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Abstract: Naturally occurring stable isotopes in foodwebs can be used to determine the relative contributions of endogenous and exogenous nutrients to avian eggs in cases where birds move between isotopically distinct biomes or habitats to breed. We measured δ^{13}C and δ^{15}N values in somatic muscle tissues and eggs of Barrow's goldeneye (*Bucephala islandica*) together with those isotope values in amphipods from wetlands used by birds breeding on the Chilcotin Plateau in central British Columbia, Canada. Females that had recently arrived on the breeding grounds had muscle tissue isotope values similar to those found in coastal wintering birds and were considerably more enriched in ^{13}C than were samples from local foodwebs. However, δ^{15}N values of amphipods were highly variable among wetlands, resulting in a nondistinct exogenous δ^{15}N endpoint for our dual-isotope mixing model. Therefore, we only used the model based on δ^{13}C values to estimate nutrient sources to eggs. In 2000, first-laid eggs were more enriched in both isotopes than fourth- or eighth-laid eggs. Considerable endogenous protein input to egg yolk and albumen was detected for the first laid egg (yolk: range = 0–92.7%, median = 23.7%; albumen: range = 0–78.6%, median = 28.7%) with less endogenous contribution of somatic lipids (first egg: range = 0–100%, median = 4.9%). Using archived tissue samples of muscle and developing ovarian follicles from birds collected in 1993–1994, we found no δ^{13}C isotopic evidence for endogenous protein contribution to egg yolk. Our results demonstrate the utility of the stable isotope approach in cases where isotopic endpoints are well established. Barrow's goldeneye showed a mixed strategy of endogenous vs. exogenous nutrient allocation to reproduction that varied by individual females, laying order, and year. We encourage managers to use this approach to quantify nutrient allocations from various biomes to reproduction in waterfowl to better understand the importance of wintering sites to reproduction.

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Birds have evolved a variety of life history strategies to optimize investment into reproduction. One important aspect of such strategies is the relative allocation of endogenous and exogenous nutrients to eggs. Drent and Daan (1980) introduced the concept of capital vs. income strategies to describe alternate reproductive investment of stored or locally ingested nutrients to clutch formation. At one extreme, capital breeders rely exclusively on endogenous reserves brought to breeding grounds for reproduction. Arctic-nesting geese that arrive on breeding grounds with few locally available foods are considered the best example of this strategy (Ankney and MacInnes 1978

2001). Correspondingly, body condition upon arrival may influence the final clutch size or volume in some species of waterfowl (Alisauskas and Ankney 1992) and thereby directly confer a fitness advantage. Understanding factors influencing fitness that occur at times and locations outside of the breeding season

mately 2.5, or intermediate between a primary herbivore and carnivore).

RESULTS

Overall, wetlands differed in amphipod mean lipid-free $\delta^{13}C$ values (range: 2.8‰, $F_{3,45} = 82.5$, $P < 0.001$, Table 1), but this was driven by a single wetland (no. 115, $\delta^{13}C = -24.6$‰) that was more enriched in ^{13}C than the others by 2.3 to 2.8‰ (Fig. 1). However, we found considerable variation among wetlands in amphipod ^{15}N values ($F_{3,45} = 71.0$, $P < 0.001$, Table 1) with some wetlands (e.g., 8,11) showing values more enriched in ^{15}N than expected (i.e., more enriched than our marine endpoint by 4.6 to 6.4‰; Fig.1

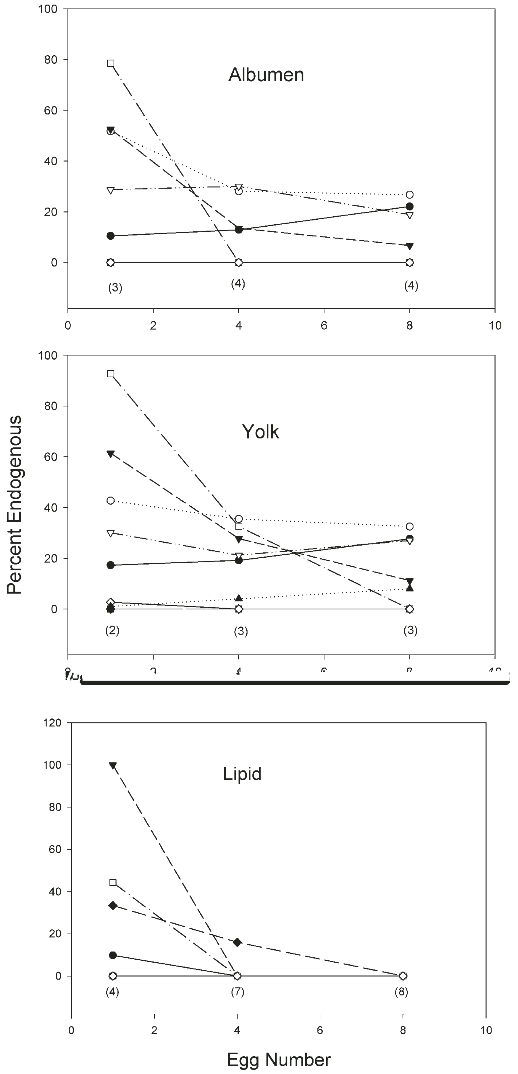

Fig. 2. Estimated percent endogenous sources to albumen, yolk, and lipid in first-, fourth-, and eighth-laid eggs of Barrow's goldeneye nesting at Riske Creek, British Columbia, Canada, 2000. Each line represents a single individual. Numbers in parentheses indicate number of females in cases where data overlap.

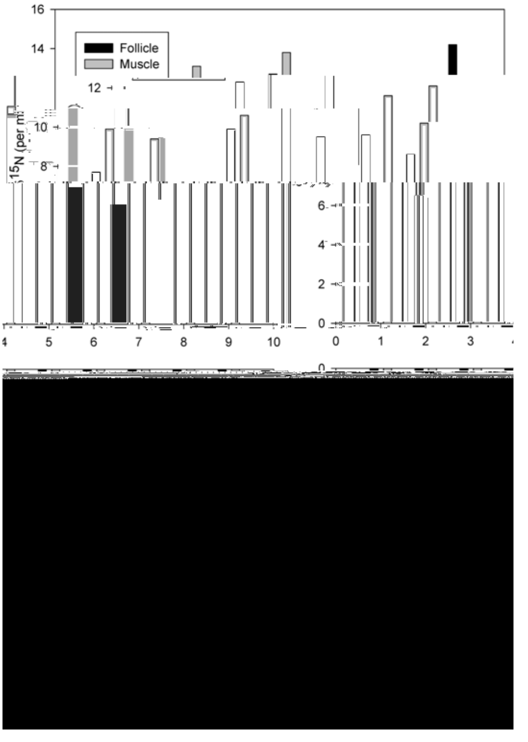

Fig. 3. Relative stable isotope values of paired muscle and ovarian follicle protein samples from female Barrow's goldeneye arriving at Riske Creek, British Columbia, Canada, 1993–1994. This figure depicts the overall somatic enrichment in both isotopes relative to those levels found in ovarian follicles, providing evidence that little endogenous protein went into follicle production at the time of formation.

foods may be less limiting to laying females. Endogenous lipid inputs to eggs may simply represent what is not used for migration (Rohwer 1992) or may be retained for use by the incubating female. However, female goldeneyes are very territorial and spend considerable time in energetically demanding aggressive behaviors (Savard and Smith 1987, Savard 1988). Somatic lipids only play an important role in fueling defense of breeding and brood-rearing territories.

Other sources of variation in nutrient allocation among females undoubtedly are related to female age and body condition at the time of RFG (Alisauskas and Ankney 1992). Although we did not address ultimate clutch size in our study of eggs from birds in 2000, it can influence the degree to which endogenous nutrients are used in egg production and involves a trade-off between nutrient investment directly into eggs and nutrients required by the female during the incubation period (Drobney 1991), and, for goldeneyes, territorial aggression, or brood rearing activities. Moreover, following arrival to breeding areas, there can be a delay of several days to weeks before laying commences (J. E. Thompson, University of Western Ontario, personal observation). Older females usually initiate clutches earlier than younger females (Gauthier 1989); thus, they may rely more on endogenous reserves.

Our original study design was based on the utility of both $\delta^{13}C$ and $\delta^{15}N$ values in discriminating between marine-derived endogenous nutrients and local exogenous freshwater nutrients on the breeding grounds. Stable-carbon isotopes were useful for this purpose, but $\delta^{15}N$ values varied considerably among wetlands with some local wetland foodwebs being as enriched in ^{15}N as marine sources. There are a number of possible explanations for this since $\delta^{15}N$ values are sensitive to both landscape- and local-level processes (Hobson 1999, Hebert and Wassenaar 2001). However, we think the most parsimonious explanation is that wetlands were used differentially by cattle. Nitrogenous waste from cattle can become enriched in ^{15}N through ammonification, a process in which isotopically lighter molecular components are lost to the atmosphere by evaporation, leaving behind isotopically heavier sources of nitrogen that are then washed into local water bodies. Some wetlands on the Chilcotin Plateau (e.g., wetlands 8, 11) were especially enriched in ^{15}N (Fig. 1). Fortunately, $\delta^{13}C$ values varied little between wetlands. Future studies could potentially use $\delta^{34}S$ as well as $\delta^{13}C$ measurements because these isotopes show considerable variation between marine and freshwater sources. Our study emphasizes the need to establish local-level isotopic endpoints when using the stable isotope approach to evaluate nutrient allocation to reproduction in migratory birds.

MANAGEMENT IMPLICATIONS

Establishing sources of nutrients to breeding females and their eggs (e.g., percent from marine vs. terrestrial freshwater sources) is fundamental to understanding the relative importance of areas occupied by waterfowl throughout their annual cycle. Such information can be used to determine the relative importance of habitats according to their influence on fitness of individuals and populations (e.g., target critical habitats that contribute most to the fall flight). We have shown that Barrow's goldeneye females are able to mobilize marine-derived nutrients acquired on wintering areas to produce early laid eggs. Furthermore, current evidence suggests that Barrow's goldeneye breeding in British Columbia likely migrate rapidly from wintering areas to breeding sites (Savard 1985). The cross-seasonal influence on fecundity we documented suggests that management efforts should place additional emphasis on maintaining the quality and availability of wintering habitat in this species.

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