

# TRACING NUTRIENT ALLOCATION TO REPRODUCTION IN BARROW'S GOLDENEYE

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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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $^{13}\text{C}$  than were samples from local foodwebs. However,  $\delta^{15}\text{N}$  values of amphipods were highly variable among wetlands, resulting in a nondistinct exogenous  $\delta^{15}\text{N}$  endpoint for our dual-isotope mixing model. Therefore, we only used the model based on  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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, but see Meijer and Drent 1999, Gauthier et al. 2003). The other extreme involves species that form clutches exclusively from local foods during egg formation such as small-bodied passerines

(Meijer and Drent 1999). Among avian taxa, waterfowl are the most well-studied group with respect to nutrient investment to eggs, and this group of birds includes species representing the spectrum of capital through income strategies (Alisauskas and Ankney 1992).

Nutrient investment strategies are not only relevant to investigating theoretical hypotheses; there is also great conservation and management interest with respect to nutrient allocation and reproduction in waterfowl. The main reason for this interest is that body condition of females arriving on breeding grounds can be influenced by factors on wintering grounds and stopover sites (Webster et al. 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 (i.e., cross-seasonal effects) currently is of great interest to conservation and evolutionary biologists (Webster et al. 2001).

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Quantifying nutrient allocation to reproduction in wild birds is difficult and has hitherto relied on indirect approaches. Conventional methods of assessing stored nutrient contributions to egg production in birds have relied mainly on tracking changes in mass of body macronutrients (i.e., protein, lipid, mineral) of laying females in relation to investment of these nutrients into eggs or, even more simply, tracking changes in total body mass in relation to a female's clutch size (Ankney and MacInnes 1978; Houston et al. 1983, 1995; Williams 1996). However, it is often unclear how much of the female's endogenous nutrients go into eggs vs. satisfy her own metabolic energy requirements. Further, conversion efficiencies of somatic and dietary nutrients to egg constituents are not well known, but they are likely significant (Spedding 1988). These unknown factors may result in overestimation of nutrients transferred from somatic stores to eggs (Meijer and Drent 1999, Gauthier et al. 2003). By contrast, measurement of naturally occurring, stable-isotopic ratios of endogenous tissues of laying females, egg macronutrients, and local diet has been proposed as an alternative and quantitative means of tracing nutrient allocation to reproduction in birds (Hobson 1995, Gauthier et al. 2003).

The abundance of several naturally occurring stable isotopes of elements found in foodwebs differ according to a variety of biogeochemical processes (reviewed by Lajtha and Michener 1994). Because isotopic signatures of consumers are related to their diets (DeNiro and Epstein 1978, 1981), somatic nutrients assume isotopic values that can differ according to the biome where they were produced. For birds that migrate between wintering and breeding grounds that differ in isotopic composition, isotopic signatures of their stored nutrients will differ from those of locally available foods; this difference allows us to directly trace patterns of nutrient allocation to eggs. Hobson et al. (1997) used the stable isotope approach to investigate sources of nutrients to eggs by analyzing  $\delta^{34}\text{S}$  and  $\delta^{13}\text{C}$  values in eggs of several species of colonial waterbirds breeding on Lake Ontario, Canada. These birds migrated from marine wintering grounds where their tissues were expected to have stable isotopic values more positive than those corresponding to breeding ground diets (see also Hobson et al. 2000). Recently, Klaassen et al. (2001) used stable isotope analyses to provide evidence for income vs. capital breeding strategies in Arctic-breeding shorebirds, at least for sources of proteins (see Morrison and Hobson 2004).

We extended the application of isotopic analyses to investigate nutrient allocation patterns during reproduction in Barrow's goldeneye. This species is ideal for such an investigation because the birds breed on inland freshwater wetlands in the intermountain region of British Columbia after wintering primarily in marine habitats along the Pacific coast of Canada. We examined isotopically somatic tissues of marine wintering birds and of birds arriving on their breeding grounds. In addition, we measured isotope ratios in ovarian follicles from collected birds and from components of the first-, fourth-, and eighth-laid eggs in clutches of known sequence. Our intention was to examine evidence for marine-derived somatic nutrient transfer into eggs and how this may be influenced by laying order.

## STUDY AREA

Our study area (52°07'N, 122°27'W) was located in the Caribou Parklands of British Columbia, Canada. Forests in this region were part of the Interior Douglas Fir (*Pseudotsuga menziesii*) zone (Krajina 1969) and were characterized by rolling grassland interspersed with mixed stands of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), Douglas fir, and black spruce (*Picea mariana*). A high density of small to moderately sized palustrine wetlands occurred in this area and provided ideal breeding habitat for Barrow's goldeneye and bufflehead (*Bucephala albeola*). Additional information on habitat and breeding waterfowl in this area is provided by Boyd et al. (1989), Savard (1991), and Savard et al. (1994). Our study population of Barrow's goldeneyes consisted entirely of birds nesting in nestboxes; a program that was initially established by Savard (1986) and continued by Thompson (1996) and Evans (2003).

## METHODS

### Egg, Somatic Tissue, and Amphipod Sampling

Our sample consisted of 2 groups. The first sample was 9 paired muscle and ovarian follicle tissue samples from female goldeneyes collected by Jonathan E. Thompson (JET) in 1993–1994. These samples consisted of lipid-free, dried, and powdered material consisting largely of protein. These birds were collected shortly after arrival on the breeding grounds. We used these archived samples opportunistically to test the hypothesis that if birds mobilized endogenous protein reserves for reproduction, their developing ovarian follicles would be enriched in  $^{13}\text{C}$  and  $^{15}\text{N}$  compared to

muscle (Hobson 1995, Gauthier et al. 2003). Our second sample consisted of first-, fourth-, and eighth-laid eggs collected from sequenced clutches of individual females monitored during the breeding season of 2000. We monitored nestboxes and determined egg order by numbering eggs as they appeared. If >1 egg appeared during the expected laying interval of 1.5 days (Thompson 1996), we considered this to be the result of brood parasitism, and we did not use that time sample. Following clutch completion, we collected the first, fourth, and eighth eggs. We stored fresh eggs frozen until stable isotope analysis.

To determine the marine isotope signal in somatic tissue of birds wintering along the coast, we collected 5 female Barrow's goldeneyes during March 1999 in the Strait of Georgia, British Columbia, Canada. We also examined isotopically the 9 early arriving female birds on the breeding grounds collected by JET during 1993–1994. We kept birds frozen, and several months later we subsampled breast muscle and abdominal fat for stable isotope analysis. We determined isotopic characterization of foodwebs associated with wetlands by collecting amphipods (*Amphipoda* spp.) during the spring of 2000. Following collection, we kept amphipod samples frozen until we conducted stable isotope analysis.

### Stable Isotope Methods

We thawed and opened frozen eggs, and we separated albumen and yolk using a syringe. We then freeze-dried these materials and removed lipids from dried yolk using a 2:1 chloroform:methanol rinse. We retrieved lipids by evaporating off the solvent in a fume hood and then kept them frozen. We washed amphipod samples with distilled water, dried and then powdered them. We removed lipids using the solvent extraction method described above. Finally, we soaked powdered, lipid-free amphipods in a 0.1N HCl solution without rinsing to remove carbonates. We freeze dried and removed lipids from pectoral muscle from wintering goldeneyes and soaked abdominal fat samples in the 2:1 chloroform:methanol solution to retrieve lipids by evaporation.

We weighed all powdered tissue samples into tin cups and analyzed for stable-carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes using continuous-flow isotope-ratio mass spectrometry (CFIRMS) using methods previously described by Hobson (1995). We reported stable isotope values in parts per thousand (‰) relative to the standards Vienna PeeDee Belemnite (VPDB) and atmospheric

air (AIR) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively (Hobson 1995). We estimated measurement precision as  $\pm 0.1$  ‰ for  $\delta^{13}\text{C}$  and  $\pm 0.3$  ‰ for  $\delta^{15}\text{N}$  values.

### Estimation of Endogenous vs. Exogenous Contributions to Eggs

Our approach was to investigate the use of a dual-isotope mixing model (Phillips 2001) to estimate the relative importance of endogenous and exogenous nutrients to egg formation. We made no a priori assumptions about the relative utility of each isotope and predicted that both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of endogenous protein and  $\delta^{13}\text{C}$  values of endogenous lipids would be enriched relative to local food isotope values for these nutrients. Hobson (1995) provided isotopic fractionation factors between diet and egg components for birds producing eggs strictly from their diet. These values allow the estimation of egg isotope values corresponding to dietary values. Fractionation factors between endogenous nutrients and eggs have not been determined directly, so we used the approach of Gauthier et al. (2003) that simply used fractionation factors associated with carnivorous income breeders as determined by Hobson (1995) as a best estimate of the fractionation associated with the breakdown of proteins and lipids and their reformation as egg components.

As determined by Thompson and Ankney (2002), Barrow's goldeneye females on our study site had a broad, primarily carnivorous diet during the egg formation period. Our challenge, then, was to determine an appropriate isotopic endpoint for local diet to estimate the proportion of eggs produced from local nutrients. Although amphipods (*Gammarus*, *Hyalella* spp.) were not prominent in the diet of female goldeneyes, they were abundant in most wetlands. Thus, we chose amphipods as a proxy animal dietary endpoint that we expected would closely approximate the bird's general diet of aquatic insects, specifically consisting of the larvae of zygoptera, chironomids, and chaoborinids (Thompson and Ankney 2002). Importantly, we needed to determine if whole foodwebs were isotopically labeled differently at each wetland in order to adjust our model for each laying female of interest. This approach follows the work of Cabana and Rasmussen (1996) who normalized trophic models among lakes based on isotopic measurements of gastropods. Our assumption was that, on average, local diets of Barrow's goldeneye consisted of aquatic invertebrates of the same trophic level as amphipods (approx-

Table 1. Summary of mean stable-carbon and nitrogen isotope values of wetland amphipods sampled in the Riske Creek, British Columbia, Canada, study area, 2000. Results of Tukey's post-hoc multiple comparisons tests are given with wetlands having the same superscript being not significantly different ( $P > 0.05$ ).

Wetland	<i>n</i>	$\delta^{13}\text{C}$ (‰)	SD	$\delta^{15}\text{N}$ (‰)	SD
8	12	-26.9 <sup>a</sup>	0.4	17.5 <sup>a</sup>	1.6
11	10	-27.0 <sup>a</sup>	0.3	15.7 <sup>a</sup>	3.0
42	12	-27.4 <sup>a</sup>	0.7	11.2 <sup>b</sup>	0.5
115	12	-24.6 <sup>b</sup>	1.2	8.6 <sup>c</sup>	0.4

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

# RESULTS

Overall, wetlands differed in amphipod mean lipid-free  $\delta^{13}\text{C}$  values (range: 2.8‰,  $F_{3,45} = 82.5$ ,  $P < 0.001$ , Table 1), but this was driven by a single wetland (no. 115,  $\delta^{13}\text{C} = -24.6$ ‰) that was more enriched in  $^{13}\text{C}$  than the others by 2.3 to 2.8‰ (Fig. 1). However, we found considerable variation among wetlands in amphipod  $^{15}\text{N}$  values ( $F_{3,45} = 71.0$ ,  $P < 0.001$ , Table 1) with some wetlands (e.g., 8, 11) showing values more enriched in  $^{15}\text{N}$  than expected (i.e., more enriched than our marine endpoint by 4.6 to 6.4‰; Fig. 1). Muscle tissues from females wintering along the British Columbia coast were predictably enriched in both  $^{13}\text{C}$  and  $^{15}\text{N}$  (mean  $\delta^{13}\text{C}$ : -19.8‰, mean  $\delta^{15}\text{N}$ : 12.0‰; Fig.

1) and did not differ from those individuals analyzed upon arrival on the breeding grounds in 1993–1994 (mean  $\delta^{13}\text{C} = -19.9$ ‰, mean  $\delta^{15}\text{N} = 11.3$ ‰;  $^{15}\text{N}$ :  $t = 0.91$ ,  $P = 0.38$ ;  $^{13}\text{C}$ :  $t = 1.43$ ,  $P = 0.17$ ). Consequently, we determined a robust marine somatic tissue signature but found enough variability in local foodweb  $\delta^{15}\text{N}$  values to preclude a generalized dual isotope approach for a corresponding local foodweb endpoint.

Given that there may have been enough trophic variation in actual and assumed foodwebs supporting individual goldeneye females, we based subsequent estimates of endogenous and exogenous inputs to eggs on a 2-endpoint, single-isotope model using only  $\delta^{13}\text{C}$  values (Table 2). Here, we applied isotopic fractionation factors determined by Hobson (1995) to the mean marine-based muscle value of -19.9‰ to obtain expected endpoint values for egg yolk and albumen derived exclusively from somatic nutrients. For all wetlands, these values were -19.0 and -19.9‰ for albumen and lipid-free yolk, respectively. Similarly, the assumed mean exogenous protein  $\delta^{13}\text{C}$  values of -24.6‰ for wetland 115 and -27.1‰ for all other wetlands corresponded to expected egg albumen and lipid-free yolk values of -23.7 and -24.6‰ for wetland 115 and -26.2 and -27.1‰ for all other wetlands, respectively. We expected egg lipid values of -28‰ for wetland 115 and -30.5‰ for all other wetlands

if derived exclusively from exogenous nutrients. We based egg lipids derived from endogenous lipids on those found for abdominal fat of overwintering birds (-30.0‰). We then calculated the mean percent endogenous contribution for eggs obtained from all wetlands using the simple single-isotope, dual-source, linear-interpolation method.

Patterns of isotopic change in eggs from early to late laid eggs showed considerable variation within and among individual females (Table 2, Fig. 2). There was a tendency for components of first-laid eggs to be more enriched in  $^{13}\text{C}$  than

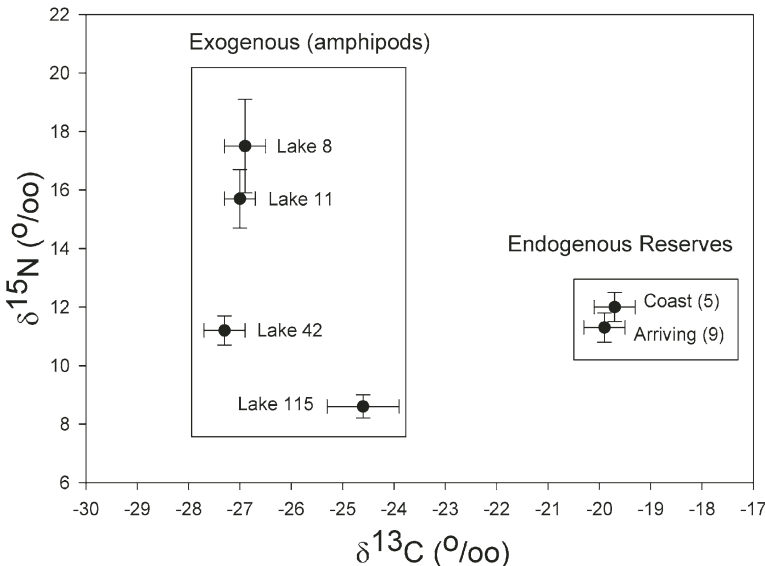


Fig. 1. Isotopic positions of local foodweb indicators (amphipods) at the Riske Creek, British Columbia, Canada, breeding sites in 2000 and somatic protein reserves (muscle) of Barrow's goldeneye from coastal wintering and early arrival samples (1993–1994) illustrating the high variability in wetland  $\delta^{15}\text{N}$  values and the more discrete  $\delta^{13}\text{C}$  values. Subsequent estimates of endogenous inputs to eggs were thus based only on the  $\delta^{13}\text{C}$  model.

Table 2. Isotopic measurements of components of first, fourth and eighth-laid eggs of Barrow's Goldeneye clutches from 8 females on 5 wetlands in the Riske Creek, British Columbia, Canada, study area, 2000.

Egg no.	Wetland	n	Tissue				
			Albumen		Yolk		Lipid
			$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
1	42	1					
		–25.5	14.3	–25.0	15.7	–30.9	
4	42	1	–25.3	14.5	–24.8	15.8	–31.4
8	42	1	–24.5	14.7	–24.1	15.3	–30.4
1	41	3	–22.1, –22.0, –24.0	10.9, 9.1, 15.4	–22.8, –21.2, –23.8	14.5, 10.5, 16.8	–28.4, –27.9, –32.3
4	41	3	–24.0, –25.3, –23.9	14.4, 13.6, 15.1	–23.4, –24.1, –24.2	15.1, 13.1, 17.0	–29.3, –30.1, –32.1
8	41	3	–24.2, –25.8, –24.8	15.0, 14.1, 15.0	–23.7, –25.5, –24.6	16.4, 15.7, 16.5	–30.0, –31.2, –32.5
1	11	1	–26.5	12.8	–26.2	15.2	–30.0
4	11	1	–26.8	13.8	–26.0	15.0	–30.2
8	11	1	–26.6	14.7	–26.2	15.7	–30.7
1	8	2	–19.7, –27.9	8.3, 16.7	–18.6, –27.7	9.4, 16.6	–24.8, –34.5
4	8	2	–27.1, –27.5	15.4, 14.9	–23.4, –27.8	13.0, 17.0	–30.1, –36.2
8	8	2	–28.3, –31.4	17.0, 6.9	–27.8, –30.5	18.5, 7.9	–33.5, –35.3
1	115	1	–28.4	6.6	–23.6	9.6	–29.3
4	115	1	–24.4	7.3	–23.8	12.2	–33.3
8	115	1	–24.2	7.5	–24.2	8.4	–30.1

fourth-laid eggs (excluding wetland 115: paired *t*-test, albumen *t* = 1.6, *P* = 0.08; yolk *t* = 1.8, *P* = 0.06; lipid *t* = 2.14, *P* = 0.04) or eighth-laid eggs (albumen *t* = 2.13, *P* = 0.04; yolk *t* = 1.78, *P* = 0.06; lipid *t* = 1.7, *P* = 0.07).

Muscle tissue of birds collected prior to laying, but that had initiated rapid follicular growth, were enriched in <sup>15</sup>N (mean  $\delta^{15}\text{N}$  = 11.3 ± 1.5‰, *n* = 9, paired *t*-test, *t* = 2.02, 1-tailed *P* = 0.04) and <sup>13</sup>C (mean  $\delta^{13}\text{C}$  = –19.9 ± 1.2‰, *n* = 9, *t* = 10.4, 1-tailed *P* < 0.0001) compared to ovarian follicles (Fig. 3; mean  $\delta^{15}\text{N}$  = 10.1 ± 2.5‰, mean  $\delta^{13}\text{C}$  = –25.0 ± 1.9‰). In the paired sample from 1993 to 1994, the follicle  $\delta^{13}\text{C}$  values overlapped completely with the endpoint expected if yolk was formed entirely from exogenous as compared to endogenous proteins.

DISCUSSION

Our study illustrated the applicability of the stable isotope approach in situations where endogenous reserves of migrating or wintering birds were labeled differently than their breeding ground foodwebs (Hobson et al. 2000, Gauthier et al. 2003). This isotopic dichotomy allowed quantification of endogenous and exogenous contributions to eggs. We determined that in 2000, goldeneyes nesting in our study area mobilized endogenous protein reserves for egg production, a surprising result given previous expectations for this carnivorous duck. Somatic lipids also were used but to a much lower degree than somatic proteins. In all cases, use of endogenous

nutrients was most pronounced in earlier- compared with later-laid eggs. Analyses of paired muscle and ovarian follicle stable isotope signatures, from birds collected in 1993–1994, suggested much lower endogenous protein contribution to eggs supporting results of the conventional approach by Thompson (1996) on these same birds. Nutrient allocation strategies for egg production in this species are apparently variable, differing among females, wetlands, and years.

Our determination that endogenous protein was allocated to eggs in 2000 is interesting because it has previously been considered rare in carnivorous ducks that feed during egg production. Common eiders (*Somateria mollissima*) and ruddy ducks (*Oxyura jamaicensis*) use somatic protein reserves for egg production (Korschgen 1977, Alisauskas and Ankney 1994). This can be attributed to low feeding rate during rapid follicular growth (RFG) in eiders and the inordinately large egg relative to body mass in Ruddy Ducks. In contrast, Barrow's goldeneyes have relatively modest daily protein requirements during laying due to extended laying intervals (Thompson 1996). This suggests that goldeneyes can be periodically protein limited during the egg-laying period, but they can rely on facultative catabolism of somatic proteins in some years (Thompson 1996). Protein abundance (i.e., aquatic insects) in wetlands during early spring can be highly variable (Boyd et al. 1989). Carbohydrates for lipid production or bioavailable lipids from



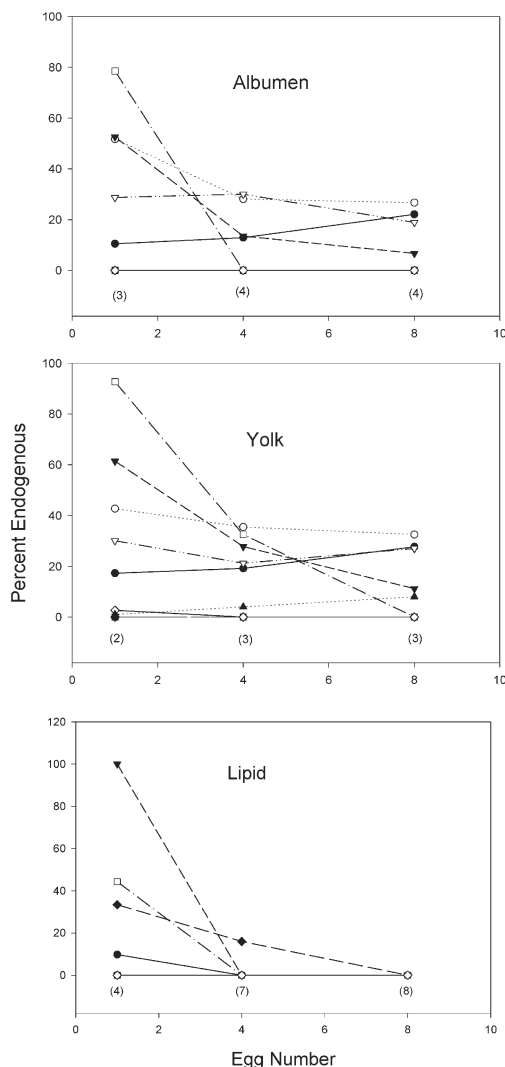


Fig. 2. Estimated percent endogenous sources to albumen, yolk, and lipid in first-, fourth-, and eighth-laid eggs of Barrow's goldeneye nesting at Riske Creek, British Columbia, Canada, 2000. Each line represents a single individual. Numbers in parentheses indicate number of females in cases where data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

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

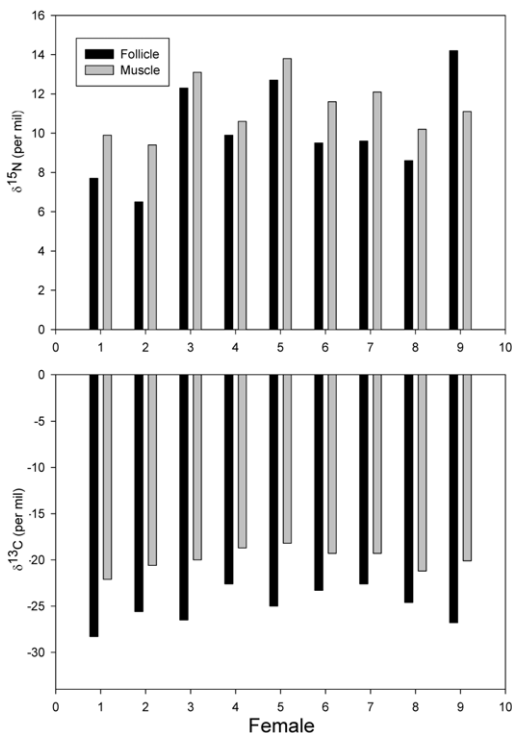


Fig. 3. Relative stable isotope values of paired muscle and ovarian follicle protein samples from female Barrow's goldeneye arriving at Riske Creek, British Columbia, Canada, 1993–1994. This figure depicts the overall somatic enrichment in both isotopes relative to those levels found in ovarian follicles,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

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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  values varied considerably among wetlands with some local wetland foodwebs being as enriched in  $^{15}\text{N}$  as marine sources. There are a number of possible explanations for this since  $\delta^{15}\text{N}$  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  $^{15}\text{N}$  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  $^{15}\text{N}$  (Fig. 1). Fortunately,  $\delta^{13}\text{C}$  values varied little between wetlands. Future studies could potentially use  $\delta^{34}\text{S}$  as well as  $\delta^{13}\text{C}$  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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