

STABLE-CARBON AND NITROGEN ISOTOPE RATIOS OF SONGBIRD FEATHERS GROWN IN TWO TERRESTRIAL BIOMES: IMPLICATIONS FOR EVALUATING TROPHIC RELATIONSHIPS AND BREEDING ORIGINS¹

KEITH A. HOBSON

Prairie and Northern Wildlife Research Center, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, SK, Canada, S7N 0X4, and Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada S7N 5E2, e-mail: keith.hobson@ec.gc.ca

Abstract. The measurement of stable-carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotope ratios in bird feathers has potential to reveal important information on trophic position and source of feeding during feather formation. This study investigated how stable-nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope ratios in feathers of insectivorous songbirds and in their supporting foodwebs differed between boreal forest sites (50 feathers representing 5 species) and upland sites associated with southern prairie agro-wetland complexes in Saskatchewan and Manitoba, Canada (108 feathers representing 12 species). No difference in feather $\delta^{13}\text{C}$ values between these biomes was found, but feathers from boreal forest songbirds were depleted in ^{15}N compared to feathers from birds in southern agricultural areas. This suggests that general trophic models cannot be constructed based on $\delta^{15}\text{N}$ values of feathers of birds from these different biomes alone unless they are related first to local foodweb isotopic signatures. However, foodweb $\delta^{15}\text{N}$ analysis in each biome indicated that the stable isotope approach could be applied successfully to delineate trophic relationships involving birds. In addition, this technique will be a useful tool for investigating the degree of frugivory or nectarivory in birds.

Key words: boreal forest, carbon-13, feathers, frugivory, migration, nectarivory, nitrogen-15, stable isotopes.

INTRODUCTION

In recent decades, the application of stable isotope analyses to studies of avian nutritional ecology and movement has increased tremendously, a trend that will undoubtedly continue with the advent of technology more readily available to avian ecologists (Kelly and Finch 1998, Hobson 1999). One of the important advances in this field has been the development of nondestructive sampling approaches that involve the isotopic analysis of bird feathers (Mizutani et al. 1990, Hobson and Clark 1992). For those cases involving birds in equilibrium with their local food web that do not rely on the mobilization of endogenous nutrient reserves obtained elsewhere (Hobson et al. 1997), stable isotope ratios in bird feathers will reflect those in their diet during the period of feather growth. Using isotopic measurements of feathers, previous studies have successfully estimated the relative importance of foods derived from freshwater and marine sources (Mizutani et al. 1990, Bearhop et al., in

press), determined trophic level (Thompson and Furness 1995, Thompson et al. 1995), and examined the relationship between trophic level and contaminant loads (Kidd 1998, Thompson et al. 1998). Recently, Hobson and Wassenaar (1997) and Chamberlain et al. (1997) demonstrated how the isotopic analysis of songbird feathers can also provide information on where feathers were grown because foodwebs may differ regionally in isotopic composition (Hobson 1999).

A fundamental assumption in the application of the stable-isotope approach is that one can reliably infer trophic level or source of feeding based on an understanding of local and regional stable isotope signatures in foodwebs. However, to date, very little attention has been paid to those factors contributing to variance in foodweb isotope ratios, particularly in terrestrial systems. There is evidence that stable-carbon and nitrogen isotope ratios in terrestrial and aquatic foodwebs can vary dramatically over both small and large spatial scales (Leavitt and Long 1988, Nadelhoffer and Fry 1994, Alexander et al. 1996). This creates both opportunity for and sets limitations on the application of stable-isotope

¹ Received 29 December 1998. Accepted 17 May 1999.

analyses of feathers or other tissues to investigate nutritional origins and trophic levels of birds that may move between isotopic regions. This study reports the results of an investigation of how $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in foodweb components and feathers of birds grown on those foodwebs varies between boreal forest and woodlands associated with agricultural wetland complexes in the central prairie region of Canada. The objective of the study was to investigate the within-site and between-site variability in stable isotope signatures in feathers in order to evaluate the utility of the technique for determining local trophic relationships and the occurrence of isotopic tracers in feathers that might provide information on geographical origins of molt in migrating or wintering birds.

METHODS

STUDY SITES

Two sites were chosen to sample birds breeding in woodlands associated with southern prairie agricultural wetland complexes. The first site, used during 1992–1995, was located in the forested dune-ridge separating Delta Marsh from Lake Manitoba, Manitoba, Canada ($50^{\circ}11'\text{N}$, $98^{\circ}19'\text{W}$, see Mackenzie 1982 for a description of study site and Mackenzie et al. 1982 for a description of the breeding bird community). The second site, used in 1992–1993, was located on the St. Denise National Wildlife Management Area ($52^{\circ}20'\text{N}$, $106^{\circ}10'\text{W}$), 30 km east of Saskatoon, Saskatchewan. Both sites host breeding forest birds in patches or linear strips of forest in close proximity to open uplands, wetlands, and agricultural land. Emergent aquatic insects were presumed to be an important component of the diets of birds at both locations, especially at Delta Marsh where chironomids typically produce superabundant food resources for passerines (Briskie and Sealy 1989). For the sampling of boreal forest birds, during 1993–1996, we used both aspen and conifer dominated mixed-wood sites in Prince Albert National Park ($53^{\circ}50'\text{N}$, $105^{\circ}50'\text{W}$) in Saskatchewan and sampled also those known boreal forest breeding birds migrating through the Delta Marsh Bird Observatory (DMBO) during the fall of 1992–1994.

Following capture using mistnets, a single outer tail feather was removed from each bird and stored in individual envelopes. Evidence of

breeding or local site use was noted using leg bands and the presence of a brood patch for females and cloacal protruberance for males. Individuals were aged to hatch-year (HY) or after hatch-year (AHY) primarily using degree of skull ossification but occasionally other criteria as outlined in Pyle et al. (1987). Plant material was obtained from live plants at collection sites and insects were collected using sweep nets.

STABLE ISOTOPE ANALYSES

Feathers were cleaned by rinsing several times in a 2:1 chloroform:methanol solution and allowed to air dry. Plant and invertebrate materials were washed in distilled water, dried in a drying oven for 48 hr at 60°C , and ground to powder using an analytical mill. All samples were loaded into tin cups and combusted in a Robo Prep elemental analyzer interfaced with a Europa 20:20 isotope ratio mass spectrometer. Stable isotope ratios were expressed in δ -notation as parts per thousand (‰) deviation from international standards (see Hobson and Schell 1998 for a more complete description of stable isotope methods). Measurement precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was estimated to be $\pm 0.1\text{‰}$ and $\pm 0.3\text{‰}$, respectively.

RESULTS

Stable-carbon and nitrogen isotope values in feathers of birds representing both southern agro-wetland complexes and boreal forest ranged considerably among individuals (Table 1, Fig. 1). Excluding raptors, adult waxwings, and hummingbirds and adult Least Flycatchers that grew their flight feathers on the wintering grounds, there was considerable isotopic segregation between feathers of individual insectivorous birds occupying boreal forest habitat compared with those from southern agricultural habitats (Wilk's lambda $F_{2,155} = 225.4$, $P < 0.001$). However this was driven entirely by $\delta^{15}\text{N}$ values (agricultural $\delta^{15}\text{N}$: $10.1 \pm 1.4\text{‰}$, $n = 108$, boreal $\delta^{15}\text{N}$: $5.2 \pm 1.2\text{‰}$, $n = 50$; Wilk's lambda $F_{1,156} = 452.2$, $P < 0.001$) that were generally more enriched in agricultural complexes compared with boreal sites, and there was complete overlap in $\delta^{13}\text{C}$ values among samples (agricultural $\delta^{13}\text{C}$: $-22.8 \pm 0.9\text{‰}$, boreal $\delta^{13}\text{C}$: $-22.8 \pm 0.6\text{‰}$; Wilk's lambda $F_{1,156} = 0.1$, $P = 0.79$).

The distinct segregation in $\delta^{15}\text{N}$ values between biomes indicated that trophic relationships using the isotopic technique could only be mod-

TABLE 1. Mean (\pm SD) stable-carbon and nitrogen isotope ratios of bird feathers sampled at southern prairie agro-wetland complexes (Delta Marsh, St. Denise WMA) and boreal forest (Prince Albert National Park and migrants passing through Delta Marsh Bird Observatory 1992–1996).

Species		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Agro-wetland Complexes				
American Robin (<i>Turdus migratorius</i>)	AHY	-22.8 ± 0.9	10.9 ± 1.7	5
Barn Swallow (<i>Hirundo rustica</i>)	AHY	-20.5 ± 1.0	9.9 ± 1.5	5
	HY	-22.6 ± 1.1	10.7 ± 1.6	6
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	AHY	-23.2 ± 0.9	4.8 ± 0.8	10
	HY	-22.9 ± 1.3	9.0 ± 1.1	9
Clay-colored Sparrow (<i>Spizella pallida</i>)	AHY	-21.9 ± 0.6	8.0 ± 0.3	3
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	HY	-24.0 ± 0.9	8.9 ± 1.1	3
Gray Catbird (<i>Dumetella carolinensis</i>)	AHY	-23.6 ± 0.5	9.3 ± 1.8	14
House Wren (<i>Troglodytes aedon</i>)	AHY	-22.1 ± 0.7	11.6 ± 2.0	11
Least Flycatcher (<i>Empidonax minimus</i>)	AHY	-22.6 ± 1.0	8.5 ± 1.4	11
	HY	-22.7 ± 0.3	11.5 ± 0.3	7
Northern Oriole (<i>Icterus galbula</i>)	AHY	-23.2 ± 0.3	11.5 ± 0.4	4
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	AHY	-22.6 ± 2.3	9.8 ± 1.3	6
Tree Swallow (<i>Tachycineta bicolor</i>)	HY	-23.9 ± 0.3	10.7 ± 1.9	7
Warbling Vireo (<i>Vireo gilvus</i>)	AHY	-23.4 ± 0.6	10.5 ± 0.8	3
	HY	-23.4 ± 1.0	11.6 ± 1.0	4
Yellow Warbler (<i>Dendroica petechia</i>)	AHY	-23.0 ± 0.5	9.6 ± 0.8	16
	HY	-21.8 ± 0.9	11.0 ± 0.9	9
Boreal Forest				
Cape May Warbler (<i>Dendroica tigrina</i>)	AHY	-22.0 ± 0.6	3.4 ± 1.5	5
Hermit Thrush (<i>Catharus guttatus</i>)	AHY	-22.6 ± 0.5	5.2 ± 1.4	5
Ovenbird (<i>Seiurus aurocapillus</i>)	AHY	-22.5 ± 0.6	5.6 ± 1.0	16
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	AHY	-24.6 ± 0.7	5.3 ± 1.6	7
	HY	-24.6 ± 0.9	7.6 ± 1.6	4
Tennessee Warbler (<i>Vermivora peregrina</i>)	HY	-23.1 ± 0.9	3.6 ± 1.1	8
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	AHY	-22.8 ± 0.5	5.8 ± 0.7	12
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	HY	-25.6 ± 1.1	7.1 ± 0.6	7
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	AHY	-23.8 ± 0.8	11.5 ± 1.1	4

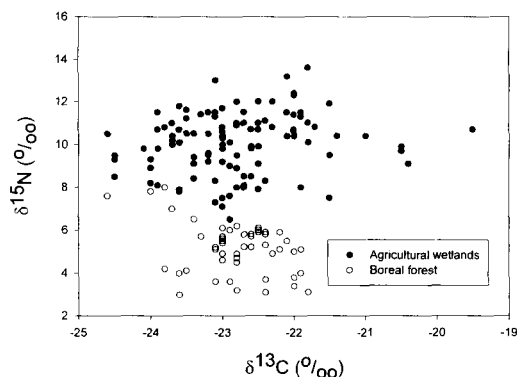


FIGURE 1. Distribution of stable-carbon and nitrogen isotope values for feathers of songbirds from two landscape types. Data correspond to the sample described in Table 1. Each point represents an individual bird.

eled within biomes. Although a complete isotope analysis of foodweb components at each site was beyond the scope of this paper, approximate trophic models were constructed based on $\delta^{15}\text{N}$ values obtained for birds, insects, and plant materials (Table 2, Fig. 2). These depictions showed clear step-wise enrichment in ^{15}N with trophic level. In boreal forest, four distinct trophic levels, from tree foliage to Sharp-shinned Hawks were found (Fig. 2a; scientific names given in Table 1). In agro-wetland systems, two parallel trophic pathways were evident, one based on frugivory or nectarivory and the other on insectivory (Fig. 2b).

Differences in $\delta^{15}\text{N}$ values between HY and AHY age classes were found for Cedar Waxwings ($F_{1,17} = 8.1, P < 0.001$) and Rufous Hummingbirds ($F_{1,9} = 9.6, P < 0.001$), a result consistent with greater incidence of lower trophic level feeding (i.e., lower $\delta^{15}\text{N}$ values, Fig. 2b) among adults compared with HY birds.

TABLE 2. Mean (\pm SD) stable-carbon and nitrogen isotope ratios of foodweb components sampled at southern prairie agro-wetland complexes and boreal forest, 1992–1996.

Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
Agro-wetland Complexes:			
Delta Marsh			
Western mountain ash (<i>Sorbus scopulina</i>)	-23.9 ± 0.7	2.7 ± 1.0	7
Chironomidae	-25.7 ± 1.3	7.5 ± 2.0	5
Lepidoptera	-23.9 ± 1.1	7.1 ± 0.6	5
Odonata	-24.9 ± 1.3	8.6 ± 1.7	7
St. Denise NWMA			
Saskatoon berries (<i>Amelanchier alnifolia</i>)	-27.7 ± 1.1	3.1 ± 0.8	5
Diptera	-28.6 ± 2.2	8.8 ± 2.8	16
Chironomidae	-29.4 ± 4.2	9.9 ± 3.2	3
Odonata	-27.6 ± 2.1	9.1 ± 1.4	6
Boreal Forest			
Prince Albert National Park			
Trembling aspen (<i>Populus tremuloides</i>) leaves	-29.1 ± 1.4	-2.5 ± 0.7	25
White spruce (<i>Picea glauca</i>) leaves	-29.1 ± 1.6	-1.7 ± 1.2	25
Spruce budworm (<i>Choristoneura occidentalis</i>)	-25.0 ± 0.6	3.3 ± 1.2	5
Large aspen tortrix (<i>Chorsitoneura conflictana</i>)	-25.6 ± 0.2	1.0 ± 0.7	5

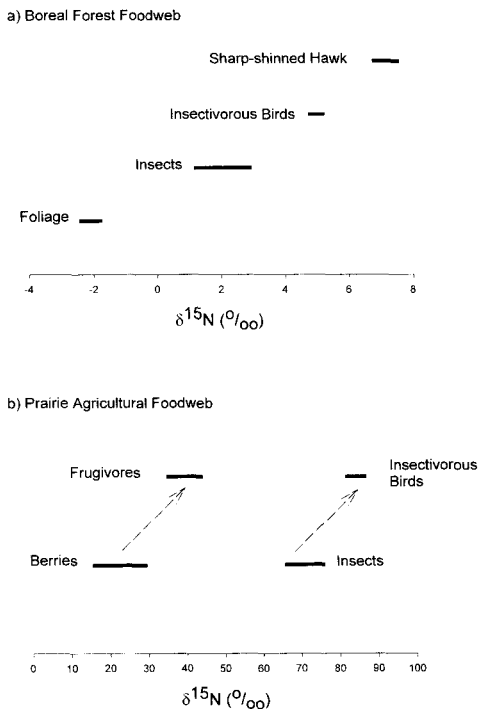


FIGURE 2. Trophic model based on 95% confidence intervals of stable-nitrogen isotope data of food web components depicting data derived from (a) boreal forest and (b) southern prairie agro-wetlands (see Tables 1 and 2). In b, frugivore endpoints were based on feather isotope values for AHY waxwings.

DISCUSSION

This study has demonstrated considerable variation in stable-nitrogen isotope signatures in feathers of birds and associated foodwebs between those individuals breeding in woodland associated with southern prairie agricultural regions and those in temperate boreal forest. Within trophic guilds, birds breeding in boreal forest were generally more depleted in $\delta^{15}\text{N}$ values compared to birds breeding farther south. This suggests that although the stable-isotope approach might be used to investigate trophic relationships among individuals feeding and growing feathers within biomes, it is not possible to include individuals from different biomes within the same model. Perhaps the most graphic example of this was revealed by the overlap in $\delta^{15}\text{N}$ measurements of raptors such as Bald Eagles and Sharp-shinned Hawks breeding in boreal areas and insectivorous songbirds breeding at Delta Marsh.

Whereas the exact origins of molt of the migratory sample of birds known to breed in the boreal forest was not known, their stable isotope values conformed to the general values we measured for breeding birds captured at our boreal forest site in Prince Albert National Park. This suggests that the isotopic pattern we observed between biomes may be relatively robust. The

occurrence of lower $\delta^{15}\text{N}$ values between assumed or confirmed northern forest birds and those known to molt in the more southern agro-wetland complexes is in agreement with our general understanding of demographic patterns of $\delta^{15}\text{N}$ values in foodwebs.

Factors determining isotopic variation in plants at the base of foodwebs will ultimately influence isotopic variation in feathers. For nitrogen, the degree of symbiotic N_2 fixation, together with natural variation in isotopic labels of soil pools, also will influence isotopic variability among plants in foodwebs supporting birds (Lajtha and Marshall 1994). Soil nitrogen is typically more enriched in ^{15}N than atmospheric N_2 (Shearer et al. 1978) and, in general, plants that obtain nitrogen from the atmosphere should be more depleted in ^{15}N than those plants that rely on soil nitrogen. Soil ^{15}N content in turn can be highly variable within and among sites (Sutherland et al. 1993), but two processes in particular may result in agricultural soils being more enriched in ^{15}N than temperate forest soils. First, isotopic fractionations during ammonia volatilization are likely unimportant in most forests, because forest soils, unlike many agricultural soils, are generally acidic enough to prevent ammonia loss (Nadelhoffer and Fry 1994). Second, highly disturbed ecosystems, such as cultivated fields, typically have high levels of biological activity that ultimately results in more ^{15}N enrichment in soils relative to unploughed forests and pastures (Mariotti et al. 1981). In their study of stable isotope signatures in tissues of shorebirds using wetlands in a prairie agroecosystem, Alexander et al. (1996) found considerable variation in $\delta^{15}\text{N}$ values of foodwebs at relatively small spatial scales. Those authors correctly questioned the applicability of the stable isotope technique in evaluating trophic relationships among birds in these agro-wetland complexes and pointed to local nitrogen fertilizer inputs as a major factor in driving local variation in stable isotope ratios within local foodwebs.

In the case of carbon, terrestrial plants fix atmospheric carbon dioxide using C-3, C-4, or Crassulacean Acid Metabolism (CAM) photosynthetic pathways (Peterson and Fry 1987, Tieszen and Boutton 1988) with the C-3 pathway typically resulting in plants with more depleted $\delta^{13}\text{C}$ values. Recent research has demonstrated further that in addition to photosynthetic pathway, isotopic variation in C-3 plants is as-

sociated with ecophysiological differences among plants, such as water-use efficiency (Lajtha and Marshall 1994). Thus, even within terrestrial C-3 plant species, environmental conditions can mediate physiological responses to ambient temperature that result in significant changes in $\delta^{13}\text{C}$ values. In general, plants subjected to hotter or more xeric conditions are more enriched in ^{13}C than those in cooler or wetter conditions (Marra et al. 1998). In closed-canopy forests, foliar $\delta^{13}\text{C}$ may increase with canopy height (Medina et al. 1986, 1991, Sternberg et al. 1989), but this is expected to be more important in tropical vs. temperate forested ecosystems. Interestingly, despite the potential for variance in $\delta^{13}\text{C}$ values among feathers grown at boreal forest and prairie woodland sites, we found no differences for this isotope.

This study was not designed to rigorously evaluate the use of the stable isotope approach to measure the incidence of frugivory in birds. However, that adult and HY waxwings and hummingbirds demonstrated isotopic patterns consistent with adult frugivory or nectarivory, and greater insectivory in HY birds of these species during periods of feather formation, alludes to the potential use of $\delta^{15}\text{N}$ measurements to investigate the importance of plant vs. insect foods to birds in general. Cedar Waxwings are largely frugivorous throughout the year but will consume insects during the breeding season (Witmer et al. 1997). Whereas sugary fruits are fed to older nestlings, insects provide important nutrition to younger birds. Our data for waxwings associated with small prairie wetlands suggests that insects may have formed the majority of the nestling diet. However, we do not know where adults grew their feathers. Ruby-throated Hummingbirds consume both flower nectar and small insects throughout the year, but nestling diet is poorly known because parents feed young by regurgitation (Robinson et al. 1996).

The distribution of stable-isotope ratios within and across local landscapes remains poorly understood. In general, stable-carbon and nitrogen isotope ratios tend to be more enriched in hot and xeric environments compared to cooler and moister environments, but there are likely several exceptions to this pattern. This study has demonstrated that it is not appropriate to directly associate stable isotope ratios with trophic level of birds or other organisms across broad geographic areas unless local isotopic data can be

used to first establish true trophic positions. This approach was used recently by Hebert et al. (in press) who inferred trophic level of Herring Gulls (*Larus argentatus*) breeding on several of the Great Lakes in Canada despite the fact that foodwebs in these lakes differed in their baseline $\delta^{15}\text{N}$ values.

Currently, stable-hydrogen isotope analyses (δD) of bird feathers hold the greatest potential for inferring origins of molt of birds in North America because there are well-established continental patterns of δD in precipitation that are ultimately transferred to feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). However, it is probable that the combined use of several stable isotopes will allow more precise tracing of origins of feather growth (Chamberlain et al. 1997). For example, enriched δD , $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values in feathers would provide convincing evidence that feathers were grown in more southern, hotter biomes than feathers showing depletion in all three stable isotopes. Investigations of demographic patterns in these and other stable isotopes are encouraged in order to increase the utility of isotopic measurements of feathers and other avian tissues.

ACKNOWLEDGMENTS

Several individuals assisted with sample collections including E. Bayne, R. G. Clark, E. Cummings, P. Farrington, H. den Haan, and S. van Wilgenburg. Isotope analyses were conducted by G. Parry at the Department of Soil Science, University of Saskatchewan. Additional laboratory facilities were provided by the Prairie and Northern Wildlife Research Center, Saskatoon. Funding was provided by The Canadian Wildlife Service, Prairie and Northern Region. I thank R. W. Furness and J. Kelly for helpful comments on an earlier draft of the manuscript.

LITERATURE CITED

- ALEXANDER, S. A., K. A. HOBSON, C. L. GRATTO-TREVOR, AND A. W. DIAMOND. 1996. Conventional and isotopic determinations of shorebird diets at an inland stopover: the importance of invertebrates and *Potamogeton pectinatus* tubers. *Can. J. Zool.* 74: 1057–1068.
- BEARHOP, S., D. R. THOMPSON, S. WALDRON, I. C. RUSSELL, G. ALEXANDER, AND R. W. FURNESS. In press. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* from inland fisheries in England. *J. Appl. Ecol.*
- BRISKIE, J. V., AND S. G. SEALY. 1989. Determination of clutch size in the Least Flycatcher. *Auk* 106: 269–278.
- CHAMBERLAIN, C. P., J. D. BLUM, R. T. HOLMES, X. FENG, T. W. SHERRY, AND G. R. GRAVES. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.
- HEBERT, C. E., J. L. SHUTT, K. A. HOBSON, AND D. V. CHIP WESELOH. In press. Spatial and temporal differences in the diet of Great Lakes Herring Gulls (*Larus argentatus*): evidence from stable isotope analysis. *Can. J. Fish. Aquat. Sci.*
- HOBSON, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, in press.
- HOBSON, K. A., AND R. W. CLARK. 1992. Assessing avian diets using stable isotopes. II: factors influencing diet-tissue fractionation. *Condor* 94:189–197.
- HOBSON, K. A., K. D. HUGHES, AND P. J. EWINS. 1997. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. *Auk* 114:467–478.
- HOBSON, K. A., AND D. M. SCHELL. 1998. Stable-carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*). *Can. J. Fish. Aquat. Sci.* 55:1–7.
- HOBSON, K. A., AND L. I. WASSENAAR. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142–148.
- KELLY, J. F., AND D. M. FINCH. 1998. Tracking migrant songbirds with stable isotopes. *Trends Ecol. Evol.* 13:48–49.
- KIDD, K. A. 1998. Use of stable isotope ratios in freshwater and marine biomagnification studies, p. 357–376. *In* J. Rose [ed.], *Environmental toxicology: current developments*. Gordon and Breach Science, Amsterdam.
- LAJTHA, K., AND J. D. MARSHALL. 1994. Sources of variation in the stable isotopic composition of plants, p. 1–21. *In* K. Lajtha and R. H. Michener [EDS.], *Stable isotopes in ecology and environmental science*. Blackwell Scientific, London.
- LEAVITT, S. W., AND A. LONG. 1988. Intertree variability of $\delta^{13}\text{C}$ in tree rings, p. 95–104. *In* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy [EDS.], *Stable isotopes in ecological research*. Springer-Verlag, New York.
- MACKENZIE, D. I. 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstorey vegetation and soil patterns. *Can. Field-Nat.* 96:61–68.
- MACKENZIE, D. I., S. G. SEALY, AND G. D. SUTHERLAND. 1982. Nest site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. *Can. J. Zool.* 60:2212–2223.
- MARA, P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable carbon isotopes. *Science* 282: 1884–1886.
- MARRIOTTI, A., J. C. GERMON, AND P. HUBERT. 1981. Experimental determination of nitrogen kinetic isotope fractionations: some principles; illustration for the denitrification and nitrification processes. *Plant and Soil* 62:413–430.
- MEDINA, E., G. MONTES, E. CUEVAS, AND Z. ROCKSANDIC. 1986. Profiles of CO_2 concentration and

- $\delta^{13}\text{C}$ values in tropical rain forests of the Upper Rio Negro Basin, Venezuela. *J. Trop. Ecol.* 2:207–217.
- MEDINA, E., L. STERNBERG, AND E. CUEVAS. 1991. Vertical stratification of $\delta^{13}\text{C}$ in closed natural and plantation forests in the luquillo mountains, Puerto Rico. *Oecologia* 87:369–372.
- MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. *Auk* 107:400–03.
- NADELHOFFER, K. J., AND B. FRY. 1994. Nitrogen isotope studies in forest ecosystems, p. 22–44. In K. Lajtha and R. H. Michener [EDS.], *Stable isotopes in ecology and environmental science*. Blackwell Scientific, London.
- PETERSON, B. J., AND B. FRY. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18: 293–320.
- PLYE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.
- ROBINSON, T. R., R. R. SARGENT, AND M. B. SARGENT. 1996. Ruby-throated Hummingbird (*Archilochus colubris*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 204. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.
- SHEARER, G. B., D. H. KOHL, AND S. H. CHIEN. 1978. The nitrogen-15 abundance in a wide variety of soils. *Soil Sci. Soc. Am. J.* 42:899–902.
- STERNBERG, L. S. L., S. S. MULKEY, AND S. J. WRIGHT. 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. *Ecology* 70:1317–1324.
- SUTHERLAND, R. A., C. VAN KESSEL, R. E. FARRELL, AND D. J. PENNOCK. 1993. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. *Soil Sci. Soc. Am. J.* 57:169–178.
- THOMPSON, D. R., S. BEARHOP, J. R. SPEAKMAN, AND R. W. FURNESS. 1998. Feathers as a means of monitoring mercury in seabirds: insights from stable isotope analysis. *Environ. Poll.* 101:193–200.
- THOMPSON, D. R., AND R. W. FURNESS. 1995. Stable isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in Northern Fulmars. *Auk* 112:493–498.
- THOMPSON, D. R., R. W. FURNESS, AND S. A. LEWIS. 1995. Diets and long-term changes in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in Northern Fulmars (*Fulmaris glacialis*) from two northeast Atlantic colonies. *Mar. Ecol. Progr. Ser.* 125:3–11.
- TIESZEN, L. L., AND T. W. BOUTTON. 1988. Stable isotopes in terrestrial ecosystem research., p. 167–195. In P. W. Rundel, J. R. Ehleringer, and K. A. Nagy [EDS.], *Stable isotopes in ecological research*. Springer-Verlag, New York.
- WITMER, M. C., D. J. MOUNTJOY, AND L. ELLIOT. 1997. Cedar Waxwing (*Bomycilla cedrorum*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 309. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.