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GEOGRAPHIC, TEMPORAL, AND AGE-SPECIFIC VARIATION IN DIETS OF GLAUCOUS GULLS IN WESTERN ALASKA[1]

JOEL A. SCHMUTZ
Alaska Biological Science Center, Biological Resources Division, U.S. Geological Survey, 1011 East Tudor Road, Anchorage, Alaska 99503, joel_schmutz@usgs.gov

KEITH A. HOBSON
Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada

Abstract. We collected boluses and food remains of adult Glaucous Gulls (*Larus hyperboreus*) at or near nests and chicks, and digestive tracts from adults at three sites on the Yukon-Kuskokwim Delta, Alaska that differed in proximity to marine and terrestrial foods. We observed both geographic and temporal variation in diet; gulls consumed proportionately more terrestrial prey after peak hatch in late June, and gulls near the coast consumed proportionately more marine prey than gulls at two inland areas. Goslings occurred in > 60% of all samples from these inland areas. We compared these data to those from a previous study in western Alaska and found no marked differences. Evidence for similar patterns of geographic and temporal variation in diet was found using measurements of stable-carbon and nitrogen isotopes in gull and prey tissues. Stable isotope analysis further revealed that adult gulls consumed proportionately more marine prey (saffron cod, *Eleginus gracilis*) than they fed to their young. Using isotopic models, we estimated that 7–22% and 10–23% of the diet of adult and juvenile Glaucous Gulls, respectively, was comprised of terrestrial species. In addition to significant age-related variation, dietary estimates varied among geographic areas and between pre- and post-hatch periods. Overall, our isotopic estimates of the contribution of terrestrial prey to the diet of Glaucous Gulls was less than what may be inferred from conventional methods of diet analysis. Our study emphasizes the benefit of combining stable-isotope and conventional analyses to infer temporal and geographic changes in diet of wild birds and other organisms.

Key words: Alaska, carbon-13, foraging ecology, geese, Glaucous Gull, Larus hyperboreus, *nitrogen-15, predation, stable isotopes.*

INTRODUCTION

Large gulls (*Larus* spp.) are well documented as opportunistic predators of young birds (Erikstad 1990, Emslie et al. 1995). In particular, Glaucous Gulls (*L. hyperboreus*) have long been known to commonly prey on young waterfowl (Strang 1976, Swennen 1989, Barry and Barry 1990). However, Glaucous Gulls are coastal marine in distribution, and in some areas they appear to rely predominantly on a marine diet, notably coastal fish and mollusks (Ingolfsson 1967). Both individual (Pierotti and Annett 1990) and intercolony (Strang 1976, Barry and Barry 1990) variations among gulls in their prey choice have been documented frequently.

The Yukon-Kuskokwim Delta (YKD), Alaska, is an expansive and important breeding area for waterfowl (Spencer et al. 1951) and shorebirds (Gill and Handel 1990). Glaucous Gulls, along with Arctic foxes (*Alopex lagopus*) and jaegers (*Stecorarius* spp.), are the only significant predators of eggs and young waterfowl on the YKD. Because of concerns about factors affecting the population dynamics of these waterfowl, Strang (1976, 1982) investigated feeding ecology of Glaucous Gulls on the YKD in 1972–1974 and 1979. He assayed the diet spectrum of gulls by examining boluses (regurgitated pellets of indigestible material) and food remains at nests or feeding areas, and digestive tracts of harvested birds. Through studies at two different sites on the YKD in different years, he demonstrated geographic and/or annual variation in diet as well as a within-year seasonal shift. At the more coastal site, Kokechik Bay (Fig. 1), where gulls nested in small colonies, Glaucous Gull diets were comprised mostly of fish species, particularly saffron cod (*Eleginus gracilis*). However, after peak hatch of gulls and geese in late June, birds also constituted a significant part of gull diets. At the more inland site, Old Che-

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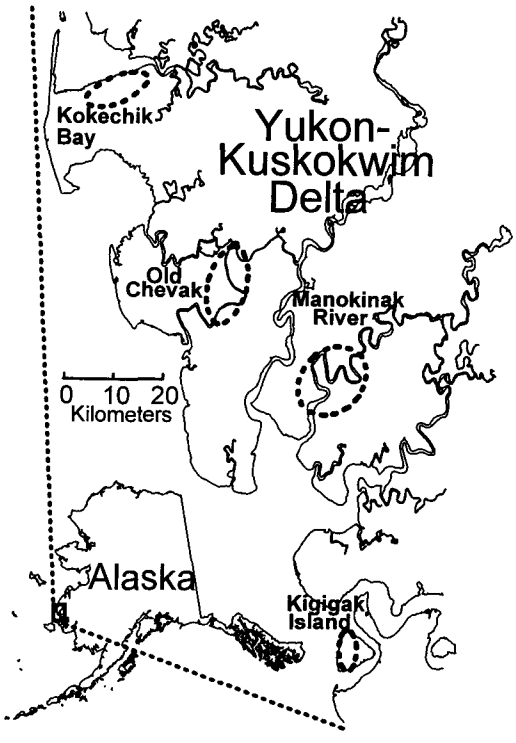

FIGURE 1. The Yukon-Kuskokwim Delta in western Alaska and the four study sites used for Glaucous Gull studies in the 1970s by Strang (1976, 1982) and/or during this study in 1993.

vak, where gulls nested as isolated pairs, gull diets were more terrestrial-based throughout the season than at Kokechik Bay, but similarly showed an apparent shift towards avian prey after peak hatch (Strang 1976, 1982).

Declines in waterfowl populations on the YKD were first noticed in the late 1960s and early 1970s (Raveling 1984). Since 1985, populations of Cackling Canada (*B. canadensis minima*) and Greater White-fronted Geese (*Anser albifrons*) have risen steadily. However, Emperor Goose (*Chen canagica*) numbers have remained relatively low (Petersen et al. 1994), and Spectacled Eiders (*Somateria fischeri*) have continued a precipitous drop in numbers (Stehn et al. 1993) and have recently been classified as a threatened species. It is unclear to what extent Glaucous Gulls have contributed to these population changes. No population estimates for Glaucous Gulls exist prior to the mid-1980s. More recently, gull numbers on the YKD in 1993 and 1994 were 45% greater than numbers estimated in 1985–1986 (Bowman et al. 1997). Thus, the ratio of predators to prey probably has varied substantially. It is unknown whether a change in the relative numbers of predator and prey would influence the magnitude of predation on waterfowl, but other studies in multiple-prey systems indicate such potential exists (Sodhi and Oliphant 1993, Dale et al. 1994).

In 1993 we initiated a study on foraging ecology of Glaucous Gulls with one of its objectives being to replicate these aforementioned aspects of Strang's (1976, 1982) work to determine whether the proportional contribution of waterfowl to the diet of Glaucous Gulls had shifted. In particular, we wanted to examine the distribution of taxa represented in boluses, food remains, and stomachs of gulls and do so at multiple areas before and after peak hatch of geese. We thus wanted to test the hypothesis that the taxonomic distributions of prey items were similar during Strang's studies and ours. We chose the same Old Chevak study site used by Strang and also conducted studies at Kigigak Island and Manokinak River (Fig. 1). Kigigak Island is a coastal site where gulls nest in small colonies, similar to the Kokechik Bay study area used by Strang. The Manokinak River site is 5–12 km inland where gulls occur in comparatively lower densities and nest as dispersed pairs, thus it is more similar to the Old Chevak site. By examining multiple sites within years, we removed the confounding influences of geographic and annual variation in diets inherent in Strang's work.

Most previous studies of seabird diets have relied upon examination of boluses, food remains, and stomachs. These conventional methods are useful for identifying specific prey taxa. However, differential digestion and assimilation of various prey species bias quantitative evaluations of how much nutrient uptake gulls derive from their prey (Hyslop 1980, Duffy and Jackson 1986, Erikstad 1990). Additionally, each sample typically constitutes a single meal, resulting in a dietary perspective that may be biased by where samples were collected, e.g., at-sea versus near a nest. A complementary method is to examine the proportional abundance of stable isotopes of various elements in tissues from both predator and prey (Tieszen and Boutton 1989, Hobson and Clark 1992a, 1992b, Sydeman et al. 1997). For species with simple, isotopically distinct diets, these methods offer a

powerful means for quantifying relative importance of various prey types. For example, the often large difference between marine and terrestrial organisms in $\delta^{13}C$ values enabled an estimate of the contribution of terrestrial prey to the diet of Western Gulls (*L. occidentalis*) (Hobson 1987), Northern Saw-Whet Owls (*Aegolius acadicus*) (Hobson and Sealy 1991), and Marbled Murrelets (*Brachyramphus marmoratus*) (Hobson 1990). Our objective was to measure stable-nitrogen and carbon isotope ratios in various tissues of gulls and in their prey in order to estimate the numerical importance of terrestrial prey to total nutrient uptake.

METHODS

STUDY AREA AND SPECIES

The YKD is an expansive coastal marsh where salt water influence extends up to 55 km inland (Tande and Jennings 1986) (Fig. 1). Distribution of gulls and geese is predominantly coastal with the vast majority within 15 km of the Bering Sea coast and associated bays. Nesting densities of geese at all study sites were > 10 nests km^{-2}, with much higher densities at localized areas, particularly at Kokechik Bay and Kigigak Island (Bowman et al. 1996). Approximately 140,000 total pairs of the four species of geese nested on the YKD in 1993. At least 17,000 Glaucous Gulls occurred in early June and 12,000 in early July, 1993–1994, on a major portion of the YKD that did not include the Kokechik Bay area (Bowman et al. 1997). Strang (1976) provides a detailed study of the general ecology of Glaucous Gulls on the YKD. Peak hatch of gulls and geese usually occurs in late June; in 1993, peak hatch was approximately 20 June (Bowman et al. 1996).

CONVENTIONAL METHODS

We examined diet of Glaucous Gulls from boluses and food remains found at feeding sites near nests or chicks, and from stomach contents of harvested adults. Nests were initially located in late May or early June. Distinct feeding areas were readily found at or near nests or within close proximity to chicks. All boluses and food remains were collected during a nest/chick visit. These collections occurred both pre- and post-hatch at Kigigak Island and Old Chevak, but only post-hatch at Manokinak River. We killed adults by shooting them, immediately removed their entire digestive tracts, and stored them in 70% ethanol. We collected gulls pre- and post-hatch at Kigigak Island and Manokinak River, but only post-hatch at Old Chevak.

Food remains, boluses, and gull stomach contents from Kigigak Island and Old Chevak were examined in the laboratory after the field season. We used reference collections to identify prey and enumerated the minimum number of individuals found within a sample. A sample constituted all boluses and food remains found during one visit or the contents of one digestive tract. Examining frequency of occurrence (Duffy and Jackson 1986), we compared the distribution of prey taxa between sites or time periods (pre- vs. post-hatch) using likelihood ratio chi-square tests. To minimize bias due to small cell frequency counts, we pooled all terrestrial prey types into one category for tests involving Kigigak Island data. To compare our data to that of Strang (1976, 1982), we pooled goslings and shorebirds into a single category and mollusks and other marine invertebrates into one category. Due to multiple tests (up to three to test for year, site, and within season effects) and some low cell frequencies, we feel a conservative *P*-value of 0.01 for interpretation of significance is warranted. We did not combine these tests into a single categorical model because comparisons with the less taxon-specific data of Strang (1976) required different pooling. For samples from Manokinak River, we obtained only a field-based and grosser level of taxonomic occurrence of food items. Thus, we did not use data from this area in chi-square analyses.

STABLE ISOTOPE METHODS

We collected approximately 1 g of breast muscle and liver, and 1 cc of blood from harvested adult gulls. We collected multiple tissues per individual as variation among tissues in metabolic activity results in different rates of isotopic turnover in those tissues (Tieszen and Boutton 1989). Thus, diet perspectives pertaining to different periods were obtained by sampling several tissue types (Hobson and Clark 1992a). We also obtained approximately 1 cc of blood from gull chicks at about four weeks of age. Tissues were temporarily cold-stored in tundra pits, then frozen until analysis at the laboratory. Prey taxa were harvested opportunistically. We collected fully developed goose embryos from eggs that failed to hatch completely. Samples from older goslings were obtained from capture mortalities

during associated studies of geese. Tundra voles (*Microtus oeconomus*) were trapped or found at gull nest sites. Intertidal invertebrates were gathered at low tides in Hazen Bay or found in stomachs of collected gulls. We collected fish using small seines or by rod and reel. We excised muscle tissue from prey for isotope analysis.

All samples were freeze dried and then powdered using an analytical mill. Lipids were extracted from tissues using a chloroform:methanol rinse according to a modification of the method described by Bligh and Dyer (1959). Samples were loaded into vycor tubes together with wire-form CuO, elemental copper and silver wire, and then sealed under vacuum before combustion at 850°C for 2 hr. After cooling overnight, sample CO_2 and N_2 was separated cryogenically and then introduced into a VG Optima isotope-ratio mass-spectrometer.

Stable isotope values are expressed as parts per thousand (‰) according to the following equation:

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

where X = ^{15}N or ^{13}C, and R = the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. $R_{standard}$ for ^{15}N and ^{13}C is that for atmospheric N_2 (AIR) and the Peedee Belemnite (PDB) standard, respectively. Using hundreds of replicate analyses of an egg albumen laboratory standard, we estimated measurement precision to be ± 0.1‰ and ± 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

We tested whether $\delta^{15}N$ and $\delta^{13}C$ values in gulls varied geographically (Kigigak Island versus Manokinak River) and/or temporally (pre- versus post-hatch) using multivariate analysis of variance (MANOVA). We ran separate analyses for muscle and liver tissues, but did not include blood in these analyses because it was not collected at all areas at all times. In addition, we did not include Old Chevak data in the MANOVA because no pre-hatch data were collected there. Because of relatively small sample sizes, we computed significance values for the MANOVAs using randomization tests as described in Manly (1991). *F*-statistics were computed from the original data and 1,000 randomizations of the data. In each randomization, each pair of $\delta^{15}N$ and $\delta^{13}C$ values were randomly assigned to a geographic and temporal category. *F*-statistics from the 1,000 randomizations were numerically ordered and then significance of the MANOVA determined by where within this rank order of *F*-statistics the *F*-statistic from the original data laid. For example, if the *F*-statistic from the original data equaled the *F*-statistic from the 994th largest *F*-statistic of the 1,000 randomizations, then $P = 0.006$. We similarly applied a randomization test to results from one-way MANOVAs to test whether stable isotope values in blood samples from chicks differed among the three study sites.

Stable-isotope values of various macronutrients (protein, lipid, carbohydrate) in foods fractionate or change when incorporated into consumer tissues according to the relationship:

$$D_t = D_d + \Delta_{dt} \quad (2)$$

where D_t = the isotope value of the consumer tissue, D_d the isotope value of the diet, and Δ_{dt} the fractionation factor between diet and consumer. Similar to Hobson (1993), we used different $\delta^{15}N$ and $\delta^{13}C$ fractionation factors for adults and chicks because young birds incorporate a greater proportion of consumed isotopes directly into new somatic tissue and so may exhibit fractionation patterns different from adults. For adults, we used 2.4‰ and 2.3‰ for ^{15}N in muscle and liver tissues, respectively, and 2.1‰ and 1.3‰ for ^{13}C in muscle and liver, respectively, as determined by Mizutani et al. (1991) for an adult Great Cormorant (*Phalacrocorax carbo*). For chicks we used 3.1‰ and −0.3‰ for fractionation of ^{15}N and ^{13}C, respectively, in whole blood as determined by Hobson and Clark (1992b) for captive-raised Ring-billed Gull chicks (*L. delawarensis*).

We used a three-source isotopic mixing model (Ben-David et al. 1997) to estimate what proportion of the Glaucous Gull diet is comprised of each of the major diet categories or sources (marine, intertidal, or terrestrial). Because of the dominance of saffron cod in gull diets (see Results) and its similar isotopic composition to that of other local marine fishes (unpubl. data), we used this species as the sole representation of the marine diet. We considered bivalve species (blue mussel, razor clam, other clam spp.) to be the intertidal prey source. Eggs (full-term embryos), voles, shorebirds, and goslings were collectively considered terrestrial prey. For each gull, we calculated how distant its $\delta^{15}N$ and $\delta^{13}C$ isotope values in bivariate space were from the mean values for each of the three diet sources after accounting for isotopic fractionation between diet and gull tissue. Proportional diet contributions

were inversely related to this distance according to the following equation (Ben-David et al. 1997):

$$P_a = D_{ag}^{-1} / (D_{ag}^{-1} + D_{bg}^{-1} + D_{cg}^{-1}) \quad (3)$$

where P_a = the proportion of the diet derived from source *a*, and D_{ag}, D_{bg}, and D_{cg} are the Euclidean distances between isotopic values of an individual gull and the mean isotopic values of prey from source *a, b,* or *c*. As an estimate of P_a was associated with each gull, we calculated standard errors based on the inherent variation among individuals. We examined variation among study areas and ages in the proportional consumption of prey by post-hatch gulls using a two-way ANOVA.

RESULTS

BOLUSES, PREY REMAINS, AND STOMACH CONTENTS

We collected 51, 91, and 58 sets of boluses and food remains from Kigigak Island, Manokinak River, and Old Chevak, respectively. We also obtained 10 gull digestive tracts from each area. Distributions of the frequency of occurrence of various prey taxa at Old Chevak in 1993 were not different from that observed by Strang (1976) in 1974 in either pre-hatch ($\chi^2_4 = 9.3$, $P > 0.05$) or post-hatch periods ($\chi^2_4 = 6.4$, $P > 0.05$). We also compared Strang's (1976) Kokechik Bay samples from 1973 with ours from Kigigak Island in 1993 because these areas were similar in their proximity to the coast and densities of gulls and geese. Prey distributions at Kokechik Bay were not statistically different from those at Kigigak Island post-hatch ($\chi^2_3 = 7.3$, $P > 0.05$). However, pre-hatch samples at these two areas were different ($\chi^2_4 = 13.8$, $P < 0.01$), primarily due to the absence of mammals in the diet of Kigigak Island gulls.

Examining just 1993 data, frequencies of occurrence of various prey taxa were different between pre-hatch and post-hatch periods, both for Old Chevak ($\chi^2_5 = 17.4$, $P < 0.01$) and Kigigak Island ($\chi^2_2 = 12.6$, $P < 0.01$, Table 1). Examining prey distributions between sites, Old Chevak and Kigigak Island were different throughout the season, both pre-hatch ($\chi^2_2 = 11.9$, $P < 0.01$) and post-hatch ($\chi^2_5 = 22.3$, $P < 0.01$). The statistical significance of all the above tests remained the same when data from stomach contents (< 20% of all samples) were excluded.

Fish was a dominant component of the diet at all areas for pre- and post-hatch periods (Table 1). Saffron cod occurred in 60% of samples with up to 9 individual fish identified in a given sample. Identified species of fish other than saffron cod occurred in 28% of analyzed sets of boluses and food remains. Mollusks, primarily razor clams (*Siliqua alta*), were rare or absent from the diet prior to hatch at both Old Chevak and Kigigak Island, but were observed in > 20% of all samples after hatch.

Terrestrial mammals, primarily tundra voles, were not recorded in the diet at Kigigak Island, but occurred in 40% of Old Chevak samples prior to hatch and 10% after hatch. Egg remains were rare at Kigigak Island, but occurred in > 20% of samples at Old Chevak and Manokinak River after hatch and nearly 60% of samples at Old Chevak prior to hatch. Goslings and shorebirds were common diet items at both Old Chevak and Manokinak River, with > 60% of post-hatch samples containing goslings. Because the distribution of hatching dates for geese may encompass 10 or more days, some goslings appeared in pre-hatch samples and some eggs in post-hatch samples.

ISOTOPE ANALYSES

Evidence for geographic and temporal variation in diet was found using stable isotope analyses. Stable isotope values in both liver ($P = 0.04$) and muscle tissue ($P < 0.01$) of adult gulls differed between Kigigak Island and Manokinak River (Table 2). Stable isotope values in muscle ($P < 0.01$), but not liver ($P > 0.05$), tissue varied between pre- and post-hatch periods. Interactions between study area and time period were not significant for either liver ($P > 0.05$) or muscle ($P > 0.05$) tissue.

The $\delta^{15}N$ and $\delta^{13}C$ values in blood from gull chicks were correlated linearly (Fig. 2), and were significantly different among sites ($P < 0.01$). Samples from Kigigak Island differed from Manokinak River and Old Chevak ($P < 0.05$, Tukey's multiple comparison test, Fig. 2). Although samples from Old Chevak were more variable than those from Manokinak River, their mean values were not different ($P > 0.05$, Tukey's multiple comparison test).

Mean (± SD) $\delta^{15}N$ and $\delta^{13}C$ for three shorebird species (Black Turnstone *Arenaria melanocephala,* Dunlin *Calidris alpina,* and Semipalmated Sandpiper *Calidris pusilla*) were 7.5 ± 0.5‰ and −25.5 ± 2.5‰, respectively (Fig. 3).

TABLE 1. Taxa found in boluses, food remains, or digestive tracts of Glaucous Gulls on the Yukon-Kuskokwim Delta, Alaska, 1993. In the first column, *n* represents the total number of occurrences of a given taxon within all samples. The other four columns refer to Kigigak Island (KI) and Old Chevak (OC) during pre- and post-hatch periods and represent the proportion of samples within a given area and time period that contained at least one occurrence of that particular taxon or taxa. The number of samples contributing to the calculated proportion is given in parentheses. Due to sample size constraints and to enable direct comparison with Strang's (1976) data, we calculated proportions for broad categories rather than each individual species.

	n	KI-Pre (13)	KI-Post (48)	OC-Pre (21)	OC-Post (47)
Marine invertebrates		0.08	0.50	0.05	0.23
Mollusks		0.08	0.50	0.00	0.23
Natica spp.	13				
Mytilus edulis	3				
Siliqua alta	101+[a]				
Unknown bivalve spp.	2				
Other marine invertebrates		0.00	0.15	0.05	0.00
Isopoda spp.	13				
Ampipoda spp.	3				
Unknown starfish spp.	2+				
Unknown sea urchin spp.	1+				
Fish		0.77	0.50	0.76	0.79
Clupea harengus	19+				
Eleginus gracilis	138				
Unknown Gadidae spp.	22				
Lycodes spp.	2				
Myoxocephalus spp.	4+				
Unknown flatfish spp.	1				
Ammodytes hexapterus	1				
Unknown fish	49+				
Birds		0.15	0.46	0.67	0.72
Geese		0.00	0.27	0.43	0.62
Branta canadensis	5				
Chen canagica	1				
Anser albifrons	2				
Unknown Anserini spp.	121+				
Ducks					
Anas acuta	2				
Somateria mollissima	1				
Unknown Anatini spp.	2				
Shorebirds		0.00	0.06	0.48	0.32
Arenaria melanocephala	7				
Calidris alpina	3				
Unknown *Calidris* spp.	16				
Limnodromus griseus	11				
Other					
Lagopus lagopus	1				
Larus canus	1				
Xema sabini	1				
Unknown Larini spp.	4				
Catharus spp.	1				
Carduelis spp.	1				
Unknown bird	18+				
Eggs		0.00	0.08	0.62	0.19
Unknown Anserini spp.	11+				
Unknown Anatini spp.	6+				
Unknown Larinae spp.	5+				
Unknown bird	5+				
Mammals		0.00	0.00	0.38	0.08
Terrestrial					
Microtus oeconomus	35				
Sorex spp.	2				
Marine					
Unknown Phocidae spp.	1+				

[a] A + indicates a minimum count because in one or more samples it was not possible to determine if there was more than one individual contained within the given sample. This was always the case for eggs.

TABLE 2. Stable-carbon (C) and nitrogen (N) isotope values (mean ± SE in ‰) of adult Glaucous Gull tissues. Gulls were collected during mid to late incubation (Pre-hatch) and ≥4 weeks after peak hatch of geese (Post-hatch).[a] $n = 5$ except for muscle and liver tissues from Old Chevak, where $n = 10$.

Tissue		Kigigak Island		Manokinak River		Old Chevak
		Pre-hatch	Post-hatch	Pre-hatch	Post-hatch	Post-hatch
Muscle	C	−19.3 ± 0.1	−18.4 ± 0.3	−20.5 ± 0.5	−20.6 ± 0.6	−20.6 ± 0.2
	N	18.0 ± 0.1	17.9 ± 0.2	17.4 ± 0.3	16.1 ± 0.6	16.8 ± 0.3
Liver	C	−19.3 ± 0.2	−19.0 ± 0.2	−20.1 ± 0.6	−21.1 ± 0.9	−21.1 ± 0.5
	N	19.1 ± 0.1	19.7 ± 0.3	19.1 ± 0.5	17.7 ± 1.0	16.8 ± 0.6
Blood	C	−18.1 ± 0.1	−17.9 ± 0.1			−19.8 ± 0.3
	N	18.2 ± 0.1	18.9 ± 0.3			17.5 ± 0.4

[a] Pre-hatch samples were collected 3–13 June and 11–13 June at Kigigak Island and Manokinak River, respectively. Post-hatch samples were collected 17–18 July at Kigigak Island, 16–17 July at Manokinak River, and 12–19 July for five Old Chevak samples and 6 August for the other five samples.

Isotopic means for embryos of Cackling Canada Geese and Greater White-fronted Geese, 4- to 5-week-old Emperor Goose goslings, and tundra voles were all similar to those for shorebirds (Fig. 3). $\delta^{15}N$ and $\delta^{13}C$ for full-term embryos from Emperor Geese were more marine than other terrestrial prey, probably as a consequence of the marine diet of Emperor Geese prior to egg laying (Petersen et al. 1994). As Emperor Goose goslings grew, their isotopic signal became similar to that of the other goose species and terrestrial prey (Fig. 3; unpubl. data). Generally, $\delta^{15}N$ was less variable than $\delta^{13}C$. Mean $\delta^{15}N$ and $\delta^{13}C$ of these six terrestrial groups was 7.1 and −25.8, respectively. Means (and SDs) for bivalves and saffron cod also are shown in Figure 3.

Using the three-source isotopic mixing model, we estimated that the contribution of terrestrial foods to the diet of Glaucous Gulls varied from 7 to 23%, depending upon time and area (Table 3). Similar to the MANOVAs on the raw isotope values (Table 2), the proportional diet contribution of terrestrial prey was greater for Manokinak River and Old Chevak than for Kigigak Island (Table 3, $P < 0.01$). Also, chicks at all three study sites consumed a diet less heavily weighted towards saffron cod than did breeding adults from these same areas ($P < 0.01$).

DISCUSSION

COMPARISON OF 1970s AND 1993 DATA WITH CONVENTIONAL METHODS

We did not find evidence of any marked change in diet of Glaucous Gulls from that observed by Strang (1976, 1982) in the 1970s. No differences in diet among years were observed at Old Chevak, the only area studied during both the 1970s and 1993. Differences between Kokechik Bay in 1973 and Kigigak Island in 1993 were driven largely by differences in the occurrence of tundra voles. The annual variability in populations of these voles (Stickney 1989) makes it likely that there is annual variability in the frequency of predation on voles by gulls. These findings are similar to what Strang (1976, 1982) concluded for variation among years in the 1970s. Overall, our observed patterns of geographic and seasonal variation in diet corroborated those of Strang (1982).

SOURCES OF ERROR IN USING ISOTOPE MODELS

Isotopic mixing models require that the different prey sources be isotopically distinct from each other in order to be treated separately (Ben-David 1996); thus the similarity between shorebirds and goslings prohibited examining these two types of prey separately. Also, mixing models are somewhat sensitive to how many different sources are included in the model. For instance, if we had excluded bivalves as a prey source, our estimates of the contribution of terrestrial prey post-hatch (mostly goslings) to chick diets would have changed from 10–23% (the range among areas) to 12–43%. Bivalves are, however, a significant prey item based upon the conventional diet results and therefore we believe our three-source model is appropriate. Incorrect inclusion (or exclusion) of less common diet sources would have less pronounced effects on our results than the above example. More taxon specific prey sources could be modeled if finer isotopic resolution could be achieved. Use of additional stable isotopes, sulfur ($\delta^{34}S$) in particular, would likely allow greater segregation of the

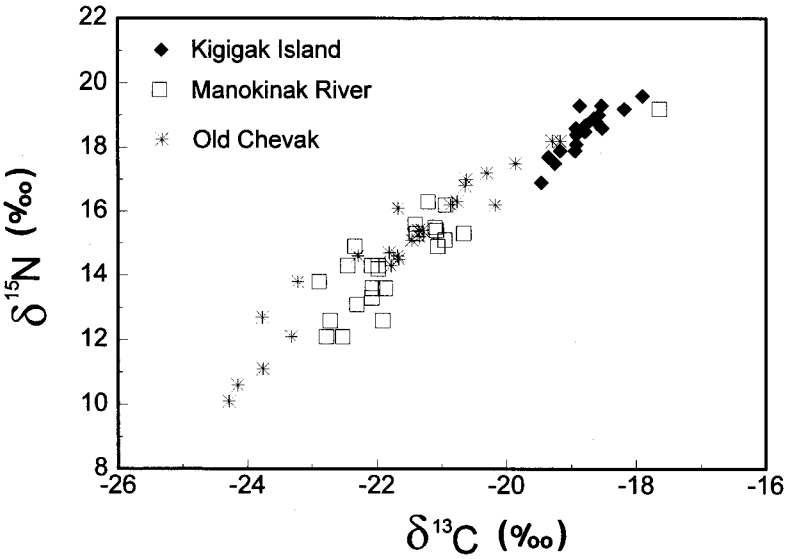

FIGURE 2. Stable-carbon and nitrogen isotope values for whole blood drawn from Glaucous Gull chicks at approximately four weeks of age at three different locations.

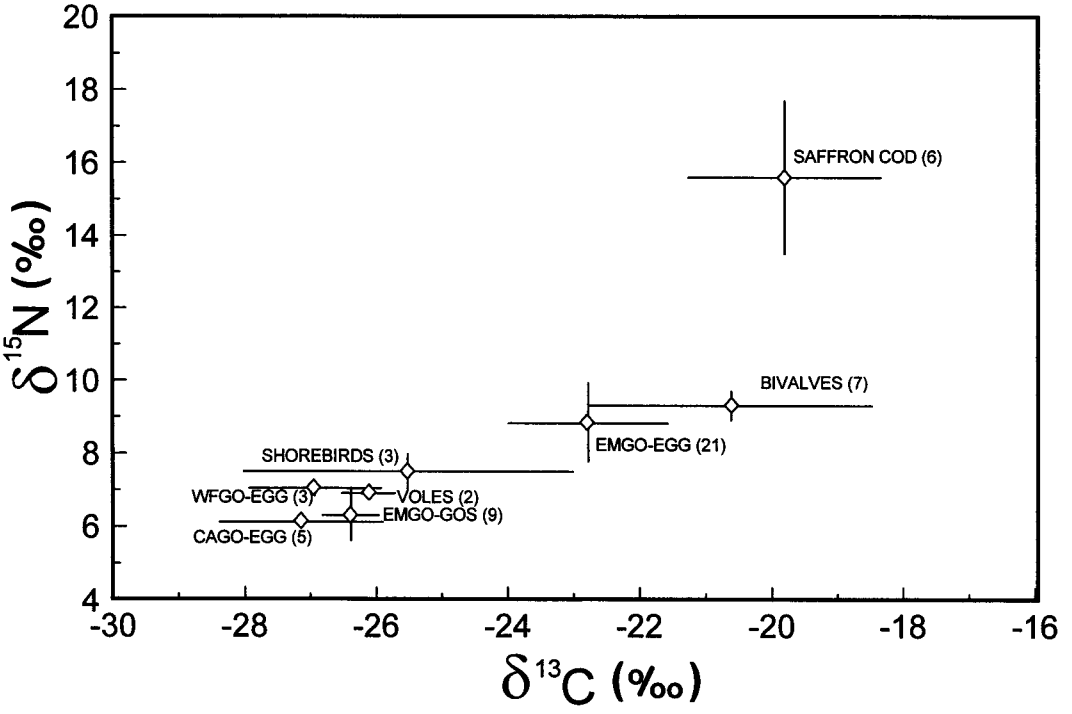

FIGURE 3. Stable-carbon and nitrogen isotope values for various taxa of Glaucous Gull prey. Specific species in each taxonomic grouping are given in the text. Means (◊) and SDs (horizontal and vertical lines) are based upon sample sizes shown in parentheses.

TABLE 3. Percent contribution (mean ± SE) of different prey in the diet of Glaucous Gulls on the Yukon-Kuskokwim Delta, 1993, as estimated from isotopic mixing models (Ben-David et al. 1997) and measures of ^{13}C and ^{15}N in muscle (adults) and blood (chicks).

	n	Goslings/ shorebirds/ eggs/voles	Saffron cod	Bivalves
Adults				
Kigigak Island				
pre-hatch	5	11.8 ± 0.7	70.0 ± 1.8	17.8 ± 1.0
post-hatch	5	6.6 ± 2.1	83.6 ± 5.3	10.0 ± 3.1
Manokinak River				
pre-hatch	5	18.4 ± 4.5	56.4 ± 3.9	25.2 ± 2.0
post-hatch	5	22.0 ± 4.2	48.0 ± 7.5	30.0 ± 3.7
Old Chevak				
post-hatch	10	20.3 ± 1.6	50.9 ± 3.4	28.7 ± 1.8
Chicks				
Kigigak Island	18	9.9 ± 0.3	73.0 ± 0.9	17.0 ± 0.6
Manokinak River	24	19.9 ± 0.7	29.2 ± 2.7	50.9 ± 2.4
Old Chevak	25	22.9 ± 2.8	39.9 ± 4.2	37.4 ± 2.6

terrestrial and marine signals within foodwebs (Hesslein et al. 1991).

Another probable source of error in the isotope models is the use of assumed isotope fractionation factors between diet and gull tissues. Although we used values derived from captive-rearing studies of piscivorous seabirds (Mizutani et al. 1991, Hobson and Clark 1992b), further studies are required to refine these estimates and to establish their general applicability across species. Fractionation values also may vary among individuals within a species (Ben-David 1996), but such differences are expected to be small (Hobson and Schwarcz 1985). Despite these limitations in developing isotopic models to estimate marine, terrestrial, and intertidal inputs to gull diets on the YKD, we are encouraged by the potential of this technique to investigate this and other questions. In particular, the strong correlation between $\delta^{13}C$ and $\delta^{15}N$ values in the blood of gull chicks with differential access to marine and terrestrial foods indicates that chick diets can be readily ascertained and monitored using routine techniques.

INFERENCES ON FEEDING ECOLOGY OF GULLS FROM STABLE ISOTOPE ANALYSES

Analyses of stable isotopes in muscle tissues revealed a pattern of geographic and seasonal differences in diet that was similar to results of the conventional diet analyses. Coastal gulls consumed less terrestrial prey than inland gulls, and the consumption of terrestrial prey was greater post-hatch than pre-hatch. Lack of a seasonal shift in isotope ratios in livers may have been a function of tissue turnover times and short-term (day-to-day or week-to-week) variations in diet. Based upon differential turnover rates among tissues, Hobson and Clark (1992a) and Hobson (1993) inferred that isotopic measurement of liver integrated dietary information over a period of about one week, whereas muscle tissue corresponded to four to six weeks. Thus, analysis of muscle tissues from the two seasonal periods in our study reflected integrations of diets throughout most of the pre-hatch and post-hatch periods, whereas liver tissues reflected only small subsets of these time periods and were therefore more sensitive to short term deviations from average diets. Overall, isotope values from Kigigak Island were less variable than those from Manokinak River and Old Chevak (Tables 2 and 3, Fig. 2). Kigigak Island gulls were almost uniformly marine feeders, whereas inland nesting gulls exhibited individual variation in how much they consumed marine prey. This pattern was evident for both adults and chicks (Tables 2 and 3, Fig. 2).

Using isotopic mixing models, estimates of the contribution of terrestrial prey to the diet of Glaucous Gulls varied from 7–22% for adults and 10–23% for chicks. Such estimates are not possible with conventional methods; nevertheless, one may be tempted to form a mental approximation of diet contributions upon examining frequency of occurrence data in Table 1 and in Strang (1976, 1982). The actual contribution

of terrestrial prey to diets of adult gulls based upon stable isotope models is lower than what one might infer from frequency of occurrence data (> 60% occurrence of goslings). Such a different perspective from examination of boluses, food remains, and stomach contents could occur simply by sampling near nests and chicks located near terrestrial prey. Soft-bodied marine prey and bones of small fishes may be completely digested by the strong gastric action in gulls (Barry and Barry 1990) before they return from their marine foraging areas. Additionally, because adults fed their young a smaller proportion of marine prey than they consumed themselves, as demonstrated by the isotopic models (Table 3), conventional food habits data collected near nests and chicks resulted in a diet perspective that is not representative of either age class alone, but rather is a composite of both adults and their young.

Dietary differences between adult gulls and their young has not been noted often. However, previous studies have recorded temporal shifts in how much fish are consumed by gulls (Murphy et al. 1984, Pierotti and Annett 1990), and Tinbergen (1960) observed that adult Herring Gulls (*L. argentatus*) consumed bivalves while feeding fish to their young. Using stable isotope techniques, Hobson (1993) determined that while Black-legged Kittiwakes (*Rissa tridactyla*) at a high Arctic colony fed their young primarily Arctic cod (*Boreogadus saida*), they depended themselves more on *Parathemisto* amphipods. These differential feeding patterns were attributed to variability in abundance (Murphy et al. 1984) and quality (Pierotti and Annett 1990) of prey. For gulls on the YKD, it is not clear why inland nesting adults fed more on marine prey than they fed to their young, but energetics of food transport and food quality are two possible contributing factors. For adults to feed marine prey (saffron cod) to their young, they would need to carry a food load farther than if they fed their young terrestrial prey (goslings and young shorebirds) that are common near gull nesting areas. It should be noted, however, that some marine foods may be accessible in and along the tidal rivers that bisect inland study areas, a pattern Strang (1976, 1982) deduced based upon average flight directions of gulls from his inland study site. Fish and gosling prey may differ in nutritive content, which also could lead to age differences in feeding if adults have different nutritive and energetic needs than their young. Goslings have high lipid content at hatch, but this steadily declines as goslings increase only muscle and skeletal mass during growth (Sedinger 1986). Proximate analyses of saffron cod have not been conducted, but Pacific herring (*Clupea harengus*), the next most common fish species in gull diets (Table 1), had high fat contents compared to other Bering sea fishes (Stansby 1976).

Sampling concerns necessitated that we focus this study on breeding gulls. However, a large number of nonbreeding Glaucous Gulls also spend some portion of the summer (mostly prehatch) on the YKD (Bowman et al. 1997). Observations of nonbreeders at coastal locations and the pattern of breeding adults favoring marine foods in contrast to what they feed their young both suggest that nonbreeding gulls on the YKD have a largely marine diet that is probably similar to that observed for breeding adults from Kigigak Island.

Our data and those of Strang (1976) indicate that there has been no large change over time in how much individual Glaucous Gulls consume gosling prey. Glaucous Gull numbers have approximately doubled during the past decade (Bowman et al. 1996, 1997). This increase corresponded with large increases in sympatrically nesting Cackling Canada Geese and White-fronted Geese; however, during the same time period numbers of the less abundant Emperor Goose stayed approximately stable (Bowman et al. 1997). It is therefore possible that while Glaucous Gull predation of geese in general has remained the same over time, predation on individual species, such as Emperor Geese, has increased.

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