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. . Nutrient-allocation models based on stable-isotope analysis are used to determine the nutrient sources birds invest in eggs. This approach is particularly useful for birds that migrate between habitats with distinct stable-isotope compositions. A crucial variable is the difference in stable-isotope values of egg tissues -
tion factors between the female's diet and embryonic down feathers (Δδ

$^{13}C = 2.1‰$ and $\Delta\delta^{15}N = 5.2‰$). Finally, we determined discrimination factors between lipid and protein in diet sources and eggs, thus enabling consideration of these nutrients separately. Our study enhances the framework for nutrient-allocation modeling in eiders and likely other sea ducks.

Factores de Discriminación de Isótopos de Carbono y Nitrógeno Estables para Cuantificar la Asignación de Nutrientes de en la Producción de Huevos

. Los modelos de asignación de nutrientes basados en análisis de isótopos estables son usados para determinar las fuentes de nutrientes que las aves invierten en los huevos. Este enfoque es particularmente útil para las aves que migran entre hábitats con composiciones distintivas de isótopos estables. Una variable crucial es la diferencia en los valores de isótopos estables de los tejidos de los huevos relativos a la dieta, lo que permite usar ajustes apropiados en los modelos que comparan los nutrientes de los tejidos con las fuentes de alimentos. Establecimos factores de discriminación (Δδ) entre la dieta y los huevos de individuos cautivos de alimentados con una dieta control. Relativos a la dieta, los valores de $\Delta\delta^{13}C$ fueron superiores para el albumen (2.6‰), la proteína de la yema (2.9‰), la cáscara del huevo (13.0‰) y la membrana de la cáscara (3.9‰), e inferiores para la yema completa (–1.6‰) y los lípidos de la yema (–3.5‰). Los valores $\Delta\delta^{15}N$ de los componentes del huevo fueron superiores relativos a la dieta (albumen 3.7‰, proteína de la yema 4.4‰, membrana de la cáscara 4.7‰ y yema completa 3.5‰). Excepto para las proteínas del huevo, estos hallazgos son generalmente consistentes con los valores publicados para otras aves. Concluimos que la selección de los factores de discriminación podría afectar marcadamente los estimados de las fuentes de contribución a los huevos y por ende permitir recomendar estimados específicos para las especies.

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INTRODUCTION

Analyses of stable carbon and nitrogen isotopes can be used to evaluate allocation of nutrients for egg production in birds that migrate between isotopically distinct regions for the nonbreeding and breeding stages of the annual cycle (Hobson et al. 1997, 2000, Hobson 2006). With this approach, mixing models can be applied to quantify sources of nutrients used for egg production (Phillips and Gregg 2001, 2003, Moore and Semens 2008). These nutrient-allocation models typically require stable-isotope values for two or more potential nutrient sources and the animal tissue, such as egg components or feathers, corrected for diet to tissue discrimination factors ($\Delta\delta$). However, there are few species-specific data available for quantifying discrimination factors in avian egg components (Hobson

considering macronutrient allocation to eggs, we separated diet and yolk samples into lipid and nonlipid components because of potential mean differences in discrimination factors. To extract lipids from diet items and whole yolk we used a 2:1 ratio of chloroform:methanol solution and followed the methods of Bligh and Dyer (1959) except we used no water because stable isotopes are analyzed as dry material. We used a vortex to mix ~5 mg of dry sample with solution, allowed samples to settle for 24 hr, and extracted lipids manually with a pipette until solvent wash was clear (Oppel et al. 2010). L

found a decrease in $\delta^{13}C$ for egg components that contain lipid (i.e., whole yolk and yolk lipid) as previously described. These lower $\delta^{13}C$ values are the result of high lipid concentration in these tissues and oxidation of these lipids during lipid synthesis (DeNiro and Epstein 1977). Finally, $\Delta\delta^{15}N$ values for albumen, whole yolk, lipid-free yolk, and shell membrane were higher than those found by Hobson (1995).

Our results also provide discrimination factors from the female's diet to embryonic down feathers, which have not been previously documented for birds. Feathers consist of proteins (Murphy 1996), and, as might be expected, discrimination factors for embryonic down feathers were similar to those for protein-based components of the egg.

We determined stable-isotope values for the whole diet, diet with lipid removed, and lipid from the diet and therefore discrimination factors from diet macronutrients (i.e., diet lipids and diet with lipids removed) to those lipid (i.e., yolk lipid) and protein portions of the egg or the embryo, respectively (i.e., albumen, lipid-free yolk, shell membrane, and down feathers). Use of macronutrient-specific discrimination factors will further increase the applicability of stable isotopes in studies of nutrient allocation to egg production because these different macronutrients may be derived from sources in isotopically distinct habitats.

Previous studies have shown that differences in isotopic discrimination of tissues may be the result of species-specific physiology (DeNiro and Epstein 1978, 1981, Hobson and

discrimination factors are a significant advancement (Hobson and Clark 1992, Hobson 1995, 2006, Dalerum and Angerbjorn 2005, Caut et al. 2008) and believe our data represent values for appropriate for the Spectacled Eider more accurately. Further experiments using artificial and natural diets varying in nutrient composition may be useful for understanding how changes in diet composition may affect isotopic discrimination factors in tissues of the Spectacled Eider, particularly for a species whose diet varies seasonally.

CONSERVATION IMPLICATIONS

The method of nutrient-allocation modeling using stable isotopes has important conservation implications for a threatened species like the Spectacled Eider. This species spends the majority of its annual cycle in offshore marine habitats (Petersen et al. 1995, 1999) and travels to freshwater tundra habitats for reproduction (U.S. Fish and Wildlife Service 1996). Potential factors leading to the decline or affecting population recovery include changes in the marine environment, such as food abundance and availability (U.S. Fish and Wildlife Service 1996, Richman and Lovvorn 2003) and shifts in marine habitats (Lovvorn et al. 2003). Because many sea ducks spend much of the winter and staging periods in marine habitats, it is plausible that their reproductive performance is correlated with the availability and quality of marine resources. However, the nutrient-allocation strategies used by breeding Spectacled Eiders are largely unknown. Tissues such as eggs and down feathers and nest-bowl contents could be useful in understanding the sources and timing of acquisition of nutrients for reproduction. Stable-isotopic discrimination factors for other species have been calculated in one study previously, but our data are the first discrimination factors reported for the Spectacled Eider. While down feathers have been used to infer percentages of nutrient sources used for egg production (Klaassen et al. 2001, 2004), stable-isotopic discrimination factors for down feathers have not been previously calculated, so these data will allow a more precise calculation for understanding proteins used for egg production in wild populations. Furthermore, down feathers as well as eggshells and eggshell membranes can be sampled noninvasively when collected from hatched eggs once the young have left the nest, which is especially important for a threatened population. Building information about strategies of nutrient acquisition and allocation will be useful for evaluating factors affecting population productivity and will contribute to conservation of the threatened Spectacled Eider.

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