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RESEARCH ARTICLE

Differential contributions of endogenous and exogenous nutrients to egg components in wild Baltic Common Eiders (*Somateria mollissima*): A test of alternative stable isotope approaches

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ABSTRACT

The relative importance of nutrients derived from feeding on breeding vs. nonbreeding grounds to the formation of eggs is crucial for predicting how the breeding success of migrating birds responds to changes in food availability during any part of their annual cycle. Eiders have been considered a classical capital breeder, but this assumption has rarely been tested. The measurement of naturally occurring stable isotopes in egg components, together with those in endogenous and exogenous nutrient endpoints, allow the estimation of the relative sources of nutrients to eggs, but these mixing models rely critically on appropriate isotopic discrimination factors that link egg isotope values with their source. A recent captive study using Spectacled Eiders (*Somateria fischeri*) provided estimates of these isotopic discrimination factors for income breeding. We applied these discrimination factors for investigating nutrient allocation strategies in Common Eiders (*Somateria mollisima*) breeding in the northern Baltic (Tvärminne, Finland) and wintering in Danish waters, sourced during 2009–2012. Our overall estimates of protein sources using isotopic mixing models were mixed for egg yolk (median: 44.5–56.5% endogenous) and overwhelmingly exogenous for egg albumen (0.4–0.7%). We tested our conclusions also with a single (δ^{15}N) model and with a more parsimonious δ^{13}C discrimination factor between diet and egg albumen, and both supported little to no endogenous reserves being used for egg albumen. A strong positive correlation between egg lipid δ^{13}C and lipid-free yolk δ^{13}C suggests similar metabolic pathways between diet sources and these egg macromolecules. The applicability of isotope discrimination factors used in nutrient allocation studies derived from captive populations needs to be tested in wild populations. Our results support the idea that potential food limitation not only at the wintering areas, but also at the breeding grounds, can limit breeding success of Baltic Common Eiders, which are currently declining.

Keywords: nutrient allocation, carbon-13, nitrogen-15, stable isotopes, capital vs. income, eggs

Contribución diferencial de nutrientes endógenos y exógenos a los componentes del huevo de individuos silvestres de *Somateria mollissima*: evaluación de enfoques alternativos de isótopos estables

RESUMEN

La importancia relativa de los nutrientes derivados de la alimentación en los sitios reproductivos y no reproductivos para la formación de los huevos es crucial para predecir cómo el éxito reproductivo de las aves migratorias responde a los cambios en la disponibilidad de alimentos durante cualquier parte de su ciclo anual. *Somateria mollissima* ha sido considerada como un ave criadora de capital clásica, pero este supuesto muy pocas veces no ha sido evaluado. La medición de isótopos estables naturales en los componentes del huevo, junto a la de los puntos finales de nutrientes endógenos y exógenos, permite estimar las fuentes relativas de nutrientes de los huevos, pero estos modelos duales dependen de modo crítico de los factores de discriminación de isótopos apropiados que vinculan los valores isotópicos del huevo con sus fuentes. Un estudio reciente de aves en cautiverio de *Somateria fischeri* brindó estimaciones sobre estos factores de discriminación de isótopos de ingreso para las crías. Nosotros aplicamos estos factores de discriminación para investigar las estrategias de asignación de nutrientes en individuos de *S. mollisima* que crían en el norte del Báltico (Tvärminne, Finlandia) e invernan en aguas danesas, entre 2009–2012. Nuestras estimaciones globales de las fuentes de proteínas usando modelos duales de isótopos fueron mixtas para la yema del huevo (mediana: 44.5 a 56.5% endógeno) y abrumadoramente exógena para la albúmina del huevo (0.4 a 0.7%). Evaluamos nuestras conclusiones también con un modelo único (δ^{15}N) y con un factor de discriminación δ^{13}C más parsimonioso entre dieta y albúmina del huevo, y ambos apoyaron la noción de un uso pequeño o nulo de las reservas endógenas para la albúmina del huevo. Una fuerte correlación positiva entre el lípido del huevo δ^{13}C y la yema libre de

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lípidos $\delta^{13}C$ sugiere rutas metabólicas similares entre las fuentes de la dieta y estas macromoléculas del huevo. La aplicabilidad de los factores de discriminación de isótopos usados en los estudios de asignación de nutrientes obtenidos de poblaciones cautivas necesita ser evaluada en poblaciones silvestres. Nuestros resultados apoyan la idea de que potenciales limitaciones de alimento, no sólo en las áreas de invernada sino también en los sitios reproductivos, pueden reducir el éxito reproductivo de *S. mollisima*, que está actualmente en disminución.

Palabras clave: asignación de nutrientes, capital vs. ingreso, carbono-13, huevos, isótopos estables, nitrógeno-15

INTRODUCTION

Birds that travel to breed at high latitudes are often faced with low food availability upon arrival; furthermore, arctic breeding seasons are short, and resources for egg production are quickly needed to enable an early start to breeding. Allocating internally stored nutrients to egg formation can alleviate this challenge but involves a cost of transporting nutrients over considerable distance as part of the body mass (reviewed by Drent 2006, Klaassen et al. 2006). For this reason, the capital breeding strategy has mainly been associated with large-bodied birds better able to cope with adverse weather conditions and more efficient at transporting stored nutrients as excess body mass. Among waterfowl, the large-bodied eiders have been considered to be capital breeders (Parker and Holm 1990, Kellet and Alisauskas 2000, Nolet 2006, Bentzen et al. 2008); however, evidence is mounting that previous assumptions regarding the life-history characteristics of migratory birds may need to be revisited. This is especially true for assumptions of capital breeding because this life-history strategy is likely less common in migratory birds than previously believed (Gauthier et al. 2003, Oppel et al. 2010, Hobson et al. 2011, Sénéchal et al. 2011, Sharp et al. 2013). The relative importance of nutrients derived from the breeding vs. wintering grounds is crucial for predicting how the breeding success of migrating birds responds to changes in food availability during any part of their annual cycle.

In wild birds, tracing nutrient allocations from diet and internally stored reserves to reproduction is challenging due to the difficulty in quantifying the mobilization of endogenous and exogenous nutrients to various egg components. Previously, this was done indirectly by assuming that female mass loss during clutch formation was due entirely to investment of endogenous stores into eggs. A more direct approach using measurements of naturally occurring stable isotopes in diets, endogenous reserves, and egg components has recently proved to be a more effective and precise method for tracing nutrient allocation into reproduction (O'Brien et al. 2000, Hobson 2005, Warner et al. 2008). The principle behind this approach is that endogenous reserves acquired away from the breeding grounds may have considerably different stable isotopic values as compared to those of the local diet at the time of egg formation (e.g., Hobson et al. 1997, 2000, 2005, Klaassen et al. 2001, Hobson and Jehl 2010), or that the isotopic discrimination or change that takes place during the mobilization of endogenous nutrients is sufficiently different from the process involved in forming eggs from local diets that distinguish these 2 potential sources of nutrients (Bond and Diamond 2010). This field of study has now benefitted from the development of Bayesian isotopic mixing models that allow reliable propagation of error, the use of informative priors, and the use of convenient web-based statistical packages (e.g., Moore and Semmens 2008, Parnell 2008). However, a current challenge with this approach is the establishment of appropriate diet-to-egg and endogenous reserve-to-egg isotopic discrimination factors that allow quantitative inferences of the relative contribution of endogenous and exogenous nutrient sources to various egg components and macromolecules. A recent study by Federer et al. (2012) provides an opportunity to use eider-specific isotopic discrimination factors that can better inform isotopic mixing models applied to estimating nutrient allocation to reproduction in wild eiders.

Tracing nutrient sources to egg components allows the consideration of individual macronutrients, in particular proteins and lipids. Isotopic studies to date have made use of metabolic routing of these macronutrients and the different allocation strategies that can be associated with them. For example, lipids present largely in egg yolk have typically been traced to local dietary sources vs. those that may have been transported as stores from other locations (Hobson 2005). This makes sense considering the fact that lipids are a preferred material to fuel migration, especially for those birds able to produce lipids from local carbohydrate-rich diets on the breeding grounds (e.g., most geese; Sharp et al. 2013). Proteins, however, can be more limiting, and endogenous allocations on the order of 50% to lipid-free yolk and albumen have been recorded using the isotope approach (Hobson 2005, Sénéchal et al. 2011, Sharp et al. 2013). Albumen proteins are also laid down rapidly just prior to shell formation and so may be more likely to be sourced from local diets compared to proteins from slower-forming yolk, but the effect of tissue formation times on potential nutrient sources to eggs is poorly understood.

In this study, we investigated the isotopic ($\delta^{13}C$, $\delta^{15}N$) composition of Common Eider (*Somateria mollisima*; Figure 1) eggs sampled in Tvärminne, Finland, Baltic Sea,

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FIGURE 1. Incubating female Common Eider (*Somateria mollisima*). Isotopic tracers indicate importance of both local diet and endogenous reserve investments to eggs. Photo credit: Grant Gilchrist

over 4 consecutive breeding seasons. In addition, we examined isotope values of female blood and used this information as a proxy for the body protein pool and their primary diet, blue mussel (*Mytilus edulis*). We used these data primarily in a Bayesian mixing model to estimate the relative endogenous and exogenous carbon (C) and nitrogen (N) contributions to egg proteins and C contribution to egg lipids. Our objectives were to re-evaluate the degree of capital breeding in Common Eiders and to shed light on inter-individual and inter-annual variations in nutrient allocation. We examined isotopic composition of several egg components (lipid-free yolk, yolk lipids, and albumen) to gain insight into relative sources of proteins and lipids for tissues formed over short and longer periods. The resource allocation patterns of Baltic eiders have previously not been analyzed using stable isotope analysis, and this is also the first documented test of the applicability of isotopic discrimination factors derived by Federer et al. (2012) for congeneric Spectacled Eiders (*Somateria fischeri*).

METHODS

Study Site and Field Sampling

The study was conducted at Tvärminne (59°50′N, 23°15′E), western Gulf of Finland, in 2009–2012. Common Eiders in this population spend the winter in Danish waters (e.g., Lehikoinen et al. 2008), and their northward migration along the Swedish east coast is rapid, usually occurring without stopping en route (Alerstam et al. 1974). Females are present close to their nesting islands for at least one month prior to laying and forage outside their breeding colonies before and during the early stages of laying (e.g., Hario and Öst 2002). Egg sampling was conducted on 11 islands spanning the entire study area (range: 1–9 islands annually). The sampling was timed to the early phases of incubation based on egg floatation (Kilpi and Lindström 1997). The egg with the darkest eggshell in each sampled clutch (Table 1), based on visual inspection, was collected, since this egg is usually the first-laid egg in the clutch (Robertson and Cooke 1993, Waldeck et al. 2004). Laying order may be important; previous

TABLE 1. Summary of the stable isotope results (mean ± SD) for Common Eider egg components (2009–2012), Common Eider blood (2010–2012) and dietary blue mussel (2012) collected in the northern Baltic Sea. Similar superscript letters indicate no significant difference ($P > 0.05$) among years for each tissue type according to Tukey's post-hoc test.

Sample	N	$\delta^{13}C$ (‰)	Range (‰)	$\delta^{15}N$ (‰)	Range (‰)	C/N
Eggs 2012						
Yolk	23	−20.5 ± 0.5^{a}	−19.7 to −21.2	12.2 ± 0.5^{a}	11.6 to 13.7	3.2
Albumen	23	−20.9 ± 0.4^{a}	−21.5 to −20.1	11.0 ± 0.5^{a}	10.1 to 12.3	3.6
Yolk Lipid	23	−26.3 ± 0.5^{a}	−27.0 to −20.4	NA	NA	NA
Blood	23	−21.2 ± 0.3^{a}	−21.7 to −20.4	11.3 ± 0.3^{a}	10.9 to 12.2	3.5
Eggs 2011						
Yolk	25	−21.1 ± 0.4^{b}	−21.8 to −20.3	11.4 ± 0.4^{b}	10.9 to 12.5	3.5
Albumen	24	−21.9 ± 1.5^{b}	−22.0 to −20.7	10.4 ± 0.6^{b}	9.5 to 12.8	3.4
Yolk Lipid	26	−26.5 ± 0.5^{a}	−27.8 to −25.6	NA	NA	NA
Blood	24	−21.5 ± 0.4^{b}	−22.4 to −20.7	10.4 ± 1.0^{b}	7.9 to 12.1	2.5
Eggs 2010						
Yolk	23	−20.2 ± 0.4^{ac}	−21.2 to −19.5	12.5 ± 0.6^{a}	10.6 to 13.4	3.5
Albumen	23	−20.9 ± 0.6^{a}	−22.7 to −20.2	11.0 ± 1.2^{a}	6.5 to 12.3	3.2
Yolk Lipid	23	−25.4 ± 0.5^{b}	−26.2 to −24.5	NA	NA	NA
Blood	23	−21.2 ± 0.6^{a}	−22.3 to −20.3	11.0 ± 0.6^{a}	9.7 to 12.2	3.7
Eggs 2009						
Yolk	24	−20.1 ± 0.4^{c}	−21.1 to −19.6	12.3 ± 0.5^{a}	11.0 to 13.1	3.5
Albumen	26	−20.8 ± 0.7^{a}	−23.2 to −19.6	11.2 ± 0.5^{a}	10.3 to 12.1	3.3
Yolk Lipid	24	−24.9 ± 0.5^{c}	−25.7 to −24	NA	NA	NA
Mussel	12	−21.0 ± 0.3	−21.3 to −20.5	7.5 ± 0.6	6.8 to 8.4	3.6

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TABLE 2. Stable isotope discrimination factors (mean ± SD) used in the mixing model to estimate endogenous and exogenous contributions to egg production in breeding Common Eiders.

Source tissue	Egg component	$\Delta^{13}C$ (‰)	$\Delta^{15}N$ (‰)	Source
Lipid-free diet	Lipid-free yolk	2.2 ± 0.3	4.2 ± 0.3	Federer et al. (2012)
Lipid-free diet	Albumen	1.9 ± 0.3	3.5 ± 0.2	Federer et al. (2012)
Diet lipid	Yolk lipid	1.9 ± 0.1	NA	Federer et al. (2012)
Body proteins	Yolk	0 ± 0.5	3.4 ± 0.5	Hobson (1995)
Body proteins	Albumen	0.9 ± 0.5	3.4 ± 0.5	Hobson (1995)
Body lipids	Yolk lipid	0 ± 0.5	NA	Hobson (1995)

studies have shown that stable isotope values may differ between first-laid and final eggs in the same clutches (Sénéchal et al. 2011).

In 2010–2012, the sampling protocol was extended to include blood samples of incubating females captured concurrent with egg sampling (as described above; Table 1). Females were captured by hand-nets, and blood samples were obtained by extracting ~1.5 mL of blood from the ulnar vein. Egg sampling and female handling procedures, including banding, were approved by the Animal Experiment Board/State Provincial Office of Southern Finland, number ESLH-2009-02969/Ym-23, and Tvärminne Zoological Station. A representative sample of blue mussels from local waters were sampled outside Tvärminne Zoological station in 2012 by scraping the mussels off a rock surface into a jar and transported immediately to the lab and stored at –20°C until freeze-drying (Table 1). The blue mussel is the preferred year-round food resource of adult females, except for a short period immediately after hatching of the brood, when brood-tending females are forced to temporarily feed on gammarid amphipods (*Gammarus* spp.; Öst and Kilpi 1999).

Isotope Analysis

Samples of whole blood from females, whole yolk and albumen from eggs, as well as tissue collected from mussels were freeze-dried to constant mass. Following drying, all samples were ground with mortar and pestle to a fine powder. Lipids from yolk and mussel samples were extracted using a solution of 2:1 chloroform:methanol (based on Bligh and Dyer 1959). To recover lipids, extracts from yolk were evaporated under a fume hood at room temperature for 1 week, or until all the solvent had evaporated.

A sample of 1.0 mg (±0.1 mg) from all tissues, excluding yolk lipid, were weighed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis. Yolk lipids were only analysed for $\delta^{13}C$ due to their extremely low N content using similar techniques. All isotope analyses were conducted using continuous-flow isotope-ratio mass spectrometry (CFIRMS) at the Environment Canada Stable Isotope Hydrology and Ecology Research Laboratory in Saskatoon, Saskatchewan. Briefly, material was combusted online using a Eurovector 3000 (Milan, Italy) elemental analyzer. The resulting CO_2 and N_2 analyte gas from the samples was separated by gas chromatograph and introduced into an Nu Horizon (Nu Instruments, Wrexham, UK) triple-collector isotope-ratio mass-spectrometer via an open split and compared to a pure CO_2 or N_2 reference gas. Stable nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) isotope ratios were expressed in delta (δ) notation, as parts per thousand (‰) deviation from the primary standards: atmospheric nitrogen and Vienna Pee Dee Belemnite (VPDB) carbonate standards, respectively. Using previously calibrated internal laboratory C and N standards (powdered keratin and gelatin), within-run precisions for $\delta^{15}N$ and $\delta^{13}C$ were better than ±0.15‰.

Mixing Model Calculations

Isotopic discrimination factors used in this study to adjust $\delta^{13}C$ and $\delta^{15}N$ values for conversion of dietary isotope values to those of egg constituents were based on a recent captive-rearing study of Spectacled Eiders by Federer et al. (2012; Table 2). Discrimination factors corresponding to the conversion of endogenous reserves to egg components have not been established experimentally for Common Eiders; however, Gauthier et al. (2003) reasoned that mobilizing nutrients from endogenous reserves to eggs is similar to the mobilization of exogenous muscle tissue to eggs in carnivorous birds. Therefore, isotopic discrimination values from the Hobson (1995) carnivore model for Peregrine Falcons (*Falco peregrinus*) feeding on Japanese Quail (*Coturnix japonica*) muscle were used to infer isotopic discrimination for the conversion of body protein to lipid-free yolk and albumen and from dietary lipids to egg lipids (Table 2). The isotopic composition of whole blood was assumed to represent the body protein pool. No isotopic discrimination is thought to occur between abdominal fat and yolk lipid because little metabolic breakdown occurs to convert stored fat into yolk lipid (Gauthier et al. 2003). Mussel samples from the study area, corresponding to dietary isotope values, were available only for 2012 and were assumed to remain isotopically constant across the study period. Blood samples of adult egg laying females were missing for 2009. We used the

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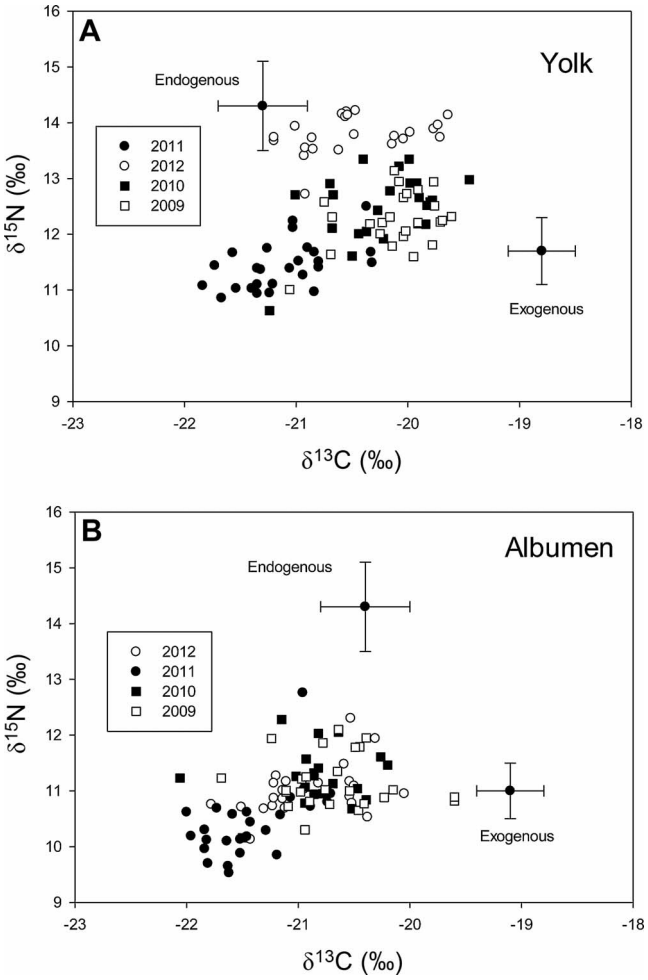


FIGURE 2. Isotopic biplot (mean ± SD) of individual egg components, (**A**) yolk and (**B**) albumen, of Common Eider breeding in the northern Baltic in 2009–2012. The endogenous endpoint was based on Common Eider blood samples for each year except for 2009. The exogenous endpoint was based on local mussel samples collected in 2012. All endpoint isotope values were corrected to represent expected Common Eider egg values using discrimination factors (see Methods). Each data point represents a single egg from a single female.

Bayesian mixing model MixSIR (v1.0; Moore and Semmens 2008) to provide an estimate of the percent endogenous contribution to egg components for each year based on the assumptions of isotopic discrimination factors outlined above. The mixing model was run using 1,000,000 iterations.

RESULTS

In general, egg yolk and albumen differed little among years 2009, 2010, and 2012 but tended to be more depleted in ^{13}C and ^{15}N in 2011 (Table 1; yolk $\delta^{13}C$: $F_{3,95} = 27.97$, $P < 0.001$; yolk $\delta^{15}N$: $F_{3,95} = 21.31$, $P < 0.001$; albumen $\delta^{13}C$: $F_{3,92} = 12.0$, $P < 0.001$; albumen $\delta^{15}N$: $F_{3,93} = 5.45$, $P = 0.002$). Egg lipid $\delta^{13}C$ values formed 3 homogenous groups, 1 each in 2009 and 2010, respectively, and 1 in years 2011 and 2012 (Table 2; $F_{3,96} = 62.2$, $P < 0.001$). Female blood was depleted in ^{15}N ($F_{2,70} = 9.08$, $P < 0.001$) and ^{13}C ($F_{2,70} = 4.29$, $P = 0.018$) in 2011 compared to 2010 and 2012.

TABLE 3. Calculated endogenous nutrient contribution (mean and 5th to 95th percentile range) to egg components of Common Eiders based on a stable isotope mixing model (MixSir) using both $\delta^{13}C$ and $\delta^{15}N$ measurements and mean endogenous nutrient contribution estimate based on a single model using only $\delta^{15}N$ measurements.

	Dual isotope model		Single isotope ($\delta^{15}N$) Model	
Sample	Yolk	Albumen	Yolk	Albumen
2009	44.5 (51.5–58.6)	0.7 (0.1–2.7)	16.2	5.4
2010	46.0 (47.5–49.4)	0.4 (0–1.6)	22.9	0
2011	56.5 (53.3–60.0)	0.4 (0.1–0.7)	NA*	NA*
2012	45.5 (41.4–48.5)	0.6 (0–2.1)	16.7	0

* Sample mean $\delta^{15}N$ fell below of the solution space

We constructed single isotopic biplots of the data for lipid-free egg yolk and albumen for all years of sampling (Figure 2). Those depictions showed that, with the exception of 2011, yolk isotope values generally fell between the endogenous and exogenous endpoints. A poor fit was found for the albumen biplot, however, with all samples generally falling to more depleted than expected values (or alternatively with endpoints requiring a different and more negative $\Delta^{13}C$ calibration). Nonetheless, based on the best available data, we conducted our Bayesian mixing model analyses to estimate endogenous contribution to lipid-free yolk and to egg albumen for each year of sampling (Table 3). Those analyses showed remarkable consistency for all years, with mean endogenous contributions to egg yolk ranging from 44.5 to 46% and to egg albumen from 0.4 to 0.7% except for 2011, which showed a mean endogenous contribution to egg yolk of 60%.

Considering only $\delta^{15}N$ as a means of tracing protein allocation to eggs (based on the observation that samples generally fell between endogenous and exogenous $\delta^{15}N$ endpoints for albumen), we used a single isotope (i.e. $\delta^{15}N$), dual-source (i.e. endogenous vs. exogenous) model. That analysis confirmed little if any contribution from endogenous reserves to albumen but also tended to predict lower endogenous contribution to yolk compared with the dual isotope model (Table 3).

We found a moderate, positive relationship between $\delta^{13}C$ and $\delta^{15}N$ values of lipid-free yolk and albumen (Figure 3a, 3b) and between $\delta^{13}C$ of egg lipids and lipid-free yolk (Figure 4a), but a weaker relationship between $\delta^{13}C$ of egg lipids and albumen (Figure 4b). Female whole

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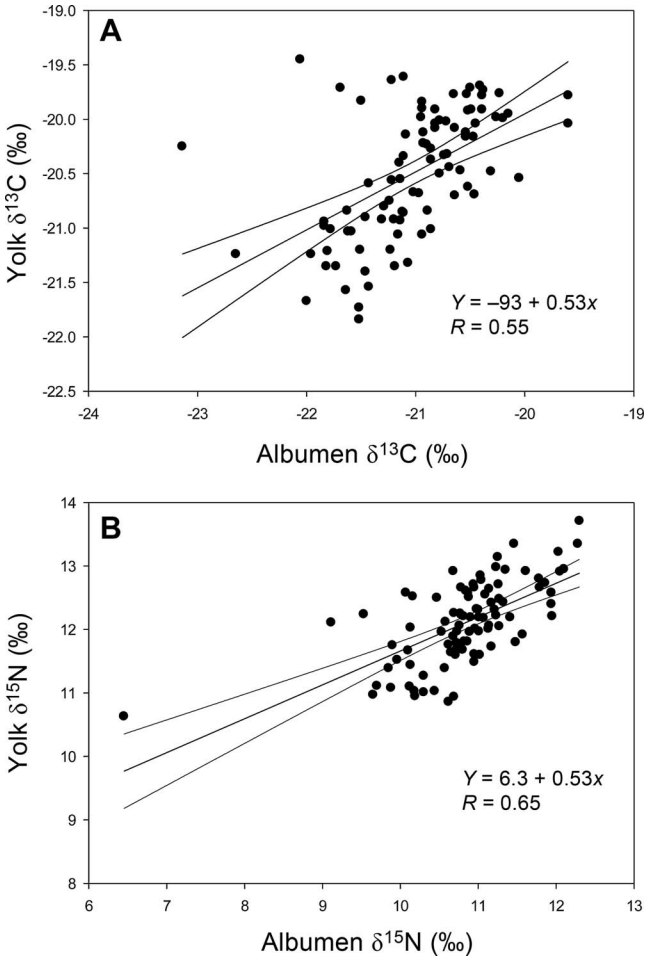


FIGURE 3. Relationship between (**A**) lipid-free egg yolk $\delta^{13}C$ and albumen $\delta^{13}C$ ($F_{1,90} = 36.8$, $P < 0.001$) and (**B**) lipid-free egg yolk $\delta^{15}N$ and albumen $\delta^{15}N$ ($F_{1,92} = 64.8$, $P < 0.001$) for Common Eiders breeding in the northern Baltic in 2009–2012. Each data point represents a single egg from a single female.

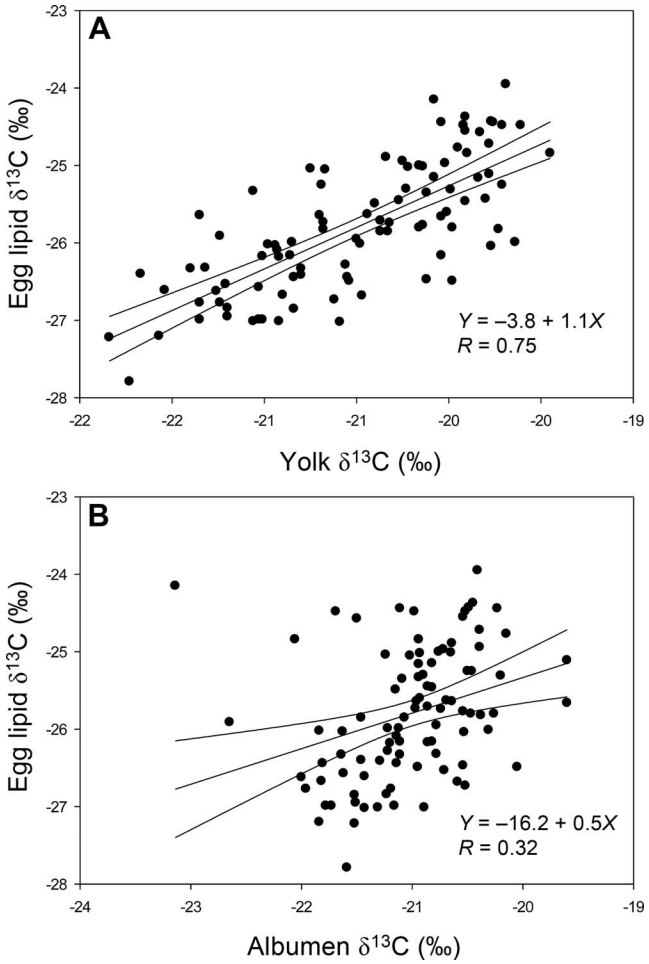


FIGURE 4. Relationship between egg lipid $\delta^{13}C$ and (**A**) lipid free yolk $\delta^{13}C$ ($F_{1,95} = 117.5$, $P < 0.001$) and (**B**) albumen $\delta^{13}C$ ($F_{1,95} = 0.76$, $P = 0.39$) for Common Eiders breeding in the northern Baltic in 2009–2012. Each data point represents a single egg from a single female.

blood $\delta^{13}C$ was almost identical to lipid-free mussel ($\Delta^{13}C \sim 0$‰), whereas blood $\delta^{15}N$ values were higher by 3.8‰ (i.e. $\Delta^{15}N = 3.8$‰; $F_{1,5} = 132.2$, $P < 0.0001$).

DISCUSSION

Our dual-isotope Bayesian mixing model provided evidence that about half of the protein forming the lipid-free egg yolk of Common Eider eggs came from endogenous protein sources, likely stored at the wintering area in the Danish sounds (Noer 1991). Intriguingly, all of the protein making up albumen came directly from local diet, in contrast to previous assumptions that eiders form eggs almost entirely from endogenous reserves (Parker and Holm 1990, but see Sénéchal et al. 2011), and emphasizes the effects that local food availability may have on eider reproductive investment. Egg albumen is produced both later in the egg development process and more rapidly than the yolk (e.g., Von Engelhardt and Groothuis 2005), which may be linked to our finding that endogenous reserves play a lesser role for albumen production than for yolk production.

Stable Isotope Models

Our dual-isotope model performed reasonably well for tracing protein sources to eggs; specifically, for 3 of the 4 years of the study, the yolk $\delta^{13}C$ and $\delta^{15}N$ values fell between the expected endogenous and exogenous endpoints in bivariate isotope space. However, the model for sources of nutrients to albumen predicted contributions falling below the range expected for $\delta^{13}C$ values of albumen derived from either endogenous or exogenous endpoints. For this reason, we also considered a single isotope model based on $\delta^{15}N$ values because all N in eggs is associated with a protein metabolic pathway. This approach confirmed there being virtually no endogenous

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contribution to albumen N and also suggested lower (i.e. 16–23%) endogenous contributions to yolk proteins than predicted by the dual-isotope model (approximately 44–57%). Because we did not sample the adipose tissue of laying females, we were unable to derive a mixing model that traced the origins of egg lipids; however, we were able to examine correlations between $\delta^{13}C$ of egg lipids and $\delta^{13}C$ of egg albumen and lipid-free yolk. The weaker relationship shown for albumen (Figure 3a) suggests that egg lipids were mainly derived from endogenous reserves. The decoupling of nutrient sources between egg yolk and albumen was also supported by the strong relationship we found between yolk lipid $\delta^{13}C$ and lipid-free yolk compared to the poor relationship between yolk lipid $\delta^{13}C$ and albumen $\delta^{13}C$. It seems that the carbon contained in the lipids transferred into eggs came from similar isotopic sources as that in yolk proteins and thus derived from previous dietary sources that were stored endogenously. These sources of lipid were not the same as those for albumen, which were in turn derived from local dietary sources. In general, then, our study provides strong evidence for Common Eider albumen being formed from the local mussel diet in all years of the study and that the nutrients allocated to yolk proteins come from both local and previously stored sources. Because Baltic eiders migrate to their breeding sites in the northern Baltic without stopping (Alerstam et al. 1974), the likeliest source of the stored nutrients are the mussel beds of the wintering area in the Danish sounds.

The stable isotope approach to tracing sources of nutrient allocation to reproduction in birds that travel across isoscapes to breed offers major advantages over previous conventional approaches (Hobson 2005). A current weakness, however, is clearly our poor understanding of the isotopic discrimination factors related to the transfer of dietary nutrients to eggs as well as the transfer of dietary nutrients first to endogenous stores and then through remobilization to egg formation. Federer et al. (2012) provided an important set of discrimination estimates specific to eiders based on their captive rearing study on Spectacled Eiders, and those were used here in a first application to a wild congeneric species. However, the Federer et al. (2012) study was limited by several factors that need to be considered; the diet of captive Spectacled Eiders was not a single homogenized source but consisted of a combination of commercial feed and Atlantic silverside (*Menidia menidia*). As a result, Federer et al. (2012) were forced to estimate the relative biomass of each of these food items to the actual diet of the birds. This is particularly concerning because the 2 diets differed dramatically in their N content (3.3% vs. 13.6%), and we know that discrimination factors are strongly influenced by the protein quality of the diet and possibly also by the protein quantity (Robbins et al. 2005, Martinez del Rio et al. 2009, Martinez del Rio and Carleton 2012). It is also not clear to what degree captive eider females use the assumed income-based allocation strategy or whether they also form eggs from body stores despite captive conditions with ad libitum access to food. Our own assumption of discrimination factors associated with the mobilization of endogenous reserves to eggs based on a carnivore income model (Hobson 1995, Gauthier et al. 2003) has also not been derived experimentally. Unfortunately, such a derivation would require captive birds in isotopic equilibrium with a known diet to be deprived of food and expected to lay eggs under a forced complete capital strategy at the stage of early egg formation.

Female blood $\delta^{15}N$ was 3.8‰ higher than the local mussel diet, which supports our assumption of this being the primary dietary item (Federer et al. 2010 estimated a $\Delta^{15}N$ value of 4.0‰ for cellular blood). However, we estimated a $\Delta^{13}C$ close to 0, which contrasts with the Federer et al. (2012) estimate of 1.9‰. Again, we suggest that the Federer et al. (2012) results are only approximations, and much more carefully controlled studies are needed on captive eiders using single homogenized diets. In our case, using a $\Delta^{13}C$ value of 0 for the discrimination between lipid-free diet (mussel) and albumen made little difference to our conclusions, with the predicted endogenous contribution for albumen ranging from 0.6% in 2011 (range: 0.1–2.5%) to 4.7% (0.6–10.3%) in 2012.

Our study assumed that the isotopic composition of mussels remained constant among years and that this was the primary prey of Common Eiders prior to laying. Both of these assumptions are reasonable (e.g., Moody et al. 2012). In our study area, Jaale (2007) examined isotopic variation among blue mussels in coastal Finland, 2002–2004, and although they did not extract lipids from mussel samples prior to isotope analysis (thereby contributing to variance in $\delta^{13}C$), within-site and between-year variance in both $\delta^{13}C$ and $\delta^{15}N$ was low (maximum difference ~1‰). Our Common Eider study population is also known to frequent the same pre-laying foraging zone of the Tvärminne archipelago (Ekroose et al. 2012) and to utilize mussels of a relatively uniform size (Öst and Kilpi 1998).

Ecological Implications and Future Research Prospects

Our study emphasizes that previous considerations of Common Eiders as largely capital breeders are unfounded. However, the annual utilization of endogenous reserves likely depends on relative mussel availability at the wintering and breeding grounds, and the higher observed reliance on endogenous reserves by laying females in 2011 may relate to this variation. Comparing this result against annual climate and Common Eider breeding parameters (Table 4) reveals consistent patterns that, although not allowing causal inferences, seem relevant in this context. Winter 2010/2011 had the largest annual maximum ice

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TABLE 4. Summary statistics of annual climate parameters (maximum Baltic ice cover; Vihma and Haapala 2009) and breeding parameters of Common Eider females (hatch date, global condition index, clutch size and their corresponding SE) from Tvärminne in 2009–2012. As a global measure of body condition, we used the standardized residuals of a regression of log-transformed projected weight at hatching on log-transformed radius–ulna length based on pooled data from all 4 years (e.g., Jaatinen et al. 2011). The data summarizing the phenology of spring migration (arrival of 5% and 50% of migrants; Lehikoinen et al. 2006) were collected at Hanko Bird Observatory, situated 20 km west of Tvärminne. The sample size of females included in the summary statistics of breeding parameters was: $n = 220$ in 2009, $n = 173$ in 2010, $n = 221$ in 2011, and $n = 187$ in 2012. Similar superscript letters indicate no significant difference ($P > 0.05$) among years for breeding parameters according to Tukey's post-hoc test.

Parameter	2009	2010	2011	2012
Hatch date	22 May ± 0.3[a]	28 May ± 0.4[b]	1 June ± 0.3[c]	30 May ± 0.4[b]
Global condition index	−0.035 ± 0.06[a]	−0.076 ± 0.07[a]	−0.158 ± 0.07[a]	−0.029 ± 0.06[a]
Clutch size (eggs)	4.96 ± 0.08[a]	4.56 ± 0.09[b]	4.7 ± 0.07[ab]	4.52 ± 0.09[b]
Days hatch-arrival 5%	60	60	66	69
Days hatch-arrival 50%	51	46	58	56
Maximum Baltic ice cover (1000 km^2) in preceding winter	110	244	315	174

extent of the Baltic Sea of the 4 study years (Table 4; http://ilmatieteenlaitos.fi/tiedote/131189). Median hatch date was latest in 2011 (Table 4), and female body condition based on residual mass (cf. e.g., Jaatinen et al. 2011) was numerically, although not statistically significantly, lower in 2011 than in the other years (Table 4). It is conceivable that cold winters like 2011 offer better foraging conditions for wintering Common Eiders because such winters positively affect individual mass and reproduction of blue mussels in the southern Baltic Sea (Waldeck and Larsson 2013). In contrast, severe ice conditions at the breeding locality (Tvärminne) may have interfered with efficient acquisition of local food resources through pre-laying foraging, as perhaps indicated by the fact that spring arrival was not later than average, whereas the onset of breeding was significantly later than usual. So the high reliance on endogenous reserves in 2011 is consistent with presumably favorable feeding conditions in the wintering area coupled with a late ice break-up at the breeding grounds. Alternatively, late breeders may lay fewer eggs, allowing them to increase the proportion of endogenous nutrients invested into each egg, which may speed up their breeding schedule and thereby minimize any additional delay (Sénéchal et al. 2011). This explanation seems less likely, however, because mean clutch size in 2011 did not differ from the other years.

Regardless of the underlying mechanisms, the complexity of annual resource allocation decisions clearly calls for more detailed investigations, preferably linking individual variation in resource use to variation in individual phenotypic traits and fitness (cf. Newsome et al. 2009, Vander Zanden et al. 2010).

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