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Use of Stable Isotope Methodology to Determine Natal Origins of Mallards at a Fine Scale Within the Upper Midwest

MICHAEL L. SZYMANSKI,[1,2] *School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA*

ALAN D. AFTON, *United States Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, LA 70803, USA*

KEITH A. HOBSON, *Environment Canada, 11 Innovation Boulevard, Saskatoon, SK S7N 3H5, Canada*

ABSTRACT Waterfowl managers often attempt to protect local breeding stocks of mallards (*Anas platyrhynchos*) from hunting pressure, but presently they cannot identify natal origins of birds shot during fall hunting seasons with certainty, unless recovered birds are banded before fledging. Accordingly, we examined whether stable isotope methodology could accurately delineate natal origins of mallards at a fine scale within the upper Midwest (USA). We determined $\delta^{13}C$, δD, and $\delta^{15}N$ values from feather samples of 102 flightless mallard ducklings collected in Minnesota, North Dakota, South Dakota, and Wisconsin, USA, from 7 July to 9 September 2002. We detected inverse relationships between latitude and $\delta^{13}C$ ($R^2 = 0.223$) and δD ($R^2 = 0.210$). We also detected a weak positive relationship between easterly shifts in longitude and $\delta^{13}C$ ($R^2 = 0.067$) and a weak negative relationship between easterly shifts in longitude and $\delta^{15}N$ ($R^2 = 0.076$). The ^{13}C and deuterium values differed ($P < 0.02$) among states: North Dakota was most depleted in ^{13}C, and South Dakota was least depleted in deuterium. Discriminant function analysis delineated natal origins of mallard ducklings in Minnesota, North Dakota, South Dakota, and Wisconsin with low-to-moderate accuracy (47%), whereas we predicted natal origins of ducklings among subregions (Prairie [ND, SD] vs. Great Lakes [MN, WI] states) with moderate accuracy (72%). We conclude that stable isotope methodology has a limited ability to determine natal origins of migratory birds along a longitudinal corridor at fine scales but that it improves across ecoregions. However, the ability of deuterium to determine natal origins of migratory birds may vary as hydrological conditions, within and among areas, change throughout time. Researchers should account for annual variation in deuterium found in surface waters when investigating natal origins of migratory birds that use food derived primarily from these waters. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1317–1324; 2007)

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Waterfowl managers often attempt to protect local breeding stocks of mallards (*Anas platyrhynchos*) from harvest pressure before arrival of migrant mallards, which presumably act as a buffer in the harvest. Successful nesting females and many local, hatch-year (HY) mallards often are present on, or near, brood marshes at the beginning of the hunting season in areas with breeding populations, and they may be especially vulnerable to hunters (Gilmer et al. 1977, Kirby et al. 1989). However, waterfowl managers presently cannot identify natal origins of mallards shot during fall hunting seasons with certainty, unless recovered birds are banded before fledging.

Special regulations, such as half-day shooting and prohibition of spinning-wing decoys early in the season, have been promulgated with objectives of protecting locally reared mallards. Such regulations are based on analysis of band recovery data, which require critical assumptions concerning banding effort, banding locations, and whether banded birds actually originated in the area where captured (e.g., Munro and Kimball 1982, Brownie et al. 1985). Preseason banding programs do not band large numbers of unfledged local age class birds. Thus, most young-of-the-year birds banded are of the HY age class, which have been flighted for unknown periods, and consequently they are of unknown origins (Gustafson et al. 1997).

For example, a relatively large proportion of the state of Minnesota's mallard bandings (9.6% of 34,928 mallards banded during 1996–2003) was local age class mallards. However, because other areas that contribute to the majority of this region's migrant mallard harvest band proportionately few (1.7% of 536,261 mallards banded in AB, SK, MB, and ON, Canada; and ND, SD, and WI, USA during 1996–2003) local age class mallards, this precludes any rigorous band analysis of differential vulnerabilities among mallards with known origins. Finally, numbers of band recoveries are inadequate to experimentally evaluate specific treatments, such as new hunting technologies (e.g., Szymanski and Afton 2005) or regulation changes that may affect derivation of the harvest at fine scales.

Stable isotope methodology has the potential to delineate natal origins of HY ducks shot during fall hunting seasons by using metabolically inert tissues (e.g., flight feathers) grown on breeding areas (Hobson 1999*b*), and it has been evaluated for ducks over coarse spatial scales (Hebert and Wassenaar 2005). Differences in photosynthetic pathways affect $\delta^{13}C$ values at the vegetative base of foodwebs (C_3 in cooler, wetter climates; C_4 in warmer, drier climates; Peterson and Fry 1987, Lajtha and Michener 1994). C_3 plants dominate in temperate areas of North America, but land-use practices and physiological mechanisms of C_3 plants to reduce water

[1] *E-mail: mszymanski@nd.gov*
[2] *Present address: North Dakota Game and Fish Department, 100 N. Bismarck Expressway, Bismarck, ND 58501, USA*

loss can result in significant variation even within C_3 systems (Marra et al. 1998, and references therein). Thus, $\delta^{13}C$ values of foodwebs in forested areas may be depleted (i.e., isotopically light compared with international standards) compared with more open grassland or crop areas. Rubenstein et al. (2002) recently reported landscape-scale patterns in $\delta^{13}C$ values of feathers of black-throated blue warblers (*Dendroica caerulescens*) in eastern North America, and Hobson et al. (1999) discovered considerable, although unexpected, structure in the pattern of $\delta^{13}C$ values of monarch butterflies (*Danaus plexippus*) throughout their eastern range.

Forest foodweb $\delta^{15}N$ values typically are lower than those found in agriculturally associated foodwebs due to tillage and fertilizer application with subsequent ammonification (or loss of isotopically lighter nitrogenous compounds to the atmosphere). The presence of animal waste nitrates also tends to enrich agricultural lands with ^{15}N (Alexander et al. 1996, Hobson 1999*a*, Hebert and Wassenaar 2001).

The discovery that patterns of deuterium in precipitation across North America are reflected in feathers grown across the continent has revolutionized the way that natal origins of migratory birds can be inferred (Chamberlain et al. 1997, Hobson and Wassenaar 1997). These patterns show decreasing δD values from southeast to northwest across North America, and they typically are useful in providing estimates of latitude of feather origin. Thus, combined use of $\delta^{13}C$, $\delta^{15}N$, and δD values of feathers has the potential to provide information on origins of birds from landscapes that differ in land-use practices and latitude.

Our objectives were to determine whether δD, $\delta^{13}C$, and $\delta^{15}N$ values of feathers collected from flightless mallard ducklings across Minnesota, North Dakota, South Dakota, and Wisconsin, USA, vary sufficiently to enable identification of local versus nonlocal mallards within states, or, given their more distinct ecological differences, between subregions of the upper Midwest (Prairie [ND, SD] vs. Great Lakes [MN, WI] states).

STUDY AREA

We visually analyzed advanced very high resolution radiometer satellite data to approximate general land use and cover ecoregions across 4 states within the upper Midwest: Minnesota, North Dakota, South Dakota, and Wisconsin (Szymanski 2004). We then selected 3 east-to-west transects, subjectively located to maximize latitude and longitude within the region, to collect feather samples from flightless mallard ducklings (age classes 2b, 2c, and 3a; Gollop and Marshall 1954) from 7 July to 9 September 2002 (Fig. 1). We attempted to collect a sample every 15–25 km where mallard ducklings were abundant. If samples were not attainable at regular intervals, we collected samples opportunistically, depending on habitat conditions, $\leq$100 km north or south of transects. Gaps in collection locations along transects represent areas where we could not locate mallard ducklings. Transects traversed 5 land-use and cover ecoregions: Agricultural, Agriculturally Dominated Forest, Agriculturally Dominated Grassland, Forest, and Grassland (Fig. 1); however, not all transects crossed all ecoregions.

METHODS

Flightless Duckling Feathers

We collected the fourth secondary and tail feathers from 102 flightless mallard ducklings that we either captured using night-lighting techniques (Bishop and Barratt 1969) or shot during daylight hours (Szymanski 2004; Louisiana State University Animal Care and Use Committee Protocol AE02–12). We then placed feather samples in small paper envelopes labeled with our scientific collection permit numbers, state of collection, and latitude and longitude coordinates from a hand-held Global Positioning System.

Stable Isotope Analysis

We cleaned feathers by rinsing them 2 times in a chloroform:methanol (2:1) solution and allowed them to air dry. We then cut samples from the upper third of secondary feathers and the lower half of tail feathers to represent similar periods of growth. We loaded feather samples into tin cups for $\delta^{15}N$ and $\delta^{13}C$ analysis and silver cups for δD analysis (for a more complete description of stable isotope methods, see Hobson and Wassenaar 1997, Hobson 1999*a*, Wassenaar and Hobson 2002). We expressed all ratios in δ-notation as parts per thousand (‰) deviations from international standards.

Statistical Analysis

Latitudinal and longitudinal relationships.—We used separate simple linear regression analyses (PROC REG; SAS Institute 1999) to describe relationships between $\delta^{13}C$, δD, and $\delta^{15}N$ values of feathers and latitudes and longitudes of collection sites. We used a critical value of $\alpha = 0.05$ in all statistical analyses.

Analysis of flightless mallard duckling feathers.—We first classified samples by state of collection (MN, ND, SD, and WI) and then by subregion (Prairie [ND, SD] and Great Lakes [MN, WI] states). We then ran 3 separate one-way analyses of variance (ANOVA; PROC MIXED; Littell et al. 1996) with state nested within subregion to test whether $\delta^{13}C$, δD, and $\delta^{15}N$ values differed among states and between subregions, and we used Tukey posthoc tests to determine differences among means.

We used linear discriminant function analysis (DFA; PROC DISCRIM; SAS Institute 1999) to develop predictive models of natal origins of mallard ducklings based on different combinations of $\delta^{13}C$, δD, and $\delta^{15}N$ values, and we subsequently determined models that most effectively predicted natal origins of ducklings by state and subregions. We alleviated biases created by slight differences in sample size among groups by specifying proportionate group membership in our DFA (PROC DISCRIM; SAS Institute 1999). Our predictive models elicited group-specific linear discriminant functions that classified each sample into the group with the highest classification score.

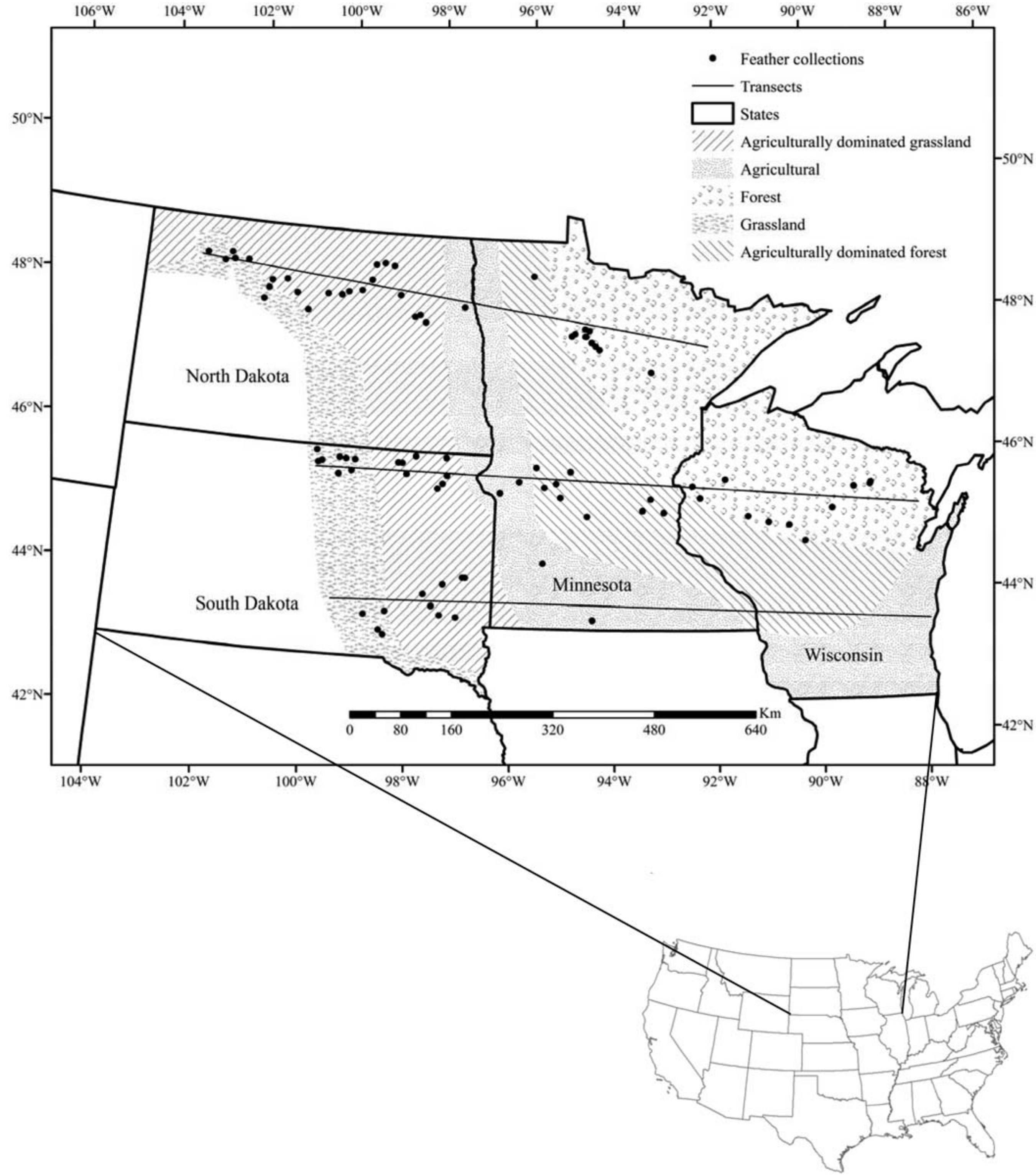

Figure 1. Map of mallard duckling feather samples collected along 3 transects traversing Minnesota, North Dakota, South Dakota, and Wisconsin within the upper Midwest (USA), 7 July to 9 September 2002.

Finally, we cross-validated the accuracy of each model by recalculating the discriminant function after removing each individual from the sample population and then reclassifying the individual with the newly calculated functions (PROC DISCRIM; SAS Institute 1999).

RESULTS

Latitudinal and Longitudinal Relationships

Simple linear regression analyses indicated that $\delta^{13}C$ and δD values decreased by 1.17‰ and 4.66‰, respectively, for each northerly degree of latitude shift; $\delta^{15}N$ values were not

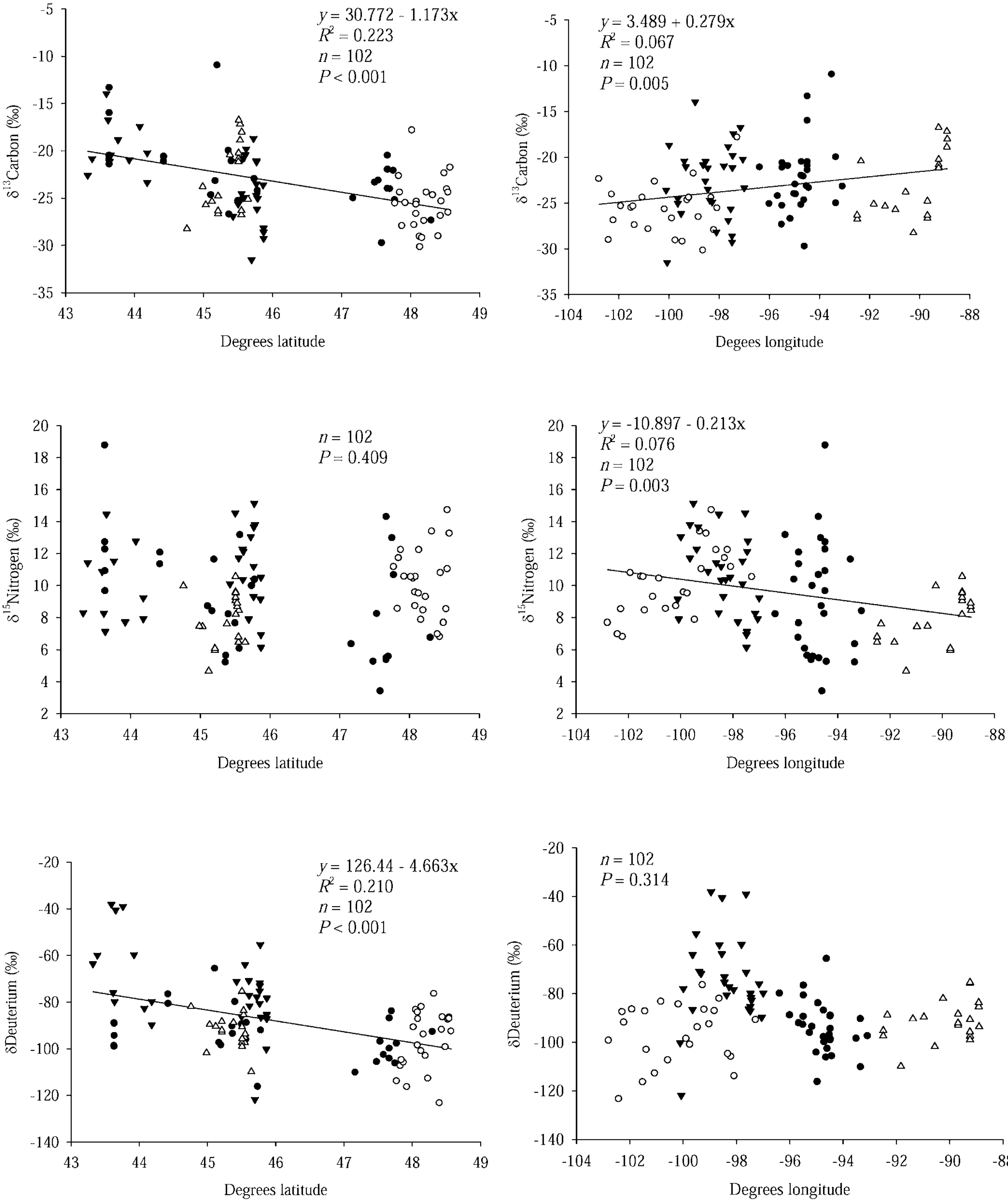

Figure 2. Relationships of feather values by isotope ($\delta^{13}C$, $\delta^{15}N$, and δD; parts per thousand [‰]) to latitude (left) and longitude (right) for flightless mallard ducklings collected or captured in Minnesota (closed circle), North Dakota (open circle), South Dakota (closed triangle), and Wisconsin, USA (open triangle), 7 July to 9 September 2002. Regression statistics are provided only for slopes that were significantly different ($P < 0.05$) from zero.

Table 1. Mean $\delta^{13}C$, δD, and $\delta^{15}N$ values (parts per thousand [‰]) and range from feathers of flightless mallard ducklings collected in Minnesota ($n = 29$), North Dakota ($n = 24$), South Dakota ($n = 29$), and Wisconsin, USA ($n = 20$), 7 July to 9 September 2002.[a]

State	$\delta^{13}C$ (‰)			δD (‰)			$\delta^{15}N$ (‰)[b]		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
MN	–22.27A	0.68	–29.75–10.97	–93.92B	2.42	–116.30–65.64	9.21	0.48	3.40–18.76
ND	–25.62B	0.74	–30.18–17.84	–96.52B	2.66	–123.32–76.76	10.19	0.53	6.80–14.72
SD	–22.76A	0.68	–31.50–13.95	–74.22A	2.42	–121.76–38.04	10.62	0.48	6.14–15.14
WI	–22.74A	0.81	–28.25–16.74	–91.22B	2.92	–109.87–75.36	7.87	0.58	4.67–10.57

[a] Means with the same letters within a column are not different ($P > 0.05$).
[b] State effect was not significant for $\delta^{15}N$ after accounting for differences among subregions in the nested model.

significantly related to latitude (Fig. 2, left). Simple linear regression analyses indicated that $\delta^{13}C$ values increased by 0.28‰ for each easterly degree of longitude shift, whereas $\delta^{15}N$ values decreased by 0.21‰ for each easterly degree of longitude shift; δD values were not significantly related to longitude (Fig. 2, right).

Comparison of Isotopes by State

Separate nested ANOVAs indicated that $\delta^{13}C$ and δD values differed among states ($\delta^{13}C$: $F_{2,98} = 4.17$, $P = 0.018$; δD: $F_{2,98} = 19.44$, $P < 0.001$) and that $\delta^{15}N$ values were not different among states ($F_{2,98} = 1.74$, $P = 0.18$). Mean comparison tests indicated that ducklings from North Dakota were approximately 1.13 times more depleted in ^{13}C than were those from other states, whereas $\delta^{13}C$ values were similar for Minnesota, South Dakota, and Wisconsin (Table 1). Ducklings from South Dakota were less depleted (0.77–0.81×) in deuterium than were those from other states, whereas δD values were similar for North Dakota, Minnesota, and Wisconsin (Table 1).

Using $\delta^{13}C$, δD, and $\delta^{15}N$ as discriminating variables, DFA achieved 47% overall classification accuracy (Table 2). Using $\delta^{13}C$ and δD as discriminating variables, DFA achieved 46% overall classification accuracy, but it did not classify any ducklings as originating in Wisconsin (Table 2). However, Wisconsin ducklings were partitioned fairly equally into other states. All other models achieved lower classification accuracy (30–45%), some with highly disproportionate rates of misclassification (e.g., δD model [0–76%]; Table 2). Expected overall classification accuracy by random assignment was 25%, and it was 28%, 24%, 28%, and 20% for Minnesota, North Dakota, South Dakota and Wisconsin, respectively. Compared with classification by random assignment, our 2 best models had low-to-moderate predictive ability (approx. 2 times better than random assignment) for classifying natal origins of mallards produced in 4 states within the upper Midwest.

Table 2. Classification accuracies by discriminant function analysis, after cross-validation, by using different combinations of $\delta^{13}C$, δD, and $\delta^{15}N$ as discriminating variables, for flightless mallard duckling feather samples collected in Minnesota, North Dakota, South Dakota, and Wisconsin, USA, 7 July to 9 September 2002.

Model	Overall model accuracy (%)	Group accuracy (%)[a]			
		MN	ND	SD	WI
$\delta^{13}C$, δD, $\delta^{15}N$	47	31	63	66	25
% of total classified as[b,c]		28	25	27	20
$\delta^{13}C$, δD	46	59	46	66	0
% of total classified as		37	31	31	0
$\delta^{13}C$, $\delta^{15}N$	37	28	58	41	20
% of total classified as		35	25	26	13
δD, $\delta^{15}N$	40	24	33	72	25
% of total classified as		33	19	30	18
$\delta^{13}C$	35	48	63	24	0
% of total classified as		40	36	24	0
δD	45	69	17	76	0
% of total classified as		57	10	33	0
$\delta^{15}N$	30	21	0	62	30
% of total classified as		38	0	45	17

[a] For example, 31% of samples from MN were classified as having MN origins.
[b] For example, 28% of all samples were classified as having MN origins.
[c] Prior proportional membership was 28%, 24%, 28%, and 20% for MN, ND, SD, and WI, respectively.

Comparison of Isotopes Between Subregions

Separate nested ANOVAs indicated that isotope values differed among subregions ($\delta^{13}C$: $F_{1,98} = 5.39$, $P = 0.022$; $\delta^{15}N$: $F_{1,98} = 12.77$, $P < 0.001$; δD: $F_{1,98} = 7.58$, $P = 0.007$). Ducklings from Prairie states were 1.08 times more depleted in ^{13}C than were those from the Great Lakes states (Table 3). Ducklings from the Great Lakes were less enriched (0.82×) in ^{15}N (Table 3), whereas those from the prairies were less depleted (0.92×) in deuterium (Table 3).

Using $\delta^{13}C$, δD, and $\delta^{15}N$ as discriminating variables, DFA achieved 70% overall classification accuracy (Table 4). However, using $\delta^{13}C$ and $\delta^{15}N$ as discriminating variables, DFA achieved 72% overall classification accuracy with equal distribution of false positives between groups (Table 4). All other models achieved <65% overall classification accuracy. Expected overall classification accuracy by random assignment was 50%, with 52% and 48% for Prairie and Great Lakes states, respectively. Compared with classification by random assignment, our 2 best models had moderate ability to predict natal origins of mallards produced in these subregions of the upper Midwest.

DISCUSSION

We detected an inverse relationship between latitude and δD at a relatively fine spatial scale in the upper Midwest, as was expected based on the similar larger scale trend in North America (Chamberlain et al. 1997; Hobson and Wassenaar 1997; Meehan et al. 2001, 2004). However, our δD values from South Dakota were substantially less depleted than

Table 3. Mean $\delta^{13}C$, δD, and $\delta^{15}N$ values (parts per thousand [‰]) and range from feathers of flightless mallard ducklings collected in 2 subregions (Prairie [ND, SD] states, $n = 53$; Great Lakes [MN, WI] states, $n = 49$) of the upper Midwest (USA), 7 July to 9 September 2002.

	$\delta^{13}C$ (‰)			δD (‰)			$\delta^{15}N$ (‰)		
Subregion[a]	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Prairie	–24.19	0.50	–31.50–13.95	–85.37	1.80	–123.32–38.04	10.40	0.36	6.14–15.14
Great Lakes	–22.50	0.53	–29.75–10.97	–92.57	1.90	—116.3–65.64	8.54	0.38	3.4–18.76

[a] Prairie and Great Lakes states differ for all 3 isotopes; all $P < 0.05$.

those from other states and explained much of the latitudinal relationship. Deuterium values that were considerably less depleted in South Dakota may have been caused by onset of drought in the region that resulted in wetlands with water levels that were receding at much faster rates than those in the other 3 states (M. L. Szymanski, North Dakota Game and Fish Department, personal observation). Variability in wetland conditions could greatly influence δD values that represent breeding origins of waterfowl, especially those with protracted nesting periods such as mallards and in environments with dynamic wetland conditions such as the Prairie Pothole Region.

Within-season effects may occur with onset of drought, causing late-hatched broods to use more permanent wetlands that possibly are more enriched in deuterium than are those used by earlier hatched ducklings. Thus, δD values from an area may differ during periods of low and high water conditions due to differences in wetland types available to breeding waterfowl (Talent et al. 1982, Rotella and Ratti 1992, Krapu et al. 2004). A goal of our sampling strategy was to maximize sampling effort for latitude and longitude in the upper Midwest. Repeated measures at locations were not feasible, and thus, sample date is confounded with location, precluding us from addressing this hypothesis posthoc. However, the overall larger scale continental trend for δD values generally should still hold true (Coplen and Kendall 2000, Kendall and Coplen 2001).

At a continental scale, we would expect a general increase in $\delta^{13}C$ values in foodwebs as biomes become more composed of C_4 plants with decreasing latitude (Sage et al. 1999). However, our documented inverse relationship between $\delta^{13}C$ and latitude was unexpected because our study lies primarily within the C_3 biome, and we speculate that this may have resulted from regional differences in chemical compositions of wetlands where ducklings were sampled (Osmond et al. 1981, Fry and Sherr 1988). Previous studies of amphipods (*Gammarus* sp. and *Hyalella* sp.) in Saskatchewan wetlands have shown similar isotopic variability in $\delta^{13}C$ related to land-use practices (K. A. Hobson, Environment Canada, unpublished data), and other researchers report strong regional influences in agricultural or grassland wetlands (Alexander et al. 1996; Fry and Sherr 1988, and references therein).

We detected weak positive and negative relationships between $\delta^{13}C$ and $\delta^{15}N$ values, respectively, and easterly shifts in longitude. We expected a much stronger relationship between $\delta^{15}N$ values and longitude given a transition of habitat types and varying amounts of land use from east to west in our study area (Fig. 1). We suspect that localized anthropogenic inputs of ^{15}N masked regional effects of this isotope (Nadelhofer and Fry 1994, Alexander et al. 1996, Harrington et al. 1998, Hobson 1999*a*, Hebert and Wassenaar 2001). For example, most wetlands in forested areas of Minnesota and Wisconsin had varying levels of anthropogenic influences ranging from adjacent farms or low numbers of cabins, to nearly complete shoreline and agricultural development (Radomski and Goeman 2001). Wetlands in the boreal forest region of Saskatchewan have foodwebs typically depleted in ^{15}N compared with those farther south and in open habitats, where anthropogenic inputs generally are more prevalent (P. Bennett and K. A. Hobson, Environment Canada, unpublished report; Nadelhofer and Fry 1994, Urton and Hobson 2005).

Isotope-based model selection may vary by area of interest (e.g., SD or MN). For example, South Dakota feather samples were classified most accurately (66% with 47% overall model accuracy) using $\delta^{13}C$, $\delta^{15}N$, and δD in our 4-state model, whereas samples from Minnesota were most accurately classified using only δD (68% with 45% overall model accuracy). These same feather samples could be classified as Prairie (ND and SD) versus Great Lakes states (MN and WI), with 72% of samples being correctly classified using $\delta^{13}C$ and $\delta^{15}N$ in our subregion model.

Table 4. Classification accuracies by discriminant function analysis, after cross-validation, by using different combinations of $\delta^{13}C$, δD, and $\delta^{15}N$ as discriminating variables, for flightless mallard duckling feather samples collected in 2 subregions (Prairie [ND, SD] and Great Lakes [MN, WI] states) of the upper Midwest (USA), 7 July to 9 September 2002.

Model	Overall model accuracy (%)	Group accuracy (%) Prairie	Great Lakes
$\delta^{13}C$, δD, $\delta^{15}N$	70	74	65
% of total classified as[a]		52	48
$\delta^{13}C$, δD	64	70	57
% of total classified as		57	43
$\delta^{13}C$, $\delta^{15}N$	72	72	72
% of total classified as		51	49
δD, $\delta^{15}N$	64	66	61
% of total classified as		53	47
$\delta^{13}C$	58	66	49
% of total classified as		59	41
δD	63	68	57
% of total classified as		56	44
$\delta^{15}N$	64	66	61
% of total classified as		53	47

[a] Prior proportional membership was 52% and 48% for Prairie and Great Lakes states, respectively.

However, it is important to determine costs versus benefits of using a model with lower overall accuracy only because it best classifies samples originating from a single area. Although the state-specific model that used only δD had only slightly lower overall classification accuracy (45%) than the 2 most accurate models (46% and 47%), and moderate-to-high classification accuracy for Minnesota, classifications were distributed such that there were many false positives for Minnesota and South Dakota.

MANAGEMENT IMPLICATIONS

We conclude that stable isotope methodology has limited abilities to determine natal origins of migratory birds along a longitudinal corridor at fine scales in anthropogenically influenced landscapes but that accuracy improves across ecoregions. Based on stark contrasts between deuterium values in ecologically and geographically similar areas (i.e., ND and SD), we suggest that researchers account for annual variation in deuterium found in surface waters when investigating natal origins of migratory birds that use food derived primarily from these waters.

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