devries, L. M. Armstrong, and J. J. Rotella (2002). Long-term response of Northern Pintails to changes in wetlands and agriculture in the Canadian prairie pothole region. *The Journal of Wildlife Management* 66:993–1010.
- Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook (2007). *Digital Distribution Maps of the Birds of the Western Hemisphere*, version 3.0. NatureServe, Arlington, Virginia, USA.
- Sagin, J., A. Sizo, H. Wheeler, T. D. Jardine, and K.-E. Lindenschmidt (2015). A water coverage extraction approach to track inundation in the Saskatchewan River Delta, Canada. *International Journal of Remote Sensing* 36:764–781.
- Schindler, D. W., and W. F. Donahue (2006). An impending water crisis in Canada's western prairie provinces. *Proceedings of the National Academy of Sciences USA* 103:7210–7216.
- Schmutz, J. K. (2001). Community conservation plan for Cumberland Marshes Important Bird Areas. <http://www.ibacanada.ca/documents/conservationplans/skcumberlandmarshes.pdf>

- Slattery, S. (2008). Status of waterfowl in the Saskatchewan River Delta. Saskatchewan River Delta Symposium Proceedings, Saskatoon, SK, Canada.
- Sowls, L. K. (1955). *Prairie Ducks: A Study of Their Behavior, Ecology and Management*. Wildlife Management Institute, Stackpole Books, Harrisburg, PA, USA.
- Stephens, D. W., J. S. Brown, and R. C. Ydenberg (Editors) (2007). *Foraging: Behavior and Ecology*. University of Chicago Press, Chicago, IL, USA.
- Szymanski, M. L., A. D. Afton, and K. A. Hobson (2007). Use of stable isotope methodology to determine natal origins of Mallards at a fine scale within the Upper Midwest. *The Journal of Wildlife Management* 71:1317–1324.
- Timoney, K. P. (2013). *The Peace–Athabasca Delta: Portrait of a Dynamic Ecosystem*. University of Alberta Press, Edmonton, AB, Canada.
- U.S. Fish and Wildlife Service (2015). Waterfowl population status, 2015. U.S. Department of the Interior, Washington, DC, USA.
- Van Wilgenburg, S. L., and K. A. Hobson (2011). Combining stable isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. *Ecological Applications* 21:1340–1351.
- Van Wilgenburg, S. L., K. A. Hobson, K. R. Brewster, and J. M. Welker (2012). Assessing dispersal in threatened migratory birds using stable hydrogen isotope (δD) analysis of feathers. *Endangered Species Research* 16:17–29.
- Wassenaar, L. I., and K. A. Hobson (2003). Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* 39:211–217.
- Webb, E. B., L. M. Smith, M. P. Vrtiska, and T. G. LaGrange (2010). Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. *The Journal of Wildlife Management* 74:109–119.
- Webster, M. S., and P. P. Marra (2005). The importance of understanding migratory connectivity and seasonal interactions. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: Unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.
- Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping* (J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu, Editors). Springer, New York, NY, USA. pp. 251–270.
- Wunder, M. B. (2012). Determining geographic patterns of migration and dispersal using stable isotopes in keratins. *Journal of Mammalogy* 93:360–367.
- Wunder, M. B., and D. R. Norris (2008). Improved estimates of certainty in stable-isotope-based methods for tracking migratory animals. *Ecological Applications* 18:549–559.
- Yerkes, T., K. A. Hobson, L. I. Wassenaar, R. Macleod, and J. M. Coluccy (2008). Stable isotopes (δD , $\delta^{13}C$, $\delta^{15}N$) reveal associations among geographic location and condition of Alaskan Northern Pintails. *The Journal of Wildlife Management* 72:715–725.



APPENDIX FIGURE 6. Hydrogen isotope ratios in feathers (δ^2H_f) of hunter-killed waterfowl in relation to date of kill in (A) 2013 and (B) 2014.