

# Nutrient allocation for egg production in six Atlantic seabirds

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**Abstract:** How species allocate nutrients to egg production is an important question in contaminant analyses. Seabird eggs are sampled frequently in such studies, so it is important to know the source of nutrients in these eggs if the source of the contaminants is to be traced. We used a stable-isotope approach to evaluate the relative importance of locally derived nutrients (income breeding) and stored nutrient reserves (capital breeding) in six species of Atlantic seabirds (Arctic Tern, *Sterna paradisaea* Pontoppidan, 1763; Common Tern, *Sterna hirundo* L., 1758; Atlantic Puffin, *Fratercula arctica* (L., 1758); Common Murre, *Uria aalge* (Pontoppidan, 1763); Razorbill, *Alca torda* L., 1758; Leach's Storm-Petrel, *Oceanodroma leucorhoa* (Vieillot, 1818)) breeding in the Bay of Fundy. We found that all species either were income breeders or adopted an intermediate strategy whereby varying proportions of locally derived nutrients were incorporated into eggs. Each species' migratory behaviour is likely a main factor in determining the amount of endogenous nutrients used in egg formation.

**Résumé :** La façon dont les espèces affectent les nutriments à la production d'œufs est une question importante lors de l'analyse des contaminants. Comme on prélève souvent des œufs d'oiseaux marins pour de telles études, il est nécessaire de connaître l'origine des nutriments dans ces œufs afin de retracer la source des contaminants. Nous utilisons une méthodologie à base d'isotopes stables afin d'évaluer l'importance relative des nutriments obtenus localement (reproduction à partir des ressources courantes) et des nutriments accumulés (reproduction à partir des réserves) chez six oiseaux marins de l'Atlantique (le sterne arctique, *Sterna paradisaea* Pontoppidan, 1763; le sterne pierregarin, *Sterna hirundo* L., 1758; le macareux moine, *Fratercula arctica* (L., 1758); le guillemot marmette, *Uria aalge* (Pontoppidan, 1763); le petit pingouin, *Alca torda* L., 1758; l'océanite minute, *Oceanodroma leucorhoa* (Vieillot, 1818)) qui se reproduisent dans la baie de Fundy. Toutes les espèces ou bien se reproduisent à partir de leurs ressources courantes ou alors adoptent une stratégie intermédiaire dans laquelle des proportions variables de nutriments d'origine locale sont incorporées dans les œufs. Le comportement migrateur de chacune des espèces est vraisemblablement un facteur majeur dans la détermination de la quantité de nutriments endogènes utilisée dans la formation des œufs.

[Traduit par la Rédaction]

## Introduction

Egg production is costly in terms of the nutrients required; in many seabird species, females lay only one egg per breeding attempt and eggs may constitute up to 27% of female body mass (Rauzon et al. 1984). The spectrum of nutrient allocation strategies spans from capital to income breeding (Drent and Daan 1980; Thomas 1983). When allocating nutrients to reproduction, capital breeders use endogenous nutrients for egg production (Reynolds 1972; Meijer and Drent 1999). At the opposite extreme are income breeders—species that use locally derived exogenous nutrients to form eggs (Drent and Daan 1980). In general, larger species need more energy and protein for egg forma-

tion than smaller species on an absolute basis, and smaller species may have difficulty in transporting nutrients in the form of fat reserves from potentially distant wintering grounds. However, seldom is a species purely a capital or income breeder; rather, it is somewhere along a continuum (Thomas 1983; Drent 2006), whereby both endogenous and exogenous nutrients contribute to egg production but in varying proportions.

Eggs also represent a significant excretory pathway for contaminants such as heavy metals and organic pollutants and can be sampled easily for contaminant studies (Pearce et al. 1979; Braune et al. 2002; Goodale et al. 2008). Female Cory's Shearwaters (*Calonectris diomedea* (Scopoli, 1769)), for example, eliminate 14% of methyl mercury via their eggs (Monteiro and Furness 2001). Interpretation of contaminant levels in eggs is, however, confounded by uncertainty in the source of contamination—are contaminants acquired locally or deposited from adult reserves accumulated elsewhere?

We used a stable-isotope approach to examine nutrient allocation in six Atlantic seabirds (Arctic Tern, *Sterna paradisaea* Pontoppidan, 1763; Common Tern, *Sterna hirundo* L., 1758; Atlantic Puffin, *Fratercula arctica* (L., 1758); Common Murre, *Uria aalge* (Pontoppidan, 1763); Razorbill, *Alca torda* L., 1758; Leach's Storm-Petrel, *Oceanodroma*

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*leucorhoa* (Vieillot, 1818)) breeding in eastern Canada. By comparing yolk and albumen to tissues synthesized at different times in the annual cycle (Hobson et al. 1997, 2000), our goal was to determine the source of nutrients for egg production and therefore the source of contaminants in eggs.

We used whole blood to represent local nutrient sources, as turnover is 2–3 weeks (Hobson and Clark 1992a), and feathers to represent nonbreeding sources. The nutrients for feather growth are exogenous (Ankney 1979; Murphy 1996) and isotope ratios are those from the time of synthesis (Hobson and Clark 1992a). Body feathers in all six species are grown in nonbreeding areas (Ainley et al. 1976; Voelker 1997; Gaston and Jones 1998; Nisbet 2002; Pyle 2008); their use in contaminant studies is recommended for clarity because of potential confusion in naming flight feathers and because they best reflect internal contaminant burdens (Furness et al. 1986; Burger 1993).

To attempt to quantify the contributions of endogenous and exogenous nutrients in egg production, we used a Bayesian stable-isotope mixing model (SIAR; Parnell et al. 2010) that provides an estimate of the proportional contribution of each source to the resultant isotope mix. We classified species that used >75% of exogenous nutrients in the production of yolk and albumen as income breeders, whereas those that used <25% exogenous nutrients in albumen or yolk formation were classified as capital breeders; all others were considered to be intermediate. Although somewhat arbitrary, this is analogous to describing categories along a continuum of forest stand composition, where stands with <25% softwood are described as “hardwood stands”, those between 25%–75% are “mixed stands”, and stands where the composition is >75% softwood are “softwood stands” (Blanchette et al. 2007). This approach also recognizes that while nutrient allocation is a continuum from capital to income, there is a desire to classify species’ nutrient allocation categorically.

## Materials and methods

### Field collection

Machias Seal Island (44°30'N, 67°6'W) is a 9.5 ha treeless island in the northern Gulf of Maine that supports a diverse seabird community (Diamond and Devlin 2003). In 2005 and 2006, we collected breast feathers, whole blood, and fresh eggs from all seabird species breeding on the island. Blood and feathers we collected from the same individuals, although eggs were not collected from the same nests. Adult birds were captured on nest sites or from the colony’s surface (Breton et al. 2005; Diamond 2007; Devlin et al. 2008; Lavers et al. 2008) and released following sampling. Warm eggs (indicative of an active, unabandoned nest) were collected as early in incubation as possible. Auks and storm-petrels have a clutch size of one, so there were no effects of laying sequence on isotope ratios. For terns, only clutches containing one egg were collected and our results only apply to the first egg (A-egg). Eggs were frozen in the field at –20 °C within 30 min of collection, which does not alter isotopic composition (Gloutney and Hobson 1998).

Blood samples from breeding adults were taken via venipuncture from the brachial vein, stored in sterile glass vials, and frozen at –20 °C in the field prior to analyses. Blood

samples were taken from adults during late incubation (terns, storm-petrels) or chick rearing (alcids), which ensures that blood isotope values represent locally acquired nutrients (Morrison and Hobson 2004), and also minimizes the chance that adults will abandon their nest. Furthermore, we have no evidence of dietary shifts during chick rearing for terns or auks in either year (Bond et al. 2006, 2007). Finally, all species arrive on the breeding ground several weeks prior to the initiation of breeding, reducing potential carry-over effects and ensuring any endogenous nutrients incorporated into eggs will be from wintering grounds or migration stopover sites. We assume that the stable-isotope values representing exogenous nutrients do not change significantly between egg laying and timing of our blood sampling in late incubation or early chick rearing. Between 4 and 8 worn breast feathers were plucked from the same birds as those sampled for whole blood and feathers were placed in sterile polyethylene bags.

We did not sex birds genetically and all species are monomorphic. Because only females contribute nutrients to egg production, we tested for differences in stable-isotope ratios in blood and feathers by classifying birds as male or female using discriminant functions developed from Machias Seal Island, or in the case of Common Terns, a nearby colony (Grecian et al. 2003; Devlin et al. 2004; Friars 2007; Nisbet et al. 2007).

### Stable-isotope analysis

Isotope analyses were done at the Stable Isotopes in Nature Laboratory (SINLAB) at the University of New Brunswick. Frozen blood and egg component samples were freeze-dried for 24–48 h in a Virtis Benchtop freeze dryer. Lipids, which are depleted in <sup>13</sup>C, were removed (Bligh and Dyer 1959) from yolk, eliminating this bias (Hobson 1995; Post et al. 2007; Logan et al. 2008). It is recommended that tissues with C:N > 4.0 should be lipid-extracted (Post et al. 2007; Logan et al. 2008); avian blood (Bearhop et al. 2000a) and feathers (Kojadinovic et al. 2008) do not require such treatment typically. Approximately 2 mL of a 2:1 chloroform:methanol solution was used to wash the samples until the supernatant appeared clear, indicating that the majority of the lipids had been removed (Bligh and Dyer 1959). Samples were freeze-dried again for 24 h to remove residual chloroform and methanol. Feather samples were washed in a 0.25 mol/L NaOH solution to remove external contamination (Bearhop et al. 2000b).

Samples were dried, powdered, and weighed, and approximately 0.2 mg was placed in a tin capsule, which was crushed and loaded to an autosampler, then combusted in a Carlo Erba NC2500 elemental analyzer. The resultant gases were delivered to a Finnigan Mat Delta XP mass spectrometer via continuous flow. Throughout analyses, internal repeats and standards (presented below as mean ± SD) were used. Values were corrected using International Atomic Energy Agency (IAEA) standards CH6 ( $\delta^{13}\text{C}$ :  $-10.49\text{‰} \pm 0.21\text{‰}$ ), N1 ( $\delta^{15}\text{N}$ :  $0.25\text{‰} \pm 0.29\text{‰}$ ), and N2 ( $\delta^{15}\text{N}$ :  $20.54\text{‰} \pm 0.17\text{‰}$ ). Internal laboratory standards of small-mouth bass (*Micropterus dolomieu* Lacepède, 1802) muscle ( $\delta^{13}\text{C}$ :  $-23.26\text{‰} \pm 0.12\text{‰}$ ;  $\delta^{15}\text{N}$ :  $12.42\text{‰} \pm 0.12\text{‰}$ ), bovine liver ( $\delta^{13}\text{C}$ :  $-18.71\text{‰} \pm 0.12\text{‰}$ ;  $\delta^{15}\text{N}$ :  $7.25\text{‰} \pm 0.18\text{‰}$ ), acetanilide (2 batches,  $\delta^{13}\text{C}$ :  $-33.60\text{‰} \pm 0.15\text{‰}$ ,  $-33.13\text{‰} \pm$

**Table 1.** Differences in discrimination factors ( $\Delta^{13}\text{C}$ ,  $\Delta^{15}\text{N}$ ) between tissue pairs (tissue–tissue discrimination factors) used to estimate the proportion of exogenous (blood) and endogenous (feather) contributions to the formation of albumen and yolk.

Discrimination type	Tissue	$\Delta^{13}\text{C}$	$\Delta^{15}\text{N}$	References
Diet–tissue	Whole blood	−0.6	−2.7	Hobson and Clark 1992 <i>b</i> ; Bearhop et al. 2002; Cherel et al. 2005
	Feather	0.0	−4.2	Hobson and Clark 1992 <i>b</i> ; Bearhop et al. 2002; Cherel et al. 2005
	Albumen	−0.9	−3.1	Hobson 1995
	Lipid-free yolk	0.0	−3.5	Hobson 1995
Tissue–tissue	Feather–albumen	−0.9	+1.1	
	Feather–yolk	0.0	+0.7	
	Blood–albumen	−0.3	+0.4	
	Blood–yolk	+0.6	−0.8	

**Note:** Diet–tissue discrimination factors were taken as means from the published literature for marine birds (see sources). Tissue–tissue discrimination factors are the differences between the “source” and the “consumer” diet–tissue discrimination factors (e.g., blood–albumen discrimination for  $\delta^{13}\text{C}$  =  $-0.9 + 0.6 = -0.3$ ).

0.14‰;  $\delta^{15}\text{N}$ :  $-3.16\text{‰} \pm 0.19\text{‰}$ ,  $-1.18\text{‰} \pm 0.19\text{‰}$ ), and nicotinamide ( $\delta^{13}\text{C}$ :  $-34.20\text{‰} \pm 0.12\text{‰}$ ;  $\delta^{15}\text{N}$ :  $-1.77\text{‰} \pm 0.14\text{‰}$ ) were also used. One standard deviation of duplicate samples within runs was  $<0.55\text{‰}$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

Results are expressed as differences in isotopic ratios expressed in parts per thousand (‰) compared with international standards (Pee Dee Belemnite (PDB) for carbon and atmospheric  $\text{N}_2$  for nitrogen) as

$$\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where  $\delta X$  is either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  and  $R_{\text{sample}}$  is the ratio of  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ , respectively, and  $R_{\text{standard}}$  is the ratio present in the international standard.

### Statistical methods

In order for stable-isotope ratios to be used to separate the contribution of nutrients from breeding and wintering grounds to egg formation, the two must be different. We used a multivariate analysis of variance (MANOVA) to test for differences between feather and blood isotope ratios (corrected for relative isotope discrimination). Because we sampled both males and females, we tested for differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  using a MANOVA for each species. We used the isotope mixing model program SIAR (Parnell et al. 2010) in R version 2.10.1 (R Development Core Team 2009) to estimate the proportional contribution of the two sources—exogenous nutrients (blood) and endogenous nutrients (feathers). To account for differences owing to isotope discrimination among the different tissues, we used the mean differences in discrimination factors between tissue pairs (e.g., the difference in discrimination factors between yolk and blood) from the literature (Hobson and Clark 1992*b*; Hobson 1995; Cherel et al. 2005) as the discrimination factors between the “consumer” (egg components) and “sources” (blood or feathers). Although there are differences in species’ tissue-specific discrimination factors that can affect mixing model output (Bond and Diamond 2010), current evidence suggests that differences in discrimination factors between tissues are constant (Quillfeldt et al. 2008; Bond et al. 2010). A summary of discrimination factors used is presented in Table 1. As we did not expect species’ ability to allocate nutrients to change between the 2 years of the study, data were pooled. Because chemical lipid extraction can affect  $\delta^{15}\text{N}$  values (Oppel et al. 2010), we also ran a

series of models in SIAR using yolk  $\delta^{15}\text{N}$  values corrected for the effects of lipid extraction ( $-1.1\text{‰} \pm 0.5\text{‰}$ , Oppel et al. 2010).

As more capital-breeding species tend to be heavier (Klaassen et al. 2001; Kullberg et al. 2005), we examined correlations between body mass, egg mass, and the proportion of body mass represented by the egg (Bond 2007; A.W. Diamond, unpublished data) to the estimated contribution of exogenous reserves to albumen and yolk formation using Pearson’s correlation coefficient ( $r$ ). All statistical tests were considered significant when  $p < 0.05$ .

### Results

There were no differences in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  in feathers or blood of birds classified as males and females for any species (Wilks’  $\lambda$ , all  $p > 0.20$ ), so all birds were considered in subsequent analyses. Within each species, isotope ratios (corrected for isotope discrimination) of feathers and blood were significantly different (Wilks’  $\lambda$ , all  $p < 0.0001$ ; Table 2). A summary of mixing model results is presented in Fig. 1. Using our criteria for categorizing capital, intermediate, or income breeders, we categorized Arctic Terns, Common Murres, and Common Terns as income breeders; Atlantic Puffins and Razorbills as intermediate breeders; and Leach’s Storm-Petrels as using endogenous reserves for yolk formation, but local nutrients for albumen formation. Mixing model performance, or model fit, as assessed by the “worst parameter  $p$  value” (Parnell et al. 2010) was generally good ( $p > 0.05$ ) for all species. After correcting  $\delta^{15}\text{N}$  for the effects of chemical lipid extraction, our estimates of exogenous nutrients in yolk were higher in all cases (Table 3).

We found no significant correlation between the estimated contribution of exogenous reserves to albumen or yolk formation and body mass (albumen:  $r = -0.42$ ,  $p = 0.41$ ; yolk:  $r = -0.12$ ,  $p = 0.82$ ), egg mass (albumen:  $r = -0.46$ ,  $p = 0.36$ ; yolk:  $r = -0.11$ ,  $p = 0.84$ ) and the proportion of body mass represented by the egg (albumen:  $r = 0.46$ ,  $p = 0.36$ ; yolk:  $r = -0.03$ ,  $p = 0.95$ ; Table 4).

### Discussion

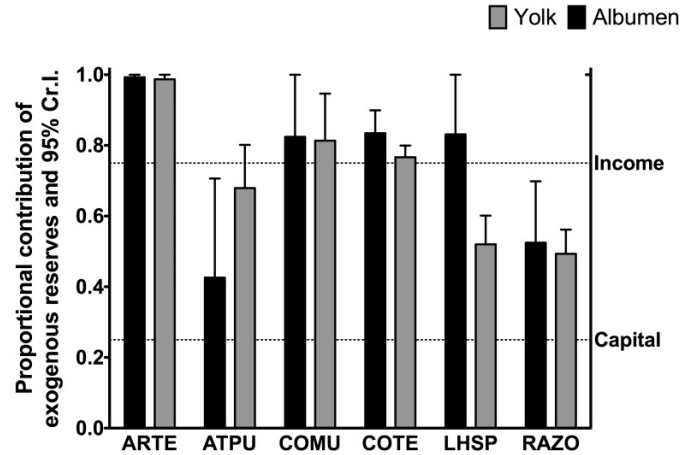
Based on evidence from stable isotopes, we conclude that Arctic Terns, Common Terns, and Common Murres are income breeders, whereas Leach’s Storm-Petrels, Razorbills,

**Table 2.** Stable-isotope ratios (‰) from whole blood, breast feathers, lipid-free yolk, and albumen from six seabird species (Arctic Tern, *Sterna paradisaea*; Common Tern, *Sterna hirundo*; Atlantic Puffin, *Fratercula arctica*; Common Murre, *Uria aalge*; Razorbill, *Alca torda*; Leach's Storm-Petrel, *Oceanodroma leucorhoa*) on Machias Seal Island.

Species	Whole blood		Breast feathers		Lipid-free yolk		Albumen	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Arctic Tern	-19.96±0.43 (23)	10.78±0.29 (23)	-24.94±1.32 (23)	8.73±0.71 (23)	-19.23±0.51 (18)	12.24±0.53 (18)	-19.90±0.66 (20)	10.68±0.25 (20)
Atlantic Puffin	-19.55±0.62 (17)	13.18±0.77 (17)	-18.07±0.58 (17)	13.76±0.53 (17)	-18.78±0.31 (16)	12.95±0.55 (16)	-19.07±0.33 (19)	12.12±0.37 (19)
Common Murre	-19.05±0.47 (6)	13.50±0.20 (6)	-17.02±0.41 (6)	15.59±0.99 (6)	-18.48±0.35 (9)	13.54±0.65 (9)	-18.91±0.26 (10)	12.56±0.28 (10)
Common Tern	-19.48±0.45 (22)	11.37±0.68 (22)	-15.18±0.87 (22)	13.45±2.15 (22)	-19.04±0.58 (11)	12.47±0.61 (11)	-19.33±0.57 (14)	11.48±0.76 (14)
Leach's Storm-Petrel	-19.53±0.57 (13)	13.09±0.52 (13)	-17.38±0.68 (13)	14.09±0.50 (13)	-18.38±0.66 (11)	13.38±0.47 (11)	-19.20±0.95 (17)	12.56±0.56 (17)
Razorbill	-18.90±0.38 (20)	13.53±0.50 (20)	-17.04±0.56 (20)	15.34±0.78 (20)	-18.51±0.57 (20)	13.66±0.30 (20)	-18.93±0.43 (20)	12.30±0.37 (20)

**Note:** Values are presented as means ± SD (*n*) and are not corrected for isotope discrimination.

**Fig. 1.** The estimated proportional contribution and 95% credible intervals (Cr.I.) of locally derived nutrients as determined in a Bayesian stable-isotope mixing model (SIAR) as the contribution of blood isotope values to the formation of egg components. When the estimated proportional contribution is >0.75, the species is classified as an income breeder; when the value is <0.25, the species is classified as a capital breeder; when the value is between 0.25 and 0.75, an intermediate strategy is adopted. Species abbreviations are ARTE (Arctic Tern, *Sterna paradisaea*), ATPU (Atlantic Puffin, *Fratercula arctica*), COMU (Common Murre, *Uria aalge*), COTE (Common Tern, *Sterna hirundo*), LHSP (Leach's Storm-Petrel, *Oceanodroma leucorhoa*), and RAZO (Razorbill, *Alca torda*).



and Atlantic Puffins adopt an intermediate strategy between income and capital breeding. Despite the more than 20-fold range in body masses (Table 4), we had both large and small species classified as income breeders and as intermediate breeders. However, because adults and eggs were not sampled from the same nests, our estimates reflect the population means of exogenous and endogenous contributions to egg formation and there may be considerable individual plasticity in nutrient allocation among females within the populations. Further research should investigate the role of individual plasticity in nutrient allocation and its consequences for reproduction, chick growth, and survival.

Both tern species migrate from wintering grounds in the southern hemisphere (Hays et al. 1999; Hatch 2002; Nisbet 2002; Egevang et al. 2010) and weigh only about 105–115 g. Furthermore, eggs comprise over 15% of body mass in both species (Bond 2007), so it is not surprising that terns use locally derived nutrients for egg production. Our results for Common Terns contrast with those from Great Slave Lake, Northwest Territories, Canada, where they were found to use endogenous reserves for egg production (Hobson et al. 2000). This suggests that nutrient allocation is a plastic trait that varies within species depending on breeding conditions and that philopatric populations might become adapted to the local environment in terms of nutrient availability and mobilization.

We suggest that puffins exhibit some carry-over effects using some nutrients acquired in wintering areas in the North Atlantic Ocean or on the southward migration to the Bay of Fundy. Interestingly, Common Murres, the largest species, were classified as an income species, whereas the



**Table 3.** The estimated contributions (%) of exogenous and endogenous nutrients to albumen and yolk production in six Atlantic seabirds (Arctic Tern, *Sterna paradisaea*; Common Tern, *Sterna hirundo*; Atlantic Puffin, *Fratercula arctica*; Common Murre, *Uria aalge*; Razorbill, *Alca torda*; Leach's Storm-Petrel, *Oceanodroma leucorhoa*).

Species	Egg component	Exogenous (%)	Endogenous (%)
Arctic Tern	Albumen	99.3 (98.1–100.0)	0.7 (0.0–1.9)
	Yolk	98.7 (96.8–100.0)	1.3 (0.0–3.2)
	Yolk (lipid-corrected)	98.5 (96.5–100.0)	1.4 (0.0–3.5)
Atlantic Puffin	Albumen	42.6 (13.9–70.7)	57.4 (4.1–12.9)
	Yolk	67.9 (56.2–80.1)	32.1 (19.9–43.8)
	Yolk (lipid-corrected)	73.3 (52.7–96.3)	26.7 (3.7–47.2)
Common Murre	Albumen	82.4 (61.6–100.0)	17.6 (0.0–38.4)
	Yolk	81.3 (68.9–94.6)	18.7 (5.3–31.1)
	Yolk (lipid-corrected)	91.0 (78.8–100.0)	9.0 (0.0–21.2)
Common Tern	Albumen	83.4 (77.4–89.9)	16.6 (10.1–22.6)
	Yolk	76.7 (57.5–79.9)	23.3 (0.5–18.8)
	Yolk (lipid-corrected)	97.0 (92.2–100.0)	3.0 (0.0–7.8)
Leach's Storm-Petrel	Albumen	83.1 (61.5–100.0)	16.9 (0.0–38.5)
	Yolk	52.0 (43.6–60.1)	48.0 (40.0–56.4)
	Yolk (lipid-corrected)	57.0 (40.4–73.9)	43.0 (26.1–59.6)
Razorbill	Albumen	52.5 (35.2–69.9)	47.5 (30.1–64.8)
	Yolk	49.3 (42.3–56.2)	50.7 (32.8–57.7)
	Yolk (lipid-corrected)	97.3 (92.6–100.0)	2.7 (0.0–7.4)

**Note:** Lipid-corrected yolk values are the result of mixing models where  $\delta^{15}\text{N}$  values were corrected for the effects of chemical lipid extraction ( $-1.1\text{‰} \pm 0.5\text{‰}$ ; Oppel et al. 2010). Values are presented as means (95% high-density regions).

**Table 4.** Fresh egg mass (g) in relation to adult body mass (g) for six Atlantic seabirds (Arctic Tern (*Sterna paradisaea*), Common Tern (*Sterna hirundo*), Atlantic Puffin (*Fratercula arctica*), Common Murre (*Uria aalge*), Razorbill (*Alca torda*), and Leach's Storm-Petrel (*Oceanodroma leucorhoa*)) from Machias Seal Island.

Species	Body mass (g)	Fresh egg mass (g)	Egg mass as percentage of body mass
Arctic Tern	105±7 (34)	18.3±3.0 (10)	17.4
Atlantic Puffin	414±33 (18)	64.3±4.2 (38)	15.5
Common Murre	880±51 (18)	114.1±6.4 (10)	13.0
Common Tern	116±7 (27)	20.3±1.0 (8)	17.5
Leach's Storm-Petrel	46±4 (17)	9.7±0.8 (10)	21.1
Razorbill	667±47 (21)	85.3±8.9 (10)	12.8

**Note:** Data are from Bond (2007) and A.W. Diamond (unpublished data), and are presented as mean ± SD (*n*).

other large auks (Atlantic Puffins and Razorbills) adopted an intermediate strategy.

Razorbills nesting on Machias Seal Island are resident in the lower Bay of Fundy year-round (Clarke 2009). With such overlap in foraging areas used in the breeding and non-breeding periods, differences in diet are more reflective of behaviour and prey availability, not geographic differences. Thus, resolving the origin of nutrients allocated to egg production in this population is challenging.

Overall, correcting for the effect of chemical lipid extraction (Oppel et al. 2010), our analyses tended to predict a greater contribution of exogenous nutrients to yolk production (Table 3), but in all species except Razorbills, our interpretation remains the same and 95% density regions overlapped between both the corrected and the uncorrected yolk model results. Correcting for the effects of lipid extraction in Razorbills increased the contribution of exogenous

nutrients to yolk formation considerably (from 49% to 97%). We urge caution in interpreting these results, however, as Razorbills are resident in the lower Bay of Fundy throughout the year (Clarke 2009), and as we mention above, resolving the contribution of exogenous and endogenous nutrients to egg production poses several challenges.

The advantage of income breeding is that there are no inventory costs of keeping nutrients from the time of acquisition to clutch initiation; it would be a useful system where there is a reliable local food source available during the prelaying and laying periods (Jönsson 1997). All species, to a certain extent, rely on locally derived nutrients, and to a lesser extent, endogenous reserves (Drent 2006). Indeed, endogenous nutrients contributed less than 50% to any egg component, except for albumen (43%) from Atlantic Puffins. The availability of nutrient-rich prey in the lower Bay of Fundy is therefore critical to the breeding of these spe-

cies, and should prey become less available, it is likely that some individuals would be incapable of acquiring sufficient nutrients to initiate breeding.

A variety of studies use seabird eggs to monitor contaminants in the marine environment (a number of studies are summarized in Bond and Diamond 2009). An implicit assumption of such studies is that the nutrients, and therefore contaminants, deposited in eggs by laying females is local in origin and that carry-over effects from migration or wintering areas are either negligible or consistent over time. This has been found to be the case in Ospreys (*Pandion haliaetus* (L., 1758)), where egg contaminant levels were correlated significantly with contaminants in prey species on the breeding ground rather than the wintering ground (Elliott et al. 2007). Determining the source of contaminants found in seabird eggs is crucial for their use as indicators of marine pollution. We have shown that all species use the prey base around the breeding colony for the formation of both albumen and yolk, although to varying degrees. Contaminants in eggs are therefore mostly derived locally and represent local contaminant levels. The Bay of Fundy and Gulf of Maine ecosystem is an area of elevated mercury contamination (Evers and Clair 2005) and has been a focus of contaminant studies for over 40 years (Zitko et al. 1972; Goodale et al. 2008; Bond and Diamond 2009).

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