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TRACING NUTRIENT ALLOCATION TO REPRODUCTION WITH STABLE ISOTOPES: A PRELIMINARY INVESTIGATION USING COLONIAL WATERBIRDS OF GREAT SLAVE LAKE

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ABSTRACT.—We investigated the use of stable-isotope analysis as a direct means of tracing allocation of endogenous protein and lipid reserves to reproduction in five gulls (*Larus canus, L. delawarensis, L. californicus, L. argentatus, L. philadelphia*), four terns (*Sterna caspia, S. hirundo, S. paradisaea, Chlidonias niger*), and one jaeger (*Stercorarius parasiticus*) breeding on Great Slave Lake (GSL) in the Northwest Territories. Our approach was based on assumptions that (1) body tissues of birds just arriving at GSL from their assumed marine-associated wintering habitats would have stable-isotope ratios more enriched than those of birds in equilibrium with the local GSL foodweb, and (2) mobilization of these reserves to reproduction could be traced by the isotopic measurement of egg macronutrients. As predicted, the pectoral muscle of six species of arriving birds was more enriched in ^{13}C ($\bar{x} = -21.5‰$) and ^{15}N ($\bar{x} = 12.7‰$) than was that of postbreeding birds (^{13}C, $\bar{x} = -23.5‰$; ^{15}N, $\bar{x} = 9.9‰$) or hatching-year birds raised at GSL (^{13}C, $\bar{x} = -24.3‰$; ^{15}N, $\bar{x} = 9.0‰$). Abdominal fat of arriving Herring Gulls and Mew Gulls was more enriched in ^{13}C ($\bar{x} = -19.7‰$) than the fat of other species ($\bar{x} = -23.4‰$), indicating lipids of marine origin. We compared isotope values of the local GSL foodweb with dietary values predicted from isotope measurements of egg macronutrients if diets were entirely derived at GSL. Isotopic analysis of lipid-free egg yolk, yolk lipid, and shell carbonate suggested that for most species, little if any endogenous protein reserves were used for reproduction, with the possible exception of Caspian Terns, whose egg protein and egg lipid values, and Common Terns, whose egg protein values, were more enriched in ^{13}C than those of the other species. Although endogenous nutrient reserves likely were important to birds during migration and the initial settling period at GSL, local food supplies were adequate to provide nutrients for reproduction. *Received 31 December 1998, accepted 3 March 2000.*

THE ALLOCATION of resources to reproduction is an important component of life-history strategies in birds (Sibley and Calow 1986, Martin 1987). In particular, evaluating the relative role of endogenous reserves acquired before or during egg formation and dietary or exogenous resources is fundamental to understanding avian reproductive ecology (Drent and Daan 1980). For example, nutritional requirements for reproduction dictate that breeding cannot take place until enough food is available or until females have accumulated sufficient body reserves. Thus, timing of breeding, clutch size, and the nutrient composition of eggs will be directly related to maternal body condition and/or local food availability (Perrins 1970, Nilsson and Svensson 1993, Williams 1994). Clutches can represent a large proportion of or may exceed female body mass, resulting in females being unable to store sufficient nutrients for reproduction (Perrins 1970). In such species, protein and fat reserves, as well as the ability of females to replenish reserves through dietary intake, will influence reproductive output (Ankney and MacInnes 1978, Fogden and Fogden 1979, Murphy 1986, Williams 1996). Larger birds should be less constrained because eggs form a relatively smaller proportion of female body mass (Lack 1968).

Despite their large body size, larids have relatively high nutritional and energetic demands during egg production (Salzer and Larkin 1990; Bolton et al. 1992, 1993). Houston et al. (1983) determined that Lesser Black-backed Gulls (*La-*

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rus fuscus) underwent declines in body protein but not fat during egg formation and that protein reserves were correlated with the total number of eggs that could be laid. In their studies of supplemental feeding in this species, Bolton et al. (1992) subsequently confirmed these findings and also determined that egg production may be further limited by specific nutrients. However, these studies were conducted on nonmigratory larids, and migratory species that are constrained by shorter breeding seasons and more seasonal food supplies may be even more dependent on body reserves for reproduction. Research on migratory waterfowl has shown the importance of protein and lipid reserves to egg formation (Alisauskas and Ankney 1992). Compared with larids, waterfowl lay large clutches, but both groups lay relatively large eggs that have high energy density (Ricklefs 1974).

Previous studies of nutrient allocation to reproduction have relied almost exclusively on indirect methods of tracing nutrient pathways. In particular, changes in body mass and composition during egg formation have been attributed to direct allocation of these resources to eggs (Houston et al. 1983, Alisauskas and Ankney 1992). Other studies have used food supplementation to evaluate the importance of female body condition or dietary nutrients that may limit clutch size, egg composition, or laying date (Hiom et al. 1991, Bolton et al. 1993, Wiebe and Bortolotti 1994). Few studies have examined the importance of specific dietary macronutrients or traced direct pathways using labeled compounds (Houston et al. 1995, Williams 1996). We studied nutrient allocation to eggs in a high-latitude assemblage of migratory gulls and terns at Great Slave Lake, Northwest Territories (hereafter GSL). Importantly, rather than relying on indirect methods of assessment, we applied the novel use of measurements of naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in body tissues, local diets, and macronutrients in eggs. This approach allowed us to trace directly the relative contributions of local exogenous (freshwater or terrestrial C-3 derived) and endogenous (marine derived) nutrients accumulated at presumed coastal wintering grounds (Hobson et al. 1997).

Marine foodwebs typically are enriched in ^{13}C, ^{15}N, and ^{34}S relative to terrestrial C-3 or freshwater foodwebs (Hobson et al. 1997). Differences in isotope signatures between foodwebs have been used to trace the relative importance of terrestrially and marine-derived nutrients in the diets of birds and other organisms (Hobson 1986, 1990; Hobson and Sealy 1991; Hobson et al. 1997), including humans (Chisholm et al. 1982, Hobson and Collier 1984). Hobson (1995) demonstrated how stable-isotope signatures in various egg components could be related to those in diets of laying females. Thus, by measuring isotope signatures in body lipid and protein reserves of migratory birds, various macronutrient components of their eggs (e.g. yolk protein, yolk lipid, albumin), and isotope signatures in local prey, we reasoned that it would be possible to determine directly whether endogenous macronutrients obtained in marine or nonlocal biomes had been deposited in eggs at GSL.

Our primary objective was to trace the origins of lipids and proteins allocated to reproduction by migratory gulls, terns, and jaegers breeding at GSL. Although we had no *a priori* hypotheses regarding body condition and isotope signatures of arriving birds, we were also interested in seeing if body condition of individuals upon arrival was in any way correlated with isotope signatures of body nutrients. This might be possible because the distance or time of travel from the wintering grounds, and the likelihood of using intermediate stopover sites, could influence the probability of arrival with nutrients obtained on the wintering grounds.

In general, we predicted that adult birds that wintered in coastal areas would arrive at GSL with isotope signatures in their tissues that were considerably enriched relative to those expected for consumers in equilibrium with a terrestrial C-3 freshwater foodweb (France 1994, 1995; Hobson et al. 1997). Thus, following arrival at GSL in spring, we expected a seasonal decline in stable carbon and stable nitrogen isotope values in pectoral muscle and abdominal fat of adults that fed from the local foodweb.

The rate of decline of the isotope signature in a bird following arrival at GSL will depend on tissue type and the dynamics of nutrient storage within the bird. Hobson and Clark (1992) determined isotope turnover rates for captive quail following an isotopic switch in their diets. Based on that study, we expect the new GSL foodweb signature to be fully integrated into

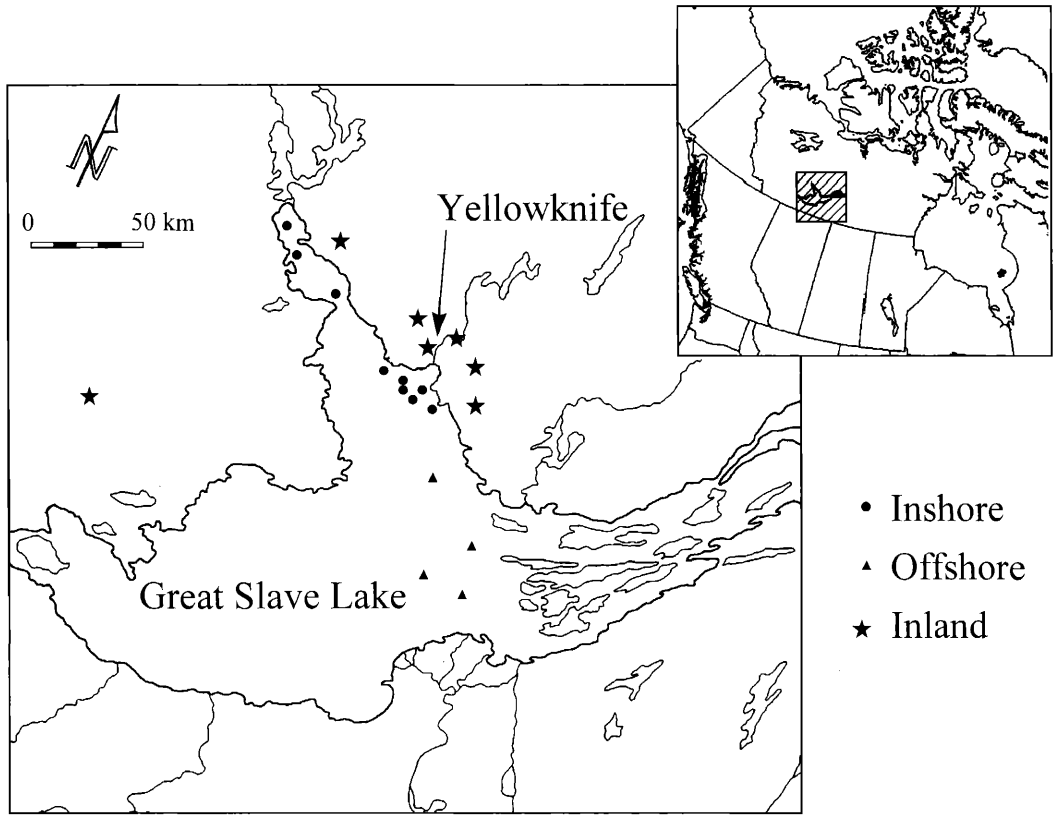

FIG. 1. Study area showing colony and collection sites. All sites on Great Slave Lake were colonial waterbird breeding colonies, those inland were additional collection sites.

muscle within about six weeks. Although it is more difficult to predict the turnover rate of abdominal fat, again we expect that birds sampled for muscle and fat late in the breeding season would reflect entirely the local foodweb signatures. The GSL system, wherein birds initiate clutches within a few weeks after arrival, provided a useful model to investigate nutrient allocation to eggs. We intended to use departures in stable-isotope signatures in egg macronutrients from those expected from models based on exclusive consumption from the local GSL foodweb to provide quantitative estimates of the proportion of nutrients allocated from parental endogenous tissues acquired before migration relative to those obtained at GSL.

METHODS

Study area.—Our study was conducted at several colonies on Great Slave Lake, Canada (62°N, 114°W), from late May through August 1995 (Fig. 1). GSL is a large (28,500 km^2) mostly oligotrophic lake with primary nutrient flow from the Slave River. The lake is surrounded by boreal forest, and a local human population of 22,000 is concentrated largely in Yellowknife. The lake is entirely ice-bound for approximately five to six months of the year, and all waterbirds breeding there are migratory (Sirois et al. 1995).

Migratory bird sample.—Five gull species (Mew Gull [*Larus canus*], Ring-billed Gull [*L. delawarensis*], California Gull [*L. californicus*], Herring Gull [*L. argentatus*], and Bonaparte's Gull [*L. philadelphia*]), four terns (Caspian Tern [*Sterna caspia*], Common Tern [*S. hirundo*], Arctic Tern [*S. paradisaea*], and Black Tern [*Chlidonias niger*]), and the Parasitic Jaeger (*Stercorarius parasiticus*) comprised our study population. Most species breeding on GSL are at the northernmost limit of their Nearctic breeding range. However, GSL represents the southern inland limit of the breeding range of most Arctic Terns and Parasitic Jaegers. All species typically arrive at GSL in mid-May and commence breeding from late May through early June.

Although precise wintering areas of the individuals sampled are unknown, we anticipated that most species wintered in coastal or marine areas. Arctic Terns and Parasitic Jaegers are the most marine or pelagic of wintering species, occurring primarily in the Southern Hemisphere (del Hoyo et al. 1996). Caspian Terns and Black Terns winter primarily in coastal areas from southern California through Central America, and Common Terns winter primarily in coastal areas from northern South America to central Brazil (Burger and Gochfeld 1991, AOU 1998). Mew Gulls and California Gulls winter primarily along the Pacific coast, but some individuals of both species winter inland in the western United States (Winkler 1996, AOU 1998). Western Ring-billed Gulls winter primarily along the Pacific coast from British Columbia south to Mexico, but some overwinter at interior locations (Ryder 1993). In eastern Canada, Herring Gulls also may winter on the Great Lakes (Hobson et al. 1997). Regardless of wintering location, our approach was to compare tissues of arriving birds with those from birds in equilibrium with the GSL foodweb and, where possible, to make inferences on nutrient allocations to reproduction based on isotope ratios in eggs. Thus, we relied primarily on the probability that birds would arrive with isotopically more enriched tissues than would result from local foodwebs, rather than on knowing the precise wintering habitat use per se.

Field methods.—We salvaged birds and eggs that had been collected as part of a large-scale study of foodwebs and contaminants. Prebreeding adults were collected as soon as possible after their arrival at Great Slave Lake, but some individuals may have been present in the area for as much as two weeks (J. Sirois pers. obs.). Adult Herring, Mew, and Bonaparte's gulls were collected along the Yellowknife Highway (9 to 12 May), whereas Caspian, Common, and Arctic terns were collected along the Yellowknife River (29 to 30 May). Postbreeding birds were collected at the north arm of Great Slave Lake (1 to 3 August).

Eggs were collected from 13 colonies between 28 May and 29 June (Fig. 1). We arbitrarily grouped sites according to inshore and offshore categories. Inshore sites were located within 5 km of the shore of the lake or on larger islands. Eggs were collected as early as possible in the breeding season, but about 20% of eggs contained partially developed embryos that were in the last half of incubation. In these cases, yolk was later subsampled from the yolk sac, and we assumed no isotopic difference between these subsamples and samples from undeveloped eggs. Birds and eggs were held individually in sterile plastic bags, labeled, stored on ice in coolers, and later frozen at −10°C within 24 h of collection for carcasses or one to five days for eggs. For purposes of comparison, we also examined archived egg tissues of marine-associated Caspian Terns breeding on the Gulf coast of Texas (Hobson et al. 1997), Ancient Murrelets (*Synthliboramphus antiquus*) breeding on Langara Island, British Columbia (Hobson et al. 1999), and Rhinoceros Auklets (*Cerorhinca monocerata*) and Cassin's Auklets (*Ptychoramphus aleuticus*) breeding on Triangle Island, British Columbia.

We recorded morphometric measures (unflattened wing chord [±0.5 mm], head length [±0.05 mm], bill height at nares [± 0.05 mm], and tarsus length [±0.05 mm]) and body mass (±0.5 g) within six months of collection. We sampled approximately 1 g each of pectoral muscle and abdominal fat, and also bone (sternum and ribs) from birds. Egg follicles (i.e. forming eggs) were removed from carcasses by dissection. Whole eggs were separated into yolk, albumen, and eggshell, and egg follicles were subsampled for yolk. Muscle and yolk samples were freeze dried and the lipids extracted using a 2:1 solution of chloroform and methanol (Bligh and Dyer 1959). Lipid-free samples were ground to a fine powder with mortar and pestle or a Wig-L-Bug dental mill. Lipids were extracted from abdominal fat and yolk samples using the solvent treatment, solvents were then evaporated, and the remaining lipid stored at −25°C prior to isotope analysis.

Stable-isotope measurements.—Mass spectrometric analyses for carbon and nitrogen isotope assays were performed on 1-mg samples of dried tissues and lipids at the stable-isotope facility of the Department of Soil Science, University of Saskatchewan, using a continuous-flow Europa 20:20 isotope-ratio mass spectrometer (CFIRMS) interfaced with a Robo Prep elemental analyzer. Based on several hundred replicate measurements of a laboratory albumen standard, we estimated measurement error to be ±0.1‰ and ±0.3‰ for stable carbon and stable nitrogen isotope ratios, respectively. We conducted stable sulfur isotope analyses on a smaller sample of egg yolk to further test for evidence of marine nutrient inputs to eggs. Stable sulfur isotope analyses were conducted on 1-mg samples by CFIRMS using a VG OPTIMA mass spectrometer interfaced with a Carlo Erba elemental analyzer at the National Hydrology Research Institute in Saskatoon. Analytical error in $\delta^{34}S$ measurements was ±0.3‰. All samples were weighed into tin cups and combusted at 1,800°C in elemental analyzers prior to isotope measurement. All isotope values are expressed in delta (δ) notation relative to the PeeDee Belemnite (PDB), atmospheric (AIR), and the Canyon Diablo Meteorite standards for carbon, nitrogen, and sulfur, respectively according to:

$$\delta X = [(R_{sample}/R_{standard}) - 1]\ 1{,}000, \qquad (1)$$

where X is ^{15}N, ^{13}C, or ^{34}S and R is the corresponding ratio $^{15}N/^{14}N$, $^{13}C/^{12}C$, or $^{34}S/^{32}S$.

Statistical analyses.—Multivariate analysis of covariance (MANCOVA) was used to analyze overall seasonal (i.e. pre- vs. postbreeding) changes in iso-

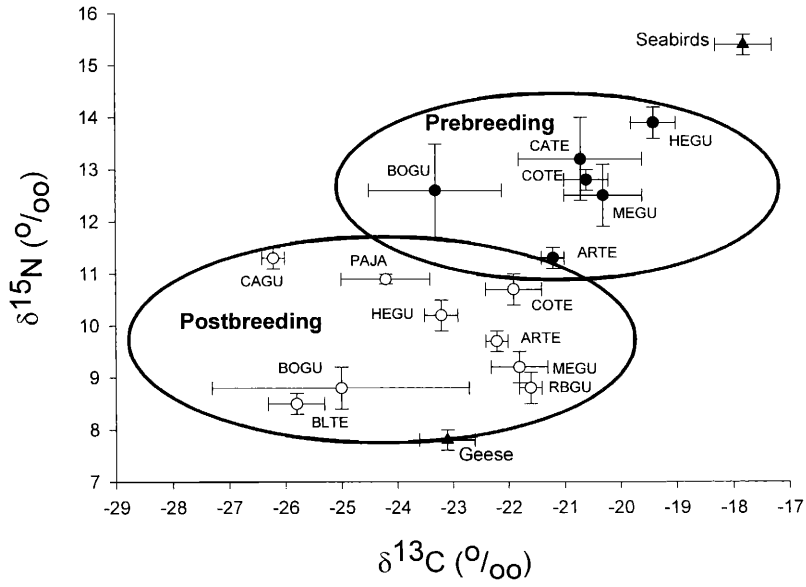

FIG. 2. Stable carbon and nitrogen isotope ratios in pectoral muscles of prebreeding and postbreeding gulls, terns, and jaegers on Great Slave Lake in 1996. For reference, collections of seabirds (K. Hobson unpubl. data) and terrestrial geese from Karak Lake, Northwest Territories (Gloutney et al. 1999), are included.

tope values for muscle with species and sex as covariates. *F*-values reported from MANCOVA were determined using Wilks' criterion. When overall MANCOVA indicated differences in stable-isotope values, we used a univariate analysis of covariance (ANCOVA) to examine these differences. Throughout, MANCOVA and ANCOVA protocol follows hierarchical procedures outlined by Alisauskas and Ankney (1994), with the final model containing only significant effects and interactions. Least-squares means were obtained from reduced models that contained significant explanatory variables.

We evaluated the relationship between body condition and $\delta^{15}N$ and $\delta^{13}C$ of muscle and $\delta^{13}C$ of abdominal fat of prebreeding adults. We obtained an index of body condition using the first principal component from a principal components analysis correlation matrix of our morphological measurements and body mass (Reyment et al. 1984). All species and sexes were combined in this analysis to index body size along a common scale. We used ANCOVA to evaluate the relationship between body condition and isotope abundance of muscle and abdominal fat of prebreeding adults. Initial tissue-specific models contained species, sex, date, and the interactions between condition and species, condition and sex, condition and date, and species and sex. Because data were not normally distributed (Wilk-Shapiro's tests, Ps < 0.05), we used Spearman rank correlation tests to evaluate the direction of any body-condition effects that were significant.

For each species and tissue type we calculated mean $\delta^{15}N$ and $\delta^{13}C$ values for prebreeding adults and eggs. Using Wilk-Shapiro tests, all means exhibited normal distributions (Ps > 0.05); consequently, we used Pearson correlations to evaluate the relationship between isotope signatures of the tissues of prebreeding adults and eggs.

RESULTS

Seasonal isotope shifts.—We tested the prediction that birds arriving at GSL have enriched $\delta^{13}C$ and $\delta^{15}N$ in body muscle compared with those feeding in isotopic equilibrium with the local GSL foodweb acquired later in the season. We found no significant effect of sex on adult muscle stable-isotope values ($P > 0.1$ in all tests), so data were pooled within pre- and postbreeding categories. While controlling for significant effects of species, overall isotope abundance ($\delta^{13}C$ and $\delta^{15}N$) of muscle changed between the two sampling periods (MANOVA, Wilks' $\lambda = 0.39$, $F = 76.0$, df = 2 and 99, $P = 0.0001$; Fig. 2, Table 1). Muscle $\delta^{15}N$ and $\delta^{13}C$ values (least-squares means ± SE) both showed overall significant seasonal declines ($\delta^{15}N$, prebreeding = 12.7 ± 0.2‰, postbreeding = 9.9 ± 0.1 ‰, $P = 0.0001$; $\delta^{13}C$, prebreeding = −21.5 ± 0.3‰, postbreeding = −23.5 ± 0.2‰, $P = 0.0001$). Herring Gulls arrived with the most

TABLE 1. Values of $\delta^{13}C$ and $\delta^{15}N$ (‰) of prebreeding and postbreeding muscle and $\delta^{13}C$ of abdominal fat from colonial waterbirds at Great Slave Lake. Values are $\bar{x} \pm$ SD (n); means with the same letter are not significantly different (Duncan's tests, $P > 0.05$).

Species[a]	Prebreeding adult muscle		Prebreeding adult abdominal fat	Postbreeding adult muscle		Fledgling muscle	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
HEGU	-19.4 ± 0.4 (10)^{A}	13.9 ± 0.3^{A}	-19.9 ± 0.7 (11)^{A}	-23.2 ± 0.3 (10)^{A,B}	$10.2 \pm 0.3^{B,C}$	-24.3 ± 0.4 (10)^{B}	9.7 ± 0.2^{A}
MEGU	-20.3 ± 0.7 (8)^{A}	$12.5 \pm 0.6^{B,C}$	-19.5 ± 0.8 (8)^{A}	-21.8 ± 0.5 (10)^{A}	$9.2 \pm 0.3^{C,D,E}$	-22.9 ± 0.4 (10)^{A}	7.9 ± 0.2^{B}
COTE	-20.6 ± 0.4 (9)^{A}	$12.8 \pm 0.2^{A,B,C}$	-24.4 ± 0.6 (8)^{B}	-21.9 ± 0.5 (9)^{A}	$10.7 \pm 0.3^{A,B}$	-23.7 ± 0.4 (10)^{A,B}	10.2 ± 0.2^{A}
CATE	-20.7 ± 1.1 (4)^{A}	$13.2 \pm 0.8^{A,B}$	-22.6 ± 0.8 (4)^{B}	—	—	—	—
ARTE	-21.2 ± 0.2 (10)^{A}	11.32 ± 0.2^{C}	-24.1 ± 0.5 (8)^{B}	-22.2 ± 0.2 (10)^{A}	$9.7 \pm 0.2^{C,D}$	-24.0 ± 0.5 (7)^{A,B}	10.2 ± 0.2^{A}
BOGU	-23.3 ± 1.2 (5)^{B}	$12.6 \pm 0.9^{A,B,C}$	-22.3 ± 2.1 (5)^{B}	-25.0 ± 2.3 (3)^{C}	$8.8 \pm 0.4^{D,E}$	-24.9 ± 0.4 (10)^{B}	8.2 ± 0.2^{B}
RBGU	—	—	—	-21.6 ± 0.2 (5)^{A}	$8.8 \pm 0.3^{D,E}$	—	—
PAJA	—	—	—	-24.2 ± 0.8 (4)^{B,C}	10.9 ± 0.1^{A}	—	—
BLTE	—	—	—	-25.8 ± 0.5 (8)^{C}	8.5 ± 0.2^{E}	-26.1 ± 0.4 (10)^{C}	7.9 ± 0.2^{B}
CAGU	—	—	—	-26.2 ± 0.2 (8)^{C}	11.3 ± 0.2^{A}	—	—

[a] HEGU = Herring Gull, MEGU = Mew Gull, COTE = Common Tern, CATE = Caspian Tern, ARTE = Arctic Tern, BOGU = Bonaparte's Gull, RBGU = Ring-billed Gull, PAJA = Parasitic Jaeger, BLTE = Black Tern, CAGU = California Gull.

enriched muscle $\delta^{15}N$ and $\delta^{13}C$ values, whereas Arctic Terns arrived with the most depleted muscle $\delta^{15}N$ values and Bonaparte's Gulls with the most depleted $\delta^{13}C$ muscle values (Table 1). However, there was considerable overlap in muscle stable-isotope values of arriving birds. Our postbreeding sample consisted of more species, and California Gulls had the lowest and Arctic Terns the highest $\delta^{13}C$ muscle values (Table 1). For muscle $\delta^{15}N$ values in postbreeding birds, Arctic Terns and California Gulls were the highest, and Black Terns, Ring-billed Gulls, and Bonaparte's Gulls were among the lowest.

For arriving birds, values of $\delta^{13}C$ in abdominal fat fell into two distinct groups, with Herring Gulls and Mew Gulls having significantly higher values than the other species (Table 1). As expected, date had a highly significant effect on tissue isotope values (Table 2). The relationship between body condition and abdominal fat $\delta^{13}C$ in prebreeding birds approached significance (Table 2), suggesting that birds in better condition had fat stable carbon isotope values that were more positive (i.e. more marine) than those in poorer body condition. However, $\delta^{15}N$ and $\delta^{13}C$ values of pectoral muscle were unrelated to body condition (Table 2).

Marine and GSL foodwebs.—We conducted an extensive isotope analysis of foodweb samples from GSL and will present those results elsewhere. The GSL freshwater foodweb showed an expected C-3 carbon-isotope composition and had relatively lower $\delta^{15}N$ values compared with those of marine foodwebs (Hobson and Welch 1992, Hobson et al. 1994). Among fish, mean $\delta^{15}N$ values ranged from 7.1‰ for spottail shiner (*Notropis hudsonius*) to 12.6‰ for lake trout (*Salvelinus namaycush*), and mean $\delta^{13}C$ values ranged from −29.3‰ for lake trout to −21.7‰ for grayling (*Thymallus arcticus*). Aquatic invertebrates had a mean $\delta^{15}N$ value of 6.1‰ and a mean $\delta^{13}C$ value of −25.5‰. As expected, within the GSL foodweb, $\delta^{13}C$ values showed a bimodal distribution consisting of relatively depleted offshore or pelagic organisms (ca. −28‰) and more enriched inshore or benthically associated organisms (ca. −22‰). Stable-isotope values for muscle of fledglings also provided evidence for isotopic endpoints expected for birds feeding exclusively within GSL (Table 1). Fledglings whose lifetime diet was derived from GSL showed a range of $\delta^{13}C$

TABLE 2. ANCOVA of effects of body condition on $\delta^{13}C$ and $\delta^{15}N$ of abdominal fat and pectoral muscle of prebreeding study species at Great Slave Lake.

	Abdominal fat $\delta^{13}C$				Pectoral muscle $\delta^{13}C$				Pectoral muscle $\delta^{15}N$			
Factor	SS	*F*	*P*	df	SS	*F*	*P*	df	SS	*F*	*P*	df
Condition	15.7	3.9	0.055	1	0.11	0.05	0.800	1	0.04	0.04	0.800	1
Date	128.2	32.0	0.0001	1	7.90	3.30	0.078	1	16.10	14.00	0.001	1
Species	—	—	—	—	37.90	3.20	0.019	5	22.20	3.80	0.010	5

values of pectoral muscle similar to that for the local foodweb. The most depleted average $\delta^{13}C$ value was for Black Tern and the most enriched for Mew Gull. Mean values for stable nitrogen isotope in muscle clustered into two groups, the most enriched ($\bar{x}$ = 10.0 ± 0.2‰, n = 3) in Herring Gulls, Common Terns, and Arctic Terns and the most depleted ($\bar{x}$ = 8.0 ± 0.2‰, n = 3) in Black Terns, Bonaparte's Gulls, and Mew Gulls. Among species, mean pectoral muscle $\delta^{13}C$ and $\delta^{15}N$ values of postbreeding adults were positively correlated with those of fledglings ($\delta^{15}N$, r = 0.85, n = 6, P = 0.032; $\delta^{13}C$, r = 0.94, P = 0.005), indicating similar adult and chick diets and similar sources of nutrients within species.

Endogenous vs. exogenous inputs to eggs.—Having established that several species arrived with endogenous muscle protein and abdominal fat reserves that were more enriched than expected based on the GSL foodweb, we investigated whether birds allocated endogenous reserves obtained on the wintering grounds to their eggs. Egg isotope values differed among species for all components (Table 3). We also investigated whether date of collection and site location (inshore vs. offshore) influenced isotope values of eggs. Initial analyses found no significant date effects ($P > 0.1$ for all egg components). When controlling for significant species effects, overall isotope abundance of egg components did not differ between inshore and offshore sites (Wilk's λ = 0.89, F = 1.43, df = 4 and 45, P = 0.24). However, when we repeated the analysis without shell carbonate, overall isotope abundance of eggs differed between sites (Wilk's λ = 0.63, F = 1,832, df = 3 and 95, P = 0.0001), with inshore sites showing enrichment in $\delta^{13}C$ and $\delta^{15}N$ (lipid-free yolk $\delta^{15}N$, inshore, $\bar{x}$ = 11.5 ± 0.3‰, offshore, $\bar{x}$ = 10.5 ± 0.5‰, P = 0.06; lipid-free yolk $\delta^{13}C$, inshore, $\bar{x}$ = −23.6 ± 0.2‰, offshore, $\bar{x}$ = −26.0 ± 0.3‰, P = 0.0001; yolk lipid $\delta^{13}C$, inshore, $\bar{x}$ = −26.9 ± 0.2‰, offshore, $\bar{x}$ = −29.3 ± 0.4‰, P = 0.0001).

In general, stable-isotope values in egg tissues of birds from GSL were similar to those of birds from other high-latitude C-3 biomes and were more depleted than those from seabirds (Table 3). Muscle $\delta^{15}N$ and $\delta^{13}C$ values of prebreeding adults were not significantly correlated with those in any egg component or $\delta^{13}C$ of follicle lipids (Ps > 0.19; Tables 1 and 3). Abdominal fat $\delta^{13}C$ in prebreeding adults tended to be negatively correlated with $\delta^{13}C$ of lipid-free yolk (r = −0.76, P = 0.078) but was not correlated with any other egg component, including follicle lipid $\delta^{13}C$ (Ps > 0.18; Table 3).

If eggs were synthesized entirely from local diets, then by using diet-tissue isotopic fractionation values established by Hobson (1995), the isotope composition of the diet of laying females can be estimated from isotope measurements of various egg components. Although isotope fractionation values between diet and egg components for fish-eating birds have not been determined experimentally, the values provided for falcons by Hobson (1995) also were probably appropriate for piscivorous birds. Following this approach, we used species-specific mean values of $\delta^{15}N$ and $\delta^{13}C$ measured for lipid-free yolk and $\delta^{13}C$ values for shell carbonates and yolk lipids presented in Table 3, and applied fractionation factors presented in Hobson (1995) to calculate isotope signatures predicted for diets of laying females. We used $\delta^{13}C$ fractionation factors of 11.2, −3.4, and 0‰ for shell carbonate, lipid, and lipid-free yolk, respectively, and a $\delta^{15}N$ fractionation factor of 3.4‰ for lipid-free yolk (Hobson 1995).

Based on mean values for lipid-free yolk and the assumption that all nutrients were derived locally, predicted overall mean $\delta^{13}C$ and $\delta^{15}N$ in diets of GSL birds (n = 10 species) during egg synthesis were −24.6 ± 1.4‰ and 7.4 ± 1.2‰,

TABLE 3. Stable-isotope values (‰) for eggshells, follicles, yolk lipid, lipid-free yolk, and corresponding predicted diets (DIET) of colonial waterbirds based on assumption that tissues are derived exclusively from diet. Diet isotope estimates based on fractionation factors for carnivores (Hobson 1995) and are 11.2, −3.4, and 0‰ for shell carbonate, egg lipids, and lipid-free yolk $\delta^{13}C$, respectively, and 3.4‰ for lipid-free egg yolk $\delta^{15}N$. For herbivores, we used −2.6 and 0‰ for yolk lipid and lipid-free egg yolk $\delta^{13}C$, respectively, and 3.4‰ for $\delta^{15}N$. Values are $\bar{x} \pm$ SD (n); means with the same letter are not significantly different (Duncan's tests, $P > 0.05$).

	Shell carbonate		Follicle lipid		Egg yolk lipid		Lipid-free egg yolk			
Species[a]	$\delta^{13}C$	DIET	$\delta^{13}C$	DIET	$\delta^{13}C$	DIET	$\delta^{13}C$	DIET	$\delta^{15}N$	DIET
Freshwater										
SNGO	—	—	—	—	−27.1 ± 0.2 (18)	−24.5	−25.0 ± 0.1 (18)	−25.0	7.2 ± 0.1	3.8
ROGO	—	—	—	—	−28.0 ± 0.1 (18)	−25.4	−25.8 ± 0.1 (18)	−25.8	7.7 ± 0.2	4.3
Great Slave Lake										
ARTE	−18.0 ± 0.6 (7)^{B,C,D,E,F}	−29.2	−24.3 ± 0.8 (4)^{A}	−20.9	−26.7 ± 0.3 (25)^{B}	−23.3	−24.8 ± 0.2 (25)^{D}	−24.8	10.1 ± 0.4^{C,D}	6.7
BLTE	−19.5 ± 0.2 (7)^{F}	−30.7	—	—	−27.4 ± 0.4 (10)^{B,C}	−24.0	−26.9 ± 0.1 (10)^{E}	−26.9	9.3 ± 0.1^{D}	5.9
BOGU	−17.6 ± 1.3 (7)^{B,C,D,E}	−28.8	−27.4 (1)^{B,C}	−24.0	−29.0 ± 0.8 (8)^{C,D}	−25.6	−24.8 ± 1.2 (8)^{D}	−24.8	10.1 ± 1.2^{B,C,D}	6.7
CAGU	−19.2 ± 0.4 (7)^{E,F}	−30.4	—	—	−30.4 ± 0.7 (10)^{D,E}	−27.0	−26.2 ± 0.2 (10)^{E}	−26.2	10.0 ± 0.3^{C,D}	6.6
CATE	−16.8 ± 0.6 (7)^{B,C}	−28.0	−24.8 ± 1.5 (2)^{A,B}	−21.4	−27.7 ± 0.9 (9)^{B,C}	−24.3	−22.8 ± 0.4 (10)^{A,B}	−22.8	11.6 ± 0.2^{A,B,C}	8.2
COTE	−14.7 ± 0.4 (7)^{A}	−25.9	−28.3 ± 0.3 (2)^{C}	−24.9	−22.8 ± 0.5 (10)^{A}	−19.4	−22.3 ± 0.3 (10)^{A}	−22.3	11.8 ± 0.2^{A,B}	8.4
HEGU	−16.4 ± 0.4 (7)^{B}	−27.6	−23.3 ± 0.4 (4)^{A}	−19.9	−30.7 ± 0.7 (24)^{E}	−27.3	−24.9 ± 0.5 (24)^{D}	−24.9	11.0 ± 0.3^{B,C,D}	7.6
MEGU	−18.5 ± 0.3 (7)^{D,E,F}	−29.7	−24.2 ± 0.5 (4)^{A}	−20.8	−27.9 ± 0.3 (23)^{B,C}	−24.5	−25.0 ± 0.3 (23)^{D}	−25.0	13.0 ± 0.8^{A}	9.6
PAJA	−18.1 ± 0.8 (7)^{C,D,E,F}	−29.3	—	—	−27.5 ± 0.3 (10)^{B,C}	−24.1	−24.4 ± 0.5 (10)^{C,D}	−24.4	11.6 ± 0.3^{A,B,C}	8.2
RBGU	−16.9 ± 0.4 (7)^{B,C,D}	−28.1	—	—	−26.8 ± 0.4 (10)^{B}	−23.4	−23.6 ± 0.3 (10)^{B,C}	−23.6	9.6 ± 0.4^{D}	6.2
Marine										
ANMU	—	—	—	—	—	—	−17.6 ± 0.3 (8)	−17.6	13.2 ± 0.3	10.2
RHAU	—	—	—	—	—	—	−20.2 ± 1.0 (20)	−20.2	15.2 ± 1.2	12.2
CAAU	—	—	—	—	—	—	−19.9 ± 0.6 (7)	−19.9	12.2 ± 0.4	9.2
CATE	−15.4 ± 0.5 (10)	−16.6	—	—	−21.2 ± 1.3 (10)	−17.8	−18.6 ± 1.0 (10)	−18.6	—	—

[a] SNGO = Snow Goose, ROGO = Ross' Goose, ANMU = Ancient Murrelet, CAAU = Cassin's Auklet, RHAU = Rhinoceros Auklet; all other species codes as in Table 1.

respectively. These values are considerably more depleted than equivalent values for eggs from the marine birds examined here ($\delta^{13}C$, $\bar{x}$ = −19.1‰; $\delta^{15}N$, $\bar{x}$ = 13.5‰; Table 3). Importantly, these egg values also are more depleted than values for pectoral muscle of birds first arriving at GSL. Common Terns and Caspian Terns had the most enriched lipid-free egg yolk $\delta^{13}C$ (i.e. −22.3‰ and −22.8‰, respectively; Table 3).

The overall mean $\delta^{13}C$ value predicted for diets based on egg lipid was −24.3 ± 2.2‰ (n = 10 species), and this value also was substantially more depleted than that predicted for the marine birds considered here (−17.8‰; Table 3). Predicted mean $\delta^{13}C$ values in the diets of laying females based on shell carbonates were more negative (−28.8 ± 1.4‰), however, and with the exception of Common Terns, all calculated dietary values were within or close to the range of isotope values measured for typical prey samples at GSL and were distinctly more depleted than comparable seabird dietary values for foodweb samples from Lancaster Sound and coastal British Columbia (Table 3).

We performed stable sulfur isotope analysis on egg yolks of four species. We found no significant difference in $\delta^{34}S$ values among Herring Gulls ($\bar{x}$ = 2.9 ± SD of 3.6‰, n = 12), Arctic Terns (5.7 ± 0.7‰, n = 6), Caspian Terns (6.4 ± 2.4‰, n = 6), and California Gulls (5.1 ± 1.2‰, n = 6; Kruskal-Wallis test, H = 6.9, P = 0.07). All sulfur-isotope values were depleted and were typical of terrestrial or freshwater biomes rather than of marine sulfates.

If we make the assumptions that $\delta^{13}C$ values in eggs of Snow Geese (*Chen caerulescens*) and Ross's Geese (*C. rossii*) provide a reasonable estimate of values to expect from nutrients derived solely from the GSL foodweb, and that values for marine birds provide a reasonable estimate of values corresponding to eggs produced solely from marine nutrients, the percent contributions of exogenous resources to egg components of GSL birds can be estimated. Here, we used mean $\delta^{13}C$ values of −27.6 and −21.2‰ for egg lipids and −25.4 and −19.1‰ for yolk protein representing eggs produced from freshwater and marine biomes, respectively (Table 3). Estimated exogenous contributions to egg lipids were 100% with the exception of Arctic Tern (86%), Black Tern (97%), Ring-billed Gull (88%), and Common Tern (25%). For egg protein, estimated exogenous contributions exceeded 90% for all species except Caspian Tern (59%), Common Tern (51%), Parasitic Jaeger (84%), and Ring-billed Gull (71%).

DISCUSSION

Seasonal isotope shifts.—Our study demonstrated that migratory gulls and terns at Great Slave Lake generally arrived on their breeding grounds with protein reserves that were isotopically more enriched in ^{13}C and ^{15}N and with fat reserves more enriched in ^{13}C than would be expected had they been derived entirely from the local freshwater C-3 foodweb. The species we investigated included individuals that possibly wintered inland as well as along coastal areas. In addition, within both temperate coastal marine and inland foodwebs, considerable scope exists for isotopic variation that depends on local conditions as well as trophic levels of species (see Rundel et al. 1988, Lajtha and Michener 1994). Within a given trophic level, stable carbon isotope values of waterbirds in marine and freshwater biomes are expected to be more enriched for inshore or benthically linked consumers compared with offshore or more pelagic feeders (Hobson et al. 1994, France 1995). These factors, in addition to variation in trophic levels, contributed to variation in $\delta^{13}C$ values among individuals of species arriving at GSL and later in equilibrium with the GSL foodweb. Nonetheless, the average $\delta^{13}C$ value of −18.6‰ calculated for pectoral muscle tissue of inshore-foraging seabirds from the Gulf of Alaska and Lancaster Sound is an appropriate value to expect from exclusively marine-foraging gulls and terns arriving at GSL.

Because $\delta^{15}N$ values of consumers are so closely correlated with trophic levels, it was not appropriate to apply a single $\delta^{15}N$ value to represent birds in equilibrium with exclusively marine or freshwater foodwebs. However, previous studies indicate that values for pectoral muscle on the order of 15‰ likely are typical for largely piscivorous marine species (Hobson and Welch 1992, Hobson et al. 1994). In contrast, assuming that isotope signatures of the GSL foodweb used by gulls did not change seasonally, isotope values we consider appropriate for muscle tissue of gulls and terns that fed exclusively in the GSL freshwater foodweb were

those obtained for fledglings or late-season adults, which averaged −21.6 and −24‰ for $\delta^{13}C$ values of inshore and offshore feeders, respectively, and 10.0‰ for $\delta^{15}N$ values. Despite the potential for high isotopic variability within each biome, we believe that the isotope segregation between birds whose tissues were derived from marine sources and those derived from the GSL freshwater foodweb were sufficiently different to permit inferences about relative nutrient allocation to eggs.

Values of $\delta^{13}C$ in muscle from the sample of arriving birds had evidence of marine carbon for Herring Gulls, Mew Gulls, Common Terns, and Caspian Terns; Arctic Terns and Bonaparte's Gulls were relatively depleted in ^{13}C. Arctic Terns winter in the Southern Hemisphere where marine $\delta^{13}C$ values typically are more depleted than in the Northern Hemisphere (Michener and Schell 1994). Protein $\delta^{13}C$ values in this species may have reflected a Southern Hemisphere marine signal or terrestrial/freshwater input acquired along the northern migration route. Bonaparte's Gulls winter on the Pacific coast from Washington to Mexico but also on the Great Lakes and the Mississippi Valley to the Gulf of Mexico. Samples of abdominal fat of arriving birds were marine in Herring Gulls and Mew Gulls but appeared less so in Common Terns, Caspian Terns, Arctic Terns, and Bonaparte's Gulls. Thus, fat and protein sources for Common Terns and Caspian Terns may be derived from different sources before or during migration.

Body condition of arriving birds was not significantly associated with evidence for endogenous allocation of nutrients to reproduction. However, there was a trend for birds in better body condition to arrive with endogenous reserves from marine versus freshwater or terrestrial C-3 sources. This may be related to the fact that marine wintering sites are closer to GSL than potential inland wintering sites and that birds in better condition traveled shorter distances to GSL from marine wintering areas.

Adult and fledgling diets, based on their pectoral muscle stable-isotope signatures, were correlated within species, suggesting that species-specific foraging patterns existed at GSL. However, isotope signatures within species were not identical between age groups, suggesting that some ecological segregation occurred between adults and young. Other isotope studies of seabirds also have suggested that diets of adults and young are not necessarily identical (Hobson 1993, Schmutz and Hobson 1998).

Endogenous vs. exogenous inputs to eggs.—The distinct isotope differences between endogenous macronutrient reserves in arriving birds and the local GSL foodweb allows us to infer the relative importance of endogenous versus exogenous contributions to eggs. Isotope values of different egg components yield information based on slightly different periods of egg formation and nutrient pathways (Hobson 1995). The calcium carbonate fraction of the shell is derived directly from plasma through the metabolism of recently assimilated food (Simkiss and Tyler 1958, Hobson 1995), which was entirely consistent with our results showing very negative $\delta^{13}C$ values in shell carbonate for all species at GSL compared with those for marine birds (Hobson et al. 1997). However, for other egg components that can be derived from endogenous reserves and local diet, it was more difficult to set cutoffs for isotope dietary predictions conforming to evidence of marine-derived endogenous nutrients because potential diets at GSL clearly varied in $\delta^{13}C$ values within and among species. Owing to differences in $\delta^{15}N$ values in eggs related to trophic level of laying females, we used this isotope only to support general conclusions based on $\delta^{13}C$ and $\delta^{34}S$ analyses.

We measured follicular lipids for Herring Gulls, Mew Gulls, Bonaparte's Gulls, Arctic Terns, Caspian Terns, and Common Terns just before or shortly after they arrived at GSL. With the exception of Common Terns and Bonaparte's Gulls, follicular lipids tended to be more enriched in ^{13}C than lipids measured for whole eggs laid later at GSL. This effect was most striking for Herring Gulls and was consistent with such lipids originating from a marine foodweb. However, comparative values from egg lipids of marine birds are lacking, the only value being that used here for Caspian Terns. For most of the species examined, it probably takes 9 to 15 days to deposit yolk in the egg (Grau 1984, Astheimer and Grau 1990). This again suggests that for some individuals, lipids in follicles were derived outside of GSL, likely from marine sources. On the other hand, lipids in egg yolk derived from eggs laid at GSL were depleted in ^{13}C, which is consistent

with values expected if eggs were formed entirely from carbon from the local foodweb. Common Terns appeared to be the only species with strong evidence that lipid sources for whole eggs came from a diet in the marine foodweb.

Predictions of diet isotope values based on the proteinaceous component of eggs generally were consistent with nonmarine origins of nutrients and were close to values found for terrestrially breeding geese. Egg protein $\delta^{15}N$ and $\delta^{34}S$ values also were generally consistent with the range of values expected if they had been derived from the GSL foodweb. However, exceptions to this trend were the Common Tern and Caspian Tern that had $\delta^{13}C$ values in egg yolks that suggested about 50% marine-derived protein inputs. The fact that such values were within the possible isotopic range of waterbird diets at GSL indicates the difficulty of using this inferential approach for eggs with intermediate isotope values. Common Terns also had the most enriched $\delta^{13}C$ values in their egg lipids, again suggesting marine-derived lipid inputs to eggs, despite the fact that abdominal fat and egg follicles of arriving Common Terns were not particularly marine in their $\delta^{13}C$ signatures. Alternatively, Common Terns may have had a very different diet from other colonial waterbirds at GSL during the egg-formation period. Based on our foodweb isotope measurements, it is possible that this species fed more on inshore aquatic invertebrates.

Ecological implications.—Jonsson (1997) noted that the storage of nutrients as endogenous reserves during breeding may be beneficial if (1) food resources are absent or very scarce, (2) food demands are very high, (3) foraging success or food demands are variable, (4) costs of obtaining food are high due to risks of predation, or (5) the time available for foraging is limited. Colonial waterbirds arrive in May at GSL, often during periods of inclement weather and when much of the lake is frozen. Initially, we considered these conditions to strongly favor the allocation of stored nutrients to reproduction that occurs from mid-May to early June. Such a capital versus income strategy (sensu Jonsson 1997) may occur in some years for some species and, as we noted, may have occurred in Common Terns at GSL. However, once open water occurs, food may not be limiting in this high-latitude system, particularly if birds can exploit a wide variety of prey types. Food may thus be relatively abundant and predictable during breeding. Predation risk probably is low for colonial waterbirds that breed on offshore reefs and islands, and because GSL experiences almost 24 h of daylight during much of the breeding season, we suspect that birds have ample time for foraging. Thus, it is possible that few of the conditions suggested by Jonsson (1997) for capital strategists apply to our study population. Rather, body protein and lipid reserves may be critical for individual maintenance prior to breeding, and nutritional capital is used as a hedge against poor conditions upon arrival.

Future research.—Our study is a preliminary investigation of the stable-isotope approach for tracing endogenous versus exogenous nutrient reserves to reproduction in birds (see Hobson et al. 1997). A potentially interesting refinement of our study could be provided by the isotopic analysis of individual yolk rings (Grau 1976) versus bulk material in eggs. This would allow reasonably precise estimates of the relative importance of endogenous versus exogenous resources to reproduction, particularly if whole clutches of known laying order were considered.

Ideally, the relative contribution of endogenous and exogenous nutrients to reproduction could be traced using a two-source mixing model, provided that these nutrient pools differed substantially in their stable-isotope signatures. For example, birds moving between two isotopically distinct foodwebs potentially can mobilize isotopically distinct inputs to eggs that correspond to body reserves of lipids and proteins and dietary lipids and proteins, respectively (Fig. 3). If we make the simplified assumption that body-protein reserves will be mobilized to egg proteins and lipid reserves to egg lipids, and consider similar macronutrient pathways for dietary sources of lipids and proteins for largely carnivorous or piscivorous birds (Hobson 1995), the stable-isotope ratio of egg macronutrients can be expressed as follows:

$$\delta_T = t_{end}(\delta_{Tend} + \Delta t_{end}) + t_{ex}(\delta_{Tex} + \Delta t_{ex}), \quad (2)$$

where δ_T is the stable-isotope ratio of the egg tissue of interest; t_{end} and t_{ex} are the proportions of the tissue derived from endogenous and ex-

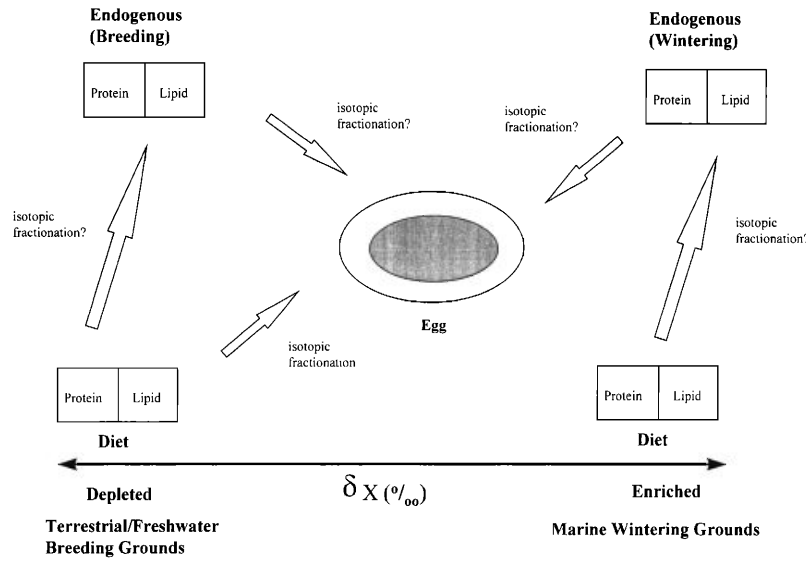

FIG. 3. Schematic diagram of potential endogenous and exogenous reserve pathways to egg formation. Equation 2 is based on the simplified two-source mixing model that considers eggs to be formed directly from the diet on the breeding grounds and endogenous reserves to be acquired on the wintering grounds (i.e. it assumes that endogenous reserves acquired on the breeding grounds prior to reproduction are negligible).

ogenous sources, respectively; δ_{Tend} and δ_{Tex} are the stable-isotope values of the endogenous and exogenous sources of the tissue, respectively; and Δt_{end} and Δt_{ex} are the isotope fractionation factors associated with converting endogenous and exogenous sources of the macronutrient into the egg tissue. Isotope fractionation factors associated with the conversion of dietary macronutrients to egg macronutrients have been estimated by Hobson (1995). However, equivalent fractionation factors associated with the conversion of endogenous macronutrients are unknown. In the case of GSL, we also lack precise estimates of δ_{Tex} because precise isotope values of diets of birds during laying were not known. We note that equation 2 undoubtedly is a simplification of a potentially much more complex process of isotopic fractionation associated with nutrient allocation during egg formation.

The technique we have described offers a convenient means of assaying individual species or whole assemblages of birds in situations where birds are known to move between distinct isotope regimes. However, research that better defines the parameters listed in equation 2 and depicted in Figure 3 is encouraged. In particular, if stable-isotope fractionation factors corresponding to the mobilization of endogenous versus exogenous reserves could be determined experimentally with captive birds, much more precise quantitative estimates of nutrient allocations to reproduction will be possible. It has not been shown experimentally that stable-isotope signatures in endogenous reserves are reflected in signatures of eggs that are produced from those reserves. However, the isotope composition of any substrate in a standard isotope mass-balance equation (i.e. equation 2) should be reflected in the products. Eggs of Emperor Geese (*Chen canagica*) in Alaska showed a much more marine isotope signal than those of Canada Geese (*Branta canadensis*) or Greater White-fronted Geese (*Anser albifrons*), which was consistent with Emperor Geese feeding on marine foods prior to egg laying (Schmutz and Hobson 1998). In addition to controlled experiments, isotope field studies involving species known to mobilize endogenous reserves for reproduction would help clarify the fractionation of stable isotopes between endogenous nutrient reserves and egg components. Further research documenting the biogeography of stable-isotope distributions also will allow insight into the ecological

situations that are appropriate for the application of this technique (Hobson 1999).

Studies of Lesser Black-backed Gulls have demonstrated that food, particularly protein, limits egg production in the form of reduced clutch size or clutch volume (Hiom et al. 1991; Bolton et al. 1992, 1993). Although we did not investigate reproductive output in the species we examined, we suspect that at GSL such measures of reproductive investment are likely to fluctuate with food supply during egg formation. Our findings indicate that the use of stored nutrients for reproduction among migratory species may be the exception rather than the rule. However, we fully recognize that the capital versus income dichotomy may be too rigid a model and that significant variation might be expected in allocation strategies among individuals and between years. We recommend that our stable-isotope approach be used more widely to test assumptions regarding nutrient allocation in other species and in other ecological situations, especially in waterfowl for which nutrient allocation has been studied with more conventional approaches (Alisauskas and Ankney 1992). In particular, the technique will be most useful in situations where birds arrive on the breeding grounds with tissue-isotope values that are substantially different from those of local foodwebs, a situation expected to be common in species that winter in marine areas and breed inland (Hobson 1999).

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