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Evaluating gull diets: a comparison of conventional methods and stable isotope analysis

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ABSTRACT. Samples such as regurgitated pellets and food remains have traditionally been used in studies of bird diets, but these can produce biased estimates depending on the digestibility of different foods. Stable isotope analysis has been developed as a method for assessing bird diets that is not biased by digestibility. These two methods may provide complementary or conflicting information on diets of birds, but are rarely compared directly. We analyzed carbon and nitrogen stable isotope ratios of feathers of Glaucous Gull (*Larus hyperboreus)* chicks from eight breeding colonies in northern Alaska, and used a Bayesian mixing model to generate a probability distribution for the contribution of each food group to diets. We compared these model results with probability distributions from conventional diet samples (pellets and food remains) from the same colonies and time periods. Relative to the stable isotope estimates, conventional analysis often overestimated the contributions of birds and small mammals to gull diets and often underestimated the contributions of fish and zooplankton. Both methods gave similar estimates for the contributions of scavenged caribou, miscellaneous marine foods, and garbage to diets. Pellets and food remains therefore may be useful for assessing the importance of garbage relative to certain other foods in diets of gulls and similar birds, but are clearly inappropriate for estimating the potential impact of gulls on birds, small mammals, or fish. However, conventional samples provide more species-level information than stable isotope analysis, so a combined approach would be most useful for diet analysis and assessing a predator's impact on particular prey groups.

RESUMEN. **Evaluando las dietas de gaviotas: una comparación de métodos convencionales y el análisis de isótopos estables**

Las muestras como las egagrópilas regurgitadas y las sobras de comida han sido tradicionalmente usadas en los estudios de las dietas de las aves, pero pueden producir estimaciones sesgadas, dependiendo de la digestibilidad de diferentes alimentos. El análisis de los isótopos estables ha sido desarrollado como un método para evaluar las dietas de las aves que no es sesgado por la digestibilidad. Estos dos métodos pueden proveer información sobre las dietas de las aves que es o no es complementaria, pero son raramente comparados directamente. Analizamos las proporciones de isótopos estables de carbón y de nitrógeno en las plumas de pichones de la gaviota *Larus hyperboreus* de ocho colonias reproductivas en el norte de Alaska, y usamos una comparación Bayesiana en modelos mixtos para generar una distribución de probabilidad sobre la contribución de cada grupo de alimento a las dietas. Comparamos estos resultados de modelo a las distribuciones de probabilidad de muestras convencionales de la dieta (egagrópilas regurgitadas y sobras de comida) de las mismas colonias y periodos de tiempo. En relación a las estimaciones de los isótopos estables, los análisis convencionales a menudo sobre-estimaron las contribuciones de aves y pequeños mamíferos a las dietas de las gaviotas y a menudo subestimaron las contribuciones de pescado y zooplancton. Los dos métodos dieron estimaciones similares para las contribuciones a la dieta de carroña de caribú, alimentos marinos misceláneos, y basura. Entonces, las egagrópilas regurgitadas y sobras de comida pueden ser útiles para evaluar la importancia de la basura en relación a ciertos otros tipos de alimento en las dietas de las gaviotas y aves similares, pero son claramente inapropiadas para estimar el impacto potencial de las gaviotas sobre las aves, pequeños mamíferos, o peces. Sin embargo, las muestras convencionales proveen mas información a nivel de especie que el análisis de isótopos estables, y por eso una metodología combinada es la mas útil para el análisis de la dieta y para evaluar el impacto de un predador sobre los particulares grupos de presa.

Key words: Alaska, Glaucous Gull, *Larus hyperboreus*, MIXSIR, predator-prey relationships

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Diet studies are used in a variety of applications to understand birds and their relationships to their habitats and communities (Montevecchi 1993, Bearhop et al. 2001, Ballard et al. 2004). Conventional methods of diet assessment, such as analyzing regurgitated pellets and food remains, can be useful in studies of the diets of predatory birds such as gulls, raptors, and ravens (Real 1996, Duhem et al. 2003, Kristan et al. 2004). These food samples are easily collected, but are typically biased toward foods with large or abundant indigestible parts (Mariano-Jelicich and Favero 2006, Lindsay and Meathrel 2008). Highly digestible foods are underrepresented or not detected. Quantifying the biases in these samples would better define the types of questions that can be answered by using these samples.

In contrast to conventional diet samples, stable isotope ratios can be used as unbiased representations of foods digested and absorbed by an animal (Hobson and Clark 1992a,b). Carbon and nitrogen stable isotope ratios in organisms vary predictably among different food webs, and foods from different habitats or trophic levels often have distinct isotopic signatures (Peterson and Fry 1987, Post 2002). For example, organisms from terrestrial food webs based on plants that use a C4 photosynthesis pathway have higher (more enriched) stable carbon isotope ratios than those from food webs based on plants that use a C3 pathway (Wooller et al. 2007). Marine organisms typically show stable carbon isotope ratios intermediate between those from terrestrial C3 and C4 pathways, but stable nitrogen isotope ratios are also higher in marine organisms so marine and terrestrial food webs can be distinguished in this way (Peterson and Fry 1987). The contribution of each food web to an organism's diet can be inferred by analyzing the stable isotope ratios of a tissue from that consumer and correcting for diet-tissue isotopic discrimination (Bearhop et al. 1999). The turnover rate of the tissue relative to changes in diet must be known (Hobson and Clark 1992a), and a fairly accurate estimate of diet-tissue discrimination is also necessary to accurately describe diets using stable isotope analysis (Vander Zanden and Rasmussen 2001).

When good information is available and an organism uses only a few types of isotopically distinct foods, calculating the contribution of each food type to the overall diet is relatively straightforward (Phillips 2001). However, determining the contributions to overall diet when organisms consume a greater variety of food items, or foods with overlapping isotopic signatures, can be difficult (Phillips and Gregg 2003; but see also Phillips et al. 2005). Recently, a Bayesian mixing model (MIXSIR) was developed to deal with overlapping prey signatures and other sources of uncertainty (Moore and Semmens 2008, Jackson et al. 2009, Semmens et al. 2009). MIXSIR accounts for uncertainty in food signatures and discrimination factors by incorporating standard deviations as well as mean values. The model deals with uncertainty and with overlapping prey signatures by giving a range of potential contributions to diet, rather than a specific estimate, for each food group. These ranges are often wide, but can be narrowed by including prior information about diet composition from other sources (e.g., stomach contents).

We used stable isotope analysis to evaluate diet information gained from regurgitated pellets and food remains produced by Glaucous Gulls (*Larus hyperboreus*) in northern Alaska. Glaucous Gulls are opportunistic predators that feed on most of the other wildlife in this area (Weiser and Powell 2010). The extent to which Glaucous Gulls use human food waste is of interest because use of anthropogenic foods can contribute to increases in gull populations (Conover 1983, Duhem et al. 2008). If gulls feed extensively on other breeding birds, these larger populations could then cause or exacerbate population declines of those birds (Guillemette and Brousseau 2001, Finney et al. 2003). An accurate evaluation of the use of garbage and bird prey by gulls is therefore of interest in many human-influenced systems. Both of these foods contain indigestible material and are easily detected in pellets and food remains, but whether the amount of indigestible material accurately portrays the use of each food source by gulls is unclear. Garbage has a distinct isotopic signature in northern Alaska because of the strong influence of corn, a C4 plant, in human foods in North America (Jahren and Kraft 2008). Most vegetation on the tundra of northern Alaska consists of grasses and sedges, most of which are C3 plants (Wooller et al. 2007), so terrestrial herbivores would show a clearly C3-based isotopic signature. Any C4-type isotopic signature (reflected in more

enriched stable carbon isotope ratios) detected in gull tissues would be due to garbage in their diet. Birds (mostly shorebirds and waterfowl) in this region typically feed on marine foods during winter and terrestrial or freshwater foods during summer so, over the summer, their tissues transition from marine (more enriched stable carbon and nitrogen isotope ratios) to terrestrial isotopic signatures (more depleted ratios). These birds thus may be isotopically distinct from some other natural foods. Stable isotope analysis could therefore be a useful tool to assess the accuracy of pellets and food remains in determining the amount of garbage and birds in gull diets.

We used MIXSIR to predict gull diets based on the stable isotope signatures of chick feathers from several Glaucous Gull colonies, and compared these results with conventional diet data from regurgitated pellets and food remains collected during the chick-rearing period at the same colonies. We predicted that foods with large or abundant indigestible parts, such as birds and small mammals, would be more strongly represented in gull pellets and food remains relative to estimates from the stable isotope models, and that more digestible prey, including fish and zooplankton, would be poorly represented in conventional samples. We were unsure how garbage would be portrayed in these food samples because the proportion of indigestible refuse gulls swallow when foraging at garbage dumps is unknown.

METHODS

Study area. We monitored the diet of Glaucous Gulls at eight colonies (three in 2008 and five in 2009) in four regions of northern Alaska (Fig. 1). Glaucous Gulls nested in small groups (5 – 30 pairs), generally on small islands in tundra lakes, sometimes with breeding geese interspersed. A variety of shorebirds and waterfowl, loons, ptarmigan, and a few sparrows nested in this region; lemmings, voles, and freshwater and marine fish were also available as potential prey. Subsistence-hunted whale, seal, caribou, and waterfowl carcasses were often available to be scavenged near residential areas. Municipal landfills were present in residential and industrial areas. The landfill at Prudhoe Bay was the largest; other areas typically incinerated garbage before disposing of ashes in landfills. Barrow had about 4000 residents, Nuiqsut had a population of about 430, and the Alpine oilfield hosted about 150 workers.

We visited each colony twice each summer, once during the period from 15 to 29 June when gulls were incubating eggs (prehatch) and again from 28 July to 11 August just before chicks began fledging (chick-rearing). We timed the first visit to each colony based on local breeding phenology and allowing for the earlier egg-laying period of more southerly colonies and later laying period of more northerly colonies (D. Troy and ELW, unpubl. data). We scheduled second

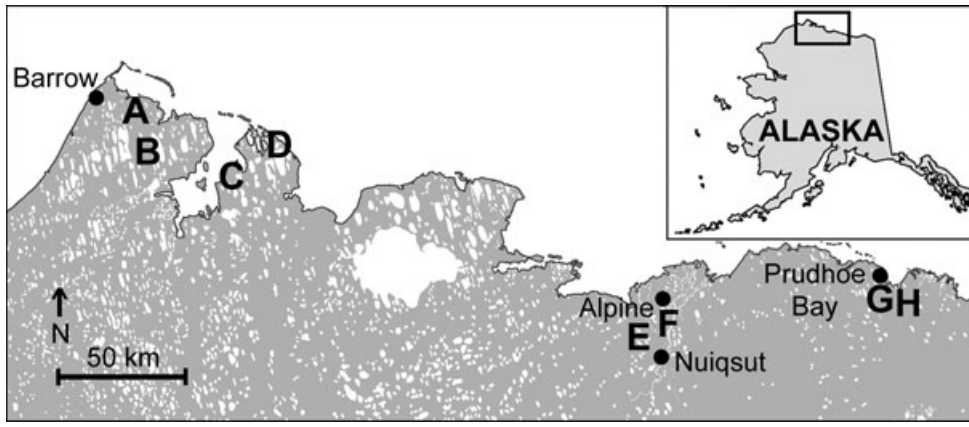

Fig. 1. Collection sites (breeding colonies) for conventional diet samples (pellets and food remains) and stable isotope samples (chick feathers) for analysis of the diet of Glaucous Gulls in northern Alaska. Colonies A, B, and D were sampled in 2008; all others were sampled in 2009.

visits based on the age of eggs during first visits, determined by floating the eggs in water (ELW, unpubl. data), and assuming a 28-d incubation period and a 42 to 48-d nestling period (Uspenski 1958). Chicks averaged 30 d old (range = 15–38 d) during second visits to colonies. We accessed one or two colonies per day by helicopter, vehicle, or foot, and traveled through colonies on foot and small inflatable rafts.

Conventional diet analysis. During each colony visit, we collected regurgitated pellets and food remains from areas around gull nests (on the nest islands and immediately adjacent shoreline). Both types of samples were composed of indigestible parts of food items; pellets were regurgitated in relatively compact form, whereas food remains were regurgitated singly or never ingested. Glaucous Gulls exclude other avian predators, such as jaegers and owls, from their colonies (ELW, pers. obs.) so we could be certain that gulls produced all samples. We collected only fresh items with no evidence of weathering (sun bleaching or epiphyte growth) to ensure that samples reflected diets during the targeted year and reproductive period. For our analysis, we used only data from samples collected during the second (chick-rearing period) colony visits. Collecting all samples from the pre-hatch period ensured that samples from the second visit were primarily representative of diets during the chick-rearing period.

We identified all food items within these samples to the lowest possible taxonomic level. We then grouped foods at the taxonomic level at which they were consistently identifiable in diet samples and so that stable isotope signatures of specific foods were similar in each food group: garbage, birds, small mammals, caribou, fish, zooplankton, and other marine foods (marine mammals and crustaceans). Anthropogenic items in diet samples, such as plastic, paper, aluminum foil, or chicken bones, indicated consumption of garbage. We could not differentiate anthropogenic from natural fish bones in the samples, so we lumped all fish remains into one category. To estimate the relative importance of each food group in the diets of gulls at each colony, we then randomly subsampled, with replacement, the original dataset from each colony. Each subsample was two-thirds the size of the original dataset. We calculated the frequency of occurrence of each food group in the subsample as the proportion of pellets and food remains containing some element of that group, then proportionally adjusted these values so that diet composition summed to 1.0. This gave the proportional contribution to diet of each food group. We repeated the subsampling procedure 100, 000 times to create a probability distribution for the contribution of each food group to diet for each colony. We truncated each of these distributions at the first and 99th percentiles to remove outliers, leaving about 98,000 subsampled estimates of diet composition for each colony. From these, we calculated the range of possible contributions and the most likely contribution (the maximum of the probability distribution) to diet for each food group.

Stable isotope analysis. For colony visits during the chick-rearing period, we used small inflatable rafts (propelled by kayak paddles) to pursue and capture as many gull chicks as possible, given wind speed, lake size, and window of helicopter availability, at each colony. We sampled one mantle feather from each chick for stable isotope analysis. These feathers are grown between 8 and 30 d of age (ELW, unpubl. data), so their stable isotope ratios represent diet during that period and do not change after feather growth is complete (Bearhop et al. 2002).

We stored feather samples in dry envelopes at room temperature. Prior to analysis, we cleaned the feathers of surface contaminants using 100% ethanol and allowed them to air dry. We submitted 0.2 to 0.4 mg of material from the distal tip of each feather to the Alaska Stable Isotope Facility (University of Alaska Fairbanks) for carbon and nitrogen isotope ratio analysis ($\pm$ 0.25‰) in a continuous-flow system with a Costech Elemental Analyzer (ESC 4010), ThermoFinnigan Conflo III interface, and Delta^{plus} XP Mass Spectrometer. We expressed the isotope ratios in delta notation relative to international standards (Vienna PeeDee Belemnite for carbon, atmospheric air for nitrogen) according to the following equation: $\delta X = ([R_{sample}/R_{standard}] - 1) \times 1000‰$, where X is either ^{13}C or ^{15}N, and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively, for the sample and the standard.

We obtained isotopic signatures of potential foods, including garbage, from the literature and from unpublished databases for northern Alaska and outlying waters (Appendix 1). We used only values from samples collected in this region

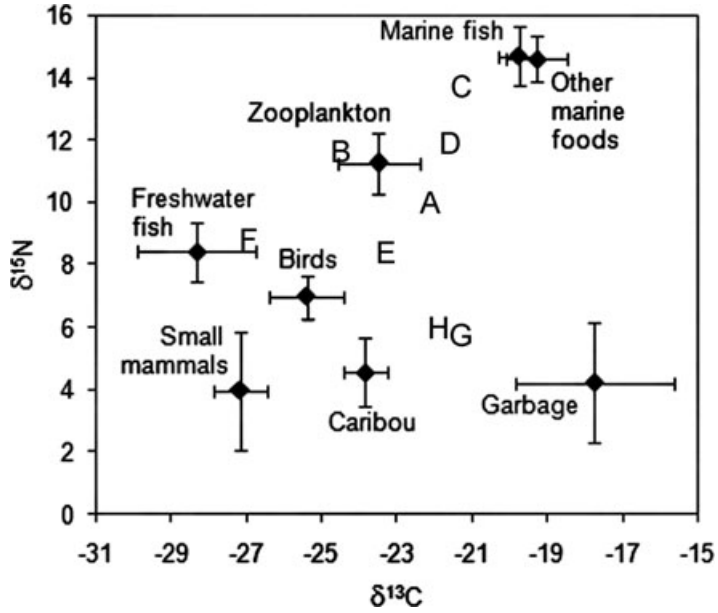

Fig. 2. Stable carbon and nitrogen isotope signatures (mean ± SD; in per mil relative to international standards) of food groups used in the stable isotope mixing models for estimating Glaucous Gull diets. Refer to Appendix for the species that make up each food group and the literature reference for each value. Letters indicate the mean stable carbon and nitrogen isotope signatures, corrected for average diet-tissue discrimination estimates, of feathers of Glaucous Gull chicks collected at each colony in northern Alaska.

during the gull breeding season (May – August) to ensure that our values represented as nearly as possible the foods actually consumed by gulls at our colonies. We supplemented these values by collecting samples of additional potential prey in 2009, including muscle tissue from unidentified crabs, marine isopods (*Saduria entomon*), and adult shorebirds and passerines found dead. We freeze-dried the tissues and submitted 0.2 to 0.4 mg subsamples for analysis at the Alaska Stable Isotope Facility.

We used the same food groups for isotopic analysis as for conventional analysis, except we separated marine and freshwater fish that have very different stable isotope signatures (Fig. 2). Grouping foods reduced the isotopic redundancy of individual foods and facilitated comparisons with conventional data. When combining isotopic values from several specific foods into one group, we used the arithmetic mean of the foods being combined, and calculated the standard deviation as:

$$\overline{SD} = \sqrt{\frac{\sum_{i=1}^{g} V(n_i - 1)}{\left(\sum_{i=1}^{g} n_i\right) - g}},$$

where V_i = variance of food i, n_i = sample size for food i, and g = number of specific foods combined into that group. We first calculated this value to combine foods within subgroups (e.g., various ducks and geese combined into "waterfowl") and then to combine subgroups into groups (e.g., waterfowl, shorebirds, and passerines combined into "birds") to avoid biasing group values by subgroup sampling effort (Appendix 1).

We used the Bayesian stable isotope mixing model MIXSIR (Semmens and Moore 2008) to estimate the range of possible contributions of each food group to gull diets at each colony based on the isotopic signatures of chick feathers. In each model, we used the mean and standard deviation of isotope signatures for each food group (Fig. 2; Appendix 1), excluding garbage from the models for two colonies (C and D) that were beyond the typical foraging range of breeding Glaucous Gulls (~60 km; D. Troy, unpubl. data) from the nearest landfill. Rather than biasing models with prior information from our conventional samples, we used an uninformative Dirichlet prior distribution in the models. We used the mean and standard

Table 1. Number of conventional diet samples (pellets and food remains) collected, number and percent (of all those present at the colony) of chicks sampled, and mean stable isotope signatures (± SD) of chick feathers from eight Glaucous Gull colonies in northern Alaska.

Colony	Conventional samples	Chicks sampled		Isotopic signatures	
		N	%	$\delta^{13}C$	$\delta^{15}N$
A	302	15	83	–20.6 ± 1.3	13.7 ± 2.1
B	211	14	37	–23.0 ± 1.8	15.3 ± 1.2
C	59	5	83	–19.8 ± 0.3	17.4 ± 0.5
D	61	6	50	–20.1 ± 0.8	15.6 ± 0.7
E	126	7	54	–21.8 ± 0.9	12.0 ± 1.0
F	200	10	40	–25.4 ± 2.1	12.4 ± 1.6
G	97	5	21	–19.8 ± 1.0	9.3 ± 1.3
H	59	6	35	–20.4 ± 1.5	9.6 ± 1.5

deviation of diet-feather discrimination values from captive studies where adult Ring-billed Gulls (*Larus delawarensis*) and Great Skuas (*Catharacta skua*) were fed a carnivorous diet (fish or beef; Hobson and Clark 1992b, Bearhop et al. 2002), and corrected for the fact that chicks in our study were growing by reducing the mean value for $\delta^{15}N$ discrimination by 0.55‰ (Sears et al. 2009). The final discrimination values used in the model were therefore + 1.5‰ ± 1.1 for $\delta^{13}C$ and + 3.7‰ ± 1.1 for $\delta^{15}N$.

We evaluated the fit of each model by checking that the number of posterior draws was over 1000, there were no duplicate draws, and the ratio of best posterior density to total posterior density was < 0.01 (Moore and Semmens 2008). If a model did not meet any one of these criteria, we ran it again with more iterations until the criteria were satisfied. For comparison with the conventional analysis, we summed the estimated contributions of marine and freshwater fish to calculate the contribution of total fishes for each colony. We then calculated probability distributions for the contribution of each food group to diet at each colony. As with the conventional probability distributions, we truncated these at the first and 99th percentiles to remove outliers and give the range of possible contributions and the most likely estimated contribution of each food group at each colony.

Differences between methods. For each food group at each colony, we compared the truncated probability distribution for contribution to diet from conventional analysis to that from the stable isotope mixing model. In each comparison, we calculated the proportion of the conventional subsamples that fell above or below the range of contributions estimated by the stable isotope model. We examined the magnitude of difference in each case by subtracting the most likely stable isotope estimate of contribution from the most likely conventional model estimate. We calculated the mean and standard deviation of these differences across colonies to evaluate general trends in biases present in conventional diet data.

RESULTS

We collected pellets and food remains (range = 59–302) from each Glaucous Gull colony just before chicks began fledging (Table 1). Conventional analysis of these samples showed that diet varied across colonies, with small mammals, birds, garbage, and fishes comprising most of the foods consumed (Fig. 3). We identified 40 species (birds, mammals, and crustaceans) in conventional samples; only one (caribou) would have been identified by the stable isotope models alone, and the models would not have been able to unequivocally confirm its presence in the diet of gulls at any colony.

We captured chicks (range = 5–15, or 21–83% of those present) at each colony (Table 1). Isotopic signatures of chick feathers varied among colonies, especially in $\delta^{15}N$ (Table 1, Fig. 2). Each of our final MIXSIR models required between 10×10^5 and 20×10^9 iterations. Each model run resulted in >1600 posterior draws with no duplicates and a ratio of best posterior density to total posterior density of < 0.008. Most models ran within a few seconds or minutes, but the two models requiring

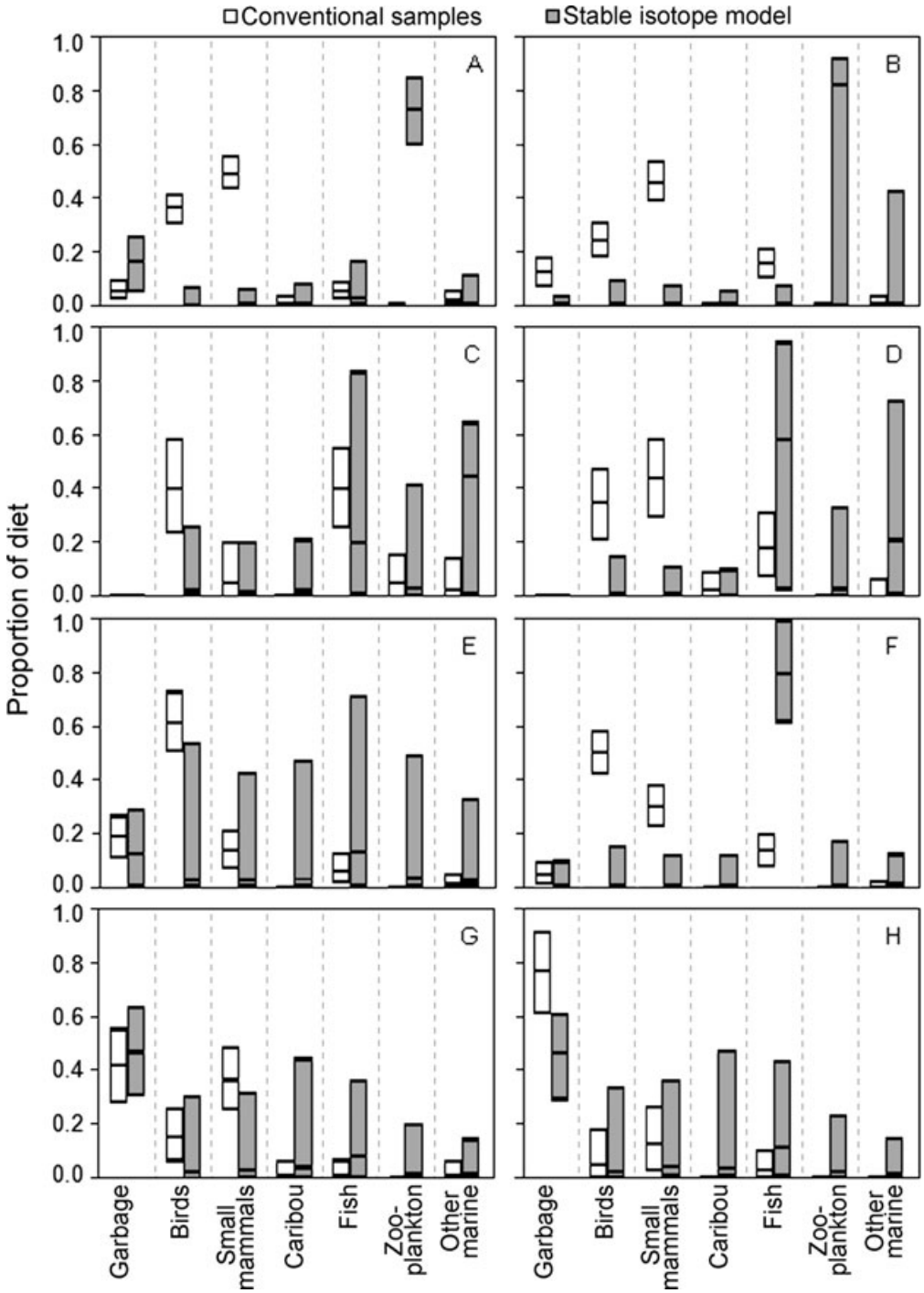

Fig. 3. Most likely value (middle line) and 98% confidence interval (outer lines) for the contribution of each food group to the diets of Glaucous Gulls at each of eight colonies in northern Alaska. White bars indicate estimates from conventional diet samples (pellets and food remains); gray bars indicate estimates from stable isotope mixing models. Where bars do not overlap, estimates are significantly different.

the most iterations each took 2.5 d to run on a 2008 laptop (2.4 GHz duo core processor, 2 GB RAM), indicating difficulty in resolving the diet estimates for those two colonies (A and B).

The range of possible contributions of each food group given by the stable isotope mixing models was often wide and poorly resolved; estimates of dietary proportions often differed substantially between methods (Fig. 3). Several food groups tended to be either over- or underestimated by conventional methods relative to stable isotope analysis, with the representation of each food group having some chance of differing between methods for at least three of the eight gull colonies, usually in the same direction each time (Table 2). The difference between methods was largest for birds and small mammals, substantial for fish and zooplankton, and minor for other food groups (Fig. 4).

DISCUSSION

Glaucous Gulls in our study consumed a variety of foods, with considerable variation among colonies. Conventional estimates of diet composition did not always agree with stable isotope estimates, and generally overemphasized contributions to diet of food groups with abundant indigestible parts. This was most pronounced for birds and small mammals, with both typically dramatically overrepresented in conventional samples relative to stable isotope estimates. Because of the large amount of indigestible material (feathers) in bird meals, gulls and related birds may produce several extra pellets per meal of avian prey (Votier et al. 2001). The fur and bones of small mammals are also largely indigestible and their presence in diet may also be overestimated by examination of conventional samples (Votier et al. 2003). Use of only conventional data would therefore overestimate the extent to which gulls feed on other birds and small mammals. Indigestible fur and feathers are not incorporated into gull tissues so stable isotope models may provide more accurate estimates of the contribution of these prey types in gull diets.

Unlike small mammals, the most likely contribution of caribou to diet was similar between the two methods. Glaucous Gulls in our study area had access to this food source by scavenging caribou remains left by local hunters. These remains included highly digestible soft parts, large bones that gulls would likely avoid swallowing, and fur that they may or may not swallow along with digestible material. The agreement between the two methods suggests that gulls swallow similar proportions of digestible material and indigestible fur from caribou remains. However, both methods indicated that caribou was a very minor part of the diet of gulls at each colony, so we cannot be certain that the methods would be in similar agreement if caribou were a more important food item.

We found that conventional and stable isotope estimates generally agreed on the proportion of gull diets made up of garbage, indicating that the indigestible waste in conventional samples accurately represented the amount of food waste ingested by gulls. The amount of garbage consumed by gulls was overrepresented by conventional samples from two colonies relative to stable isotope estimates, but the difference was substantial for only one colony. For the remaining colonies, the two methods agreed on the importance of garbage, relative to other food groups, in gull diets. Because of the near-absence of C4 terrestrial plants in our study area, the stable isotope models easily differentiated between garbage and natural terrestrial food sources; these two groups would be less distinct where both C3 and C4 plants occur naturally or where the corn signature is less prevalent in human foods.

The two methods also generally agreed on the proportion of miscellaneous marine foods in gull diets. These foods potentially included scavenged whale and seal carcasses and crustaceans. Scavenged carcasses of whales and seals would consist mostly of highly digestible meat, and gulls would likely be unable to swallow the large indigestible bones. However, the remains of crab and isopod shells were easily detected in pellets and food remains. Agreement between methods on the use of marine foods suggests that gulls generally consumed similar amounts of digestible and indigestible marine prey. However, at two colonies (C and D), stable isotope models indicated much higher contributions of marine foods to gull diets than conventional samples, suggesting that gulls at these colonies may have relied more on scavenged whale and seal carcasses.

As expected, stable isotope models generally produced higher estimates of the use of highly digestible foods (zooplankton and fish)

Table 2. Proportion of subsamples of conventional data from each colony that gave overestimates (a) or underestimates (b), relative to the range of possible contributions estimated by the stable isotope model, for the contribution of each food group to diets of eight Glaucous Gull colonies in northern Alaska.

Colony	Garbage	Birds	Small mammals	Caribou	Fish	Zoo-plankton	Other marine
(a) Proportion of overestimates							
A	0	1.00	1.00	0	0	0	0
B	1.00	1.00	1.00	0	0	0	0
C[a]	-	0.99	0	0	0	0	0
D[a]	-	1.00	1.00	0	0	0	0
E	0	0.96	0	0	0	0	0
F	0	1.00	1.00	0	0	0	0
G	0	0	1.00	0	0	0	0
H	1.00	0	0	0	0	0	0
(b) Proportion of underestimates							
A	0.43	0	0	0.02	0	1.00	0
B	0	0	0	1.00	0	1.00	0.07
C[a]	-	0	0.03	1.00	0	0.07	0.14
D[a]	-	0	0	0.26	0	1.00	0.52
E	0	0	0	1.00	0	1.00	0.26
F	0	0	0	1.00	1.00	1.00	0.52
G	0	0	0	0.27	0.27	1.00	0.27
H	0	0	0	1.00	0.26	1.00	1.00

[a]Garbage was not available to gulls at this colony and was not included in the isotope model.

than conventional data. Because zooplankton are likely easy to digest, we did not expect this food item to be well represented in conventional diet samples. Our stable isotope models indicated high use of zooplankton at two colonies (A and B), but we did not detect this prey in gull diets at these colonies in conventional samples. At other colonies, both methods indicated that zooplankton were a minor food source. However, where gulls consumed zooplankton, conventional diet samples did not accurately indicate its importance in diet.

Differences between methods in estimates of the amount of fish in gull diets at some colonies were also pronounced. In most cases, stable isotope models estimated a greater contribution

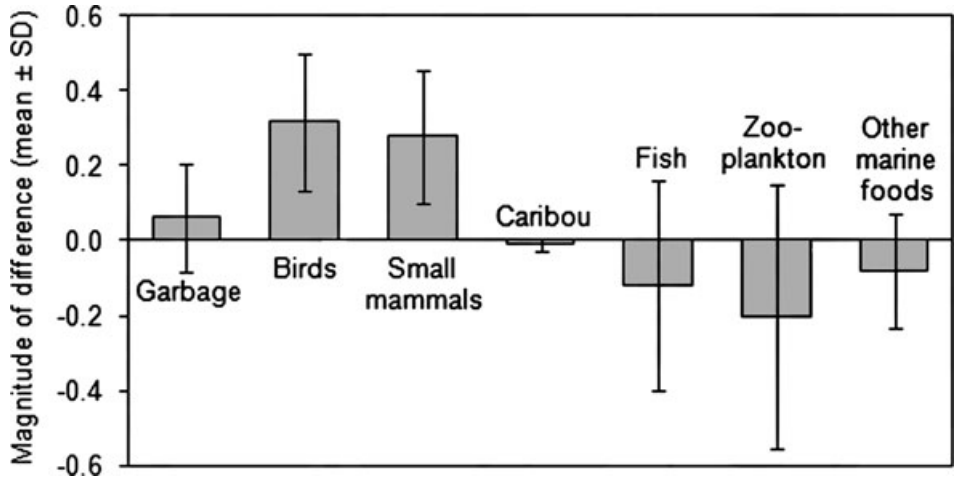

Fig. 4. Differences between conventional methods and stable isotope models in estimates of the most likely contributions of different food groups in the diet of Glaucous Gulls breeding at eight colonies in northern Alaska.

to diet than conventional data. Glaucous Gulls appear to efficiently digest bone (e.g., 99% of lemming and vole skulls in pellets were represented only by mandibles, teeth, and small skull fragments) and may digest many fish bones rather than regurgitating them. As also found in previous studies (Votier et al. 2003, Mariano-Jelicich and Favero 2006, Lindsay and Meathrel 2008), we found that pellets and food remains are not useful for assessing the amount of fish and other highly digestible prey in diets of predatory birds.

Aside from differences in what our two methods of diet assessment could detect, several aspects of our study design could explain discrepancies between conventional estimates and stable isotope models. We used conventional samples that had accumulated between our first and second visit to each colony, so these represented diet during the period from just before hatching to just before fledging. Stable isotope models, however, were based on isotope ratios of feathers grown between approximately 8-d-old and either sampling age or 30-dold, whichever came first. This difference in time periods sampled is potentially significant because some gull species may feed chicks different foods at different ages (Brousseau et al. 1996, Ramos et al. 2009). Our conventional samples represented diet at all ages whereas stable isotope samples did not represent diet during the first week after hatching or the last 10 d before fledging. If the diet of Glaucous Gull chicks changes with chick age, this difference would result in a discrepancy between the two methods in diet estimates. Similarly, if gulls at these colonies fed their chicks different prey than they consumed themselves (Schmutz and Hobson 1998), our conventional samples, representative of both chicks and adults, would provide a different estimate of diet than the analysis of chick feathers. Additionally, individuals in many species of gulls specialize on certain foods (Pierotti and Annett 1991, Watanuki 1992, Annett and Pierotti 1999), so diet may vary among individuals. If this is the case with Glaucous Gulls, our conventional samples would have represented diets averaged across each colony because we sampled all nests present, but our chick samples may have represented only certain breeding pairs and may have been influenced by individual specialization. Unfortunately, we could not assign chicks to particular nests because all chicks in a colony grouped together in the water as we approached. Finally, although we collected conventional samples from all nests at each colony, not all nests necessarily produced chicks that survived to near fledging. Diet is known to affect gull reproductive success (Baird 1990, Pierotti and Annett 1991), so our feather samples represented only those diets associated with reproductive success. Gulls that attempted to breed, but did not produce fledglings, would have been included in our conventional samples, but not in the stable isotope assessment. This discrepancy could further account for differences between the two methods in diet estimates. For example, fish is a high-quality food for gulls and can be associated with high reproductive success (Pierotti and Annett 1991). This could help explain why chick feathers indicated more fish in gull diets than conventional samples that represented both successful and unsuccessful breeders.

As in most stable isotope studies of animal diets, our models were based on several assumptions. We assumed that our stable isotope values for potential foods were correct, even though we did not have values for all species. We included stable isotope values for 12 of 22 families identified in our diet samples, and all families excluded were identified in $<1\%$ of conventional samples. However, we do not know if the values we included encompassed the full range of variation in isotopic signatures of each food group. In addition, our models assumed that diet–tissue discrimination values, including the correction for growth, were accurate for wild Glaucous Gull chicks. These values were the best available values relevant to our study species, and when we used them to correct gull feather stable isotope ratios for discrimination, the signatures fell within the isotopic space delineated by potential food sources (Fig. 2), suggesting the values were reasonable. Overall, we believe any potential biases in our stable isotope models were minor compared to the biases inherent in conventional methods of diet analysis. Therefore, where estimates based on the two methods differed substantially, the stable isotope model estimates were probably closer to true dietary proportions and can be used to identify trends for biases in the conventional data.

Although well-suited for examining broad patterns in food webs and trophic levels, stable

isotope analysis typically cannot provide species-level information on diet composition (Peterson and Fry 1987, Post 2002). Our conventional samples identified 39 species of prey in gull diets that would not have been identified by stable isotope analysis. These were species for which we did not have stable isotope signatures or that had similar signatures and could not reliably be distinguished isotopically.

Conventional diet data generally agreed with stable isotope model estimates of the importance of garbage in the diet of Glaucous Gulls and, therefore, could be a convenient and effective method for monitoring the use of garbage by human-subsidized birds. In contrast, conventional diet samples strongly disagreed with stable isotope model assessments of gull use of fish, birds, small mammals, and zooplankton. Using pellets and food remains to assess the impact of gulls on these types of prey, therefore, is probably not appropriate. Thus, conventional samples will continue to be useful for identifying prey species in the diets of avian predators, and stable isotope models, used in conjunction with conventional methods, could provide an assessment of the predator's impact on particular prey groups.

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Appendix 1. Stable carbon and nitrogen isotope values of potential prey of Glaucous Gulls in northern Alaska. Species were averaged into subgroups, then subgroups were averaged into food group values used in the stable isotope mixing models to estimate Glaucous Gull diets at eight colonies in northern Alaska.

Food group	Subgroup	Species	Tissue	Lipid-extracted?	Mean $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{13}C$	SD $\delta^{15}N$	*N*	Reference[a]
Garbage	Meat	Chicken	Chicken fillets	No	−17.4	2.3	0.5	0.3	158	1
		Beef	Burger patties	No	−18	6.1	2.9	0.6	165	1
					−17.7	4.2	2.1	1.9	323	
	Garbage average									
Birds	Waterfowl	*Somateria spectabilis* egg	Yolk + albumen	Yes	−22.5	9.3	1.5	1.1	39	2
			Yolk + albumen	Yes	−22.5	8.9	2.2	1.6	117	3
		S. spectabilis embryo	Feather	No	−22.4	9.9	0.9	1.8	14	3
		S. spectabilis spring female	Muscle	No	−17.8	14.5	0.5	0.8	8	3
		S. spectabilis prenesting	Red blood cells	No	−19.3	14.7	0.8	0.9	51	3
		S. spectabilis nesting female	Red blood cells	No	−21.2	12.3	1	0.9	6	3
		S. spectabilis postbreeding	Whole blood	No	−21.9	6.9	1.8	0.4	7	3
		S. spectabilis average			−20.5	11.6	0.9	0.7	242	
		Clangula hyemalis	Yolk + albumen	Yes	−22.3	9.1	2	1.4	29	2
		Chen caerulescens egg[b]	Yolk + albumen	Yes	−24.9	5.5	0.4	0.9	20	4
			Yolk + albumen	Yes	−24.6	5.8	0.7	0.9	20	4
			Yolk + albumen	Yes	−24.2	6	0.9	1.5	25	4
		C. caerulescens adult[b]	Muscle	No	−22.3	6.3	0.9	0.4	19	4
			Muscle	No	−19.6	7	1.3	0.6	25	4
			Muscle	No	−20.8	6.7	1.3	0.4	20	4
		C. caerulescens average			−22.7	6.2	1	0.9	129	
		Waterfowl average			−21.8	9	1.1	0.8	400	
	Passerines	*Calcarius lapponicus*	Muscle	No	−26.5	5.9			1	5
		Plectrophenax nivalis	Muscle	No	−26.7	6.4			1	5
		Carduelis flammea	Muscle	No	−25.2	2.9			1	5
		Passerine average			−26.1	5.1	0.8	1.9	3	
	Shorebirds	*Phalaropus lobatus*	Muscle	No	−26.6	7.9			1	5
		Pluvialis dominica	Muscle	No	−29.5	7.0			1	
		Shorebird adult average			−28.1	7.4	2.1	0.7	2	
		Shorebird eggs	Yolk + albumen	No	−28.8	5.1	2.8	1.1	327	6
		Shorebird average			−28.3	6.9	0.9	0.3	329	
					−25.4	7	1	0.7	732	
	Bird average									
Small mammals		*Spermophilus parryii*	Muscle	No	−26.9	3.7	1	1.9	4	7
		Dicrostonyx, Lemmus, Microtus spp.	Muscle	No	−27.5	4.2	0.6	1.9	15	7
					−27.2	4	0.7	1.9	19	7
	Small mammal avg.									
Caribou		*Rangifer tarandus*	Hair	No	−23.8	4.6	0.6	1.1	12	7
Freshwater fish[c]		*Catostomus catostomus*	Muscle	No	−28.2	8.2	0.5	0.5	16	8
		Thymallus arcticus	Muscle	No	−27.8	8.6	0.9	0.6	22	8
		Pungitius pungitius	Muscle	No	−29	8.4	2.3	1.4	25	8
					−28.3	8.4	1.6	1	63	

(Continued)

Appendix 1. *(Continued)*

Food group	Subgroup	Species	Tissue	Lipid-extracted?	Mean $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{13}C$	SD $\delta^{15}N$	*N*	Reference[a]
	FW fish average									
Marine fish		*Eleginus gracilis*	Whole	No[d]	−20.0	14.2			1	9
		Ammodytes hexapterus	Whole	No[d]	−20.5	14.6			1	9
		Boreogadus saida	Whole	No[d]	−18.9	15.5	0.4	1	24	9
		Osmerus mordax	Whole	No[d]	−19.2	14.8	0.8	1	10	9
					−19.8	14.7	0.5	1	36	
	Marine fish average									
Zooplankton	Unsorted	Unidentified	Whole	No	−24.9	10.4	0.7	1.2	21	9
			Whole	No	−20.3	9.9	0.6	0.8	13	9
			Whole	No	−22.6	10.2	0.7	1.1	34	9
	Copepods[b]	*Paraeuchaeta* sp.	Whole	No	−25.4	11.9	0.1	0.1	3	10
			Whole	No	−28	13.1	0.4	0.6	3	10
			Whole	No	−27	12.9	0.8	0.4	2	10
		Metridia longa	Whole	No	−25.4	12.2	2.4	1.4	8	10
		Calanus hyperboreus/glacialis	Whole	No	−26.7	9.4	0.4	0.4	4	10
			Whole	No	−25.9	10.5	1.1	1.2	4	10
			Whole	No	−25.7	9.6	0.3	0.6	3	10
			Whole	No	−26.4	9.3	0.2	0.6	3	10
			Whole	No	−25.4	9.8	0.6	0.7	3	10
			Whole	No	−25.7	10.2	0.1	0.2	3	10
			Whole	No	−25.8	9.6	1.3	1.1	7	10
		Copepod average	Whole	No	−26.1	10.8	1.3	0.9	43	
	Euphausiids	Unidentified	Whole	No	−21.8	12.8	0.6	0.3	3	5
			Whole	No	−23.5	11.3	1.1	1	80	
	Zooplankton average									
Other marine	Marine mammals	*Erignathus barbatus*	Muscle	No	−17.1	16.7	0.6	0.9	47	11
		Phoca hispida	Muscle	No	−18.5	16.9	0.8	0.6	78	11
		Balaena mysticetus	Muscle	No	−20.6	13.4	0.9	0.7	122	11
		Marine mammal average			−18.7	15.7	0.8	0.7	247	
	Crabs	Unidentified	Muscle	No	−18.8	14.4	0.5	1.1	8	5
	Isopods	*Saduria entomon*	Whole	No	−20.7	14.3	0.5	0.9	3	9
		S. entomon	Muscle	No	−19.8	13	0.7	0.8	10	5
		Isopod average			−20.3	13.7	0.6	0.8	13	
					−19.3	14.6	0.8	0.7	268	
	Other marine average									

[a] 1 = Jahren and Kraft (2008), 2 = Lawson (2006), 3 = S. Oppel, unpubl. data, 4 = Gauthier et al. (2003), 5 = this study, 6 = Jamieson (2009), 7 = Alaska Department of Fish and Game, unpubl data, 8 = Kline et al. (1998), 9 = Dehn et al. (2007), 10 = Iken et al. (2005), and 11 = Dehn et al. (2006)

[b] SD calculated from standard error reported in the publication ($SD = SE \times \sqrt{n}$).

[c] Values estimated from Figure 2 in Kline et al. (1998).

[d] Adjusted by adding 2‰ to $\delta^{13}C$ (Lawson 2006) to account for lower stable carbon ratio of lipid fraction (Tieszen et al. 1983, Hobson and Clark 1992b). Other tissues that were not lipid extracted typically had low lipid content.