Changes in Isotopic Niches across Stages of the Annual Cycle in the Arctic Tern (*Sterna paradisaea*)

Isabeau Pratte,[1] Kelly A. Boadway,[2] Antony W. Diamond[2] and Mark L. Mallory[1,3]

ABSTRACT. Arctic Terns (*Sterna paradisaea*) are iconic seabirds of polar latitudes, whose successful reproduction is thought to depend on local food supplies near breeding colonies. We used stable isotopes of carbon and nitrogen in eggs, blood, and feathers of terns breeding in the Canadian High Arctic to compare their isotopic niche between life history stages and between two years. The isotopic niche of terns was smaller during incubation than during pre-breeding or winter. Over two breeding seasons, isotopic profiles of Arctic Terns suggested the high importance of local, exogenous nutrient supplies to form eggs (i.e., an income breeding strategy). Our results illustrate that using stable isotopes to assess the niche of a seabird population during critical periods of its annual cycle could be an essential tool in determining the influence that local forage conditions have on breeding decisions, especially for species that mostly rely on exogenous sources of nutrients and energy for egg production.

Key words: diet; Arctic seabird; winter; niche overlap; Arctic Tern; *Sterna paradisaea*

RÉSUMÉ. La sterne arctique (*Sterna paradisaea*) est un oiseau de mer emblématique des latitudes polaires, dont la reproduction réussie dépendrait de l'approvisionnement en aliments à proximité des colonies de nidification. Nous avons utilisé les isotopes stables du carbone et de l'azote provenant des œufs, du sang et des plumes des sternes se reproduisant dans l'Extrême-Arctique canadien pour comparer leur niche isotopique entre divers stades de leur cycle biologique ainsi qu'entre deux années différentes. La niche isotopique des sternes était plus petite pendant l'incubation qu'avant la reproduction ou que pendant l'hiver. Au cours des deux saisons de reproduction, les profils isotopiques des sternes arctiques ont laissé entrevoir la grande importance d'approvisionnements en nutriments locaux et exogènes pour la formation des œufs (soit une stratégie de reproduction à approvisionnement). Nos résultats illustrent que l'utilisation des isotopes stables pour évaluer la niche de la population d'oiseaux de mer pendant les périodes critiques de leur cycle annuel pourrait constituer un outil essentiel pour déterminer l'influence qu'ont les conditions d'alimentation locales sur les décisions de reproduction, surtout pour les espèces qui dépendent de sources d'énergie et de nutriments exogènes pour la production des œufs.

Mots clés: régime alimentaire; oiseau de mer de l'Arctique; hiver; recoupement des niches; sterne arctique; *Sterna paradisaea*

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INTRODUCTION

Seabird foraging strategies vary throughout the breeding season according to the distribution and availability of prey items and the food requirements of growing chicks at the nest site (Suryan et al., 2002; Navarro et al., 2007; Ceia et al., 2014; Delord et al., 2016). In the Arctic, migratory birds arriving at their breeding site after spring migration experience low but increasing ecosystem productivity, but foraging conditions may still be suboptimal compared to the pulse of food supplies that become available during the summer period (e.g., Laidre et al., 2008). Since optimal marine productivity is not yet attained, individuals could specialize on certain prey types in response to the constraints associated with limited prey resources during pre-breeding compared to later in the breeding season (Bolnick et al., 2003; Araújo et al., 2011), and females may seek particular prey to meet physiological requirements of breeding (e.g., Boersma et al., 2004). Conversely, optimal foraging theory suggests that individuals could also assume a more generalist foraging strategy—foraging for themselves, traveling farther, and selecting easily obtained prey of various sizes and types (Stephens and Krebs, 1986)— because their foraging range is less constrained by colony attendance during pre-breeding than during incubation and chick-rearing, when constraints are maximal. Given that many seabird species use exogenous sources of energy and nutrients for egg production (Mallory and Forbes, 2008; Bond and Diamond, 2010; Sénéchal et al., 2011), their diet immediately prior to breeding influences their reproductive decisions and consequently their reproductive success (Sorensen et al., 2009; Kowalczyk et al., 2014).

[1] Department of Biology, Acadia University, 33 Westwood Avenue, Wolfville, Nova Scotia B4P 2R6, Canada
[2] Atlantic Laboratory for Avian Research, University of New Brunswick, PO Box 45111, Fredericton, New Brunswick E3B 6E1, Canada
[3] Corresponding author: mark.mallory@acadiau.ca

The Arctic Tern (*Sterna paradisaea*) is a classic example of an income breeder (Hobson et al., 2000; Bond and Diamond, 2010) that uses resources obtained near the breeding site for egg production. This species feeds at the surface and cannot pursue prey to depths (Hatch, 2002), which may limit its capacity to adjust to adverse foraging conditions in the spring. Specifically, Arctic Terns are not able to plunge-dive to more than 50 cm below the surface, and they cannot store captured prey but rather carry one or few items at a time (Hatch, 2002). Consequently, they feed fairly close to their colony during the breeding season (Black, 2006; Rock et al., 2007; Robertson et al., 2014). Given their small size and their limited diving ability, Arctic Terns cannot easily compensate for lack of food by diving deeper or increasing their foraging range. The trophic niche of Arctic Terns may be particularly sensitive to changes in ocean conditions, compared to those of larger diving species; thus, monitoring of this niche may provide early indications of such changes (Furness and Camphuysen, 1997).

We studied the trophic ecology of Arctic Terns breeding at a colony located in Nunavut, High Arctic Canada, close to the northern limit of their breeding range (Mallory et al., 2017). Other than an adjacent polynya (about 10 km^2 next to the colony), our study site was surrounded by sea ice early and throughout the breeding season, which limited the area available for foraging, especially during the pre-breeding and incubation periods. We examined the isotopic niche of Arctic Terns during these critical early periods of their breeding season, as well as their trophic ecology in winter, after Arctic Terns have migrated to the Antarctic Ocean (Egevang et al., 2010; Fijn et al., 2013). We used stable isotope ratios of nitrogen (δ^{15}N) and carbon (δ^{13}C) in different tissues to assess and compare the isotopic niche of adults during the winter (when feathers are replaced; Hatch, 2002), pre-breeding (eggs), and incubation (blood) periods during two years of data collection (2007 and 2008). Many previous studies have demonstrated the utility of δ^{15}N for providing insights into the trophic level at which a species feeds (higher δ^{15}N for species feeding higher in food webs), while δ^{13}C provides information on foraging locations in the marine environment (higher δ^{13}C generally indicating nearshore or benthic foraging; reviewed in Hobson, 2006). Using feather and blood samples, we also determined the extent to which these High Arctic terns used endogenous (feather) or exogenous (blood) sources of nutrients for egg production: that is, whether Arctic Terns nesting at the northern limit of their breeding range in Canada are income breeders (i.e., relying on resources found nearby their breeding site for egg production).

Given the constraints (low productivity, extensive sea ice) on foraging availability and accessibility in the marine environment surrounding their breeding colony during spring, we expected to see differences in the isotopic niche of Arctic Terns across life history stages, and potentially across years. Arctic Terns exhibit considerable plasticity in their diet, feeding on terrestrial insects, zooplankton, marine worms, and fish (Hatch, 2002). The availability of these prey presumably changes through the breeding season; at our field site, for example, terrestrial insects are not available during pre-breeding, and access to marine invertebrate prey will vary with ice cover and timing of their seasonal abundance (Falkenhaug et al., 1997; Ji et al., 2013). We predicted that earlier in the season, when individuals are less constrained by time and colony attendance, pre-breeding terns would generalize on various prey types, leading to a broader dietary niche than during the incubation period, when terns would specialize on certain prey types and have a narrower dietary niche. In the winter, terns should be relatively unconstrained in foraging, and thus we predicted that their dietary niche would be large. Considering the extreme migration this species undertakes (Egevang et al., 2010; Fijn et al., 2013), and evidence from colonies to the south that Arctic Terns are principally income breeders (Hobson et al., 2000; Bond and Diamond, 2010), we expected terns nesting at this High Arctic colony to rely almost entirely on nutrients acquired locally for egg production.

METHODS

Study Site and Sample Collection

Nasaruvaalik Island, Nunavut (75°49′ N, 96°18′ W) is a 1.4 km^2 island surrounded by sea ice early in the season, except for a polynya adjacent to the island that provides a suitable foraging environment for multiple species of breeding seabirds (Maftei et al., 2015). A colony of about 900 Arctic Terns, split into two subcolonies, one at each tip of the crescent-shaped island, has been studied since 2007. Arctic Terns arrive at this colony in mid-June, initiate egg laying in the first week of July, incubate for ~21 d, and hatch their young in late July (Mallory et al., 2017). Formation of eggs takes about one week, with a two-day interval between laying dates of the two-egg clutch (Hatch, 2002). Thus, to assess isotopic niche, trophic position, and nutrient allocation in eggs, we collected samples from three different tissues that would represent diet during winter (feathers), pre-breeding (eggs), and breeding (adult blood) of Arctic Terns.

In 2007, as part of another project, adult Arctic Terns were collected (shot) at the colony at different periods of the breeding season (Provencher et al., 2014), and whole blood was collected and kept frozen for measurements of stable isotope ratios. Whole blood turns over isotopically in two to four weeks (Hobson and Clark, 1992a), meaning that whole blood collected approximately one week into chick rearing reflects the diet of the birds during the incubation period (i.e., the same period reflected by plasma collected from birds late in the incubation period, since plasma turns over in few days; Boecklen et al., 2011). In 2008, near the end of the incubation period, we caught Arctic Terns on their nests using a bownet trap and took blood samples

from 10 individuals by pricking the brachial vein with a 27-gauge needle and collecting approximately 150 µL of blood in heparinized capillary tubes (Gaunt et al., 1999). Within 5 h, the blood was spun in a micro-hematocrit centrifuge for 5 min to separate the plasma from the red blood cells (Howlett, 2000). Each fraction was placed in a separate micro-centrifuge tube and kept frozen. Whole blood of chick-rearing adult terns and plasma of terns late in incubation were used to assess the isotopic niche during incubation, as well as nutrient allocation to egg production. Prey consumed by adults (worms, crustaceans, fish) did not exhibit obvious trends in the relative proportions of different items throughout the breeding season and was similar to the prey fed to chicks (M.L. Mallory, unpubl. data based on hundreds of hours of observation). However, prey vary considerably in their isotopic values, which can be reflected in tern tissues, as we have described previously from this site (Clayden et al., 2015; Pratte et al., 2017).

In both 2007 and 2008, tern eggs were collected to assess isotopic niche of pre-breeding adult birds and nutrient allocation to egg production. In 2007, we gathered all eggs from the nests of terns that had been collected (shot; see above). In 2008, eggs were collected as described in Akearok et al. (2010). To determine the extent to which these terns used exogenous resources for egg production, we used plasma collected during incubation (2008) and the whole blood collected during early chick-rearing (2007).

Breast feathers were plucked from adult terns in both years, from either dead (2007) or live (2008) birds, to use as an indicator of winter diet. Arctic Terns grow body feathers at their wintering grounds (Hatch, 2002), and feathers are isotopically inert once grown (Pearson et al., 2003; Inger and Bearhop, 2008), so breast feathers reflect the isotopic value of the diet during winter.

Sample Analyses

Blood samples were either dried in a convection oven at 60°C for 12–24 h or freeze-dried for 6–12 h. To remove potential contaminants (including preen oils) from surfaces, the feathers were triple-washed in a 0.25 M NaOH solution, rinsed with distilled, deionized water (Bearhop et al., 2000a, 2002; Catry et al., 2008; Ramos et al., 2009), and dried at 60°C in a convection oven. Eggs were homogenized, freeze-dried, and ground, and lipids were removed with 2:1 chloroform:methanol rinses, using a modified Bligh and Dyer (1959) method. After lipid extraction, eggs were dried in a convection oven at 60°C, as were plankton samples. All samples, except feathers, were ground into a homogenous powder prior to analysis. The distal tips of three cleaned feathers per bird were cut with scissors into small pieces. All tissue samples, except the 2008 egg samples, were analyzed by the Stable Isotopes in Nature Laboratory (SINLAB) at the University of New Brunswick. The 2008 eggs were analyzed at the University of Ottawa G.G. Hatch Stable Isotope Laboratory. At both labs, samples were combusted in an elemental analyzer,

and gases were sent to the isotope-ratio mass spectrometer using a continuous-flow interface. Similar standardization procedures were used at both labs, including internal repeats and international standards. For SINLAB, international standards measured as follows: $\delta^{13}C$ – IAEA-CH6 −10.4 ± 0.06, IAEA-CH7 −31.88 ± 0.06; $\delta^{15}N$ – IAEA-N1 0.40 ± 0.10, IAEA-N2 20.47 ± 0.35. For the G.G. Hatch laboratory, $\delta^{13}C$ – IAEA-CH6 −10.4, NBS-22 −29.91; USGS-40 −26.24, USGS-41 37.76; $\delta^{15}N$ – USGS-40 −4.52, USGS-41 47.57, IAEA-N1 0.40, IAEA-N2 20.3. Eight internal standards varied within 0.4% for $\delta^{13}C$ and 4% for $\delta^{15}N$. Data are reported as differences in isotopic ratios, for which the units are parts per thousand (‰) compared to Vienna-Pee Dee Belemnite for carbon and to atmospheric nitrogen (air) for nitrogen.

Because lipids were not extracted from blood samples, we normalized $\delta^{13}C$ for lipid content in the plasma samples (Post et al., 2007) using the formula:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$$

We did not correct the whole blood samples given that $\delta^{13}C$ in whole blood is less affected by the lipid content (Bearhop et al., 2000b) and that the average C:N ratio in those samples was 3.95 ± 0.49 SD (e.g., Post et al., 2007).

Statistical Analyses

Prior to isotopic niche analyses, $\delta^{15}N$ and $\delta^{13}C$ values were corrected for tissue-specific discrimination factors by subtracting the tissue-tissue discrimination factor differences against whole blood from each value, thus eliminating the effect of tissue between the life-history stages of the individuals. We obtained tissue-tissue discrimination factors by gathering diet-tissue discrimination factors from the literature (Table 1) and using the differences between the diet-tissue discrimination factors as the tissue-tissue discrimination factors (Table 2). Discrimination factors were not specific to Arctic Terns, and very few data are available from captive studies, so we assumed that tern discrimination factors were similar to those we found for other species, but we note that additional research is required to confirm these values. We used the differences between lipid-free homogenized egg and feather or whole blood discrimination factors in the nutrient allocation Bayesian Stable Isotope Analysis in R (SIAR) model (see below).

The isotopic niche area (‰²) of Arctic Terns at different stages of their annual cycle was assessed using the Stable Isotopes Bayesian Ellipses in R package (SIBER; Jackson et al., 2011). We used Standard Ellipse Area corrected for small sample size (SEA$_c$) to determine the degree of isotopic niche overlap between years and between stages of the annual cycle following this equation:

$$\%\,Niche\;overlap = \left[\frac{(\text{area of overlap between SEA}_{c1} \text{and SEA}_{c2}) \times 2}{\text{SEA}_{c1} + \text{SEA}_{c2}} \right] \times 100$$

TABLE 1. Mean diet-tissue discrimination factors as reported in the literature. Because discrimination factors vary greatly with species and size of individuals (McCutchan et al., 2003), the studies listed below were chosen because they contained discrimination factors for species of similar size to Arctic Terns or of similar diet.

Tissue	$\Delta^{13}C$ (‰)	$\Delta^{15}N$ (‰)	Species	Literature source
Whole blood	+0.5	+3.0	Ring-billed Gull (*Larus delawarensis*), Dunlin (*Calidris alpina*)	Hobson and Clark, 1992b; Ogden et al., 2004
Plasma	+0.5	+3.3	Dunlin (*Calidris alpina*)	Ogden et al., 2004
Feather	+0.2	+3.0	Ring-billed Gull (*Larus delawarensis*)	Hobson and Clark, 1992b
Albumen	+0.9	+4.5	Gentoo Penguin (*Pygoscelis papua*)	Polito et al., 2009
Lipid-free yolk	+0.1	+3.5	Gentoo Penguin (*Pygoscelis papua*)	Polito et al., 2009
Lipid-free homogenized egg[1]	+0.1	+3.9		

[1] Calculated from diet-tissue discrimination values of albumen and lipid-free yolk, above, using the weighted average of each albumen and lipid-free yolk in eggs as reported in Østnes et al. (1997) for Arctic Terns.

TABLE 2. Differences in tissue-tissue discrimination factors based on the diet-tissue discrimination factors reported in Table 1 for carbon and nitrogen isotopes. These values were used to adjust for tissue type scaled against whole blood prior to niche width analyses and to determine nutrient allocation to eggs. Whole blood/plasma and feathers were used as proxies of breeding colony and wintering ground diets, respectively, and their discrimination values against lipid-free homogenized egg were used as discrimination factors in the SIAR model.

Tissue pairing	$\Delta^{13}C$ (‰)	$\Delta^{15}N$ (‰)
Lipid-free homogenized egg – whole blood	−0.4	+0.9
Lipid-free homogenized egg – feather	−0.1	+0.9
Feather – whole blood	−0.3	0.0
Plasma – whole blood	0.0	+0.3

We also used a probabilistic method to assess whether differences in isotopic niche between years and stages were significant following a posteriori distribution of estimated Bayesian-simulated Standard Ellipse Areas (SEA$_b$; Jackson et al., 2011). To assess whether differences in isotopic niche between years and stage were significant, we obtained a posterior distribution of estimated Bayesian-simulated Standard Ellipse Areas (SEA$_b$; Jackson et al., 2011) generated from a series of 10 000 subsampled iterations from the data. We compared the proportion of SEA$_b$ that differed between the groupings (year and stage) to estimate a probability that one group has a larger or smaller isotopic niche area than the other. Thus, given this Bayesian approach, a null probability (i.e., $p_b = 0$) is possible if the 10 000 iterations for a group year-stage are different from the 10 000 iterations of the compared group year-stage. The probability p_b represents the number of iterations for a group year-stage SEA$_b$ that are smaller (or greater) than the number of iterations for the compared group year-stage SEA$_b$:

$$p_b = \frac{\sum(SEA_{b1} < SEA_{b2})}{\text{total number iterations}}$$

The extent to which terns at this colony are income breeders (using local resources for egg production) or capital breeders (using nutrients and energy obtained before arrival at breeding site) was established using a Bayesian SIAR mixing model (Parnell et al., 2010). This modeling application takes into account different diet-tissue discrimination factors (reported in Table 2), and it allows for the determination of what proportion of the nutrients for egg production came from endogenous reserves or exogenous sources. In our case model, feathers and blood isotopic values (whole blood and plasma corrected against whole blood) were used as sources of nutrients from endogenous and exogenous origin (winter diet and local diet), respectively, while egg isotopic values corresponded to the "consumer." In 2007, we used whole blood taken during chick-rearing to ensure that isotopic turnover had occurred and the blood would thus reflect local isotopic sources obtained during incubation, while in 2008, we used plasma taken during late incubation to represent the local diet.

To test for potential differences between males and females, and to examine whether using eggs (i.e., female diet) to compare the isotopic niche and trophic position across stages reflects the entire population, we compared isotopic values of known-sex birds (from dissections) using a multivariate model (MANOVA) for $\delta^{15}N$ and $\delta^{13}C$ values in feathers in both years and in whole blood in 2007. Too few plasma samples were available (10 samples; 1 male) to test for the effect of sex on plasma isotopic values in 2008.

RESULTS

We found no significant differences between the sexes either in stable isotope ratios from feathers in either year or in whole blood in 2007 (MANOVA; all $F \leq 1.74$, $p \geq 0.20$, df = 2), so data from sexed and unsexed birds were pooled for all further analyses, including for the SIAR model assessing the sources of nutrients for egg production.

In 2007, Arctic Terns had a significantly larger isotopic niche in the winter (Southern Ocean) compared to the pre-breeding and the incubation periods in the High Arctic ($p_b = 0$). This difference was not found in 2008, when isotopic niche did not differ between the pre-breeding and the winter periods ($p_b = 0.1$, Fig. 1); however, as in 2007,
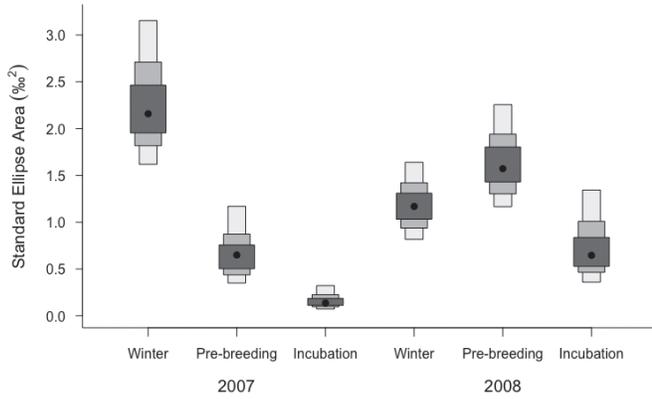
FIG. 1. Density plots with 50%, 75%, and 95% credible intervals resulting from posterior estimates of Bayesian-simulated standard ellipse areas (SEA$_b$; Jackson et al., 2011) in 2007 and 2008 based on δ^{13}C and δ^{15}N values of Arctic Terns at different stages of their life history. Winter values were derived from samples of feathers, and prebreeding values, from eggs. Samples representing incubation were from whole blood collected at chick rearing in 2007 and from plasma collected at late incubation in 2008. The degree of overlap of the credible intervals shows the degree of similarity between years and stages.

TABLE 3. Mean ± SE of isotopic values of Arctic Terns breeding at Nasaruvaalik Island, Nunavut, in 2007 and 2008. Winter, Pre-breeding, and Incubation represent isotopic values assessed in feathers, lipid-free eggs, and whole blood (2007) or plasma (2008), respectively. Each tissue was corrected for differences in discrimination factors against whole blood to allow comparison across life-history stages (Table 2). In 2007, whole blood collected during chick-rearing was assumed to represent the diet during incubation considering whole blood isotopic turnover rate; in 2008, plasma was collected during the late incubation period.

Life-history stage	δ^{13}C	δ^{15}N	n
2007:			
Winter	−24.14 ± 0.20	8.73 ± 0.10	36
Pre-breeding	−17.48 ± 0.12	13.37 ± 0.16	12
Incubation	−18.35 ± 0.11	14.69 ± 0.09	8
2008:			
Winter	−23.80 ± 0.12	9.52 ± 0.14	32
Pre-breeding	−17.03 ± 0.10	14.60 ± 0.15	35
Incubation	−17.03 ± 0.20	14.41 ± 0.12	10

incubating birds in 2008 had a smaller niche compared to pre-breeding birds (both years, $p_b < 0.02$, Fig. 1). The isotopic niches of pre-breeding and incubating individuals in 2008 were highly overlapping (82%; Fig. 2), suggesting that individuals were relying on similar prey types during those two periods. Considering only pre-breeding or incubation, we found no overlap between years in the isotopic niche area (Fig. 2). The winter isotopic niche was smaller in 2008 than in 2007 ($p_b = 0.005$), and overlap between the two years was limited (28%; Fig. 2).

Our models, which are based on isotopic values (Table 3), suggested that Arctic Terns derived most of the nutrients for egg production from exogenous, local food sources, acquired presumably in the waters surrounding the breeding colony, a pattern consistent in both 2007 and 2008 (Table 4).
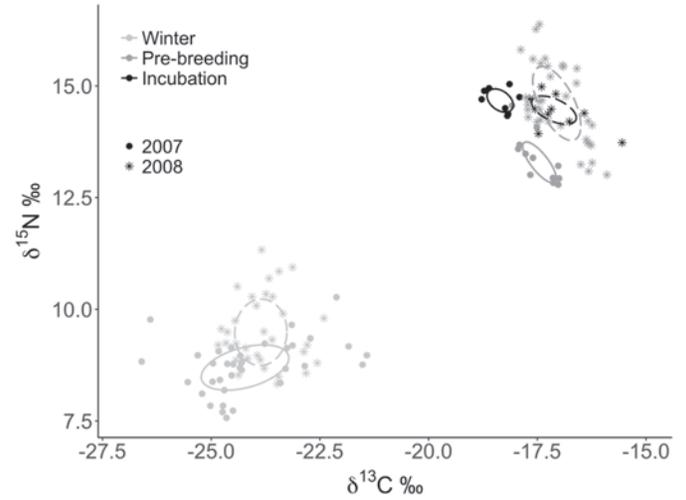

FIG. 2. Isotopic niche area represented by standard ellipses corrected for small sample size with 40% credible interval (Jackson et al., 2011) based on δ^{13}C and δ^{15}N values of Arctic Terns in 2007 and 2008, and at different stages of their life history (details as in Fig. 1). Isotopic values were corrected for differences in tissue-tissue fractionation values against whole blood, as reported in Table 2.

TABLE 4. Median (95% credible interval) proportional nutrient contribution to Arctic Tern eggs from local exogenous sources and endogenous reserves at Nasaruvaalik Island, Nunavut, in 2007 and 2008, as determined using a Bayesian SIAR modeling approach. In this model, δ^{13}C and δ^{15}N values in whole blood ($n = 8$; collected during chick-rearing in 2007) and plasma ($n = 10$; collected during late incubation and corrected for tissue-tissue differences in discrimination factor against whole blood in 2008) acted as proxies for the local breeding diet, and δ^{13}C and δ^{15}N values in feather acted as the proxy for distant wintering diet.

Year	Exogenous sources (%)	Endogenous reserves (%)
2007	98.1 (92.4–99.9)	1.9 (0.1–7.6)
2008	99.5 (97.6–100.0)	0.5 (0.0–2.4)

DISCUSSION

By looking at stable isotopes in different tissues of breeding Arctic Terns, we noted differences in Arctic Tern isotopic niche width between life history stages and between years of the study. Our results from the northern limit of the Arctic Tern breeding range in Canada were also consistent with those of previous studies, which suggests that terns rely principally on exogenous sources of nutrients for egg formation.

During the winter, Arctic Terns travel to the Antarctic Ocean (Egevang et al., 2010), and the δ^{13}C values assessed in the breast feathers of individuals in both 2007 and 2008 corresponded to the values of seabirds foraging south of the Antarctic polar front (Cherel and Hobson, 2007; Phillips et al., 2009; Jaeger et al., 2010). Overlap of the isotopic niche areas in the two years was limited. In 2007, the diversity of basal resources used by terns (δ^{13}C range), as represented in the overall isotopic niche width, was much wider than

in 2008, which suggests that the birds were more widely dispersed along a latitudinal gradient south of the polar front (Cherel and Hobson, 2007). The generally wider niche area of wintering Arctic Terns supports the hypothesis that trophic niche width of individuals increases when the birds are no longer constrained to be central place foragers (Cherel et al., 2007). Such an increase could represent use of a greater variety of prey types, or the likely geographic widening of habitat use by the terns in the Southern Ocean, or both. Such widening in trophic niche could also apply to pre-breeding birds that are not yet totally constrained by colony attendance (below).

Compared to pre-breeding individuals, incubating terns foraged later in the Arctic season, when the primary productivity pulse initiated by the spring sea-ice melt had allowed reproduction and growth or increased availability of preferred prey items (e.g., fish, copepod swarms; Søreide et al., 2010; Leu et al., 2011). Consequently, larger prey and greater prey diversity are likely more available at incubation time than in the pre-breeding period. We speculate that the narrower niche width of Arctic Terns during incubation might represent this growth spurt of preferred prey items and their selection by the terns (Martínez del Rio et al., 2009; Polito et al., 2015). In both years, the size of the tern niche area was smaller during incubation and more enriched in nitrogen. This pattern suggests that individuals relied more on a similar diet of prey enriched in nitrogen during that time, which is consistent with our predictions that terns would specialize on certain prey types and have a narrower niche width later in the breeding season. In contrast, the relatively broader isotopic niche areas of terns during the pre-breeding period in both 2007 and 2008 suggests that females preyed upon a wider variety of prey items during that time. Although the broader isotopic niche could represent females seeking particular elements for egg formation (e.g., Boersma et al., 2004), we suspect it more likely that it is associated with suboptimal foraging conditions (Bolnick et al., 2003; Tinker et al., 2008; Matich et al., 2011), and such conditions could prevail in the spring in this High Arctic marine ecosystem. However, in 2008, we observed extensive overlap in the isotopic niche areas of pre-breeding and incubating birds, along with generally larger niche width for both periods, compared to 2007. Such interannual variation in the size of niche width likely indicates differential foraging conditions that led individuals to broaden their diet in 2008 relative to 2007 (Bolnick et al., 2007; Araújo et al., 2011). We noted that in 2008, sea-ice breakup occurred about two weeks earlier near Nasaruvaalik Island (M.L. Mallory, unpubl. data) than in 2007, which may have influenced the phenology and distribution of prey. In general, we believe the larger isotopic niche widths of Arctic Terns in 2008 suggested a response to annual variation in foraging conditions. However, we note that terns appear well adapted to this annual variation; mean body mass, clutch size, and nest initiation were effectively identical in 2007 and 2008 (Mallory et al., 2017).

Our data strongly suggest that Arctic Terns rely principally on exogenous sources of nutrients for egg production, which emphasizes the importance of pre-breeding conditions for energy acquisition and breeding decisions in this species. The High Arctic is a relentless environment characterized by stochastic, adverse weather events and only a short favourable weather window in which to complete a successful reproductive attempt (e.g., Mallory et al., 2009). Consequently, animals likely rely on specific cues gathered over a short period after their arrival at the breeding site to make their reproductive decision and initiate breeding (e.g., Moe et al., 2009; Love et al., 2010). Environmental cues such as snow and sea-ice cover, but also foraging conditions within that restricted time, are likely critical in determining upcoming breeding decisions and success (Frederiksen et al., 2004; Gaston et al., 2005a, b; Reed et al., 2009; Ramírez et al., 2016; Mallory et al., 2017).

In both 2007 and 2008, Arctic Tern breeding parameters (nest initiation, clutch size, nesting success) were similar (Mallory et al., 2017) suggesting that despite differences in the isotopic niche width of pre-breeding Arctic Terns between those years, it is unlikely that these affected tern reproductive decisions and fitness. The diet of pre-breeding seabirds during years of low abundance of energy-rich prey can negatively influence breeding success (Sorensen et al., 2009; Kowalczyk et al., 2014). However, many seabirds exhibit phenotypic and behavioural plasticity and are able to adjust to changing conditions of food availability; these dietary changes do not necessarily impair their fitness (e.g., Little Auk *Alle alle*; Jakubas et al., 2016; Common Guillemot *Uria aalge*; Reed et al., 2009). Under extremely adverse conditions, such as extensive sea ice, cold temperatures, and delayed primary productivity, terns may forego breeding, as has been seen in other seabird species (e.g., Gaston et al., 2005a; Reed et al., 2009). For example, at this colony in 2013 and 2014, terns were present at the site, but none attempted to nest (Pratte et al., 2016). This behavior may have been influenced in part by high numbers of predators (Levermann and Tøttrup, 2007; Pratte et al., 2016); however, except for eiders, most species at the site did not nest in those years, which strongly suggests that poor food supplies may have limited the ability of female terns to acquire sufficient body condition for egg production and breeding (Mallory et al., 2017). Using stable isotopes to assess the niche width of a seabird population during critical periods of its annual cycle is one of several powerful tools for determining the influence that local forage conditions have on breeding decisions, especially for species that mostly rely on exogenous sources of nutrients and energy for egg production. Identifying which specific attributes of local or regional environmental conditions terns use to decide whether to breed or not, and when they make that decision, will likely prove crucial to modeling future Arctic seabird populations in a changing climate (Howell et al., 2009; Provencher et al., 2012; Post et al., 2013).

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