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RESEARCH ARTICLE

Shorebird hunting in Barbados: Using stable isotopes to link the harvest at a migratory stopover site with sources of production

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ABSTRACT

Understanding spatial connectivity of long-distance migrants is important for effective management and conservation of both game and nongame species. Hunting of Nearctic-breeding shorebirds occurs in the Caribbean and northern South America; however, the origins of harvested individuals are generally unknown. We used stable hydrogen isotopes ($\delta^2\text{H}$) in feathers of juvenile shorebirds to infer the origins of birds harvested at 2 sites in Barbados using probabilistic assignments based on a terrestrial–freshwater $\delta^2\text{H}$ isoscape. We used tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to filter individuals that had derived nutrients from marine sources. Natal origins of juvenile American Golden-Plover (*Pluvialis dominica*), Stilt Sandpiper (*Calidris himantopus*), Short-billed Dowitcher (*Limnodromus griseus*), and Lesser Yellowlegs (*Tringa flavipes*) were predicted to be mainly from the eastern parts of their breeding ranges in eastern Canada, with American Golden-Plover, Stilt Sandpiper, and Short-billed Dowitcher also having high potential areas of origin in parts of Alaska, USA. Results from our study should help to modify prior estimates of sustainable harvest levels for these species. We identify sources of uncertainty in determining shorebird origins using stable isotopes, including a lack of shorebird-specific calibration equations and the apparent lack of an appropriate tissue for breeding ground assignment for adults.

Keywords: carbon-13, deuterium, harvested species, fall migration, migratory connectivity, nitrogen-15, shorebirds, stable isotopes

Chasse aux limicoles à la Barbade : utilisation d'isotopes stables pour relier la récolte sur une halte migratoire à des sources de production

RÉSUMÉ

Comprendre la connectivité spatiale des migrants est important pour assurer une gestion et une conservation efficaces des espèces gibiers et non gibiers. Une chasse aux limicoles nichant dans le Néarctique a lieu dans les Caraïbes et le nord de l'Amérique du Sud mais l'origine des individus récoltés est généralement inconnue. Nous avons utilisé des isotopes stables de l'hydrogène ($\delta^2\text{H}$) dans les plumes de limicoles juvéniles afin d'inférer les origines des oiseaux récoltés sur deux sites de la Barbade à l'aide d'affectations probabilistes basées sur un paysage isotopique terrestre/d'eau douce de $\delta^2\text{H}$. Nous avons utilisé des valeurs de $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$ provenant des tissus pour filtrer les individus tirant leurs nutriments de sources marines. Selon les prédictions, les juvéniles de *Pluvialis dominica*, *Tringa flavipes*, *Limnodromus griseus* et *Calidris himantopus* étaient originaires principalement des parties est de leurs aires de nidification dans l'est du Canada, alors que *P. dominica*, *C. himantopus* et *L. griseus* avaient également des aires d'origine potentielles dans certaines parties de l'Alaska. Les résultats de notre étude devraient permettre de modifier les estimations antérieures de niveaux de récolte durables pour ces espèces. Nous identifions les sources d'incertitude dans la détermination des origines des limicoles à l'aide des isotopes stables, dont l'absence d'équations de calibration propres aux limicoles et l'absence apparente d'un tissu approprié pour l'affectation des aires de nidification pour les adultes.

Mots-clés : carbone 13, deutérium, espèce récoltée, migration automnale, connectivité migratoire, azote 15, limicoles, isotopes stables

INTRODUCTION

Connecting breeding, staging, and wintering sites of long-distance migratory birds is important due to clear

implications for effective conservation and management of species over their full life cycle (Webster et al. 2002, Hobson 2005, Brown et al. 2017). For hunted migratory birds, harvest can occur across many jurisdictions; thus,

optimal conservation strategies require knowledge of migratory connectivity as well as the coordination of regulations and policies among jurisdictions (Klaassen et al. 2008, Hobson et al. 2009a, Marra et al. 2011). Shorebirds are among the groups of highest conservation concern in the world (IWSG 2003, Piersma 2007), with 3 times as many species declining as increasing (Wetlands International 2006, Nebel et al. 2008). Substantial population declines have been reported in 65% of the Nearctic-breeding shorebird species that migrate via the Atlantic Flyway (Bart et al. 2007, Andres et al. 2012). Although the proximate causes of these declines are poorly understood for most species, harvest along migration routes and on the wintering grounds has emerged as a threat or potential contributing factor in shorebird declines worldwide (Zöckler et al. 2010, Morrison et al. 2012, Watts et al. 2015, Pearce-Higgins et al. 2017). In the Americas, shorebird harvest occurs in several countries and may negatively affect shorebird populations in the Western Atlantic Flyway (e.g., Hutt 1991, Vermeer and Castilla 1991, Canevari and Blanco 1994, Ottema and Spaans 2008, Burke 2009).

Protection of migratory birds and associated legislation, including hunting regulations, vary widely across the Americas (Bayney and Da Silva 2005, Watts and Turrin 2016), complicating efforts to manage these species. The bulk of the harvest of Nearctic-bred shorebirds is thought to occur in the Caribbean and northern regions of South America. For instance, the annual shorebird harvest in Barbados ranges from 12,000 to 35,000 birds (Hutt 1991, E. T. Reed personal observation), and harvest levels are suspected to be similar in several other countries (Andres 2011). Furthermore, a recent evaluation of the harvest in Barbados showed that 18 species were recorded in hunting logs, with 6 species making up ~98% of the harvest: Lesser Yellowlegs (*Tringa flavipes*; 54–67% of the harvest), Pectoral Sandpiper (*Calidris melanotos*; 11–23%), Stilt Sandpiper (*Calidris himantopus*; 6–8%), Short-billed Dowitcher (*Limnodromus griseus*; 4–11%), Greater Yellowlegs (*Tringa melanoleuca*; 3–7%), and American Golden-Plover (*Pluvialis dominica*; 1–6%; Wege et al. 2014). Although the harvest levels of these species in Barbados are apparently within continental-scale sustainable limits (Watts et al. 2015), their overall hemispheric harvest is unknown and could negatively affect some populations (Hutt 1991, Clay et al. 2010).

Determining the source populations of individuals hunted at nonbreeding sites is challenging for species such as shorebirds that have broad breeding distributions and occur at low densities, often in remote northern locations. Migratory movements of shorebirds in North America have been studied primarily through banding programs and remote tracking approaches such as satellite and VHF telemetry or light-sensing geolocators (e.g.,

Warnock and Takekawa 2003, Dunn et al. 2010, Niles et al. 2010, Brown et al. 2017). Band return data are of limited value because capture and marking of a sufficient sample of birds is daunting and, to date, have produced low returns (Hobson 2003, Dunn et al. 2010; but see Lanctot et al. 2009). Exogenous markers such as satellite telemetry transmitters and archival tags such as geolocators suffer from similar issues: it is challenging to equip a representative sample of the population and/or to recapture a sufficient number of individuals due to potentially low return rates (Hobson et al. 2014, Weiser et al. 2016), particularly at stopover sites where individuals may stay for only a few days or hours.

Intrinsic biogeochemical markers such as stable isotopes have become particularly useful tools for understanding migratory connectivity (Rubenstein and Hobson 2004, Hobson and Wassenaar 2008) as well as for determining the origins of harvested birds (Hebert and Wassenaar 2005, Asante et al. 2017). For instance, in North America, the average abundance of deuterium in amount-weighted precipitation ($\delta^2\text{H}_p$) follows well-described, continent-wide patterns (Bowen et al. 2005). Local deuterium is incorporated into food webs, allowing the creation of continent-wide, tissue-dependent “isoscapes” that can be used to assign individuals to approximate regions of origin (Wunder et al. 2005, Hobson et al. 2014). The application of stable isotopes to determining the origins of migratory animals can target the segment of the population exposed to harvest and has been used effectively to describe the origins of many migratory species, including shorebirds (Atkinson et al. 2005, Catry et al. 2012, 2016, Franks et al. 2012). However, their application has been limited to only a few species and populations, and most studies have not used probabilistic models to determine likely areas of origin.

The objective of this study was to use stable-hydrogen ($\delta^2\text{H}_f$) measurements of feathers to delineate the probable natal origins of 4 shorebird species (American Golden-Plover, Stilt Sandpiper, Short-billed Dowitcher, and Lesser Yellowlegs) harvested in Barbados. Feathers, which are grown on breeding sites by juveniles but not by adults (Pyle 2008), are faithful indicators of the location where they were developed. Limited information on connectivity is available for most Arctic-breeding shorebird species (but see Lanctot et al. 2016, Brown et al. 2017); however, we developed hypotheses based on flyway population delineations for other shorebird species (BirdLife International and NatureServe 2015, J.-F. Lamarre personal communication). We expected that most birds and species harvested at migratory stopover sites in Barbados would originate from the eastern parts of their ranges in northeastern North America. However, we expected that a portion of American Golden-Plover samples might also originate from the Alaskan, USA, part of their range, based on

recent results from geolocators (Johnson et al. 2018, J.-F. Lamarre personal communication, <https://doi.org/10.13140/RG.2.2.20167.60329>). Given that nesting phenology tends to be later at higher latitudes (Klima and Jehl 2012, Johnson et al. 2018), we predicted that $\delta^2\text{H}_f$ values would decrease with the date of harvest, indicating that birds that arrive earlier in Barbados during fall migration originate from more southerly natal areas. Similarly, we predicted that feather carbon ($\delta^{13}\text{C}_f$) and nitrogen ($\delta^{15}\text{N}_f$) isotope values, which can be used to identify marine-derived resource use (Hobson 1999, Cross et al. 2014, Hobson and Kardynal 2016), would decrease with harvest date for Short-billed Dowitcher and Lesser Yellowlegs, indicating that birds that originate from marine-influenced areas (potentially more abundant in the southern part of these species' ranges in coastal areas of James and Hudson bays, Canada) arrive before more northern birds, reflecting a chain migration. Marine isotopic values typically derive from individuals foraging in coastal areas (e.g., mudflats and wetlands); however, aerosolic transport (i.e. sea spray) can also affect inland (~ 100 km) continental regions (Zazzo et al. 2011, Hobson and Kardynal 2016). Therefore, we used $\delta^{13}\text{C}_f$ and $\delta^{15}\text{N}_f$ values as filters to remove birds with feather growth potentially influenced by marine resources, which provides unreliable assessment of natal origins using terrestrial patterns of $\delta^2\text{H}$ (Hobson and Wassenaar 2008).

METHODS

Species and Study Area

We conducted this study in Barbados ($13^\circ 10' \text{N}$, $59^\circ 33' \text{W}$), one of the nearest potential migratory stopover sites in the Caribbean for shorebirds using the southbound trans-Atlantic migration route from the North American Atlantic coast to South America (Williams 1985). Fall passage of migrants through Barbados is typically of short duration, with most birds spending only a few hours on site. In Barbados, only 4 shorebird species are protected from hunting under the Barbados Wild Birds Protection Act of 1907, 1985: Upland Sandpiper (*Bartramia longicauda*), Hudsonian Godwit (*Limosa haemastica*), Ruff (*Philomachus pugnax*), and Buff-breasted Sandpiper (*Calidris subruficollis*). All other shorebird species are therefore unprotected during a traditional July 15 to October 15 shorebird hunting season (Watts and Turrin 2016). Shorebird hunting in Barbados occurs only at private hunting clubs known locally as shooting swamps. These areas are composed of a series of diked impoundments that are mechanically prepared and flooded to attract migrating shorebirds to a landscape mainly devoid of natural wetlands (Jackman 1901, Hutt 1991). Daily and seasonal bag limits are not regulated by the government but by the Barbados Wildfowlers Association, which



FIGURE 1. Location of the study area where we investigated the natal origins of harvested shorebirds. Wings and claws of harvested shorebirds were collected at Fosters and Tom's Pond shooting swamps, Barbados, in July–October of 2013 and 2014.

represents shorebird hunters in Barbados and sets bag limits and rules for hunting that are voted on by members. Individual shooting swamps can implement stricter bag limits and rules than those agreed upon by the Wildfowlers Association. There were 8 shooting swamps active in 2013 and 2014 (Wege et al. 2014). Two shooting swamps provided samples for this study: Fosters, in the Parish of St. Lucy, and Tom's Pond, in St. Philip Parish (Figure 1).

We collected one wing from all birds harvested: American Golden-Plover and Lesser Yellowlegs were collected in 2013, and Stilt Sandpiper, Short-billed Dowitcher, and Lesser Yellowlegs were collected in 2014 (Table 1). Each wing was identified to species and age (juvenile or adult) based on plumage characteristics (Jehl et al. 2001, Pyle 2008). We divided the hunting season into 13 7-day periods from July 15 to October 15, and in each period randomly selected up to 20 juvenile birds of each species for isotopic analysis (Table 1). When <20 birds of a given species were available during a period, all individuals were selected for analysis. In the case of American Golden-Plover, Stilt Sandpiper, and Short-billed Dowitcher, we wanted to maximize the overall sample size and thus

TABLE 1. Number of wings collected from juvenile American Golden-Plover (AMGP), Stilt Sandpiper (STSA), Short-billed Dowitcher (SBDO), and Lesser Yellowlegs (LEYE) at 2 shooting swamps in Barbados 2013 and 2014, and number of individuals (i.e. feathers) randomly sampled for data analysis by species and by week of the hunting season. Assignment to natal origin was made using the filtered dataset, wherein individuals with marine-influenced isotope values ($\delta^{13}\text{C}_f > -20\text{‰}$ and $\delta^{15}\text{N}_f > 10\text{‰}$) or enriched in ^2H ($\delta^2\text{H}$ within 2 standard deviations greater than -69.8‰) were removed. The hunting season ran from July 15 to October 15.

Species	Year	Sample	Week													Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	
AMGP	2013	Wing	0	0	0	0	0	0	0	4	1	0	4	5	1	15
		Feather	0	0	0	0	0	0	0	4	1	0	4	5	1	15
		Filtered	0	0	0	0	0	0	0	0	0	0	1	5	1	7
STSA	2014	Wing	0	0	0	0	2	0	3	7	0	7	4	0	0	23
		Feather	0	0	0	0	2	0	3	7	0	7	4	0	0	23
		Filtered	0	0	0	0	2	0	1	2	0	5	3	0	0	13
SBDO	2014	Wing	0	0	0	0	0	19	39	34	13	10	0	0	0	115
		Feather	0	0	0	0	0	19	39	34	13	9	0	0	0	114
		Filtered	0	0	0	0	0	17	30	33	13	9	0	0	0	102
LEYE	2013	Wing	0	0	0	0	0	23	79	132	99	45	44	27	14	463
		Feather	0	0	0	0	0	20	20	20	20	21	19	20	13	153
		Filtered	0	0	0	0	0	13	14	18	19	17	16	19	12	128
LEYE	2014	Wing	0	1	11	54	28	20	34	125	14	170	86	75	34	652
		Feather	0	1	11	20	20	20	20	20	14	20	20	20	20	206
		Filtered	0	0	0	0	2	15	18	10	12	16	18	18	18	127

selected all birds for which we had wings. Some periods contained few or no samples of certain species or age groups as they occurred outside the migratory passage period of those assemblages. The tip (2 cm) of the 10th primary feather was cut from all randomly selected juvenile samples in both years of the study and used for stable isotope analysis. We also collected claw samples from harvested adult American Golden-Plovers and Lesser Yellowlegs to determine whether this tissue could be used to assign adults to areas of breeding origin; however, claws were grown during migration and thus integrated resources from across a broad geographic area (Appendix Figure 4).

Stable Isotope Analysis

All feathers were cleaned of surface oils in 2:1 chloroform:methanol solvent rinse and prepared for $\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ analysis at the Stable Isotope Laboratory of Environment and Climate Change Canada (Saskatoon, Saskatchewan, Canada). The $\delta^2\text{H}$ of the nonexchangeable hydrogen of feathers was determined using the method described by Wassenaar and Hobson (2003), based on 2 calibrated keratin hydrogen isotope reference materials (CBS (caribou hoof standard): -197‰ ; KHS (kudu horn standard): -54.1‰). Hydrogen isotopic measurements were performed on H_2 gas derived from high-temperature ($1,350^\circ\text{C}$) flash pyrolysis (Eurovector 3000, Milan, Italy) of $350 \pm 10 \mu\text{g}$ feather subsamples and keratin standards loaded into silver capsules. Resultant separated H_2 was analyzed on an interfaced Isoprime (Crewe, UK) continuous-flow isotope-ratio mass spectrometer. Measurements of the 2 keratin laboratory reference materials corrected

for linear instrumental drift were both accurate and precise with typical within-run SD ($n = 5$) of $<2\text{‰}$. All results are reported for nonexchangeable H expressed in typical delta notation, in parts per mil (‰), and normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale.

For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, between 0.5 and 1.0 mg of feather was combusted and CO_2 and N_2 separated online using a Eurovector 3000 elemental analyzer interfaced with a Nu Horizon (Nu Instruments, Wrexham, UK) triple-collector isotope-ratio mass spectrometer via an open split and compared with a pure CO_2 or N_2 reference gas. Stable nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) isotope ratios were expressed in delta (δ) notation as parts per mil (‰) deviation from the primary standards of atmospheric nitrogen and Vienna Pee Dee Belemnite carbonate (VPDB) standards, respectively. Using previously calibrated internal laboratory C and N standards (powdered keratin and gelatin), within runs ($n = 7$), precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was better than $\pm 0.15\text{‰}$.

Statistical Analysis and Assignment to Origin

We used multivariate analysis of variance (MANOVA) with Pillai's trace statistic to test for differences in feather isotope ($\delta^2\text{H}_f$, $\delta^{13}\text{C}_f$, $\delta^{15}\text{N}_f$) composition by year of harvest in juvenile Lesser Yellowlegs; no other species was collected in both years. The F -statistic provided in the MANOVA results is the "approximate" value. Changes in feather isotope values were tested against the ordinal date of harvest using multivariate regression for the 3 isotopes combined and using univariate regression for individual isotopes. These analyses were conducted to determine

whether individuals from different geographic areas, as represented by isotopic composition, migrated through Barbados at different times. The predicted relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ breaks down in food webs influenced by marine-derived nutrients; however, we retained all data for the regression analyses since they may still provide insight into the timing of migration of individuals from disparate coastal (i.e. influenced by nutrients of marine origin) and inland areas. For instance, we would expect Lesser Yellowlegs with natal origins in southern breeding areas and near Hudson Bay to arrive earlier in Barbados than those that bred in northern areas and adjacent to the Beaufort Sea.

However, probabilistic assignments using individuals with marine-influenced isotope values do not provide accurate depictions of potential geographic origins for those individuals (Yerkes et al. 2008, Ashley et al. 2010, Hobson and Kardynal 2016). Therefore, we filtered our dataset based on $\delta^{13}\text{C}_f$ and $\delta^{15}\text{N}_f$ values and assumed that samples with $\delta^{13}\text{C}_f > -20\text{‰}$ and $\delta^{15}\text{N}_f > 10\text{‰}$ had marine influence (Peterson et al. 1985, Kelly 2000); these individuals were removed from all further analyses of assignment to origin. Even after filtering, some juvenile Lesser Yellowlegs with ^2H -enriched feathers could not be placed in feather terrestrial isoscapes. Therefore, we removed individuals with $\delta^2\text{H}_f$ within 2 standard deviations greater than the highest value in the calibrated feather isospace (-69.8‰ ; see below). Results of statistical tests were considered significant at $P < 0.05$ and slope coefficients (± 1 SE) are provided for regressions.

To delineate the probable natal origins of juvenile shorebirds, we applied a spatially explicit likelihood assignment method (Royle and Rubenstein 2004, Hobson et al. 2009b) to each species separately. First, we converted an amount-weighted growing season precipitation surface from Bowen et al. (2005) to a feather isospace using the calibration equation for juvenile Lesser Scaup (*Aythya affinis*; $\delta^2\text{H}_f = -27.88 + 0.95 \cdot \delta^2\text{H}_p$; Hobson et al. 2009b) because we lacked similar species- or guild-specific equations for shorebirds. Similarly to many shorebird species, Lesser Scaup forage on aquatic invertebrates, and thus represented the most appropriate available calibration equation. The standard deviation of the residuals of the linear regression model ($\text{SD} = 12.6\text{‰}$) from the calibration of the Lesser Scaup feather isospace was incorporated into the origin assignments as an estimate of error (Hobson et al. 2009b). We used digital range maps obtained from BirdLife International and NatureServe (2015) to delineate known breeding areas for all 4 species; breeding ranges for American Golden-Plover in northern Quebec, Canada, and Stilt Sandpiper in eastern Nunavut and western Northwest Territories, Canada, were modified based on secondary sources (Québec Breeding Bird Atlas: http://www.atlas-oiseaux.qc.ca/index_en.jsp, Andres 2006) and

other regional surveys (Andres 2006). The calibrated feather isospace was then restricted ("clipped") to the resulting breeding range maps for use in species-specific origin assignments of juvenile birds.

Similarly to Hobson et al. (2009b), we used an odds ratio of 2:1 to assign individuals to their potential natal origin, where cells in the isospace in the upper 67% of probabilities were considered likely (1) origins and all others were considered unlikely (0). Assignments conducted for feather samples resulted in a spatially explicit binary surface for each individual; surfaces were summed across assignments for all individuals of a species to represent potential origins for that species. Manipulation of digital files and assignment to origin analyses were conducted using multiple packages, including raster 2.5-8 (Hijmans 2016), maptools 0.8-39 (Bivand and Lewin-Koh 2016), and permute 0.9-4 (Simpson 2016), in the R 3.3.2 statistical computing environment (R Core Team 2016) and ArcMap 10.1 (ESRI, Redlands, California, USA).

RESULTS

Tissue samples that could be aged accurately were collected from 1,359 harvested birds in 2013 and 2,110 birds in 2014. Lesser Yellowlegs was the most numerous species in each year. The proportion of juvenile birds in the harvest was variable across species: it was high for Short-billed Dowitcher (59% of juveniles in the harvest, $n = 196$ individuals harvested and collected), moderate for Lesser Yellowlegs (42%, $n = 2,643$), and low for Stilt Sandpiper (8%, $n = 291$) and American Golden-Plover (5%, $n = 329$). Adults tended to be harvested earlier in the season than juveniles for all species. The range of harvest dates was: July 22–October 8 (adults) and September 8–October 8 (juveniles) for American Golden-Plover; July 18–September 18 (adults) and August 16–September 27 (juveniles) for Stilt Sandpiper; July 22–September 3 (adults) and August 24–September 20 (juveniles) for Short-billed Dowitcher; and July 15–October 10 (adults) and July 26–October 10 (juveniles) for Lesser Yellowlegs. A subsample of 511 juvenile birds was selected for isotopic analysis (Table 1).

Isotopic Composition

There were no significant differences in juvenile Lesser Yellowlegs feather isotope composition in different years ($F_{1,355} = 2.45$, $P = 0.06$); therefore, all data for this species were combined for further analyses. Using the full, unfiltered dataset, feather isotope values were significantly different among juvenile shorebird species for $\delta^{13}\text{C}_f$ ($F_{3,505} = 12.09$, $P < 0.001$) and $\delta^{15}\text{N}_f$ ($F_{3,505} = 20.29$, $P < 0.001$), but not $\delta^2\text{H}_f$ ($F_{3,505} = 2.11$, $P = 0.10$). Multivariate linear regression models indicated significant changes in juvenile feather isotope ($\delta^2\text{H}_f$, $\delta^{13}\text{C}_f$ and $\delta^{15}\text{N}_f$) composition with

ordinal date for American Golden-Plover ($F_{1,13} = 7.59$, $P = 0.01$) and Lesser Yellowlegs ($F_{1,355} = 68.68$, $P < 0.001$), but not for Stilt Sandpiper ($F_{1,21} = 2.28$, $P = 0.11$) or Short-billed Dowitcher ($F_{1,112} = 2.49$, $P = 0.06$; Figure 2). Linear models indicated that $\delta^2\text{H}_f$ decreased with ordinal harvest date for American Golden-Plover ($\beta = -52.27 \pm 12.08$, $r^2 = 0.59$; $F_{1,13} = 18.73$, $P < 0.001$) and Lesser Yellowlegs ($\beta = -36.12 \pm 2.52$, $r^2 = 0.37$; $F_{1,355} = 204.10$, $P < 0.001$), suggesting that individuals of these species with natal origins in coastal or southern regions arrived in Barbados before conspecifics from inland or more northerly regions. However, we did not find evidence of differential migration timing using $\delta^2\text{H}_f$ for Stilt Sandpiper ($\beta = -12.21 \pm 7.73$, $r^2 = 0.11$; $F_{1,21} = 2.49$, $P = 0.13$) or Short-billed Dowitcher ($\beta = 0.77 \pm 1.25$, $r^2 = 0.003$; $F_{1,112} = 0.38$, $P = 0.54$).

Feather $\delta^{13}\text{C}$ decreased with ordinal harvest date for Lesser Yellowlegs ($\beta = -1.30 \pm 0.21$, $r^2 = 0.10$; $F_{1,355} = 39.68$, $P < 0.001$) and Short-billed Dowitcher ($\beta = -0.56 \pm 0.25$, $r^2 = 0.04$; $F_{1,112} = 4.75$, $P = 0.03$), but there was no relationship for the other 2 species ($P > 0.10$). Using $\delta^{13}\text{C}_f$ only, this suggests that Lesser Yellowlegs and Short-billed Dowitchers that originated near coastal areas may have arrived in Barbados earlier than conspecifics from northern and western regions, respectively. For American Golden-Plover ($\beta = -2.85 \pm 0.79$, $r^2 = 0.50$; $F_{1,13} = 13.05$, $P = 0.003$) and Lesser Yellowlegs ($\beta = -0.44 \pm 0.12$, $r^2 = 0.04$; $F_{1,355} = 13.01$, $P < 0.001$), $\delta^{15}\text{N}_f$ decreased in relation to harvest date, but there was no relationship with ordinal date for Stilt Sandpiper ($\beta = 0.42 \pm 0.48$, $r^2 = 0.03$; $F_{1,21} = 0.76$, $P = 0.39$) or Short-billed Dowitcher ($\beta = -0.20 \pm 0.20$, $r^2 = 0.009$; $F_{1,112} = 1.05$, $P = 0.31$). These results suggest that American Golden-Plover and Lesser Yellowlegs from coastal areas arrived in Barbados before northern inland birds. Considering the results from all regression analyses, evidence for differential timing of migration (for coastal and southern birds arriving earlier in Barbados) is strongest for Lesser Yellowlegs and American Golden-Plover and weakest for Short-billed Dowitcher and Stilt Sandpiper.

Shorebird Origins

A total of 377 juveniles were retained in the analysis assigning birds to natal origin after accounting for individuals without the complete set of 3 isotopes and applying filters for marine-influenced tissues based on $\delta^{13}\text{C}_f$ and $\delta^{15}\text{N}_f$ as well as $\delta^2\text{H}_f$ (Table 1). Our assignment to origin analysis using probabilistic models resulted in considerable spatial structure in natal origins for juveniles of all species. The highest probability of origin of harvested juvenile American Golden-Plover (total $n = 7$ after applying the filters) was the southeastern portion of the range in southern Nunavut near Hudson Bay (Coats and Southampton Islands) and southern Baffin Island and/or an area spanning much of the latitudinal range in central

Alaska (Figure 3A). Harvested juvenile Stilt Sandpiper (total $n = 13$) most likely originated from far western Alaska (North Slope) and/or the Manitoba and Nunavut portions (near western Hudson Bay) of the breeding range (Figure 3B). The southern and eastern parts of the Short-billed Dowitcher's (total $n = 102$) breeding range in southeastern Manitoba, around James Bay (northeastern Ontario), and in central Quebec, as well as the far western part of the range on Kodiak Island in Alaska, were likely areas of natal origin for juvenile birds of this species (Figure 3C). The highest number of juvenile Lesser Yellowlegs (total $n = 255$) likely originated from the southeastern part of the breeding range, mainly centered on James Bay in northern Ontario (Figure 3D). However, a high proportion of birds also originated from central and western parts of the species' range, throughout a large area of the Northwest Territories and Alaska.

DISCUSSION

Our isotopic investigation into the probable origins of juvenile shorebirds harvested in Barbados during fall migration has shown considerable structure in the breeding regions that likely contributed the most to harvest. Discrete catchment areas were identified for each species using our assignment to origin method. This will allow the development of conservation and management options for these species that are better targeted at the segments of the population exposed to harvest. For example, a recent evaluation of North American breeding shorebird sustainable harvest levels was based on demographic and population parameters from potential production areas within the breeding range of the 4 species included in our study as identified by expert opinion (Watts et al. 2015). Applying results from our study will allow estimates of sustainable harvest levels to be indicative of Nearctic population segments that are likely exposed to harvest in Barbados, and will allow the use of regional demographic estimates when available.

Results from our assignment analyses generally aligned with our predicted regions of natal origins for juvenile birds, with the highest numbers of individuals originating in the eastern portions of their breeding ranges. However, probabilistic assignments for all species indicated that juveniles harvested in Barbados could also have origins in parts of Alaska in the western portion of their breeding ranges. Watts et al. (2015) assumed that only the Canadian portion of the American Golden-Plover population was exposed to harvest, while our results indicate that Alaskan individuals (juveniles) may also comprise a portion of the birds harvested in Barbados. In the case of the Short-billed Dowitcher, our results indicate that it was mostly juveniles of the eastern subspecies (*L. g. griseus*) that had high probabilities of being harvested in Barbados, whereas

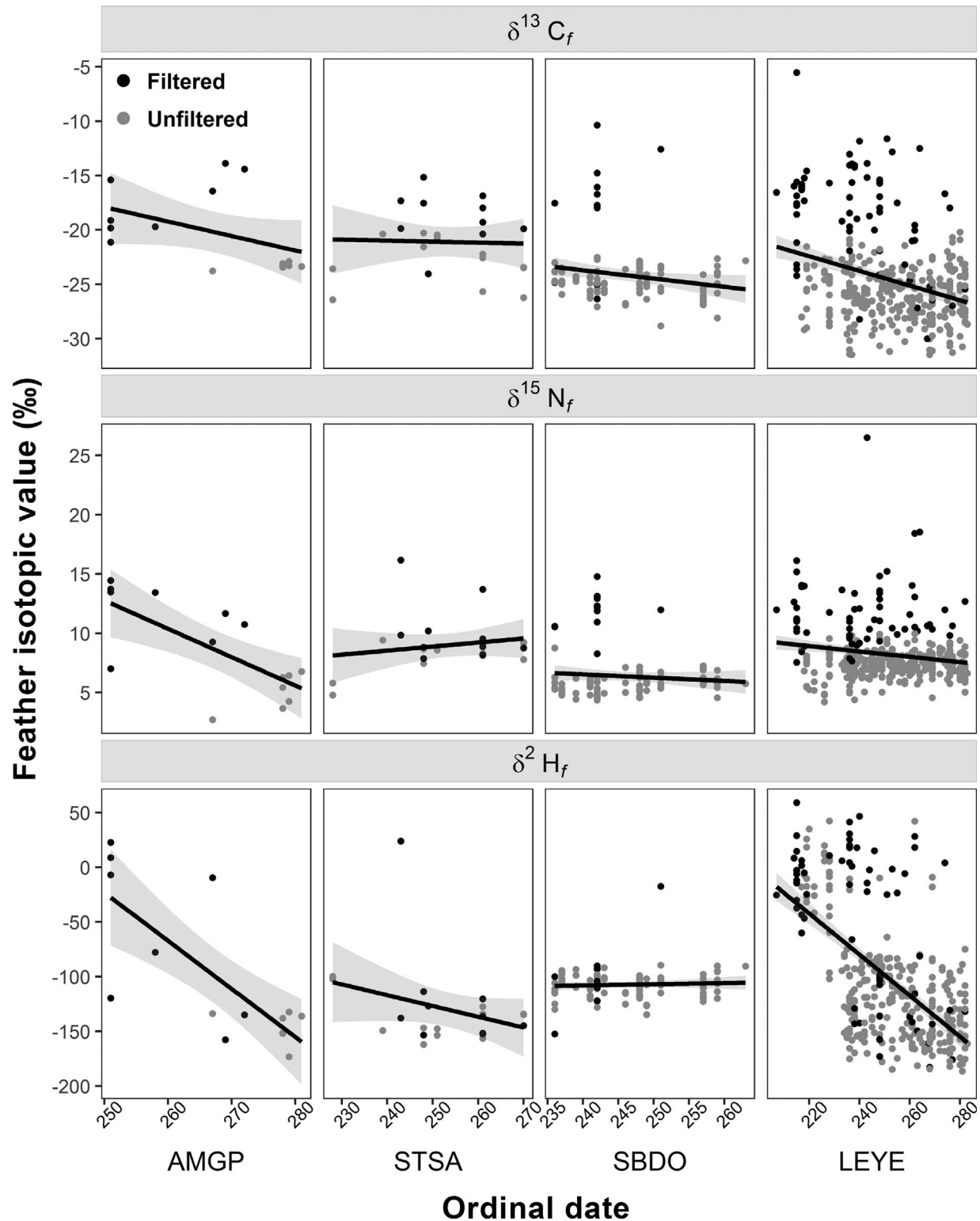


FIGURE 2. Linear models showing variation in feather isotope (δ^2H_f , $\delta^{13}C_f$, and $\delta^{15}N_f$) values (‰) from juvenile American Golden-Plover (AMGP), Stilt Sandpiper (STSA), Short-billed Dowitcher (SBDO), and Lesser Yellowlegs (LEYE) harvested during fall migration in Barbados in July–October of 2013 and 2014 as a function of the date of harvest. Data shown here represent all isotope values prior to filtering the dataset for potential marine-influenced birds as well as posterior to applying the filter. Dots indicate data values for filtered and unfiltered samples, and the line and pale gray shaded area represent the linear model with associated 95% confidence interval for the unfiltered dataset

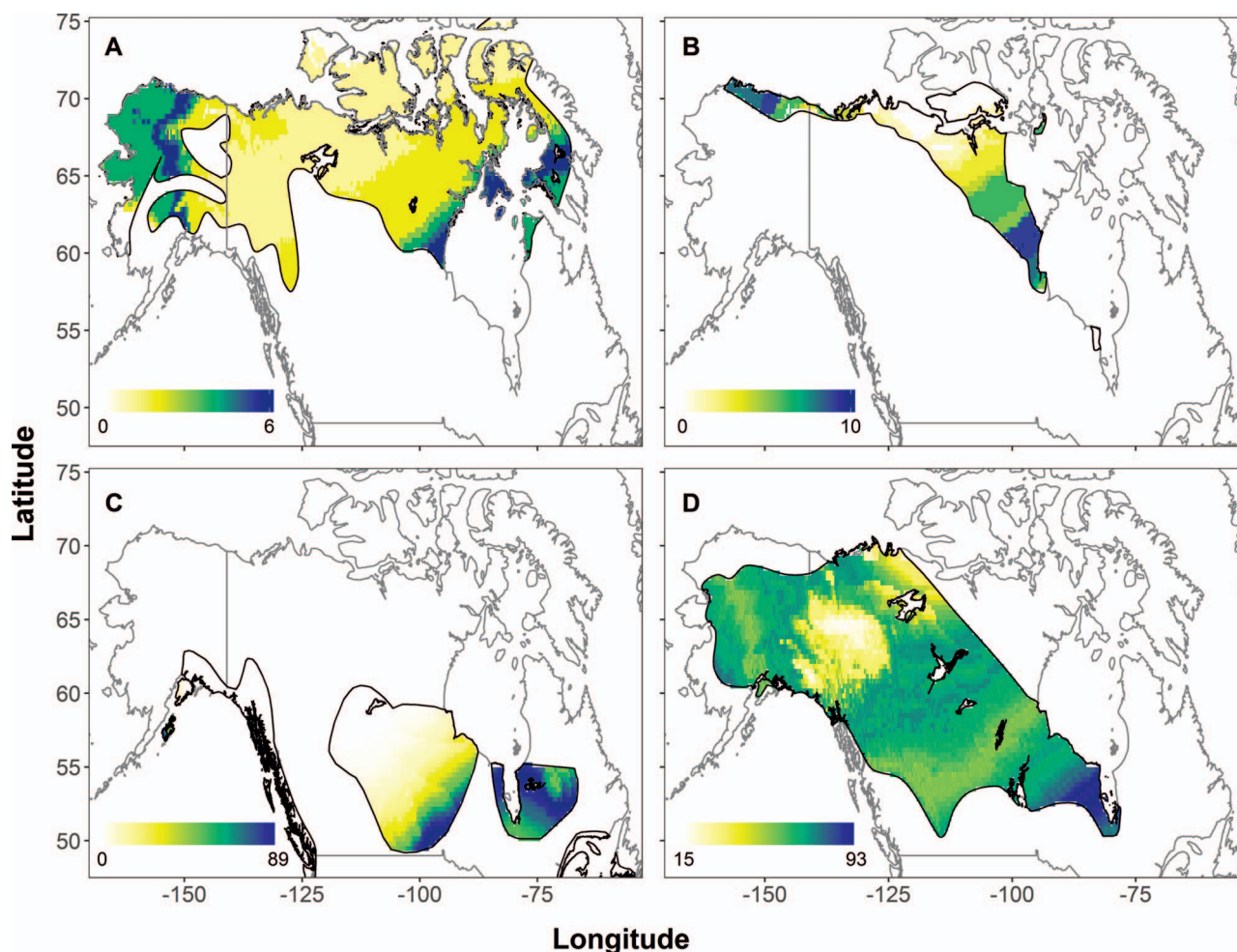


FIGURE 3. Assignment of shorebirds harvested in Barbados in July–October of 2013 and 2014 to their probable natal origins in North America using feather $\delta^2\text{H}$ of juvenile (A) American Golden-Plover, (B) Stilt Sandpiper, (C) Short-billed Dowitcher, and (D) Lesser Yellowlegs. Assignments were restricted to each species' breeding range (black outline). Legend values indicate the potential number of individuals originating from a single cell ($\sim 37 \text{ km} \times 37 \text{ km}$) in the raster.

Watts et al. (2015) assumed that both the subspecies that breed in the midcontinental region (*L. g. hendersoni*) and the eastern subspecies (*L. g. griseus*) were equally exposed to harvest in the Western Atlantic Flyway.

The proportion of juveniles to adults in the harvest also provides evidence for differential migration pathways between age classes of American Golden-Plover and Stilt Sandpiper. Based on the low percentage of juveniles of these species in the harvest, it appears that a large proportion of juvenile American Golden-Plovers and Stilt Sandpipers may use a different fall migration flyway than adults and thus may bypass Barbados. Juvenile American Golden-Plovers are known to use a more westerly fall migration route than adults, moving through the mid-continental region of North America and likely island-hopping through the Caribbean Basin (Johnson et al. 2018). Adults using the more easterly trans-Atlantic flyway likely originate from the same breeding areas, as supported

by recent research on migration patterns of American Golden-Plovers fitted with geolocators (J.-F. Lamarre personal communication, <https://doi.org/10.13140/RG.2.2.20167.60329>). The low prevalence of juvenile American Golden-Plovers and Stilt Sandpipers resulted in low sample sizes, but nevertheless represented the entirety of the harvest at the 2 swamps where samples were collected. Little information exists on age-specific differential fall migration pathways for the Short-billed Dowitcher. Our results suggest that estimated sustainable continental harvest levels (Watts et al. 2015) could possibly be revised upward for American Golden-Plover and downward for Short-billed Dowitcher. However, more information would be required on the routes and migratory connectivity of adult birds to provide definitive management recommendations.

Feather isotopic composition ($\delta^2\text{H}_f$, $\delta^{13}\text{C}_f$, and $\delta^{15}\text{N}_f$) of juvenile Lesser Yellowlegs did not vary between our 2 yr of

samples, indicating that the population being harvested likely originated from the same catchment area in both years and suggesting limited variation in population exposure to hunting over time. For American Golden-Plover and Lesser Yellowlegs juveniles, birds harvested earlier in the season generally had higher $\delta^2\text{H}_f$ values, indicating coastal or more southerly natal origins from within the breeding range. As the season progressed, harvested birds of these 2 species became more likely to have originated from more northerly latitudes (i.e. lower $\delta^2\text{H}_f$ values). This provides potential evidence for a chain migration pattern, in which birds from more southern areas arrive at stopover sites before birds from more northern areas. American Golden-Plover, Short-billed Dowitcher, and Lesser Yellowlegs also showed a negative temporal trend in either or both $\delta^{13}\text{C}_f$ and $\delta^{15}\text{N}_f$ values, supporting the notion that individuals that originated from coastal areas potentially arrived in Barbados earlier in the season than birds from other areas. This suggests that a larger proportion of birds that originated from the southern portion of the range (which we assume corresponded to a higher probability of encountering marine-influenced habitats during the pre fledging period) arrived in Barbados first, a result consistent with our predictions for Short-billed Dowitcher and Lesser Yellowlegs, but not American Golden-Plover. Marine-influenced Short-billed Dowitcher and Lesser Yellowlegs potentially originated from the James and Hudson Bay regions, consistent with the known distributions of these 2 species, which mainly inhabit inland boreal habitats at higher latitudes (Jehl et al. 2001, Tibbitts and Moskoff 2014). Marine-influenced American Golden-Plover potentially originated in greater proportion from the Hudson Bay and Foxe Basin area, despite significant amounts of coastal habitat in other portions of their range (Johnson et al. 2018). However, results for the temporal analysis of American Golden-Plover should be interpreted with caution, given the small weekly sample sizes.

Similarities in the $\delta^2\text{H}_p$ isoscape between Alaska and eastern parts of North America impeded our ability to determine whether birds with $\delta^2\text{H}_f$ values similar to those areas originated from the western or eastern parts of their ranges. Probabilistic assignments using stable isotopes can be made more accurate or precise when multiple isotopes are used in combination or when isotopic information is combined with nonisotopic information (e.g., band encounter data, geolocator locations, genetics; Van Wilgenburg and Hobson 2011, Rundel et al. 2013, Hobson and Kardynal 2016). Regional species abundance data can potentially be used to refine assignments for species when sufficient data are available. However, abundance data are currently available for only ~20% of the breeding ranges of the Arctic species (Arctic PRISM; Bart and Johnston 2012, K. J. Kardynal personal observation), and the other 2

species (Short-billed Dowitcher and Lesser Yellowlegs) are not well surveyed by other programs (e.g., the Breeding Bird Survey). Further, use of this prior also assumes an equal probability that a bird from any part of its range will migrate through Barbados, thus ignoring any potential migration flyway structure. Thus, inclusion of such priors can introduce bias into assignments and this topic requires further investigation. However, the hypothesis that Alaskan Golden-Plover, Stilt Sandpiper, and Lesser Yellowlegs are exposed to harvest in Barbados can now be tested with more targeted sampling and use of alternative methods. Additional species-specific information for our study species would allow further refinement of our analyses of assignment to origin. For example, more refined species distributions, density estimates, flyway structure, and habitat selection models could potentially be used as prior information in a Bayesian analysis to increase the accuracy of results from assignment algorithms.

Our use of a Lesser Scaup calibration algorithm linking $\delta^2\text{H}_p$ with $\delta^2\text{H}_f$ potentially has implications for our results because the use of an inaccurate calibration may skew probabilistic assignments, particularly latitudinally. However, general and species-specific shorebird equations are currently unavailable, and Lesser Scaup are the closest match to shorebirds for which a calibration algorithm is available as both have a diet primarily composed of invertebrates. To develop a shorebird- or species-specific calibration algorithm, sampling of shorebird tissues grown on the breeding grounds across broad geographical gradients will be required (Hobson and Wassenaar 2008) but is currently not performed because flight feathers are difficult to sample near the nest from precocial juvenile shorebirds. Alternatively, captive birds subjected to simulated latitudes using carefully selected or “spiked” food and drinking water could potentially be used for such calibrations (Hobson et al. 1999a, 1999b). Meanwhile, using the Lesser Scaup calibration algorithm appeared to fit the data reasonably well and our choice of variance from the calibration algorithm was of a similar magnitude to that seen previously (Hobson et al. 2014).

Tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can be useful for providing information on the origins of birds in some areas (Hobson and Kardynal 2016). However, the lack of described gradients of these isotopes in the Arctic precluded their use in probabilistic assignments for our study species. Instead, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements in general are more valuable for providing insights into diet and trophic position, and in this study were used to discriminate between terrestrial vs. marine influences using thresholds (Hobson and Wassenaar 2008). Further, analysis of these isotopes in relation to harvest date indicated that some latitudinal and inland vs. coastal population structure may have existed in the timing of passage through Barbados for some species. The proportion of individuals removed from

the filtered analysis due to potential marine influence was small for 2 of our study species (Stilt Sandpiper and Short-billed Dowitcher), but not for juvenile American Golden-Plover (30% of samples had marine influence) and juvenile Lesser Yellowlegs in 2014 (12% of samples). Since the assignment of birds to origin using precipitation isoscapes can only be done in terrestrial systems, it was not possible to determine the potential origins of individuals with such marine influence, and therefore we could not assess whether this introduced a bias into our assignments (e.g., if individuals from a particular region were more likely to forage in marine environments) for these 2 species.

Adult (after-second-year) shorebirds typically have higher annual survival and productivity than juvenile birds (Sandercock 2003); therefore, understanding the origins of these older birds would likely have a greater impact on the conservation of these species through the setting of harvest limits that would afford protection to that segment of the population. However, we were not able to identify a tissue that could be used to assign adults to breeding areas. Most adult shorebird species grow their feathers during the nonbreeding season, making this tissue unusable for determining breeding origins using probabilistic methods. Other tissues used to assess diet and trophic positioning such as claws, muscle, and liver are chemically active and represent resources accumulated over the previous weeks to months (Bearhop et al. 2003, Hahn et al. 2014). For example, we analyzed isotopes in claws from adult birds harvested in Barbados, and probabilistic assignments of adult American Golden-Plover and Lesser Yellowlegs using claw $\delta^2\text{H}$ ($\delta^2\text{H}_c$) revealed potential origins of these species during fall migration across broad areas of North America (Appendix Figure 4) and therefore were not useful for determining potential breeding or refueling locations. Adult Lesser Yellowlegs were harvested throughout the hunting season, from July to October, whereas American Golden-Plover adults were mainly harvested from late August to October, therefore $\delta^2\text{H}_c$ of adult shorebirds harvested in Barbados likely reflected $\delta^2\text{H}$ integrated over at least the migration period. Values of $\delta^2\text{H}_p$ are not available for many of the Caribbean islands and are generally not useful due to the strong marine effect in local precipitation and sea spray. Based on $\delta^2\text{H}_c$ values, adult shorebirds in our study were assigned to areas much farther north than Barbados, and confirm that birds being harvested had not been in the study area for sufficient duration (i.e. several weeks) to exhibit more local or even southern U.S. $\delta^2\text{H}_c$ values.

Hunting has emerged as a potential factor contributing to the declines of some North American–breeding shorebirds (Morrison et al. 2012, Watts et al. 2015). Our study is the first to identify the potential natal origins of juvenile birds exposed to harvest in Barbados using probabilistic methods. This information will allow the

identification of populations or subspecies that may be negatively affected by harvest or able to sustain current levels. Barbados hunters have taken voluntary measures to limit the harvest of American Golden-Plover and Lesser Yellowlegs based on results from a recent evaluation of the sustainability of their harvest (Watts et al. 2015, E. T. Reed personal observation), but it is not clear what proportion of hunters adhere to these voluntary restrictions or how heavily these species are hunted outside Barbados. Results from our study can be used to refine estimates of sustainable harvest levels in Barbados for the species studied, as these estimates can now more accurately be based on the size of the population exposed to hunting estimated from published sources (e.g., Andres et al. 2012), as opposed to using continental population estimates or estimates of population segment size determined through expert opinion.

Shorebird hunting occurs in several countries in the Western Hemisphere. A broader study of migratory connectivity and identification of species and populations exposed to harvest at the scale of the Americas is urgently needed to determine populations at risk of overharvesting. We therefore suggest that similar studies should be undertaken in key hunting areas, especially in the Caribbean and along the northern coast of South America. This will undoubtedly require exceptional cooperation from local hunting organizations as well as governments. While we were able to assign probable natal origins of harvested juvenile birds, it is adult survival that has the greatest influence on population growth in long-lived species such as shorebirds (Hitchcock and Gratto-Trevor 1997). Therefore, identification of appropriate tissues to determine breeding origins of adults, development of shorebird- and shorebird species-specific precipitation-to-feather calibrations, and more precise understanding of tissue isoscapes in general are needed so that we can better understand the contribution of populations and/or subspecies to the hemispheric harvest. Finally, information on the distributions and densities of Nearctic, Arctic, and boreal shorebirds across their breeding ranges is needed to better evaluate the relative contribution of different population segments to the hemispheric harvest.

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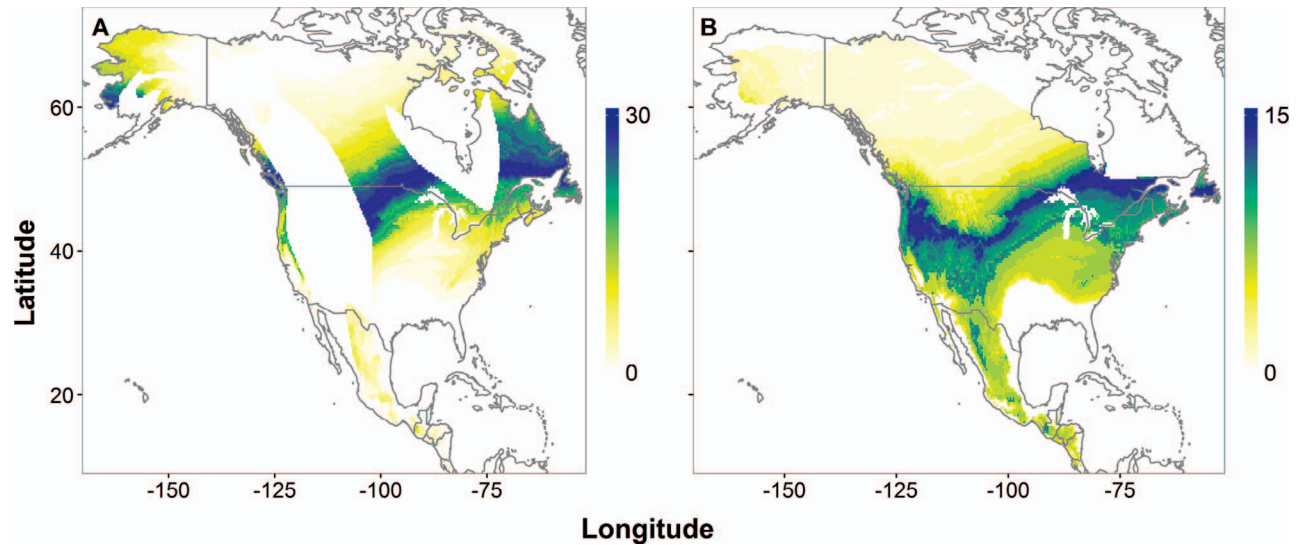
Author contributions: E.T.R., J.A.H., and K.A.H. formulated the questions; E.T.R. and J.A.H. collected data and supervised research; K.A.H. and K.J.K. analyzed the data; and E.T.R., K.J.K., and K.A.H. wrote the paper.

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APPENDIX FIGURE 4. Assignment of adult birds to areas of claw growth in North and Central America using $\delta^2\text{H}$ values from the claws of (A) American Golden-Plover and (B) Lesser Yellowlegs harvested in Barbados during fall migration in July–October of 2013 and 2014. Potential areas of claw growth were limited to possible breeding and migration areas. Legend values indicate the potential number of individuals originating from a single cell in the raster. Claw $\delta^2\text{H}$ was converted to an equivalent feather value using a transfer function from Hobson et al. (2006).