

King eiders use an income strategy for egg production: a case study for incorporating individual dietary variation into nutrient allocation research

Steffen Oppel · Abby N. Powell · Diane M. O'Brien

Received: 9 March 2009 / Accepted: 15 March 2010 / Published online: 4 April 2010
© US Government 2010

Abstract The use of stored nutrients for reproduction represents an important component of life-history variation. Recent studies from several species have used stable isotopes to estimate the reliance on stored body reserves in reproduction. Such approaches rely on population-level dietary endpoints to characterize stored reserves (“capital”) and current diet (“income”). Individual variation in diet choice has so far not been incorporated in such approaches, but is crucial for assessing variation in nutrient allocation strategies. We investigated nutrient allocation to egg production in a large-bodied sea duck in northern Alaska, the king eider (*Somateria spectabilis*). We first used Bayesian isotopic mixing models to quantify at the population level the amount of endogenous carbon and nitrogen invested into egg proteins based on carbon and

nitrogen isotope ratios. We then defined the isotopic signature of the current diet of every nesting female based on isotope ratios of eggshell membranes, because diets varied isotopically among individual king eiders on breeding grounds. We used these individual-based dietary isotope signals to characterize nutrient allocation for each female in the study population. At the population level, the Bayesian and the individual-based approaches yielded identical results, and showed that king eiders used an income strategy for the synthesis of egg proteins. The majority of the carbon and nitrogen in albumen (C: $86 \pm 18\%$, N: $99 \pm 1\%$) and the nitrogen in lipid-free yolk ($90 \pm 15\%$) were derived from food consumed on breeding grounds. Carbon in lipid-free yolk derived evenly from endogenous sources and current diet (exogenous C: $54 \pm 24\%$), but source contribution was highly variable among individual females. These results suggest that even large-bodied birds traditionally viewed as capital breeders use exogenous nutrients for reproduction. We recommend that investigations of nutrient allocation should incorporate individual variation into mixing models to reveal intra-specific variation in reproductive strategies.

Communicated by Elisabeth Kalko.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1619-z) contains supplementary material, which is available to authorized users.

S. Oppel · A. N. Powell · D. M. O'Brien
Department of Biology and Wildlife, University of Alaska,
211 Irving 1, Fairbanks, AK 99775-6100, USA

A. N. Powell
Alaska Cooperative Fish and Wildlife Research Unit,
US Geological Survey, University of Alaska,
Fairbanks, AK 99775-7020, USA

A. N. Powell · D. M. O'Brien
Institute of Arctic Biology, University of Alaska,
311 Irving 1, Fairbanks, AK 99775-6020, USA

S. Oppel (✉)
Royal Society for the Protection of Birds, The Lodge,
Sandy, Bedfordshire SG19 2DL, UK
e-mail: steffen.oppel@gmail.com

Keywords Capital breeding · Eggshell membranes · Migratory birds · Mixing models · Stable isotopes

Introduction

The use of stored nutrients in reproduction represents an important component of life-history variation (Stearns 1992). In environments with seasonal fluctuations in resource availability, animals may have to reproduce at a time when food availability is low (Monaghan and Nager 1997; Perrins 1996). One way to overcome this challenge is

to carry nutrients from earlier annual cycle stages to fuel the reproductive effort, a strategy referred to as capital breeding (Drent and Daan 1980; Jönsson 1997; Meijer and Drent 1999). The alternate strategy, income breeding, describes animals that rely entirely on current diet from the local environment for nutrients needed in reproduction.

Capital and income breeding are the two extremes of a continuum of breeding strategies. Where along that continuum a species falls depends on the general life history of the species as well as on the resource availability at the place and time of reproduction (Bonnet et al. 1998; Houston et al. 2007; Jönsson 1997). Many recent studies have used stable isotope applications to trace the origin of nutrients used for reproduction, in insects (O'Brien et al. 2000, 2005), fish (Jardine et al. 2008), reptiles (Warner et al. 2008), mammals (Dalerum et al. 2007), and especially in migratory birds (Bond et al. 2007; Morrison and Hobson 2004; Schmutz et al. 2006). The techniques used to quantify the allocation of nutrients via isotopic mixing models have advanced rapidly in the recent past (Moore and Semmens 2008; Parnell 2008; Phillips et al. 2005). However, so far no method has incorporated individual variation in diet choice into nutrient allocation models, despite substantial evidence that individual specialization in foraging behavior affects animal isotope ratios (Araújo et al. 2007; Bearhop et al. 2006; Matthews and Mazumder 2004; Woo et al. 2008). Capturing individual variation in diet and reproductive allocation is of particular importance in studies of migratory birds, in which reproductive strategies can be closely linked to migration strategies (Béty et al. 2004; Drent et al. 2003; Prop et al. 2003). Variation in nutrient allocation strategies at the species level has been linked to body size (Nolet 2006), distance to areas where reserves can be accumulated (Klaassen et al. 2006), quality of these areas in relation to breeding grounds (Drent et al. 2007), and costs associated with accumulating and transporting reserves from distant staging areas (Alerstam 2006). Because variation in nutrient allocation strategies fundamentally affects life-history characteristics, a technique to explore variation at the individual level would have broad ecological utility (Hamel et al. 2009; Wheatley et al. 2008).

In this study we investigate nutrient allocation to egg production of king eiders (*Somateria spectabilis*) by using stable isotopes of carbon and nitrogen to quantify the proportion of egg proteins derived from body reserves (Hobson 2006). King eiders migrate and winter at sea, but nest in freshwater ecosystems of the circumpolar Arctic; thus, we used the well-described isotopic differences between marine and freshwater environments (Peterson and Fry 1987) to distinguish egg nutrients accumulated in marine staging areas from nutrients derived from breeding areas (Hobson 2006). Eiders are the largest carnivorous

waterfowl breeding in the Arctic and rely on body reserves to fuel their metabolism during incubation (Bentzen et al. 2008; Kellett and Alisauskas 2000; Parker and Holm 1990). Based on allometric equations of energy expenditure during migration and clutch formation (Nolet 2006), eiders should be able to carry sufficient reserves to pursue a capital strategy for egg formation. However, the source of nutrients for egg synthesis in eiders has not been quantified.

King eiders exhibit large individual variation in several aspects of their ecology (Merkel et al. 2007; Opper et al. 2008, 2009b; Suydam 2000), and such individual variation needs to be incorporated into studies of nutrient allocation. Thus, we evaluated nutrient allocation in two ways. We first estimate nutrient allocation to egg proteins in king eiders at the population level using a Bayesian isotope mixing model (Jackson et al. 2009; Moore and Semmens 2008; Semmens et al. 2009). We then introduce an approach to account for individual variation in diet choice of king eiders on breeding grounds. We show that this approach yields identical results as a Bayesian analysis at the population level, but provides additional information on the extent of variability in nutrient allocation at the individual level. This information facilitates future investigations of how migratory and reproductive strategies interact to affect individual fitness.

Materials and methods

Study area

We studied king eiders in June and July 2005–2007 at two sites located on the Arctic coastal plain of Alaska. “Olak” was near Teshekpuk Lake, approximately 30 km south of the coast of the Beaufort Sea (70° 26' N, 153° 08' W), and “Kuparuk” was ~150 km to the east within an active oilfield 10 km south of the coast (70°20' N, 149°45' W). Both sites consisted mainly of low-lying tundra with numerous ponds, lakes, and wetland complexes. Satellite telemetry has shown that king eiders arrive in the study areas in the first two weeks of June, and do not commute between breeding grounds and marine foraging sites after arriving on the tundra (Phillips et al. 2007). Thus, nutrients obtained during foraging on breeding grounds are entirely terrestrial and/or freshwater, and thus should exhibit a different isotopic signature than nutrients derived from the marine diet during migration (Peterson and Fry 1987). King eiders nesting in both study areas winter in the Bering Sea and use the eastern Chukchi Sea for approximately three weeks during spring migration, which is a likely site for reserve accumulation (Opper et al. 2009a). The eastern Chukchi Sea is approximately 400 km west of our study area.

Field measurements

We located king eider nests by systematically searching each study site between mid-June and mid-July, and estimated the incubation stages of detected nests by candling eggs on the day the nest was found (Weller 1956). We calculated the day of nest initiation as the day the nest was found minus the incubation stage (in days) of the oldest egg in the nest minus 2 days to adjust for the initial laying stage during which eggs are not incubated (Suydam 2000). Mean dates of nest initiation in our study areas were 19 June 2005 (range 7 June–1 July, $n = 70$), 18 June 2006 (9 June–3 July, $n = 68$), and 19 June 2007 (12–30 June, $n = 43$).

Tissue and food source collection

We collected one egg from each clutch in 2006 and 2007, and all infertile eggs and eggs from abandoned or partly depredated nests in 2005–2007. We collected eggs between 12 June and 15 July 2006 at an average age of 5 days (± 5 days, $n = 69$), and between 17 June and 5 July 2007 at an average age of 4 days (± 5 days, $n = 42$). In 2005, the collection of fresh eggs was not possible due to another ongoing study, and we collected eggs between 15 June and 15 July at an average age of 8 ± 6 days ($n = 24$). All eggs collected at ages >17 days were infertile and had not undergone embryonic development, and we did not analyze eggs that no longer contained white albumen or yellow yolk.

We also collected all remaining eggshell membranes (hereafter: membranes) from depredated and hatched nests. Eggshell fragments were sorted to ensure that each membrane sample represented an individual egg. Membranes were stored individually in paper envelopes and kept dry. Whole eggs were boiled in the field and subsequently kept frozen until analysis (Gloutney and Hobson 1998).

All king eiders at our study sites migrate past Point Barrow, Alaska, in spring (Phillips et al. 2007), approximately 150 and 300 km west of Olak and Kuparuk, respectively. In 2003, eight female king eiders shot by subsistence hunters during the spring migration hunt in Barrow (15–25 May) were collected for another study. We excised sections of breast muscle from those birds to analyze the isotope ratios of king eider protein stores before arrival on breeding grounds (Gauthier et al. 2003).

In 2006 and 2007 we captured 21 female king eiders on the breeding grounds during the pre-nesting period (10–22 June) using mist net arrays and decoys. Although only two of these birds were individually identified via recapture on the nests sampled in our study, it is likely that all 21 females represented birds nesting in our study area because they were captured after their spring migration had ended. At the time of capture, the females had been foraging on

breeding grounds for 0–20 days (Oppel and Powell 2010), thus encompassing the expected time range elapsing between arrival and egg formation for individual eiders in our study area. We collected 1 ml of blood from each bird by jugular venipuncture. Blood samples were separated into blood plasma and red blood cells (RBC) using a portable centrifuge and a precision syringe. We stored plasma and RBC samples frozen in liquid nitrogen until analysis.

We collected potential food items by manually sieving through mud in ponds and lakes of the study areas in July 2005, and by netting pelagic invertebrates in June 2006 and August 2007. We sampled invertebrates in 19 shallow (<1 m deep) ponds 10–200 m in diameter where female king eiders were observed foraging during the pre-breeding period. We used a 1 mm mesh net to capture invertebrates in the water column and floating sediment layer throughout ponds <40 m in diameter, and within 30 m of the shoreline of larger ponds, corresponding to the areas that are ice-free during spring and thus available as foraging habitat for king eiders during the pre-breeding period. We kept all invertebrate samples frozen until analysis. In 2006 we also collected aquatic plant leaves (mostly *Carex* spp., Cyperaceae) from the same ponds. We air-dried plant samples and kept them dry until analysis.

Stable isotope analysis of tissues

We separated whole eggs manually into yolk, albumen, membrane, and shell. Membranes were cleaned with a small brush in deionized water to remove surface contaminants, oven-dried at 60°C for 24 h, and then crumbled in a plastic bag. Albumen and yolk were freeze-dried to constant mass for 48 h, and then ground into powder using mortar and pestle. We extracted yolk lipids by using several rinses with a 2:1 chloroform:methanol solution (Bligh and Dyer 1959; Hobson 1995), and evaporated all remaining solvent from the remaining protein fraction under a fume hood. We cleaned breast muscles in deionized water, freeze-dried and ground them into powder, and extracted lipids from breast muscle using a 2:1 chloroform:methanol solution (Gauthier et al. 2003). We also freeze-dried plasma and RBC samples and homogenized them using mortar and pestle. We did not remove lipids from blood or membrane samples, as these tissues contain too little lipid to significantly alter isotope ratios (Burley and Vadehra 1989; Cherel et al. 2005).

We removed calcified shells from freshwater invertebrates, rinsed soft parts in deionized water, oven-dried them at 60°C for 24 h, and then ground them into powder using mortar and pestle. We used an arithmetic correction for lipid content in invertebrate samples based on mass balance and the C/N ratio of samples (Smyntek et al. 2007). Tadpole shrimps and fairy shrimps (Crustacea: Branchiopoda)

collected in August 2007 were lipid-extracted with a 2:1 chloroform:methanol solution, and we analyzed extracted lipid-free body tissues separately.

All dried and homogenized materials were analyzed for carbon and nitrogen isotope ratios at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) using continuous flow stable isotope ratio mass spectrometry with a Costech ECS4010 elemental analyzer (Costech Scientific Inc., Valencia, CA, USA) interfaced to a Finnigan Delta Plus XP isotope ratio mass spectrometer via the Conflo III interface (Thermo-Finnigan Inc., Bremen, Germany). We report results of carbon and nitrogen isotope analyses in delta (δ) notation relative to international standards (Vienna PeeDee belemnite for C, atmospheric nitrogen for N) according to the following equation: $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1,000$, with X denoting either ^{13}C or ^{15}N , and R representing the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. The standard deviation of replicate measurements of laboratory peptone standards run concurrently with samples was less than $\pm 0.2\text{‰}$ for carbon and $\pm 0.2\text{‰}$ for nitrogen.

Calculation of source contribution

Nutrients in king eider eggs were derived either from marine nutrients stored as body reserves, or from freshwater nutrients obtained by foraging on breeding grounds. We used a two-source mixing model to quantify the contributions of these two sources to a mixture (egg components) using a single isotopic dimension. We performed these calculations for both carbon (C) and nitrogen (N), to assess whether allocation patterns differed between these elements. We estimated the contribution of each source separately for albumen and lipid-free yolk. As we found no differences in egg isotope signatures among years (all Bonferroni-corrected $P > 0.05$), we pooled eggs from all years for analysis.

Avian egg yolk contains $>50\%$ lipids (Oppel et al. 2010; Sotherland and Rahn 1987); therefore, the origin of lipids in yolk of migratory birds is also of interest in studies of nutrient allocation. We measured the carbon isotope ratios of yolk lipids, female adipose tissues, and invertebrate lipids, and these data are available in the “[Electronic Supplementary Material](#)” (Table S1). However, because our measurements of female adipose tissue and prey lipids did not sufficiently constrain the possible sources of yolk lipids, and adequate estimates of discrimination between dietary lipids, adipose tissues, and yolk lipids were lacking, we omitted lipids from our estimates of nutrient allocation.

We characterized the isotope ratios of body reserves and nutrients obtained by foraging on breeding grounds (hereafter referred to as capital and income endpoints,

respectively) specifically for the protein components (albumen and lipid-free yolk). We averaged lipid-corrected isotope signatures of freshwater invertebrates as income endpoint, and used RBC as capital endpoint. RBC are an effective proxy for body protein reserves, as most protein is likely stored in muscles and RBC and muscles turn over at similar rates (Evans Ogden et al. 2004; Hobson and Clark 1993). Thus, we account for any turnover in our capital endpoint that occurs as a result of foraging in a freshwater environment after arrival on breeding grounds (Morrison and Hobson 2004; Schmutz et al. 2006).

We used a Bayesian mixing model to quantify the contribution of each source to egg components (Moore and Semmens 2008). This model incorporates variability in endpoints and discrimination factors to calculate a posterior probability distribution of source contributions (Jackson et al. 2009; Moore and Semmens 2008; Semmens et al. 2009). Because we found considerable variation in isotope ratios of freshwater prey items (Table 1), and we included uncertainty in isotopic discrimination factors, the ability of the Bayesian method to incorporate such variation made it particularly appropriate for this study. We applied corrections for isotopic discrimination between diet, body reserves, and egg components following the approach of Gauthier et al. (2003). We used the mean and SD of published discrimination factors of spectacled eiders (*S. fischeri*) (Federer 2009), peregrine falcons (*Falco peregrinus*), gyrfalcons (*F. rusticolus*), and prairie falcons (*F. mexicanus*) (Hobson 1995) to account for uncertainty around discrimination factors in king eiders, resulting in the use of the following discrimination factors in our model: invertebrates–albumen: $+1.8 \pm 1.5\text{‰}$ for $\delta^{13}\text{C}$ and $+3.3 \pm 0.6\text{‰}$ for $\delta^{15}\text{N}$; RBC–albumen: $+2.2 \pm 0.9\text{‰}$ and $+3.3 \pm 0.6\text{‰}$, invertebrates–lipid-free yolk: $+1.0 \pm 2.0\text{‰}$ and $+3.5 \pm 1.0\text{‰}$; RBC–lipid-free yolk: $+1.5 \pm 0.7\text{‰}$ and $+3.6 \pm 0.8\text{‰}$.

Because discrimination between body reserves and egg components is unknown, and only assumed to be reflected by a carnivore income model (Gauthier et al. 2003), we also explored whether our results would change if this assumption was incorrect. If proteins used for egg synthesis exist in a similar form in body reserves, it is possible that there is no isotope discrimination between body reserves and egg components. Hence, we also calculated source contributions to lipid-free yolk and albumen assuming that there was no discrimination in either C or N between body reserves and egg components.

We used SIAR v 2.07 in R 2.8.0 (Parnell 2008) to create posterior probability distributions for endogenous and exogenous contributions. We estimated means and 95% credible intervals of source contributions, and graphically present the posterior probability distribution for our main model.

Table 1 Stable carbon and nitrogen isotope ratios of relevant sources of nutrients, body tissues, and egg tissues of king eiders in northern Alaska

	$\delta^{13}\text{C}$					$\delta^{15}\text{N}$				
	<i>n</i>	Mean	SD	Min	Max	<i>n</i>	Mean	SD	Min	Max
King eider body tissues										
Breast muscle	8	−17.8	0.5	−18.4	−16.9	8	14.5	0.8	13.5	15.6
Red blood cells (pre-nesting)	21	−19.5	0.8	−20.7	−18.3	21	14.5	0.6	13.4	15.5
Plasma (pre-nesting)	19	−23.1	2.0	−26.9	−19.8	19	11.4	2.2	9.1	16.6
Food on breeding grounds										
Invertebrates ^a	59	−26.6	3.5	−33.0	−20.3	59	4.8	2.3	0.0	9.9
Plants (<i>Cyperaceae</i>)	15	−28.3	1.2	−30.0	−26.4	15	−0.3	5.6	−12.9	10.9
King eider egg tissues										
Eggshell membrane	262	−21.2	2.1	−26.8	−14.6	262	9.2	1.3	5.5	12.9
Albumen	117	−22.9	2.1	−28.8	−18.1	117	7.9	1.2	4.3	12.0
Lipid-free yolk	142	−22.1	2.2	−29.1	−16.4	142	9.9	1.6	6.2	15.7
Whole yolk	20	−24.0	2.4	−26.9	−17.9	20	9.2	1.4	7.2	12.1

^a $\delta^{13}\text{C}$ corrected for lipid content using C/N ratio and mass balance model according to Smyntek et al. (2007)

Incorporating individual variation

We found a wide range of isotopic values in both invertebrate prey items and blood plasma of females during egg formation (Table 1), which suggested that individual females foraged consistently on prey items with different isotope ratios (Bolnick et al. 2002; Matthews and Mazumder 2004). Due to this variation in available and consumed diet items, a mean isotope signature reflecting exogenous nutrients (income endpoint) for all individuals may mask real variation in allocation strategies and lead to significant error in the estimation of source contributions to individual eggs. To address that problem specifically, blood samples could be taken from females captured on nests, but capture and blood sampling of incubating females frequently leads to nest abandonment (Crisuolo 2001). To overcome this problem, we explored the approach of estimating an income endpoint for every individual nest by using the isotope ratios of eggshell membranes.

Eggshell membranes are thought to reflect current diet in seabirds, as reviewed elsewhere (Schaffner and Swart 1991). We found previously that the isotope ratios of eggshell membranes in king eiders do not change during incubation (Oppel et al. 2009c). In addition, experimental data from captive quail showed that eggshell membranes reach an isotopic equilibrium following a diet switch as rapidly as blood plasma (Hobson 1995), a widely acknowledged indicator of recent diet (Evans Ogden et al. 2004; Hobson and Clark 1993; Pearson et al. 2003). Because captive quail are not an ideal model organism for resource use in wild migratory birds, we further evaluated

whether using eggshell membranes indicates current diet in king eiders by comparing the results of the population-level Bayesian mixing model with results obtained using membrane isotope ratios as income endpoints at the individual level. The results were very similar at the population level (see “Results” below), and thus supported the use of eggshell membranes to represent income for individual females. This finding does not rule out the presence of some marine-derived capital resources in eggshell membranes, but it does indicate that any such contribution is insufficient to substantially alter our estimates of resource use at the population level.

We used the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of all membranes collected from a clutch to describe the isotope signature of each laying female’s diet. This approach enabled us to estimate endogenous and exogenous source contributions to egg formation at the individual level. We used established values to correct for discrimination between diet and membranes (Hobson 1995), and calculated source contribution at the individual level using simple linear mixing models (Phillips 2001). We used a membrane-albumen discrimination of -2.3‰ for $\delta^{13}\text{C}$ and -0.6‰ for $\delta^{15}\text{N}$ (obtained by subtracting the diet-membrane discrimination factor from the diet-albumen discrimination factor given by Hobson (1995)), and a similarly derived membrane-lipid-free yolk discrimination of -3.2‰ for $\delta^{13}\text{C}$ and -0.3‰ for $\delta^{15}\text{N}$. Because we found large variations in $\delta^{13}\text{C}$ of freshwater prey items, some of the freshwater prey items approached the $\delta^{13}\text{C}$ of the marine endpoint used in our models. Thus, we excluded eggs from source contribution calculations if the difference between the discrimination-corrected income and capital endpoints was $<2\text{‰}$ in $\delta^{13}\text{C}$

or $\delta^{15}\text{N}$ (12 of 140 for yolk and 10 of 116 for albumen), as the error in calculations increases exponentially with decreasing isotopic difference between endpoints (Phillips and Gregg 2001; Vander Zanden and Rasmussen 2001).

Statistical analysis

We report all results as mean \pm SD. We used nonparametric Wilcoxon tests or Kruskal–Wallis tests to test for significant differences among groups at $\alpha = 0.05$. In multiple comparisons, we used a Bonferroni correction to adjust the error rate to the number of comparisons. We used an ANOVA to examine whether within-clutch variation in nutrient allocation was larger than variation among clutches, and we restricted this analysis to clutches from which we estimated nutrient allocation of more than two eggs. All analyses were carried out using SPSS 11.0 and R 2.8.0.

Results

Isotopic signatures of body tissues

Plasma and RBC of birds captured prior to nesting on breeding grounds did not differ between years (all $P > 0.1$), so we pooled samples from 2006 and 2007. Muscle $\delta^{13}\text{C}$ of female king eiders collected on spring migration was enriched by 1.7‰ over RBC $\delta^{13}\text{C}$ collected from birds on breeding grounds during the pre-nesting period ($W = 167.0$, $P < 0.001$), but muscle and RBC did not differ in $\delta^{15}\text{N}$ ($W = 81.0$, $P = 0.90$, Table 1). Isotope ratios of RBC of king eiders captured during the pre-nesting period did not differ between sites ($\delta^{13}\text{C}$: $W = 26.0$, $P = 0.12$, $\delta^{15}\text{N}$: $W = 38.0$, $P = 0.64$, $n = 21$). We therefore used the pooled sample of RBC $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from both sites as our capital endpoint ($\delta^{13}\text{C}$: $-19.5 \pm 0.8\text{‰}$, $\delta^{15}\text{N}$: $14.6 \pm 0.6\text{‰}$).

Isotopic signatures of diet on breeding grounds

We found large variation in freshwater invertebrates collected on breeding grounds, ranging from -33.0 to -20.3‰ in $\delta^{13}\text{C}$ and from 0.0 to 9.9‰ in $\delta^{15}\text{N}$ (Table 1). Aquatic plants were on average about 1.7‰ depleted in $\delta^{13}\text{C}$ compared to all invertebrates, but fell completely within the range of $\delta^{13}\text{C}$ variation of invertebrates (Table 1).

Proportional contribution of exogenous nutrients to eggs

Based on the results of the Bayesian mixing model, N in both albumen and lipid-free yolk was predominantly

derived from nutrients consumed on breeding grounds (Fig. 1; Table 2). The majority of C in albumen was also derived from exogenous nutrients, while C in lipid-free yolk was derived almost equally from exogenous and endogenous sources (Fig. 1; Table 2). Thus, the exogenous N contribution was almost 30% higher than the exogenous C contribution for both albumen and lipid-free yolk.

Because discrimination between body reserves and egg components is poorly known, we also calculated source contributions assuming no discrimination between body reserves and egg components. With an assumed discrimination of 0‰, the mean of the exogenous C contributions to albumen and to lipid-free yolk decreased by 10% each, whereas the exogenous N contributions to albumen and to lipid-free yolk decreased by 2 and 9%, respectively (Table 2).

With the exception of C in lipid-free yolk, the majority of proteins in king eider eggs were derived from nutrients obtained on breeding grounds, leading to large variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of egg components as a result of large variation in dietary isotope ratios (Table 1; Fig. 1).

Evidence for individual differences in diet

Isotopic variation in eggshell membranes was similar to variation in diet items (Table 1). We found evidence that nesting king eiders foraged consistently on isotopically

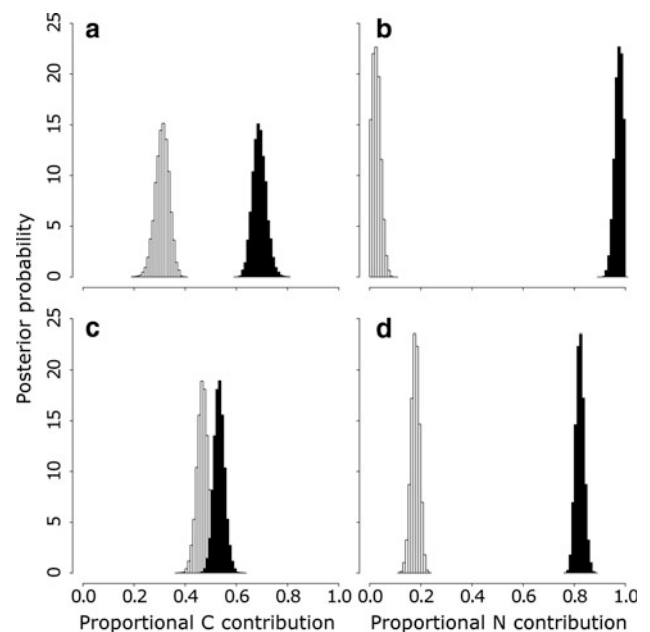


Fig. 1 Posterior probability distribution of exogenous (black) and endogenous (white) nutrient contributions to king eider (*Somateria spectabilis*) eggs from northern Alaska, calculated with a Bayesian isotope mixing model at the population level. **a** Carbon and **b** nitrogen contributions to albumen, and **c** carbon and **d** nitrogen contributions to lipid-free yolk

Table 2 Mean (and 95% credible interval) proportional contribution of exogenous nutrients to albumen and lipid-free yolk of king eider eggs in northern Alaska estimated with a Bayesian mixing model for C and N

	Model 1			Model 2		
	$\Delta\delta^{13}\text{C}$ (‰)	Mean	95% CrI	$\Delta\delta^{13}\text{C}$ (‰)	Mean	95% CrI
C in albumen	2.2	0.69	0.64–0.74	0	0.59	0.54–0.65
N in albumen	3.3	0.97	0.95–1.00	0	0.95	0.90–0.99
C in lipid-free yolk	1.5	0.53	0.49–0.58	0	0.43	0.37–0.49
N in lipid-free yolk	3.6	0.82	0.79–0.86	0	0.73	0.68–0.77

The two models presented differ in the assumption of isotopic discrimination ($\Delta\delta^{13}\text{C}$) between body reserves and egg components

distinct prey items by calculating the within-individual component of the isotopic variance in membranes (Bolnick et al. 2002). We found that within-nest membrane isotopic variance (within-individual component, WIC) was small compared to the total variance (total niche width, TNW) in the population ($\delta^{13}\text{C}$ WIC/TNW = 0.24, $\delta^{15}\text{N}$ WIC/TNW = 0.30, based on 57 nests with >1 membrane), and concluded that individual female king eiders forage on isotopically different prey items during egg formation.

Estimating source contribution with individual income endpoints

To account for individual differences in dietary isotope ratios, we estimated the nutrient source contribution for every egg by using membrane isotope ratios of the respective nest as income endpoints. Among individual females, capital and income endpoints differed from 2.3 to 11.5‰ in $\delta^{13}\text{C}$ and 2.6–11.1‰ in $\delta^{15}\text{N}$. Exogenous N contributed 87–142% to albumen ($109 \pm 10\%$, $n = 116$). Values exceeding 100% reflect the propagation of errors in either endpoints or discrimination factors through mixing model calculations (Wolf et al. 2009); however, the mean contribution of exogenous N to albumen was indistinguishable from 100%. If we adjusted N contributions to egg albumen to a maximum value of 100% (in $n = 96$ eggs), the average contribution of exogenous N was $99 \pm 1\%$ ($n = 116$). In lipid-free yolk, $90 \pm 15\%$ of the N was derived from exogenous sources. Averaged across all individuals, these results were highly consistent with the results from the population-wide Bayesian mixing model, differing from the mean of the posterior probability distribution by only 2% for N in albumen and 8% for N in lipid-free yolk. Only 4% of the eggs had exogenous N contributions of <60%, and most eggs (82%) had very little (0–20%) endogenous N invested in lipid-free yolk ($n = 137$, Fig. 2).

Exogenous C made up $86 \pm 18\%$ (range 26–149%, $n = 106$) of albumen C, with most eggs (65%) having exogenous C contributions of >80% (Fig. 2). Exogenous C contributions to yolk protein were significantly lower than

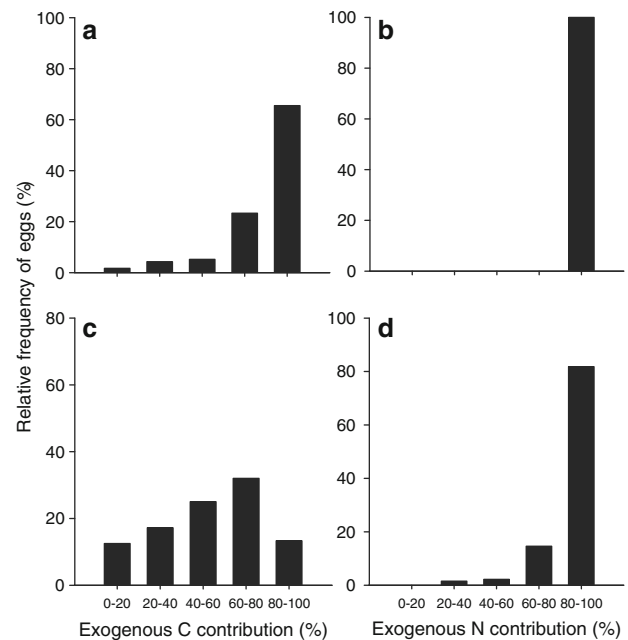


Fig. 2 Relative frequencies of exogenous **a** carbon and **b** nitrogen contributions to albumen, and exogenous **c** carbon and **d** nitrogen contributions to lipid-free yolk in king eider eggs, calculated with individual isotope mixing models using eggshell membranes as nest-specific income endpoint. Eggs for which mixing model results exceeded 100% were included in the 80–100% category (17 for C and 96 for N in albumen, 2 for C and 27 for N in lipid-free yolk)

those to albumen, with an average of $54 \pm 24\%$ (range 0–148%, $n = 128$) of the lipid-free yolk C derived from tundra food sources. These average results across individuals differed from the mean of the posterior probability distribution of the population-level Bayesian mixing model by only 1% in lipid-free yolk and by 12% in albumen. We found large variation in C allocation to lipid-free yolk among eggs, with similar proportions of eggs having almost none (0–20%) and almost all (80–100%) C derived from exogenous sources (Fig. 2).

C and N allocation to yolk protein were positively correlated ($b = 1.16 \pm 0.13$, $P < 0.001$, $R^2 = 0.38$), but the proportion of exogenous N allocations to yolk protein was on average 30% larger than exogenous C allocation

(paired samples t test, $t_{127} = 20.59$, $P < 0.001$); this difference in individual mixing models was identical to the difference found in the population-level Bayesian mixing model.

Variation in nutrient allocation

The large variation in C allocation we found among eggs could be due to either variation in nutrient allocation within a clutch or variation in nutrient allocation among females. Within-clutch variation could be caused by laying order, whereas variation among females could be a result of individual nutrient allocation strategies. We examined whether the variation in C allocation was a result of differences among individual females for seven nests from which we collected more than two eggs. Exogenous C contributions to yolk protein were less variable within than among nests ($F_{6,21} = 3.79$, $P = 0.01$). Similarly, exogenous C contributions to albumen were less variable within than among nests ($F_{5,18} = 14.94$, $P < 0.001$, Fig. 3). Nest initiation date did not explain variation in nutrient allocation among those nests ($P = 0.15$, Fig. 3).

Discussion

Traditionally, large-bodied birds migrating to breed in the Arctic have been viewed as capital breeders, producing eggs mainly from stored body reserves (Ankney and MacInnes 1978). Although recent studies have shown that several Arctic-nesting species use exogenous nutrients for egg production (Gauthier et al. 2003; Klaassen et al. 2001; Morrison and Hobson 2004), capital breeding should be feasible for large-bodied species like king eiders (Klaassen et al. 2006; Nager 2006; Nolet 2006). In contrast to our expectation, we found that king eiders in northern Alaska largely use an income strategy to produce egg proteins. This result is surprising given their body size, allometric considerations of transport costs (Nolet 2006), and the relatively short distance of <500 km to the main spring staging site in the Chukchi Sea.

Variation in isotopic signatures and nutrient allocation

We used two different approaches to estimate nutrient allocation to egg proteins in this study: a Bayesian mixing model using population level dietary endpoints, and an approach using individual nest-specific endpoints based on eggshell membranes. The individual approach was necessary because we found strong evidence that individual female king eiders foraged consistently on isotopically distinct prey sources: both plasma and eggshell membranes exhibited very large isotopic variation, reflecting the

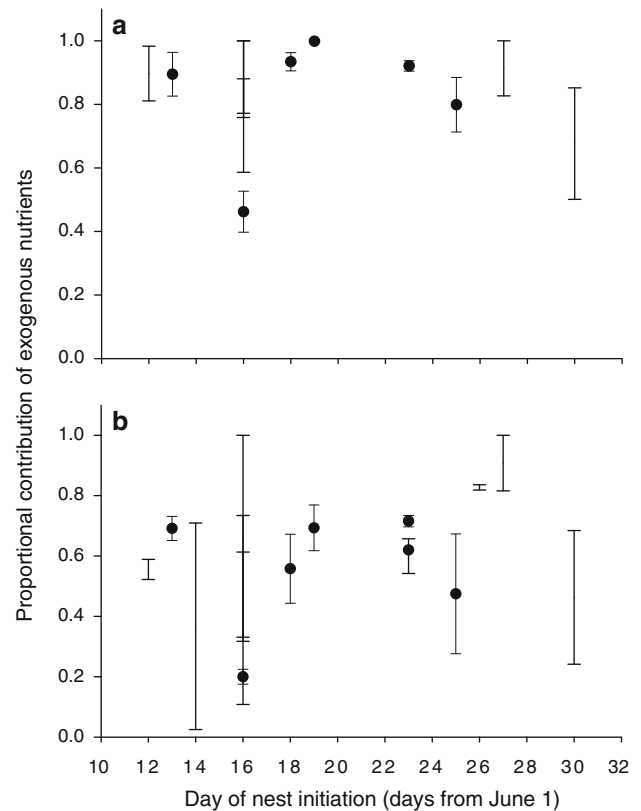


Fig. 3 Proportional contributions of exogenous carbon to **a** albumen and **b** lipid-free yolk in eggs of 16 king eider nests in relation to nest initiation date. Points represent averages (\pm SE) from clutches with >2 sampled eggs, lines represent range in clutches from which only two eggs were analyzed

variable diets consumed by laying females on breeding grounds. Isotopic variability among diets may be caused by eiders consuming different prey taxa, foraging in water bodies with different primary productivity and origin of dissolved inorganic carbon (Peterson and Fry 1987; Post 2002), or by intraspecific variation in prey organism isotope ratios (Grey et al. 2004; Kiljunen et al. 2006). The average results of our individual mixing models were consistent with the results of our Bayesian mixing models at the population level. If membranes had contained significant amounts of endogenous nutrients, the estimates from our individual mixing models would have yielded much higher estimates of exogenous proportions. Because we did not find that pattern in our study, we conclude that using eggshell membranes as individual-specific income endpoints is a reasonable approach.

Furthermore, this approach revealed substantial variation in the origin of nutrients among eggs (Fig. 2) and individual females (Fig. 3). This variation would be obscured by approaches using a population-wide average endpoint for exogenous sources. We thus recommend examining whether a population consists of individual specialists (Bearhop et al. 2004; Matthews and Mazumder

2004; Woo et al. 2008) before using population-wide average estimates of diet isotope ratios in nutrient allocation studies. Similarly, individual endpoints for endogenous sources could be required for animals storing reserves in isotopically different locations, or by foraging on isotopically different prey items. In our case, king eiders exhibited little variation in RBC among individuals, hence individual capital endpoints were not required.

Reviews of the capital-income dichotomy have emphasized that the breeding strategies of most species likely fall along the continuum between the two extremes of pure capital and income breeding (Jönsson 1997; Klaassen et al. 2006; Meijer and Drent 1999). Our study shows that with respect to egg proteins, nutrient allocation strategies can vary even within a species. Intraspecific variation in nutrient allocation has been found in mammals (Hamel et al. 2009; Wheatley et al. 2008) and reptiles (Madsen and Shine 1999; Warner et al. 2008), and may be a result of individual quality, size, age, or the timing of nest initiation. Migratory schedules differ among individuals in our study area (Oppel et al. 2008), and the time between arrival and nest initiation may have a large influence on nutrient allocation. Future studies should investigate migratory schedules of individuals as causes of individual differences in nutrient allocation to reveal potential trade-offs between migratory and reproductive strategies (Bêty et al. 2004; Ely et al. 2007; Prop et al. 2003).

In addition to the variation in endogenous protein contribution among eggs, we found a generally lower contribution of endogenous N than C to egg components in both the individual and the population level approaches. The higher endogenous carbon contribution may result from catabolism of body reserves and incorporation of some of this endogenous C into eggs (Podlesak and McWilliams 2006). This finding is important because traditional dual-isotope mixing models that do not account for concentration dependence (Phillips and Gregg 2001, 2003) assume that C and N are similarly allocated into tissues and eggs (Becker and Beissinger 2006; Benstead et al. 2006; Gauthier et al. 2003; Thompson et al. 1999). We thus recommend that C and N allocation is analyzed separately in investigations quantifying the nutrient allocation strategy of migratory birds.

Uncertainty in discrimination factors is a major concern when reconstructing source contributions to diets or eggs using stable isotopes (Martínez del Rio et al. 2009). Discrimination factors between body reserves and egg components have to our knowledge never been determined experimentally, but we demonstrated that the endogenous contributions of N to albumen and lipid-free yolk were relatively insensitive to variation in this discrimination factor. Similarly, the majority of C in albumen was derived from exogenous sources, even when we assumed no body

reserve–albumen discrimination. For lipid-free yolk, we found the contributions of endogenous and exogenous nutrients to be similar regardless of the discrimination factor used; however, the contribution of endogenous nutrients exceeded that of exogenous nutrients when we assumed no body reserve–yolk discrimination. We recommend that researchers using stable isotopes to study nutrient allocation consider different discrimination factors to evaluate the robustness of their results towards deviation of discrimination factors from assumed values taken from the literature.

Do eiders retain body reserves for incubation?

Although we found that king eiders rely mostly on exogenous proteins to produce eggs, female king eiders lose about 30% of their arrival body mass during the breeding season, suggesting that endogenous nutrients are still likely to be important to successful reproduction (Bentzen et al. 2008; Kellett and Alisauskas 2000). Because only some of these body reserves are invested into eggs, we hypothesize that they may support metabolic costs during the incubation period when eiders rarely leave the nest to forage (Bentzen et al. 2008; Kellett and Alisauskas 2000). A bird of similar mass, the dark-bellied brent goose (*Branta bernicla*), arriving with a mass of 1,500 g at breeding grounds in the Siberian Arctic, invested half of the available body reserves into eggs (Spaans et al. 2007). However, these geese laid the entire clutch within a week of arrival. In contrast, mean arrival and nest initiation dates are two weeks apart for king eiders in our study area, and none of the females collected on spring migration in Barrow showed enlarged follicles. Thus, rapid follicle growth is likely initiated after arrival on breeding grounds in most individuals, offering an explanation for large proportions of exogenous proteins even in yolk.

During incubation, king eiders forage for less than 30 min per day (Bentzen et al. 2008), as opposed to brent geese foraging an average of 3 h per day (Spaans et al. 2007). Thus, while brent geese invest their body reserves into eggs and therefore have to forage extensively during incubation, king eiders may use exogenous resources for egg formation in order to retain body reserves for incubation (Bond et al. 2007; Gorman et al. 2008). As a consequence, there is potential for both endogenous and exogenous nutrient sources to be limiting to king eider reproduction.

Conclusion

King eiders primarily use an income strategy for the synthesis of egg proteins, suggesting that changes of

freshwater foraging habitats on breeding grounds could have significant consequences for reproductive output. Individual females varied in their reliance on endogenous nutrients for egg production, with few producing egg proteins mostly from body reserves. Therefore, we caution against assigning a single nutrient allocation strategy to this species, and encourage researchers to incorporate individual variation into their studies of nutrient allocation in other animals. Our approach enables investigations that focus on individual variation in reproductive strategies and will improve current theories of reproductive and life-history strategies.

Acknowledgments We thank the US Geological Survey Outer Continental Shelf Program and the Minerals Management Service for funding, and the North Slope Borough, ConocoPhillips Alaska Inc., R. Suydam, C. Rea, A.S. Kitaysky, and N. Gundlach for logistical support during fieldwork. S.O. was supported by a Ph.D. fellowship from the German Academic Exchange Service (DAAD). We are grateful to R. Federer and the Alaska Sea Life Center for sharing unpublished data on discrimination factors. S. Sekine, A. Hoffmann, R. Bentzen, C. Latty, A. Patterson, J. Liebezeit, and J. Rogalla assisted in bird captures, nest searches, and egg and membrane collection, and S. Sekine performed laboratory preparations of egg components. K. Hobson, J. Bond, and S. Lawson offered advice on laboratory techniques. T. Howe and N. Haubstock conducted isotope analyses. R. Inger, A. Jackson, and A. Parnell assisted with Bayesian analysis. We appreciate the comments of J. Schmutz, D. Esler, E. Murphy, and two anonymous reviewers on an earlier draft of the manuscript. The work described in this article was approved by the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks under protocol #05-29. Mention of trade names or commercial products is for descriptive purposes only and does not imply endorsement by the US Government.

References

- Alerstam T (2006) Strategies for the transition to breeding in time-selected bird migration. *Ardea* 94:347–357
- Ankney CD, MacInnes CD (1978) Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459–471
- Araújo M, Bolnick D, Machado G, Giarretta A, dos Reis S (2007) Using $\delta^{13}\text{C}$ stable isotopes to quantify individual-level diet variation. *Oecologia* 152:643–654
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- Bearhop S, Phillips RA, McGill R, Chere Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar Ecol Prog Ser* 311:157–164
- Becker BH, Beissinger SR (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conserv Biol* 20:470–479. doi:10.1111/j.1523-1739.2006.00379.x
- Benstead JP, March JG, Fry B, Ewel KC, Pringle CM (2006) Testing Isosource: stable isotope analysis of a tropical fishery with diverse organic matter sources. *Ecology* 87:326–333. doi:10.1890/05-0721
- Bentzen RL, Powell AN, Williams TD, Kitaysky AS (2008) Characterizing the nutritional strategy of incubating king eiders *Somateria spectabilis* in northern Alaska. *J Avian Biol* 39:683–690
- Bêty J, Giroux J-F, Gauthier G (2004) Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behav Ecol Sociobiol* 57:1–8
- Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Can J Biochem Physiol* 37:911–917
- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. *Ecology* 83:2936–2941
- Bond J, Esler D, Hobson K (2007) Isotopic evidence for sources of nutrients allocated to clutch formation by Harlequin Ducks. *Condor* 109:698–704
- Bonnet X, Bradshaw D, Shine R (1998) Capital versus income breeding: an ectothermic perspective. *Oikos* 83:333–342
- Burley RW, Vadehra DV (1989) The avian egg: chemistry and biology. Wiley, New York
- Cherel Y, Hobson KA, Hassani S (2005) Isotopic discrimination between food and blood and feathers of captive penguins: Implications for dietary studies in the wild. *Physiol Biochem Zool* 78:106–115
- Crisuolo F (2001) Does blood sampling during incubation induce nest desertion in the female common eider *Somateria mollissima*? *Mar Ornithol* 29:47–50
- Dalerum F, Bennett NC, Clutton-Brock TH (2007) Longitudinal differences in $\delta^{15}\text{N}$ between mothers and offspring during and after weaning in a small cooperative mammal, the meerkat (*Suricata suricatta*). *Rapid Commun Mass Spectrom* 21:1889–1892
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- Drent R, Both C, Green M, Madsen J, Piersma T (2003) Pay-offs and penalties of competing migratory schedules. *Oikos* 103:274–292
- Drent R, Eichhorn G, Flagstad A, Van der Graaf A, Litvin K, Stahl J (2007) Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. *J Orn* 148:S501–S514
- Ely CR, Bollinger KS, Densmore RV, Rothe TC, Petrus MJ, Takekawa JY, Orthmeyer DL (2007) Reproductive strategies of Northern Geese: why wait? *Auk* 124:594–605
- Evans Ogden LJ, Hobson KA, Lank DB (2004) Blood isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) turnover and diet-tissue fractionation factors in captive Dunlin (*Calidris alpina pacifica*). *Auk* 121:170–177
- Federer R (2009) Quantifying diet to tissue isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) fractionation factors in captive spectacled eiders (*Somateria fischeri*): implications for nutrient allocation and foraging. MSc thesis, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, p 101
- Gauthier G, Bêty J, Hobson KA (2003) Are Greater Snow Geese capital breeders? New evidence from a stable-isotope model. *Ecology* 84:3250–3264
- Gloutney ML, Hobson KA (1998) Field preservation techniques for the analysis of stable-carbon and nitrogen isotope ratios in eggs. *J Field Ornithol* 69:223–227
- Gorman KB, Esler D, Flint PL, Williams TD (2008) Nutrient reserve dynamics during egg production by female Greater Scaup (*Aythya marila*): relationships with timing of reproduction. *Auk* 125:384–394. doi:10.1525/auk.2008.06151
- Grey J, Kelly A, Jones RI (2004) High intraspecific variability in carbon and nitrogen stable isotope ratios of lake chironomid larvae. *Limnol Oceanogr* 49:239–244
- Hamel S, Côté SD, Gaillard J-M, Festa-Bianchet M (2009) Individual variation in reproductive costs of reproduction: high-quality females always do better. *J Anim Ecol* 78:143–151

- Hobson KA (1995) Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. *Condor* 97:752–762
- Hobson KA (2006) Using stable isotopes to quantitatively track endogenous and exogenous nutrient allocations to eggs of birds that travel to breed. *Ardea* 94:359–369
- Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. *Auk* 110:638–641
- Houston AI, Stephens PA, Boyd IL, Harding KC, McNamara JM (2007) Capital or income breeding? A theoretical model of female reproductive strategies. *Behav Ecol* 18:241–250. doi:10.1093/beheco/arl080
- Jackson AL, Inger R, Bearhop S, Parnell A (2009) Erroneous behaviour of MixSIR, a recently published Bayesian isotope mixing model: a discussion of Moore & Semmens (2008). *Ecol Lett* 12:E1–E5. doi:10.1111/j.1461-0248.2008.01233.x
- Jardine TD, Chernoff E, Curry RA (2008) Maternal transfer of carbon and nitrogen to progeny of sea-run and resident brook trout (*Salvelinus fontinalis*). *Can J Fish Aquat Sci* 65:2201–2210
- Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78:57–66
- Kellett DK, Alisauskas RT (2000) Body mass dynamics of King Eiders during incubation. *Auk* 117:812–817
- Kiljunen M, Grey J, Sinisalo T, Harrod C, Immonen H, Jones RI (2006) A revised model for lipid-normalizing $\delta^{13}\text{C}$ values from aquatic organisms, with implications for isotope mixing models. *J Appl Ecol* 43:1213–1222
- Klaassen M, Lindström A, Meltofte H, Piersma T (2001) Arctic waders are not capital breeders. *Nature* 413:794
- Klaassen M, Abraham KF, Jefferies RL, Vrtiska M (2006) Factors affecting the site of investment, and the reliance on savings for arctic breeders: the capital-income dichotomy revisited. *Ardea* 94:371–384
- Madsen T, Shine R (1999) The adjustment of reproductive threshold to prey abundance in a capital breeder. *J Anim Ecol* 68:571–580
- Martínez del Rio C, Wolf N, Carleton SA, Gannes LZ (2009) Isotopic ecology ten years after a call for more laboratory experiments. *Biol Rev* 84:91–111
- Matthews B, Mazumder A (2004) A critical evaluation of intrapopulation variation of $\delta^{13}\text{C}$ and isotopic evidence of individual specialization. *Oecologia* 140:361–371
- Meijer T, Drent R (1999) Re-examination of the capital and income-dichotomy in breeding birds. *Ibis* 141:399–414
- Merkel F, Mosbech A, Jamieson S, Falk K (2007) The diet of king eiders wintering in Nuuk, Southwest Greenland, with reference to sympatric wintering common eiders. *Polar Biol* 30:1593–1597
- Monaghan P, Nager RG (1997) Why don't birds lay more eggs? *Trends Ecol Evol* 12:270–274
- Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol Lett* 11:470–480. doi:10.1111/j.1461-0248.2008.01163.x
- Morrison RIG, Hobson KA (2004) Use of body stores in shorebirds after arrival on high-arctic breeding grounds. *Auk* 121:333–344
- Nager RG (2006) The challenges of making eggs. *Ardea* 94:323–346
- Nolet BA (2006) Speed of spring migration of Tundra Swans *Cygnus columbianus* in accordance with income or capital breeding strategy? *Ardea* 94:579–591
- O'Brien DM, Schrag DP, del Rio CM (2000) Allocation to reproduction in a hawkmoth: a quantitative analysis using stable carbon isotopes. *Ecology* 81:2822–2831
- O'Brien DM, Boggs CL, Fogel ML (2005) The amino acids used in reproduction by butterflies: a comparative study of dietary sources using compound-specific stable isotope analysis. *Physiol Biochem Zool* 78:819–827
- Oppel S, Powell A (2010) Carbon isotope turnover in blood as a measure of arrival time in migratory birds using isotopically distinct environments. *J Orn* 151:123–131. doi:JORN-D-09-00037
- Oppel S, Powell AN, Dickson DL (2008) Timing and distance of King Eider migration and winter movements. *Condor* 110:296–305
- Oppel S, Dickson DL, Powell AN (2009a) International importance of the eastern Chukchi Sea as a staging area for migrating King Eiders. *Polar Biol* 32:775–783
- Oppel S, Powell AN, Dickson DL (2009b) Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck. *J Anim Ecol* 78:524–531. doi:10.1111/j.1365-2656.2008.01513.x
- Oppel S, Powell AN, O'Brien DM (2009c) Using eggshell membranes as a non-invasive tool to investigate the source of nutrients in avian eggs. *J Orn* 150:109–115. doi:10.1007/s10336-008-0325-7
- Oppel S, Federer R, O'Brien DM, Powell AN, Hollmén T (2010) Effects of lipid extraction on stable isotope ratios in avian egg yolk: is arithmetic correction a reliable alternative? *Auk* 157:72–78
- Parker H, Holm H (1990) Patterns of nutrient and energy expenditure in female common eiders nesting in the high arctic. *Auk* 107:660–668
- Parnell A (2008) The SIAR package: stable isotope analysis in R v. 2.07. <http://cran.r-project.org/web/packages/siar/siar.pdf>. Accessed 15 Sept 2008
- Pearson SF, Levey DJ, Greenberg CH, Martinez del Rio C (2003) Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia* 135:516–523
- Perrins CM (1996) Eggs, egg formation and the timing of breeding. *Ibis* 138:2–15
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Ann Rev Ecol Syst* 18:293–320
- Phillips DL (2001) Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* 127:166–170
- Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia* 127:171–179
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136:261–269
- Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144:520–527
- Phillips LM, Powell A, Taylor EJ, Rexstad EA (2007) Use of the Beaufort Sea by King Eiders nesting on the North Slope of Alaska. *J Wildl Manage* 71:1892–1899
- Podlesak DW, McWilliams SR (2006) Metabolic routing of dietary nutrients in birds: effects of diet quality and macronutrient composition revealed using stable isotopes. *Physiol Biochem Zool* 79:534–549
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- Prop J, Black JM, Shimmings P (2003) Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103:403–414
- Schaffner FC, Swart PK (1991) Influence of diet and environmental water on the carbon and oxygen isotopic signatures of seabird eggshell carbonate. *Bull Mar Sci* 48:23–38
- Schmutz JA, Hobson KA, Morse JA (2006) An isotopic assessment of protein from diet and endogenous stores: effects on egg production and incubation behavior of geese. *Ardea* 94:385–397
- Semmens BX, Moore JW, Ward EJ et al (2009) Improving Bayesian isotope mixing models: a response to Jackson et al. (2009). *Ecol Lett* 12:E6–E8. doi:10.1111/j.1461-0248.2009.01283.x

- Smyntek PM, Teece MA, Schulz KL, Thackeray SJ (2007) A standard protocol for stable isotope analysis of zooplankton in aquatic food web research using mass balance correction models. *Limnol Oceanogr* 52:2135–2146
- Sotherland PR, Rahn H (1987) On the composition of bird eggs. *Condor* 89:48–65
- Spaans B, van't Hoff CA, van der Veer W, Ebbinge BS (2007) The significance of female body stores for egg laying and incubation in Dark-bellied Brent Geese *Branta bernicla bernicla*. *Ardea* 95:3–15
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Suydam RS (2000) King Eider (*Somateria spectabilis*). In: Poole A, Gill F (eds) The birds of North America, no. 491. The Birds of North America Inc., Philadelphia
- Thompson DR, Lilliendahl K, Jon S, Furness RW, Waldron S, Phillips RA (1999) Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. *Condor* 101:898–903
- Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol Oceanogr* 46:2061–2066
- Warner DA, Bonnet X, Hobson KA, Shine R (2008) Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *J Anim Ecol* 77:1242–1249
- Weller MW (1956) A simple field candler for waterfowl eggs. *J Wildl Manage* 20:111–113
- Wheatley K, Bradshaw C, Harcourt R, Hindell M (2008) Feast or famine: evidence for mixed capital–income breeding strategies in Weddell seals. *Oecologia* 155:11–20
- Wolf N, Carleton SA, Martínez del Río C (2009) Ten years of experimental animal isotopic ecology. *Funct Ecol* 23:17–26
- Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J Anim Ecol* 77:1082–1091