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# TROPHIC RELATIONS OF THE RED-NECKED GREBE ON LAKES IN THE WESTERN BOREAL FOREST: A STABLE-ISOTOPE ANALYSIS

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*Abstract.* We compared trophic ecology of grebes inferred from stable-isotope analysis to that from gut contents, and compared isotopic ratios of Red-necked Grebes (*Podiceps grisegena*) from lakes differing in their food webs. Analyses of different grebe tissues (egg yolk and albumen, pectoral and leg muscle, breast and primary feathers) also allowed us to assess the effectiveness of these tissues at representing grebe trophic relations. Isotopic ratios from pectoral and leg muscles were similar, based on comparisons within individual birds. Enriched values of $\delta^{15}N$ and $\delta^{13}C$ suggested that breast and primary feathers were molted over winter, and therefore reflected a marine food web. Albumen and yolk of grebe eggs and muscle tissues from downy chicks, however, matched isotopic characteristics of the local food web, indicating that female Red-necked Grebes use nutrients from the breeding lake for egg formation. Eggs, therefore, can provide excellent material for isotopic analysis aimed at assessing trophic relations of Red-necked Grebes on breeding lakes. Gut contents and stable isotopes both indicated that grebes from lakes with fish consumed a mixed diet of fish and macroinvertebrates and occupied the highest trophic level, at or above the level of piscivorous fishes. In contrast, grebes from lakes lacking fish occupied a lower trophic position.

*Key words: diet, egg, food web,* Podiceps grisegena, *Red-necked Grebe, stable-carbon isotope ratios, stable-nitrogen isotope ratios.*

## Relaciones Tróficas de *Podiceps grisegena* en Lagos del Bosque Boreal del Oeste: Un Análisis de Isótopos Estables

*Resumen.* Comparamos la ecología trófica de *Podiceps* inferida a partir de análisis de isótopos estables con la de contenidos estomacales y comparamos las relaciones isotópicas de *P. grisegena* entre lagos que difieren en sus redes tróficas. Los análisis de diferentes tejidos de *P. grisegena* (yema y albumen del huevo, músculo pectoral y de la pierna, plumas del pecho y primarias) también nos permitieron evaluar la efectividad de estos tejidos para representar las relaciones tróficas de *P. grisegena*. Las relaciones isotópicas de los músculos pectorales y de las piernas basadas en comparaciones realizadas para cada ave individual fueron similares. Valores enriquecidos de $\delta^{15}N$ y $\delta^{13}C$ sugirieron que las aves mudaron las plumas del pecho y las primarias durante el invierno, y por lo tanto reflejaron una red trófica marina. El albumen y la yema del huevo de *P. grisegena* y los tejidos musculares de pichones emplumados, sin embargo, coincidieron con las características isotópicas de la red alimenticia local, indicando que las hembras de *P. grisegena* usan nutrientes del lago donde nidifican para la formación de los huevos. Los huevos, por lo tanto, pueden constituir un material excelente para análisis isotópicos centrados en evaluar las relaciones tróficas de *P. grisegena* en los lagos donde se reproducen. Los contenidos estomacales y los isótopos estables indicaron que los individuos de *P. grisegena* provenientes de lagos con peces consumieron una dieta mixta de peces y macroinvertebrados y ocuparon la posición trófica más alta, al mismo nivel o por arriba de los peces piscívoros. En contraste, los individuos provenientes de lagos sin peces ocuparon una posición trófica menor.

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## INTRODUCTION

The roles of aquatic birds in lake ecosystems are of growing interest to aquatic ecologists (Kerekes 1994). Birds that nest on freshwater lakes in the north temperate zone have diverse trophic relationships that can affect their competitive interactions (Eadie and Keast 1982), reproductive success (Gingras and Paszkowski 1999), and exposure to contaminants and parasites (Stock and Holmes 1987, Scheuhammer et al. 1998). Many aquatic birds consume mixed diets of plants and invertebrates that cause their trophic position and even their morphology to change with time of year and concurrent nutritional demands (Kehoe and Ankney 1985). Even in carnivorous species, such as loons and grebes, feeding patterns can be complex, as either fish or invertebrates can dominate diets depending on habitat, season, and local prey availability (Gingras 1997, Stout and Nuechterlein 1999). Furthermore, species that overwinter on marine waters may (or may not) import energy to the freshwater ecosystem by using marine-derived energy for eggs (Hobson et al. 1997, Hobson, Sirois, and Gloutney 2000).

Lakes of the boreal mixedwood forest region of western Canada support diverse and abundant aquatic birds (Paszkowski and Tonn 2000, Pierre 2001, Morrison 2002). It seems likely that aquatic birds are important players in the ecosystem dynamics of these lakes, yet information available to assess avian roles is limited.

Because the nature of a lake's fish assemblage can strongly influence the structure of its food web through top-down effects on benthic and planktonic invertebrates (Brönmark et al. 1992, Carpenter and Kitchell 1993), the type of fish assemblage could affect the trophic relationships of the aquatic birds and their position in the food web. Because of an interplay between winter hypoxia, predation, and access to refuges or recolonization routes, the small, shallow, and highly productive lakes of the boreal mixedwood forest can be fishless, dominated by small-bodied fish species (stickleback [*Culaea* spp.] and cyprinids) that tolerate low oxygen conditions, or dominated by large-bodied species that include piscivores (northern pike [*Esox lucius*], yellow perch, [*Perca flavescens*]; Robinson and Tonn 1989, Conlon 2002). Overall, there is concordance between the fish assemblage of a lake and its aquatic bird assemblage, highlighting the interplay among birds, fish, and the lake environment (Paszkowski and Tonn 2000).

Many species of birds, however, nest on all three kinds of lakes (Gingras and Paszkowski 1999, Paszkowski and Tonn 2000). Included among these species, perhaps unexpectedly, are the Common Loon (*Gavia immer*) and Red-necked Grebe (*Podiceps grisegena*), often considered specialist piscivores (McIntyre and Barr 1997) or at least known to include a large proportion of fish in their diets (Stout and Nuechterlein 1999, Kloskowski 2003). How do these differences in fish assemblage, including the absence of fish altogether, affect the trophic relations of such bird species?

Stable-isotope analysis can be used to trace migratory patterns, describe diets, and understand trophic interactions of organisms (Peterson and Fry 1987, Hobson 1999, Kelly 2000). Stable-isotope analysis determines the ratios of naturally occurring stable isotopes of common elements, such as carbon and nitrogen, in plant and animal tissue. Fractionation, or a change in the ratio of heavy to light isotopes of carbon ($^{13}C$:$^{12}C$) and nitrogen ($^{15}N$:$^{14}N$), can result from a variety of physical and physiological processes (Gannes et al. 1997). Because there is relatively little (usually $<1‰$) enrichment of $^{13}C$ between trophic levels, the $^{13}C$:$^{12}C$ ratio of a consumer is very similar to that of its prey, and thus reflects diet and connections to particular primary producers and habitats (Peterson and Fry 1987). In contrast, tissue becomes progressively enriched in $^{15}N$ as it passes up a food web, so the $^{15}N$:$^{14}N$ ratio can be used to determine the trophic level of species of interest (DeNiro and Epstein 1981, Peterson and Fry 1987). In the present study, we investigate the use of stable isotopes of carbon and nitrogen as a means of characterizing the trophic relationships of Red-necked Grebes on lakes within the boreal mixedwood forest of Alberta, Canada. We also use stable-isotope analysis to investigate whether the materials and energy used in egg formation are imported from the overwintering (marine) habitat or from the local freshwater lake.

Stable-isotope analysis offers an attractive technique to ecologists interested in avian diets. It integrates feeding histories and can allow less destructive and disruptive sampling of birds through the use of tissues like blood, feathers, and eggs (Hobson and Clark 1992, Hobson

TABLE 1. The location, area, and maximum depth of lakes in northern Alberta where Red-necked Grebes were collected. The fish species within each lake and the age-class, range of mass (g), number (*n*) of individuals, and sex of Red-necked Grebes collected from each lake are also presented. F = female; M = male.

| Lake (Lat-long) | Area (ha) | Max. depth (m) | Fish species present | Grebes sampled | | |
|---|---|---|---|---|---|---|
| | | | | Age | Mass range (g) | *n* (F, M) |
| Armstrong Lake (54°39′N, 113°38′W) | 217.0 | 4.5 | Brook stickleback<br>Fathead minnow<br>Northern pike<br>White sucker<br>Yellow perch | Adults<br>Juvenile<br>Chicks | 1000–1260<br>720<br>65–68 | 3, 2<br>0, 1<br>2[a] |
| Gilbert Lake (54°30′N, 113°10′W) | 12.8 | 1.2 | None | Adults | | 0, 2 |
| Jackfish Lake (54°49′N, 113°06′W) | 214.7 | 6.0 | Brook stickleback | Adult | 1301 | 0, 1 |
| SPH-20 (55°25′N, 113°42′W) | 157.0 | 8.5 | Northern pike<br>White sucker<br>Yellow perch | Adult | 1189 | 1, 0 |
| N26 (56°49′N, 116°27′W) | 200.0 | 5.8 | Brook stickleback<br>Fathead minnow<br>White sucker | Adult | 1178 | 1, 0 |

[a] Sex unknown.

1995). However, stable-isotope analysis has limitations that must be factored into its use and interpretation. For example, different tissues within an individual organism display inherently different isotopic ratios as a result of differential allocation of dietary nutrients to specific tissues (Gannes et al. 1997). Different tissues are also characterized by different turnover rates that range from days to years (Hobson and Clark 1992). Similarly, localities separated by a few kilometers can diverge substantially in their background isotopic ratios (Beaudoin et al. 2001), and starving animals can show an increase in their stable-nitrogen-isotope ratio relative to animals in good nutritional condition (Hobson et al. 1993). Likewise, deciphering specific sources of nutrition for generalist feeders from isotopic values alone can be challenging (Beaudoin et al. 2001). One method that can aid the interpretation of stable-isotope analysis is to couple it with feeding observations or gut analyses (Vander Zanden and Vadeboncoeur 2000, Hart and Lovvorn 2002).

To assess the trophic relationships of the Red-necked Grebe on lakes in the western boreal forest and the usefulness of stable-isotope analysis in examining trophic interactions of birds in these systems, we addressed the following questions: (1) How do trophic positions of grebes inferred from stable-isotope analysis compare with gut contents of birds? (2) How do stable-isotope ratios differ among grebe tissues; specifically, are eggs and feathers more, or less, representative of diets during the breeding season than muscle? (3) How does trophic structure (i.e., fish assemblage) of a lake affect the trophic position of grebes, as revealed by stable-isotope analysis?

## METHODS

### STUDY AREA

The study centered on Armstrong Lake, near Rochester, Alberta, Canada (Table 1). The lake is 217 ha, eutrophic (43 $\mu$g $L^{-1}$ total phosphorus), and shallow (maximum depth 4.5 m), with a largely undeveloped shoreline (<10 residences) and uplands in agriculture. The lake supports >25 species of aquatic birds (Paszkowski and Tonn 2000), including about 40 nesting pairs of Red-necked Grebes. The fish assemblage is dynamic due to periodic winterkills and since 1986 has contained varying abundances of northern pike, yellow perch, and white suckers (*Catostomus commersonii*), along with fathead minnows (*Pimephales promelas*), and brook sticklebacks (*Culaea inconstans*; Robinson and Tonn 1989, Jones and Paszkowski 1997). Although we focused on the trophic interactions within Armstrong Lake, we supplemented our stable-isotope analysis with samples from Red-necked Grebes from four other lakes, including one that

was fishless, all located within 200 km of Armstrong Lake (Table 1).

### DIETARY ANALYSIS

Gut content analysis was performed on five adult grebes that had drowned in gill nets set as part of a fisheries study of Armstrong Lake in May and June 1994 (Table 1). Nets were set late at night (ca. 22:00) and checked a few hours after dawn (ca. 06:00). Red-necked Grebes become active at dawn, so it is unlikely that caught birds were dead for more than a few hours before they were collected. We assumed that there was no differential regurgitation of prey prior to the birds' deaths. In addition, gut contents were examined from one large, fledged male bird-of-the-year (referred to here as a juvenile) found dead on Armstrong Lake in August 1994. Cause and time of death were unknown, although the bird appeared quite fresh and in good condition (PHK, pers. obs.). Gut contents were also obtained from two adult grebes found dead with head and neck wounds near their nests at Gilbert Lake in June 1995 (Table 1), possibly killed by a Great Horned Owl (*Bubo virginianus*). Birds were frozen whole within hours of discovery. After thawing, the entire digestive tract was dissected; items found therein were counted, dried to a constant weight, and identified to the lowest taxonomic level possible. For the purposes of this paper, prey organisms are characterized using broad taxonomic categories, but Stout and Nuechterlein (1999), to which we contributed our diet data in greater taxonomic detail, reveal the substantial diversity found at the family level and below.

### STABLE-ISOTOPE ANALYSIS

*Prey.* Using organisms found in the guts of Red-necked Grebes as a guide, we collected representatives of 11 taxa of aquatic invertebrates, plus fathead minnows (mean total length ± SD = 65.5 ± 4.7 mm) and brook sticklebacks (50.2 ± 1.9 mm), from Armstrong Lake in June 1997. To more fully describe the food web in which the grebes operated, we subsequently collected arthropods from along the lake shore, northern pikes (690 ± 2.1 mm), small (116.5 ± 0.2 mm) and large (249.7 ± 1.0 mm) yellow perch, and additional fathead minnows in September 1999. All invertebrates were held in water for at least 24 hr to allow gut clearance, chilled or anesthetized with soda water, then frozen and stored in aluminum foil. Fish were collected from gill nets or euthanized with an overdose of MS-222 (tricaine methanesulfonate; Kelsch and Shields 1996), then frozen and stored in foil. Stable-isotope analysis was performed on a sample of epaxial trunk muscle from each fish.

*Grebe tissues.* To assess the trophic relations of the grebes, we performed stable-isotope analysis on a variety of tissues. Pectoralis major muscle was analyzed from the eight previously described birds from Armstrong and Gilbert Lakes, as well as from two downy chicks found dead on Armstrong Lake in 1995. Pectoral muscle was also analyzed from three adult grebes each salvaged from a different lake that contained at least one species of fish (Table 1). Other species of grebes (e.g., Eared Grebe [*Podiceps nigricollis*]; Jehl 1997) undergo major shifts in the relative mass of body tissues as part of their annual cycle, including a decrease in breast muscle and an increase in leg muscle while on the breeding grounds. Thus, we also performed stable-isotope analysis on leg (iliotibialis) muscle for all of the grebes from Armstrong and Gilbert Lakes, except downy chicks.

As avian muscle tissue has a turnover rate on the order of months (Hobson and Clark 1992), we also explored the usefulness of other tissues for stable-isotope analysis. For the 11 fully fledged birds, we performed stable-isotope analysis on the first primary feather and on breast contour feathers. Feather samples consisted of the 5-cm tip of the first primary and 10–20 breast feathers. On 8 June 1997 we collected the cleanest egg from 10 Red-necked Grebe nests (clutch size = 2–7 eggs) on Armstrong Lake; based on the previous day's survey, eggs were >1 day old. Eggs were wrapped in aluminum foil and frozen for later analysis of yolk and albumen. Two eggs were eventually discarded because embryos were substantially more developed than in the other eight, and extensive vascularization prevented the collection of pure samples of yolk and albumen.

*Sample preparation and processing.* For aquatic and terrestrial invertebrates, a single sample typically consisted of one whole animal (two ants were required to provide sufficient mass). Invertebrates were thawed, washed with 1 M HCl to remove inorganic carbon (Boutton 1991), and then washed three times for 10-min intervals in a 1:1 methanol:chloroform mixture to remove lipids (Kling et al. 1992). Washed

samples were then freeze-dried and ground into a fine powder with a mortar and pestle.

Thawed muscle samples from fish and Red-necked Grebes were also washed in methanol: chloroform to remove lipids, freeze-dried, and ground. Although lipid extraction may affect stable-isotope ratios of some fish tissues (Sotiropoulos 2002), Kelly (2000) suggested that it does not create a consistent bias in results for avian muscle. Samples of albumen and yolk were extracted from thawed grebe eggs with a syringe, freeze-dried, and ground. Prior to drying, yolk samples were washed with chloroform to remove lipids (Hobson 1995). All feathers were washed and rubbed thoroughly with distilled water (while wearing gloves) to remove any organic film that might have been present, then freeze-dried and ground.

Stable-carbon and -nitrogen analyses were performed on 1.0 ± 0.1 mg subsamples of powdered tissue. Samples were loaded into 5 × 8 mm tin capsules, combusted at ~1800°C in a Robo Prep elemental analyzer (MWG Biotech Ag., D85560 Ebersberg, Germany), and the resultant gases analyzed using an interfaced Europa 2020 continuous flow isotope ratio mass spectrometer (CFIRMS; PDZ Europe, Northwich, Cheshire, UK) at the Stable Isotope Facilities, Department of Soil Science, University of Saskatchewan (Saskatoon, Saskatchewan, Canada). Stable isotope results are presented as the difference (δ) between the ratios of the sample and a standard expressed in parts per thousand (‰), following the equation: $\delta x = ([R_{sample}/R_{standard}] - 1) \times 10^3$, where $X$ is $^{13}C$ or $^{15}N$ and $R = {}^{13}C{:}{}^{12}C$ or $^{15}N{:}^{14}N$; standards are PeeDee Belemnite limestone for $\delta^{13}C$ (Craig 1957) and atmospheric $N_2$ for $\delta^{15}N$ (Ehleringer and Rundel 1989). Measurement accuracy was within 0.01‰ for carbon and 0.3‰ for nitrogen.

### STATISTICAL ANALYSIS

We used two-tailed paired *t*-tests to compare $\delta^{13}C$ or $\delta^{15}N$ values between tissue types from individual Red-necked Grebes or eggs. We used two-tailed *t*-tests to compare $\delta^{13}C$ or $\delta^{15}N$ values between grebes and other organisms from Armstrong Lake. Pearson correlations were used to determine if carbon or nitrogen ratios from the pectoral muscle of the 10 adult Red-necked Grebes changed in relation to the date of collection (Hobson, Brua, et al. 2000). Results were judged significant at a *P*-value of 0.05.

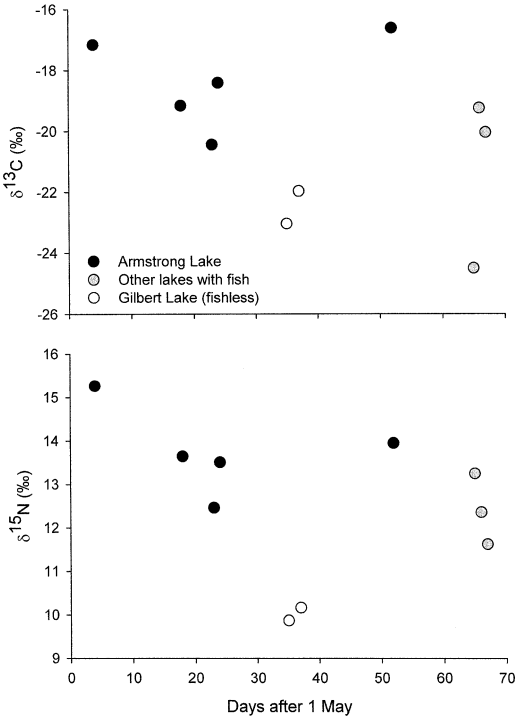


FIGURE 1. $\delta^{13}C$ (upper) and $\delta^{15}N$ (lower) values for pectoral muscle of nine adult Red-necked Grebes from several northern Alberta lakes as a function of the number of days after 1 May that birds were collected. Neither relationship was significant.

## RESULTS

### STABLE-ISOTOPE RATIOS IN GREBE TISSUE

The $\delta^{13}C$ and $\delta^{15}N$ values of pectoral muscles from the 10 adult grebes were not significantly correlated with the number of days after 1 May that birds were collected ($\delta^{13}C$: $r = -0.34$, $P = 0.34$; $\delta^{15}N$: $r = -0.33$, $P = 0.36$; Fig. 1). Stable-isotope ratios of paired leg and pectoral muscles from adult and juvenile birds from Armstrong and Gilbert Lakes did not differ for either carbon or nitrogen (paired *t*-tests, $n = 8$, $\delta^{13}C$: $t_7 = 0.7$, $P = 0.49$; $\delta^{15}N$: $t_7 = -0.1$, $P = 0.93$). However, within Armstrong Lake, isotopic ratios in pectoral muscle were higher in the five adult grebes than in the three younger birds (two-sample *t*-tests, $\delta^{13}C$: $t_6 = 3.9$, $P = 0.01$; $\delta^{15}N$: $t_6 = 4.0$, $P = 0.01$; Fig. 2).

Isotopic ratios for pectoral muscle from adult grebes on Armstrong Lake ($n = 5$ adults) also differed from ratios for both albumen and yolk ($n = 8$ eggs; two-sample *t*-tests, $\delta^{13}C$ albumen: $t_{11} = -6.7$, $P < 0.01$; $\delta^{15}N$ albumen: $t_{11} = -4.4$,

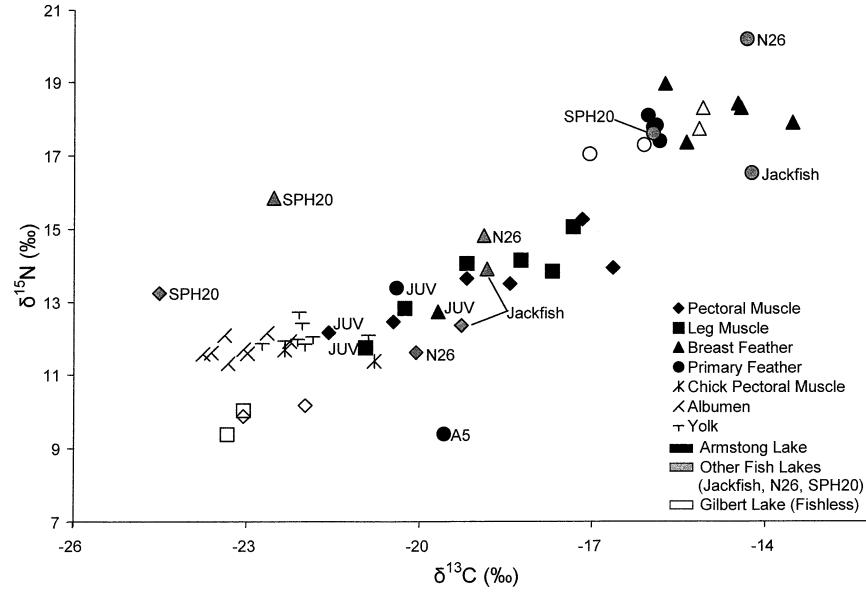


FIGURE 2. Comparison of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (‰) for different tissues of Red-necked Grebes from several Alberta lakes. Samples were from five adults, one juvenile (JUV), two chicks, and eight eggs from Armstrong Lake, adults from three other fish-bearing lakes in the region (Jackfish, SPH20, and N26; one bird each), and from fishless Gilbert Lake. See text for discussion of the feather sample from Armstrong Lake adult A5.

$P = 0.01$; $\delta^{13}C$ yolk: $t_{11} = -5.1$, $P < 0.01$; $\delta^{15}N$ yolk: $t_{11} = -3.6$, $P = 0.02$). Isotopic ratios of egg tissues, however, did not differ from pectoral-muscle ratios of chick and juvenile grebes from Armstrong Lake (two-sample *t*-tests, $\delta^{13}C$ albumen: $t_9 = 3.2$, $P = 0.06$; $\delta^{15}N$ albumen: $t_9 = 0.001$, $P = 0.99$; $\delta^{13}C$ yolk: $t_9 = -0.9$, $P = 0.44$; $\delta^{15}N$ yolk: $t_9 = 1.5$, $P = 0.24$). Isotopic ratios from yolk were always higher than albumen ratios, on average by 1.1‰ for $\delta^{13}C$ and 0.4‰ for $\delta^{15}N$ (paired *t*-tests, $n = 8$, $\delta^{13}C$: $t_7 = -12.3$, $P < 0.001$; $\delta^{15}N$: $t_7 = -6.7$, $P < 0.001$; Fig. 2).

Isotopic ratios of primary feathers from the 10 adult birds were generally similar to each other (Fig. 2), but differed from the ratios of pectoral muscle taken from the same individual (paired *t*-tests, $\delta^{13}C$: $t_9 = -3.9$, $P < 0.01$; $\delta^{15}N$: $t_9 = -3.8$, $P < 0.01$). In nine of 10 cases, primary feathers displayed distinctly higher $\delta^{13}C$ (mean difference = 4.6‰) and $\delta^{15}N$ (mean = 5.2‰) values than muscle. In contrast, ratios for the primary feather from the juvenile bird differed only slightly from ratios from its muscle (Table 2, Fig. 2). The primary feather from one adult grebe (''A5''; see Fig. 2) displayed exceptionally low $\delta^{13}C$ and $\delta^{15}N$ values, even lower than those of the juvenile bird. Analysis of the first primary from the other wing showed a consistent pattern of low values ($\delta^{13}C$:−19.2‰, $\delta^{15}N$: 9.5‰). Isotopic ratios for all other tissues from this bird (including breast feathers), however, were comparable to those of other adults.

Stable-isotope ratios of breast feathers of the 10 adult birds also differed from ratios of their pectoral muscle (paired *t*-tests, $\delta^{13}C$: $t_9 = -4.6$, $P < 0.01$; $\delta^{15}N$: $t_9 = -6.8$, $P < 0.001$), and again, feather ratios were higher (Fig. 2; mean difference $\delta^{13}C = 3.7$‰, $\delta^{15}N = 4.6$‰). The values for breast feathers did not differ from those for primary feathers (paired *t*-tests, $\delta^{13}C$: $t_9 = -0.3$, $P = 0.81$; $\delta^{15}N$: $t_9 = 0.2$, $P = 0.84$), although breast feathers showed greater variability among birds (Fig. 2). Isotopic ratios of both the breast and primary feathers of the juvenile bird, in contrast, were very similar to ratios from its muscles, displaying low levels of enrichment compared to values from adults (Table 2).

## FOOD WEB RELATIONS DETERMINED WITH STABLE ISOTOPES

*Nitrogen.* Stable-isotope ratios from aquatic and terrestrial invertebrates, fish, and Red-necked Grebe muscle suggested the existence of four

TABLE 2. Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values for terrestrial invertebrates, herbivorous and carnivorous aquatic invertebrates, fish muscle, and various tissues from Red-necked Grebes collected from Armstrong Lake, Alberta. Each sample represented one organism, except for ants (which required two for sufficient sample mass).

| Taxon or tissue (no. of samples) | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) |
|---|---|---|
| Terrestrial invertebrates | | |
| Araneae (3) | –23.7 ± 1.0 | 9.6 ± 0.8 |
| Coleoptera (3) | –25.5 ± 0.8 | 7.6 ± 0.5 |
| Hymenoptera (3) | –25.9 ± 0.5 | 6.0 ± 0.3 |
| Orthoptera (3) | –26.8 ± 0.4 | 3.9 ± 0.2 |
| Trichoptera (adults, 3) | –23.6 ± 0.8 | 8.4 ± 0.1 |
| Herbivorous aquatic invertebrates | | |
| Amphipoda (*Gammarus*) (3) | –24.5 ± 0.4 | 2.8 ± 0.9 |
| Pulmonata (*Lymnaea*) (3) | –26.6 ± 1.2 | 4.9 ± 0.2 |
| Trichoptera (*Limnephilus*) (3) | –26.5 ± 1.2 | 2.4 ± 0.9 |
| Carnivorous aquatic invertebrates | | |
| Coleoptera (*Dytiscus*) (3) | –25.0 ± 0.2 | 7.2 ± 0.1 |
| Coleoptera (*Hydroporus*) (3) | –24.8 ± 0.3 | 5.8 ± 0.8 |
| Coleoptera (*Gyrinus*) (3) | –25.5 ± 0.7 | 5.3 ± 0.6 |
| Odonata (*Aeshna*) (3) | –23.5 ± 2.4 | 6.5 ± 1.4 |
| Odonata (*Enallagma*) (3) | –25.3 ± 0.8 | 6.7 ± 0.5 |
| Pharyngobdillida (*Nephelopsis*) (3) | –23.3 ± 0.4 | 8.5 ± 0.6 |
| Rhynchobdellida (*Placobdella*) (3) | –23.6 ± 3.2 | 11.4 ± 1.5 |
| Fish | | |
| Brook stickleback (3) | –22.8 ± 1.0 | 9.8 ± 2.6 |
| Fathead minnow (6) | –22.5 ± 0.6 | 10.7 ± 0.5 |
| Small yellow perch (4)[a] | –21.3 ± 0.7 | 11.2 ± 0.7 |
| Large yellow perch (2)[a] | –21.2 ± 0.1 | 12.9 ± 0.1 |
| Northern pike (2) | –22.4 ± 0.2 | 13.2 ± 0.4 |
| Red-necked Grebe | | |
| Egg albumen (8) | –23.1 ± 0.5 | 11.7 ± 0.3 |
| Egg yolk (8) | –22.0 ± 0.5 | 12.1 ± 0.3 |
| Chick pectoral muscle (2) | –21.6 ± 1.1 | 11.5 ± 0.2 |
| Juvenile pectoral muscle (1) | –21.6 | 12.2 |
| Juvenile leg muscle (1) | –20.9 | 11.8 |
| Juvenile primary feather (1) | –20.4 | 13.4 |
| Juvenile breast feather (1) | –19.7 | 12.7 |
| Adult pectoral muscle (5) | –18.4 ± 1.5 | 13.8 ± 1.0 |
| Adult leg muscle (5) | –18.5 ± 1.2 | 14.0 ± 0.8 |
| Adult primary feather (5) | –16.6 ± 1.6 | 16.1 ± 3.8 |
| Adult breast feather (5) | –14.7 ± 0.9 | 18.2 ± 0.6 |

[a] Small yellow perch were 116.5 ± 0.2 mm (mean total length ± SD); large were 249 ± 1.0 mm.

levels of consumers in the food web of Armstrong Lake (assuming a 3–5‰ change in $\delta^{15}N$ per level; Minagawa and Wada 1984; Fig. 3, Table 2). The $\delta^{15}N$ values for aquatic invertebrates indicated that they belonged to two lower trophic levels of macroconsumers: herbivores–detritivores, such as snails, amphipods, and caddisfly larvae, and carnivores, such as aquatic diving beetles, odonate larvae, and predaceous leeches. Based on $\delta^{15}N$ values, the terrestrial arthropods occupied similar trophic levels as aquatic invertebrates (Fig. 3). Fathead minnows, brook stickleback, and juvenile yellow perch displayed higher $\delta^{15}N$ values (Fig. 3) and occupied the second-highest trophic level in the lake (Table 2). At the highest trophic level were adult grebes and the large piscivorous fishes (northern pike and adult yellow perch). The $\delta^{15}N$ values of these two groups did not differ (two-sample *t*-test, $t_8 = 1.6$, $P = 0.19$, based on grebe pectoral muscle).

Stable-nitrogen isotope ratios of pectoral muscle from adult grebes from fishless Gilbert Lake ($n = 2$) were lower than the ratios from adult

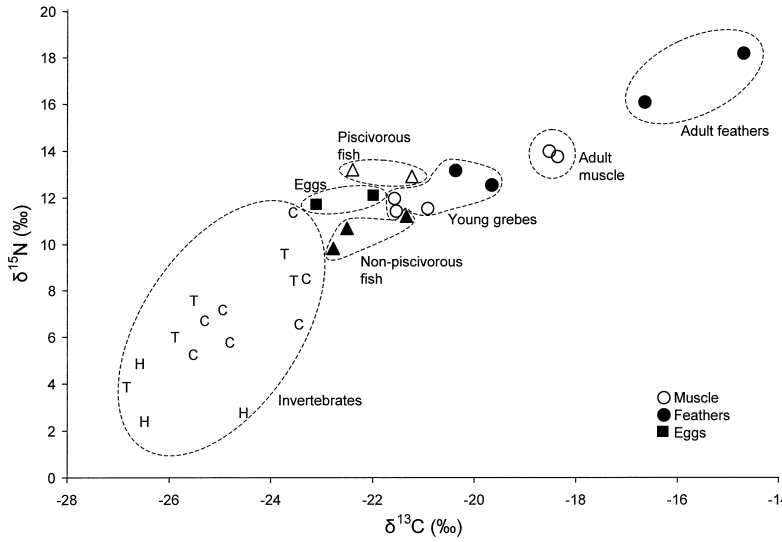


FIGURE 3. Stable-isotope signatures of Red-necked Grebes and other food-web components from Armstrong Lake, Alberta, based on mean stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (‰). Grebe tissues analyzed included pectoral and leg muscle from five adults and three young birds (unfilled circles), and breast and primary feathers from the adults and one of the young birds (a juvenile; filled circles), and the albumen and yolk of eight eggs (filled squares). Piscivorous fish included adult Northern Pike and Yellow Perch; non-piscivorous fish included brook stickleback, fathead minnow, and juvenile perch. Invertebrates were classified as terrestrial (T), carnivorous aquatic (C), and herbivorous aquatic (H). Data points correspond to samples in Table 2.

grebes from the other four lakes with fish ($n$ = 8; two-sample $t$-test, $t_7 = 7.6$, $P < 0.001$; Fig. 2). The $\delta^{15}N$ values from Gilbert Lake adult grebe muscle were also lower than values from pectoral muscle from the Armstrong Lake juvenile and downy chicks, as well as from egg albumen and yolk.

*Carbon.* The $\delta^{13}C$ values increased, generally by 1–2‰, with each trophic level (Fig. 3). The $\delta^{13}C$ values for adult Red-necked Grebe muscles were higher than values from any other organism sampled in or around Armstrong Lake, including piscivorous fish and juvenile grebes that had similar $\delta^{15}N$ values (Fig. 3, Table 2).

### DIETARY ANALYSIS

Guts of all six Red-necked Grebes from Armstrong Lake contained both aquatic invertebrates and fish (Table 3). The five adult birds had also eaten terrestrial arthropods. Invertebrate counts ranged from 7 to 487 individuals, with aquatic taxa contributing a larger proportion than terrestrial forms. All birds from Armstrong Lake ate aquatic coleopterans, and these plus odonates made up a substantial proportion of the invertebrate biomass. Although the number of fish in guts ranged from only 2 to 9, fish were nevertheless the dominant prey based on mass. Brook sticklebacks were eaten more frequently than fathead minnows; two grebes had eaten both species.

The two Red-necked Grebes from fishless Gilbert Lake contained few prey items, 19 and 24 invertebrates total. Terrestrial invertebrates and herbivorous aquatic species were poorly represented; large diving beetles (e.g., *Dytiscus alaskanus*) dominated gut contents (Table 3).

## DISCUSSION

The Red-necked Grebe is one of the most widespread aquatic birds on lakes and wetlands in northern Alberta (Semenchuck 1992). By combining traditional gut-content analysis and technologically sophisticated stable-isotope analysis, our study offers an initial picture of the trophic role of the species in these productive systems. Stable-isotope analysis of a range of tissues from Red-necked Grebes also proved useful in examining other aspects of the species' biology related to energy allocation and the annual cycle of reproduction and feather molt.

TABLE 3. The frequency of occurrence (number of grebes with prey type present in gut) and the mean (± SD) percentage by number and dry mass of terrestrial and aquatic invertebrates and fish found in guts of six Red-necked Grebes from Armstrong Lake and two Red-necked Grebes from fishless Gilbert Lake.

| Taxa | Armstrong Lake | | | Gilbert Lake | | |
|---|---|---|---|---|---|---|
| | Frequency (max = 6) | % by number | % by mass | Frequency (max = 2) | % by number | % by mass |
| Invertebrates | 6 | 84 ± 21 | 46 ± 26 | 2 | 100 | 100 |
| Terrestrial | 5 | 33 ± 29 | 10 ± 16 | 1 | 3 ± 4 | <1 |
| Coleoptera | 5 | 21 ± 22 | 4 ± 5 | 1 | | |
| Hymenoptera | 4 | 12 ± 14 | 2 ± 4 | 0 | | |
| Other[a] | 2 | <1 | <1 | 0 | 3 ± 4 | <1 |
| Herbivorous aquatic | 5 | 8 ± 9 | 4 ± 8 | 0 | | |
| Amphipoda | 2 | 2 ± 5 | 4 ± 9 | 0 | | |
| Veneroida | 3 | 4 ± 5 | 1 ± 1 | 0 | | |
| Other[b] | 4 | 1 ± 2 | <1 | 0 | | |
| Carnivorous aquatic | 6 | 43 ± 25 | 24 ± 27 | 2 | 97 ± 4 | 96 ± 5 |
| Coleoptera, Dyticidae | 6 | 9 ± 12 | 2 ± 3 | 2 | 58 ± 29 | 81 ± 26 |
| Coleoptera, Gyrinidae | 3 | 8 ± 12 | 1 ± 2 | 0 | | |
| Coleoptera (all other) | 5 | 18 ± 18 | 6 ± 7 | 2 | 12 ± 5 | 4 ± 4 |
| Hemiptera | 3 | 3 ± 5 | <1 | 1 | 17 ± 24 | 1 ± 2 |
| Odonata | 4 | 5 ± 7 | 14 ± 22 | 1 | 8 ± 12 | 9 ± 13 |
| Other[c] | 6 | 1 ± 1 | 7 ± 11 | 1 | 2 ± 3[d] | 5 ± 7 |
| Fish | 6 | 16 ± 21 | 55 ± 26 | | | |
| Brook stickleback | 5 | 8 ± 10 | 19 ± 37 | | | |
| Fathead minnow | 2 | 8 ± 13 | 36 ± 24 | | | |
| Total gut contents[e] | | 127 ± 183 | 973 ± 1013 | | 22 ± 4 | 668 ± 42 |

[a] Araneae, Hemiptera, Homoptera.
[b] Ephemeroptera, Trichoptera.
[c] *Rhynchobdellida* and unknown aquatic insects.
[d] Plus fragments of unknown aquatic insects.
[e] Mean ± SD; mass is in grams.

## DIET

Although breeding Red-necked Grebes in Sweden avoid lakes inhabited by large-bodied fishes and prefer fishless lakes (Wagner 1997), the species shows considerable versatility in habitat selection and use in western Canada and elsewhere in North America (Stout and Nuechterlein 1999, Nuechterlein et al. 2003) and Europe (Kloskowski 2003). Similarly, our study indicates a greater dietary flexibility of Red-necked Grebes in Alberta than in Sweden, which was related largely to the local fish assemblage. For example, the grebe from SPH-20, a lake that lacks small-bodied fish species, had eaten a 141-mm yellow perch, as well as numerous invertebrates. In Armstrong Lake, where small-bodied fish species were present, grebes ate fathead minnows and brook sticklebacks (ca. 50–65 mm), along with a wide range of aquatic and terrestrial invertebrates. In contrast, gut analysis indicated that the two birds from fishless Gilbert Lake primarily ate aquatic arthropods. Observations of foraging grebes suggest that leeches are also an important food (PHK, unpubl. data), but were likely underrepresented in guts because of their soft bodies and rapid digestion. This flexibility in diet is consistent with our observations of Common Loons breeding on small lakes in Alberta, where loons feed their chicks small fish where these prey are available but provide only invertebrates, primarily odonates and leeches, to chicks on fishless lakes (Gingras 1997). This pattern even extends across classes in the highly productive boreal Alberta lakes; diets of typically piscivorous northern pike indicate that they too eat significant numbers of macroinvertebrates, and that some individuals and populations even specialize on this prey type (Beaudoin et al. 1999, Venturelli 2004).

## TROPHIC WEBS AND STABLE ISOTOPES

The trophic web of Armstrong Lake, as constructed with stable-isotope analysis, was typical of lakes of the Boreal Plain (Beaudoin et al.

1999, 2001). Muscle, a tissue commonly used for vertebrates in stable-isotope studies (Kelly 2000), proved reasonably successful at representing the trophic level of adult Red-necked Grebes, as determined from gut analyses. The rather modest increase of $\delta^{15}N$ (2–3‰) in the muscle tissue of grebes, compared to muscle from small-bodied fishes, was consistent with grebe gut contents, which showed that birds regularly ate both fish and macroinvertebrates. Although $\delta^{15}N$ values from grebe muscle varied among our study lakes, the variation appeared to be consistent with the short-term diets indicated by gut contents, rather than underlying differences in isotopic regimes among lakes. For example, $\delta^{15}N$ values of grebe muscle from Gilbert Lake complemented gut analyses and suggested a lower trophic position of birds there, compared to birds from the four lakes containing fish.

In contrast, $\delta^{13}C$ values of muscle from adult grebes from Armstrong Lake were substantially elevated (3–8‰) compared to tissues from all other species examined in the food web, and also 3–4‰ above values for eggs and chicks from this lake. Although some (ca. 1‰) increase in $\delta^{13}C$ is expected as one moves up trophic levels (Peterson and Fry 1987), the degree of enrichment we measured was well beyond this. This result might indicate additional, unidentified prey for adult grebes or the enrichment of muscles as a result of mobilization of muscle protein for egg production (Gannes et al. 1997). However, there was no relationship between $\delta^{13}C$ levels in grebe muscle and the number of days after 1 May that the bird was found, and feathers of adult grebes were also enriched. Instead, we suggest that stable-carbon isotopic ratios of adult grebe muscle tissue most likely reflected, at least in part, their winter feeding in marine habitats, where $\delta^{13}C$ levels are generally higher (e.g., marine fish $\delta^{13}C$ values range from ca. −17‰ to −21‰ vs. freshwater fish from ca. −26‰ to −29‰) than in terrestrial and freshwater ecosystems (Hobson 1990, Sydeman et al. 1992, Kline et al. 1998, Hobson, Sirois, and Gloutney 2000). Nitrogen ratios are also often higher in marine food webs (Hobson 1999, Kelly 2000) and grebes may be more piscivorous while on marine wintering habitats (Stout and Nuechterlein 1999). Thus, lingering marine influences among $\delta^{15}N$ values may have made breeding grebes appear more dependent on fish, and less dependent on invertebrates, than they actually were.

## GREBE TISSUES AND STABLE ISOTOPES

During nesting, the flight muscles of Eared Grebes diminish substantially in relative mass while leg muscles increase (Jehl 1997). We hypothesized that tissues of Red-necked Grebes might undergo similar seasonal remodeling and that the isotopic signal of leg muscle might more closely mirror the trophic position of birds on the breeding lake than pectoral muscle. Contrary to expectations, the isotopic signatures of leg muscles were very similar to values for pectoral muscle. These results suggest that the reallocation of muscle protein or the muscle-tissue turnover rate is lower in Red-necked Grebes than in the smaller Eared Grebe, based on anatomical work (Jehl 1997), or in captive Japanese Quail (*Coturnix japonica*), based on stable-isotope analysis (Hobson and Clark 1992). Because of tissue turnover, we also expected that isotopic ratios from adult muscle would converge with local, freshwater values and thus be negatively correlated with the time an individual had spent on its breeding lake. However, unlike six species of colonial waterbirds from Great Slave Lake (Hobson, Sirois, and Gloutney 2000), adult grebes from Armstrong Lake did not display a strong relationship between date of collection and isotopic signatures of muscle.

Feathers offer a potentially attractive means of conducting stable-isotope analysis without destroying birds and have been used to determine trophic status of aquatic birds in the wild (Thompson and Furness 1995, Romanek et al. 2000). Feathers are metabolically inert after maturation, however, and thus isotopic composition of feathers reflects diet and habitat at the time they were grown (Mizutani et al. 1990, Hobson and Clark 1992). Traditional natural history reports suggest that adult Red-necked Grebes molt their primary feathers on the freshwater breeding grounds prior to fall migration and the red breast feathers on the marine wintering grounds prior to spring migration (Bent 1963). Grebes from Alberta winter on the Pacific Ocean (Stout and Nuechterlein 1999).

Although feathers are typically among the most enriched tissues in birds for both $^{13}C$ and $^{15}N$ (Mizutani et al. 1992, Kelly 2000), $\delta^{13}C$ and $\delta^{15}N$ values of grebe feathers were dramatically higher than other grebe tissues and other fresh-

water and terrestrial organisms. As well, feathers of grebes from fishless Gilbert Lake showed the same level of enrichment as adults from lakes with fish. Thus, although stable-isotope analysis supports natural-history reports that the bright nuptial plumage of the neck and breast is developed in marine wintering habitats, our results also indicate that Red-necked Grebes breeding in Alberta molt at least some of their flight feathers in marine habitats, following fall migration. Interestingly, Stout and Cooke (2003) recently documented that Red-necked Grebes migrate to special locations to undergo wing molt and regrowth before proceeding to wintering sites. In particular, Boundary Bay, British Columbia, was identified as a major molt site for Pacific-wintering populations, which include birds from Alberta. This type of migration to a molting area is similar to the well-documented molt migrations of the Great Crested Grebe (*Podiceps cristatus*, Piersma 1987) and the Eared Grebe (Jehl 1990, Boyd and Jehl 1998). Stout and Cooke (2003) also suggested that similar patterns occur for Horned Grebe (*Podiceps auritus*) and, in some cases, Western Grebe (*Aechmophorous occidentalis*). Because of these enriched, marine-derived values, the breast and primary feathers of birds in our study were considerably less successful than muscle tissue at reflecting the position of adult grebes in the trophic webs of their breeding lakes. In contrast, isotopic ratios for both feather types from the juvenile collected in August, although slightly enriched ($<1.7‰$, as expected for integumentary structures), otherwise matched the $\delta^{13}C$ and $\delta^{15}N$ values characteristic of Armstrong Lake's food web and values from the bird's own muscles.

As was true of muscle, stable-isotope analysis results for feathers also varied among individuals and localities. Most striking was the extremely low $\delta^{13}C$ and $\delta^{15}N$ values of the primary feathers of one adult Red-necked Grebe (A5) from Armstrong Lake. Values for its other tissues were not unusual. This bird may have produced its flight feathers in a freshwater habitat, in contrast to the other nine adults. Perhaps this grebe had hatched the previous year and still possessed its first set of primary feathers grown on its natal lake. Stable-isotope ratios of breast feathers from adult grebes breeding on Jackfish Lake, SPH20, and N26 were also not as enriched as ratios from Armstrong and Gilbert Lakes, nor as enriched as their own primaries. These birds may have molted their breast feathers in a different trophic setting than their primaries, although other studies have shown that isotopic signals can vary among feather types, even for species that are strictly marine (Thompson and Furness 1995). Thus, while our results indicate that stable-isotope ratios of adult grebe breast feathers and possibly primary feathers may be used to track migratory patterns and help determine molting and staging areas (e.g., Hobson and Wassenaar 1997, Hobson, Brua, et al. 2000, Hobson et al. 2001), they should be used with caution when interpreting trophic patterns on breeding lakes.

In contrast to adult feathers, stable-isotope analysis of eggs appears to be well suited for assessing trophic relationships of Red-necked Grebe during the breeding season. The impact of limited egg collections on grebe populations should be relatively small as median clutch size on lakes in our study area was five eggs, but median brood size was only two chicks (CAP, unpubl. data). Both albumen and yolk isotopic ratios aligned strongly with values sampled from the local food web and organisms found in the gut contents of adult grebes. Isotopic ratios from eggs were also very similar to values from muscle and feathers from young grebes.

Red-necked Grebes typically arrive on northern Alberta lakes around 1 May and initiate clutches around 20 May (CAP, unpubl. data). In the habitats we studied, it appears that female grebes obtain materials for egg formation by feeding on the breeding lake, not by importing reserves from marine wintering sites. This pattern is common among other groups of birds that winter in marine habitats but breed on northern freshwater systems (e.g., Pelicaniformes and Charadriiformes; Hobson et al. 1997, Hobson, Sirois, and Gloutney 2000). Our study provides the first evidence, to our knowledge, that Red-necked Grebes use exogenous materials from the local breeding area to form egg yolk and albumen. An analysis of $\delta^{13}C$ values of eggshells also indicated that Western Grebes use nutrients from freshwater feeding for egg formation (Schaffner and Swart 1991).

The western boreal forest has recently gained recognition as a key habitat for aquatic birds in North America (Morrison 2002). Supporting an estimated 13 million breeding ducks, it is the focus of a number of large-scale research and conservation initiatives. Although our sample

size may limit broad conclusions, our study of the Red-necked Grebe indicates that stable-isotope analysis is a powerful ecological tool for exploring trophic relations of aquatic birds in this region, as well as addressing questions concerning migration patterns, habitat use, and energy allocation.

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