COMPARATIVE REPRODUCTIVE STRATEGIES BETWEEN LONG-TAILED DUCKS AND KING EIDERS AT KARRAK LAKE, NUNAVUT: USE OF ENERGY RESOURCES DURING THE NESTING SEASON

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Shona Louise Lawson

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ABSTRACT

Energy demands can be particularly high in arctic-nesting birds that face harsh, unpredictable conditions during the breeding season. Consequences of these demands, particularly energy-partitioning during egg laying and incubation, are fundamentally important for arctic nesters. This study investigated differences in breeding strategies between Long-tailed Duck (*Clangula hyemalis*) and King Eider (*Somateria spectabilis*) in the central Canadian arctic. The focus was on ecological variables and influences of variation in nutrient resources used during incubation and egg production. Research was done at Karrak Lake, Nunavut, where both species nest sympatrically at relatively high densities, permitting comparative research about breeding strategies.

This study used stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis to investigate origins and allocation of endogenous (stored) and exogenous (external) nutrients used in egg production. Remote temperature sensors were placed in nests to estimate and compare incubation rhythms and gain insight into capital and income incubating strategies of both species. Results suggest that breeding Long-tailed Ducks and King Eiders used a “mixed” breeding strategy, that is they relied on both exogenous and endogenous resources for reproduction. Close correspondence between $\delta^{13}C$ and $\delta^{15}N$ values of egg components and potential diet items indicated that King Eiders allocated exogenous nutrients for egg production (albumen 98.1%, yolk protein 96.8%, whole yolk 98.4%, and yolk lipids 84%). Female King Eiders relied on endogenous nutrients for incubation, as evidenced by high incubation constancy (96%). Conversely, the range of $\delta^{13}C$ values in components of Long-tailed Duck eggs and $\delta^{13}C$ values of diet items suggested that although some females allocated endogenous reserves for egg production, most females allocated exogenous resources for egg production (albumen 98.5%, yolk protein 78.3%, whole yolk 84.9%, and yolk lipids 38.3%). Long-tailed Duck females had an 84% incubation constancy, suggesting less reliance on endogenous nutrients for incubation than was estimated for female King Eiders. Knowledge about the relative importance of endogenous reserves and exogenous nutrients for egg production and incubation may help direct management decisions to specific winter/staging and or breeding areas used by King Eiders and Long-tailed Ducks.

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DEDICATION

I would like to dedicate this thesis to all the scientists, past, present and future, who provide inspiration, encouragement and support.

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1.0 GENERAL INTRODUCTION

1.1. BREEDING STRATEGIES OF LONG-TAILED DUCKS AND KING EIDERS

Drent and Dann (1980) theorized that breeding birds use either a capital strategy, relying on stored (endogenous) energy sources, or an income strategy, relying on external (exogenous) sources. Energy and nutrient reserves are essential during the breeding season for successful reproduction in many waterfowl species (Ankney et al. 1991, Alisauskas and Ankney 1992), and are crucial to the egg-laying and incubation processes (Afton and Paulus 1992). Reliance on energy and nutrient reserves for reproduction is a ubiquitous adaptation by breeding waterfowl to meet high energy demands of breeding (Alisauskas and Ankney 1992). The degree to which a breeding female relies upon endogenous and exogenous nutrient sources determines the breeding strategy as either, capital or income (Drent and Dann 1980). Recent research has demonstrated that many species occupy a continuum between the two extremes (Bonnet et al. 1998, Thomas 1988, Meijer and Drent 1999, Gauthier et al. 2003, Morrison and Hobson 2004).

The analysis of naturally occurring stable-isotopes in avian eggs can provide dietary information and insights into metabolic pathways linking endogenous reserves and exogenous nutrients to reproduction (Hobson 1995). Nutrients required for egg production are derived from either nutrient reserves or directly from the diet of laying females, making eggs particularly amenable to stable-isotope analysis (Hobson et al. 1997). Stable isotope analysis of eggs can help determine the relative proportion of endogenous or exogenous nutrients allocated to egg production (Hobson 1995). In addition, the technique can determine if nutrients utilized for egg production were obtained from either a freshwater or marine ecosystem (Hobson et al. 1997). Stable-isotope techniques have been used successfully to investigate capital and income breeding strategies of several species (Hobson 1995, Hobson et al.1997, Hobson et al. 2000, Klassen et al. 2001, Morrison and Hobson 2004, Hobson et al. 2004).

In addition to the physiological costs of egg formation, incubation behaviour is also fundamentally important to reproductive success (Mallory and Weatherhead 1993). A few of the major functions of avian incubation relate to maintaining favorable temperature conditions within nests for embryonic development, while minimizing likelihood of predation and allowing incubating females to maintain a favorable energy balance. The optimum balance of time spent on and off the nest is an adaptation that maximizes likelihood of successful hatch against costs of conflicting variables (Flint and Grand 1999). Blums and Clark (1991) suggested that in northern-most breeding areas, reliance on endogenous reserves during incubation might be more important than in more southern areas because of lower ambient temperatures. The various physiological costs of incubation to breeding females has lead to the suggestion that incubation behavior is driven by tradeoffs between the loss of body condition, maintenance of egg viability and predation risks (Thompson and Raveling 1987, Afton and Paulus 1992). These combined costs and tradeoffs have lead to theories related to the reliance by breeding females on either a capital or income strategy for incubation.

Capital incubators are typically considered larger-bodied birds, such as geese, as larger body size may enable a greater storage of endogenous reserves (stored body reserves) before the breeding season, permitting greater use of these stores during the egg-laying and incubation periods. Income incubators, typically smaller-bodied birds, such as shorebirds, are thought to rely almost exclusively on exogenous stores (local diet resources) during the same periods, since their size may restrict the amount of energy that they can be stored for reproduction prior to arrival on the breeding grounds. Due to past technological difficulties in obtaining data on continuous nest attentiveness by incubating birds few studies have examined these variables simultaneously (Mallory and Weatherhead 1993). However, recent technological advances allow researchers to investigate such variables concurrently. Data loggers for automatically recording temperatures are one such technological advance, whereby incubation constancy can be easily measured since nest temperature will decrease and increase when a female leaves and returns to the nest respectively.

Energy demands are expected to be particularly high in arctic-nesting sea ducks, which face harsh, often unpredictable conditions. However, few studies have researched the use of endogenous and exogenous resources (i.e. capital and income breeding strategies, respectively) in arctic-breeding sea duck species. Long-tailed Ducks (*Glangula hyemalis*) and King Eiders (*Somateria spectabilis*) winter and breed in arctic and subarctic regions, coming to coastal and inland freshwater areas during the breeding period. King Eider’s are large-bodied ducks (Palmer 1976, Portenko 1972 in Suydam 2000, Kellett and Alisauskas 1997), while Long-tailed Ducks are medium-sized (Peterson and Ellarson 1979, Leafloor et al. 1996, G.J.R. Gilchrist and H.G. Gilchrist Unpubl.). Afton and Paulus (1992) found that larger bodied waterfowl relied more on endogenous reserves, during incubation because of less time available for feeding recesses due to their high incubation constancy. Alternatively, smaller-bodied waterfowl had short fasting endurance, and instead relied more on exogenous energy sources (Afton and Paulus 1992). These findings suggest that body size is a significant factor in the breeding ecology of waterfowl (Afton and Paulus 1992).

Long-tailed Ducks were found to lose most of their fat reserves during spring migration and egg laying and body mass declined by 7 - 13% during incubation (Peterson and Ellarson 1979, Kellett et al. 2005). Fat deposition in Long-tailed Ducks appears to fulfill two requirements 1) supplying energy for migration, and 2) as energy reserves for meeting existence requirements during winter periods when food intake could be limited (Peterson and Ellarson 1979). King Eiders may rely exclusively on endogenous energy reserves during both egg production and incubation, losing an average of 30% of their pre-incubation body mass during incubation (Kellett and Alisauskas 2000). Common Eiders (*Somateria mollissima*) also lost ~30% body mass during incubation (Parker and Holm 1990), despite recent findings from the Baltic that suggested reliance on exogenous nutrients from the local breeding ground for egg production, (Rigou and Guillemette Unpubl.). These findings suggest that sea ducks may use different breeding strategies for reproduction, with Long-tailed Ducks as income breeders, King Eiders as capital breeders and Common Eiders as “mixed” breeders.

Karrak Lake, Nunavut, Canada is an ideal research area for this study as both King Eiders and Long-tailed Ducks are found nesting at relatively high densities, permitting comparative research about breeding strategies, and allocation of nutrients for reproduction. Results regarding breeding strategies of Long-tailed Ducks and King Eiders with respect to variation in endogenous and exogenous resources in both egg production and incubation could provide insight into factors that influence reproductive success and may help direct management decisions to specific winter/staging or breeding areas.

1.2 STUDY SPECIES

Long-tailed Ducks and King Eiders belong to the Mergini Tribe, along with all sea ducks. This primarily marine group are considered ancient in origin, and includes some of the most specialized species within the family Anatidae (Johnsgard 1965). These two species, are circumpolar in distribution, share sympatric breeding and wintering ranges, and are considered among the most northerly- nesting waterfowl species in North America. Both species exhibit high sexual dimorphism in plumage, vocalization and behavior (Johnsguard 1965). Pair bonds are renewed with elaborate courtship displays each year on wintering grounds before spring migration (Johnsguard 1965, Parmelee 1967, Lamothe 1973, Alison 1975). Long-tailed Ducks and King Eiders reach sexual reproductive maturity at two years of age (Johnsguard 1965, Livezey 1995). Mark-recapture data on King Eiders breeding at Karrak Lake suggests they do not begin breeding before three years of age (Alisauskas Unpubl.). Adult females have cryptic and disruptive plumage (Johnsguard 1965) and are ground nesters. Only females incubate and they are likely to produce only one clutch per breeding season, as with most arctic-nesting waterfowl, and if the first attempt fails, the nest is abandoned or predated (Parmelee 1967, Lamothe 1973, Pehrsson 1986, Alison 1975, Kellett and Alisauskas 1997).

Long-tailed Ducks and King Eiders, considered the two deepest diving sea ducks (Ehrlich et al. 1988), are carnivores that rely on various prey species as primary sources of food (Weller 1964a). However, both species feed occasionally on plant matter on breeding grounds (Cottam 1939, Preble and McAtee 1923). Interspecific differences in bill morphology and dive depth allow exploitation of different niches and food resources while sharing habitats (Livezey 1995). King Eiders are circumpolar in distribution, wintering in marine habitats and coming inland to freshwater habitats during the breeding season. The King Eider is a large-bodied duck weighing between 1200 and 2100g (Palmer 1976, Portenko 1972), Kellett and Alisauskas 1997). King Eiders have an average clutch size ranging from 4 – 5.5 (Lamothe 1973, Cotter et al. 1997, Kellett and Alisauskas 1997) and incubate on average for 23 days (Lamothe 1973, Kellett and Alisauskas 1997). King Eiders take short infrequent incubation recesses throughout incubation, maintaining an incubation constancy between 94% - 99% (Chapter 3, McGuire et al. Unpubl.). King Eider's, like other North American waterfowl have two plumage phases - basic and alternate and molt twice a year (Palmer 1976).

The Long-tailed Duck is also a circumpolar species that breeds in freshwater arctic and subarctic regions, and winters in marine and freshwater areas. Long-tailed ducks are a medium-sized sea duck: females weigh approximately 700g and males weigh approximately 800g (Peterson and Ellarson 1979, Leafloor et al. 1996, G.J.R. Gilchrist and H.G. Gilchist Unpubl.). Average clutch size ranges from 6 – 7.9 (Alison 1975, Bengston 1971, Kellett et al. 2005) and the incubation period is 26 days (Alison 1975, Kellett et al. 2005). Long-tailed Ducks take frequent incubation recesses of longer duration than those of King Eiders, maintaining an incubation constancy of 84% (Chapter 3). Long-tailed ducks, unlike other North American waterfowl species have 3 plumage phases (basic, supplemental and alternate) and molt occurs three times a year (Palmer 1976).

1.3 STUDY OBJECTIVES

Noted population declines for both species along with sparse information about reproductive life history generated interest in this research (Sea Duck Joint Venture Management Board 2001, Prairie and Northern Region Sea Duck Team 2000). In addition, sparse knowledge about arctic breeding ecology, and shared phylogeny of Long-tailed Ducks and King Eiders motivated this research. Energy demands are expected to be particularly high in arctic-nesting sea ducks, which face harsh, often unpredictable conditions during the breeding season. Environmental variables may influence the amount of energy reserve needed to complete reproduction successfully. Some Eider species rarely leave the nest during incubation suggesting reliance upon stored (endogenous) energy sources (Parker and Holm 1990, Kellett and Alisauskas 2000). Conversely, Long-tailed Ducks frequently leave their nests during incubation suggesting a greater reliance on local food (exogenous) resources (Kellett et al. 2005). Consequently, Long-tailed Ducks may use a markedly different nutritional strategy for reproduction than King or Common Eiders. Isotope analysis of avian eggs may provide dietary information and insights into metabolic pathways linking endogenous and exogenous reserves to reproduction (Hobson 1995) and can provide information on source of nutrients for egg production (Hobson et al. 1997, Gauthier et al. 2003, Morrison and Hobson et al. 2004, Hobson et al. 2004). Stable-isotope techniques were used to analyze stable-carbon and nitrogen (δ^{13}C and δ^{13}N, respectively) values of 1) eggs collected from both species and 2) potential diet items, to investigate contributions and allocation to egg production of endogenous versus exogenous sources of nutrients, from wintering and breeding ground habitats. Constancy of incubating females was measured by placing remote temperature data loggers in nests.

Field work consisted of 1 field season extending from May 2004 to August 2004. The objectives were to:

1. Estimate allocation of endogenous and exogenous resources in eggs of Long-tailed Ducks and King Eiders using naturally-occurring stable isotopes.

2. Estimate frequency, timing, and duration of incubation recesses of Long-tailed Ducks and King Eiders.

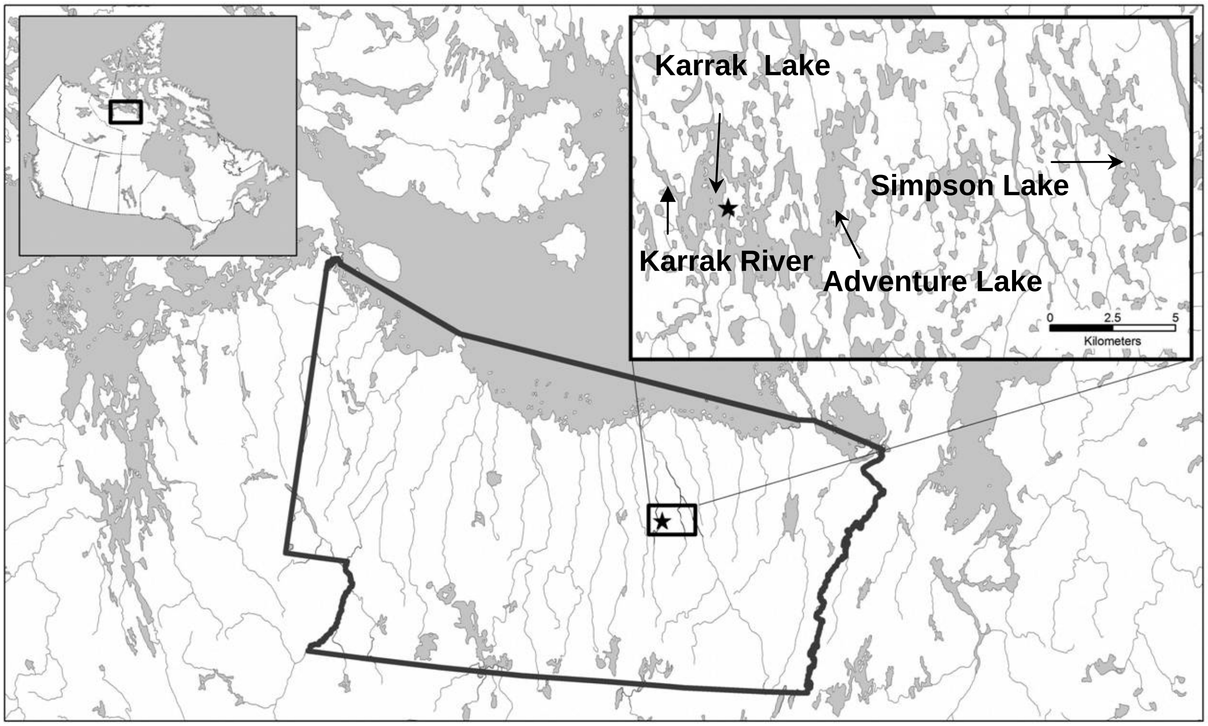
2.0 STUDY AREA AND GENERAL METHODS

2.1 STUDY AREA

Karrak Lake, Nunavut (67°14' N, 100°15' W) is ~60km south of the Queen Maud Gulf in the Queen Maud Gulf Bird Sanctuary in the Central Canadian Arctic (Figure 2.1). Karrak Lake supports a large colony of ~1 million nesting Lesser Snow Geese (*Chen caerulescens caerulescens*) and Ross's Geese (*Chen rossii*). The area also supports the highest known density of "semi-colonial" nesting King Eiders (Kellett and Alisauskas 1997, 2000) and the highest known density of nesting Long-tailed Ducks in North America (Kellett et al. 2005). The area consists of sedge meadows, marshy areas and rock outcrops interspersed with shallow tundra ponds (Slattery 1994). Much of the vegetation within the goose colony has been altered by feeding and nest-building by high densities of the geese (Alisauskas et al. 2006). Karrak Lake covers 16.1 km^2 (Kellett and Alisauskas 2000), averages a depth of 1.2m (Ryder 1972) and is interspersed with 2.5 km^2 of various sized islands (Kellett and Alisauskas 2000). Adjacent to Karrak Lake, is Adventure Lake which is 8.8 km^2 in size, averaging 2.5m in depth and containing 0.2km^2 of various sized islands (Kellett and Alisauskas 2000). Islands in both lakes are predominately rock and gravel outcrops with some low-lying vegetation (Kellett and Alisauskas 2000). Islands vary in habitat and nesting bird assemblages with different proportions of nesting King Eiders, Long-tailed Ducks, Glaucous Gulls (*Larus hyperboreus*), Herring Gulls (*Larus argentatus*), Arctic Terns (*Sterna paradisaea*), Lesser Snow Geese, Ross's Geese, Canada Geese (*Branta Canadensis*) , Red-throated Loons (*Gavia stellata*), Arctic Loons (*Gavia arctica*), and Red-breasted Mergansers (*Mergus serrator*). Simpson Lake (67°16' N, 99°54' W) is located 8 km east of Adventure Lake and is10.26 km^2 in size with 0.314 km^2 of islands. Islands in Simpson Lake are predominantly grassy with low lying vegetation and a mixture of rock and gravel outcrops.

There are one-hundred and seven islands on Karrak and Adventure Lakes of which King Eiders and Long-tailed Ducks used twenty and ten, respectively for nesting during the 2004 breeding season. Simpson Lake has thirty-five islands and King Eiders and Long-tailed Ducks were found nesting together or separately on twelve.

Figure 2.1. Study area Karrak, Adventure and Simpson Lakes and Karrak River. The star represents the Karrak Lake Canadian Wildlife Service Research Station (67°14’ N, 100°15’ W).



2.2.0. GENERAL FIELD METHODS

2.2.1. Weather Data

Meteorological weather variables of daily maximum and minimum ambient temperatures (^{0}C), precipitation (mm/day), and wind speed (km/hour) and direction (degrees 0 – 360^0) were recorded daily. In additional, timing of ice break-up as well as arrival times for both sexes of King Eiders (Kellett and Alisauskas 1997) and Long-tailed Ducks were recorded (Alisauskas Unpubl.).

2.2.2. Nest Searching, Monitoring and Egg Collection

Islands were searched for nests starting in mid-June, corresponding with late egg-laying and early incubation for both King Eiders and Long-tailed Ducks. Nests were visited every 5 - 10 days to determine final clutch size, egg attrition rate, and nest fate. As predicted hatching dates neared, nests were visited more often, at intervals of 1 – 4 days. King Eiders and Long-tailed Ducks were assumed to have respective incubation periods of 23 days (Parmelee et al 1967, Kellett 1999) and 26 days (Alison 1975, Kellett et al. 2005), and eggs are laid at an interval of one per day (Lamothe 1973); hatch dates were calculated from estimated initiation dates. Remote temperature sensors (Hobo XT, Onset Computer Corporation) were placed in 29 Long-tailed Duck and 26 King Eider nests during incubation to record incubation and recess frequency, duration and timing. Nests were visited on predicted hatching dates to capture and mark incubating females and hatching ducklings. Remote temperature probes were placed in nests on several islands. Remote temperature probes were placed in nests on several islands with the aim of placing an equal number of remote temperature probes in both Long-tailed Duck and King Eider nests on each island.

Nest locations were marked with small-numbered wood stakes placed 1 m north of nests. Nests with remote temperature probes were marked with a small plain 6” wooden stake placed underneath the nest bowl. This was done to minimize likelihood of predation (Picozzi 1975). Gulls (*Larsus*) and Parasitic Jaegers (*Sterocoraius parasiticus*) observed robbing nests of Long-tailed Ducks were the primary predators although mammalian predators, such as Grizzly Bears (*Ursus horribilis*) and Arctic Foxes (*Alopex lagopus*) have depredated sea duck nests at Karrak Lake (S.L. Lawson per. obs.). Avian predators (gulls and jaegers) nesting close to nesting King Eider and Long-tailed Ducks may have increased predation or robbing of duck nests.

Both King Eiders and Long-tailed Duck eggs were numbered with indelible ink, and egg length (± 0.1mm) and width (± 0.1mm) was measured using dial calipers and recorded. Long-tailed Duck and King Eider eggs were obtained during the same time period. Thirty and twenty–nine eggs of Long-tailed Ducks and King Eiders, respectively, were collected from active nests at Simpson Lake early in incubation, in early July 2004. One to two eggs and one to three eggs per nest were collected from active King Eider and Long-tailed Duck nests respectively. A nest was considered active if incubated and/or females were flushed from nest. Another forty-seven King Eider and nineteen Long-tailed Duck eggs were collected from failed and abandoned nests at Simpson, Karrak and Adventure Lakes throughout the breeding season (mid June – early August). Nest fates included (1) *abandoned* (if eggs are at the same stage of incubation as last visit and were cold) (2) *failed* (no depredated evidence of eggs or shells were found) or (3) *depredated* (Klett et al. 1986) were recorded. All salvaged eggs present in a nest when it was determined to be abandoned or failed were collected. Salvaged eggs collected ranged from one to four per nest. Collected eggs were boiled and frozen at Karrak Lake to preserve them until transportation to Canadian Wildlife Service laboratory in Saskatoon (Gloutney and Hobson 1998, Hobson per. comm.) where egg components were prepared and analyzed for stable-carbon and nitrogen analyses. As I was unable to detect laying order or obtain a large enough sample of whole clutches and due to the close correspondence of δ^{15}N and δ^{13}C values within species and between species I did not test for a clutch effect. Egg component (albumen, yolk protein, whole yolk and yolk lipid) δ^{15}N and δ^{13}C values from the same nest were averaged to investigate contribution of exogenous versus endogenous nutrient allocation on a per nest basis. Egg component δ^{15}N and δ^{13}C values hereafter refer to the mean δ^{15}N and δ^{13}C values of each nest sampled. Egg components of twenty-nine Long-tailed Duck and forty-four King Eider nests were used in the δ^{15}N and δ^{13}C stable isotope analysis.

2.2.3. Diet sampling and Storage

King Eiders and Long-tailed Ducks congregate before and during the nesting season on Karrak and Adventure Lakes (S. Lawson per. obs.). Groups of molting Long-tailed Ducks also congregate on Karrak Lake after the nesting season. Samples of potential diet items (hereafter referred to as diet items), Ninespine Sticklebacks (*Pungitius pungitius*) and unidentified fish and invertebrates (*Copepoda, Eubranchiopoda, Tipulidae, Haliplidae, and Chironomidae*), were collected in 2004, during and after the breeding season, using a dip net at several locations along the Karrak River and Karrak Lake (Figure 2.1) during and after nesting. Diet items were also collected at several sites on Adventure Lake in 2005 during and after nesting (Figure 2.1). Specimens were placed in 70% ethanol to avoid deterioration of stable isotopes during storage and transfer from field to laboratory (Hobson per. comm.). Ethanol preservation of aquatic invertebrates did not affect either $\delta^{15}N$ or $\delta^{13}C$ isotope values of specimens (Sarakinos et al. 2002). The $\delta^{13}C$ and $\delta^{15}N$ signatures of diet items from these wintering grounds were obtained from the literature (Table 4.2).

2.3 GENERAL LABORATORY METHODS

Frozen egg components, whole yolk and albumen, were separated and placed into separate 20ml vials and then freeze-dried in the laboratory. A portion of each dried whole yolk sample was put into a separate 20ml vial. This second whole yolk sample from each egg, hereafter referred to as yolk protein, was soaked in a 2:1 chloroform: methanol mixture to remove lipids. Lipids moved into the chloroform fraction which was then poured off and the remaining sample placed in a fume-hood to air dry. Albumen samples were powdered using a mortar and pestle. Diet items were rinsed in distilled water and placed in individual 20ml vials, freeze-dried and soaked in a 2:1 chloroform: methanol mixture to remove lipids and then allowed to air-dry in a fume-hood.

Whole yolk, yolk protein, albumen and diet items were weighed (1.0 milligram) in tin cups and combusted in a Roboprep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Europa Scientific, Crewe, UK; Hobson and Schell 1998) at the Department of Soil Science, University of Saskatchewan. All stable isotope values are reported in δ notation relative to the Pee Dee Belemnite (PDB) and atmospheric air standards for stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) measurements. Measurement precision is based on thousands of measurements of our albumen lab standard and is estimated to be ± 0.1 ‰ for $\delta^{13}C$ measurements and 0.3 ‰ $\delta^{15}N$ measurements (see Hobson 1995). Isotope values are expressed as $\delta^{13}C$ and $\delta^{15}N$ (with units of ‰) according to the following equation:

$$\delta^{13}C, \delta^{15}N = [\,(R_{sample}/R_{standard}) - 1] \times 1000 \quad \text{Where } R = {}^{13}C/{}^{12}C,\ {}^{15}N/{}^{14}N \quad (2.1)$$

3.0 INCUBATION RHYTHMS OF LONG-TAILED DUCKS AND KING EIDERS AT KARRAK LAKE, NUNAVUT

3.1. INTRODUCTION

Incubation behavior is fundamentally important to reproductive success in avian species. Incubation must maintain relatively stable temperature conditions within the nest for embryonic development, while maintaining a favorable energy balance for incubating females (Flint and Grand 1999). These costs of breeding have led to theories that incubation behavior has evolved in response to tradeoffs between the loss of body condition, reliance upon energy and nutrient reserves, maintenance of egg viability, and to minimize predation risks (Thompson and Raveling 1987, Afton and Paulus 1992, Ankney et al. 1991, Alisauskas and Ankney 1992). Incubating birds have a restricted behavioural repertoire governed by the need to maintain contact between the eggs and bird's incubation patch in order to maintain the appropriate temperature for the developing embryo (Deeming 2002). Drent and Daan (1980) suggested that incubating birds rely on either a capital or income strategy for incubation. Capital incubators are typically considered to be larger-bodied birds, as their body size enables them to store sufficient endogenous reserves before arrival at breeding grounds and then draw from these reserves during the incubation period to meet their own metabolic requirements (Drent and Daan 1980). Income incubators, typically smaller-bodied, may be limited by their body size from arriving at breeding grounds with sufficient endogenous (stored) reserves to sustain themselves during incubation, and therefore rely almost exclusively on exogenous resources i.e. directly from their diets, during this portion of the breeding cycle (Drent and Daan 1980).

Deeming (2002) suggested that the pattern of incubation behavior adopted by different bird species likely reflects restrictions imposed upon them by their environment. As a result, closely related species can adopt markedly different patterns of incubation behavior, thus confounding any relationship between phylogeny and incubation patterns (Deeming 2002). Only females incubate in most species of waterfowl, an incubation strategy found in 37% of bird families. Female-only incubation is characterized by three incubation behaviour patterns (1) a single recess of long duration during the day, (2) several recesses taken during the 24 hour period and (3) uninterrupted incubation for several days (Williams 1996). Lengths of both the incubation sessions and recesses are highly variable (Kendiegh 1952, Skutch 1962). In addition, the number of sessions a bird undertakes during the incubation period can also vary considerably (Deeming 2002).

Many incubating birds are often required to endure adverse weather conditions (Deeming 2002). Weather conditions have a profound affect on the degree of incubation constancy particularly for females involved in a female-only incubation strategy (Deeming 2002). Afton (1980) showed that weather variables explained more of the components of incubation rhythms in small ducks than in larger geese and swans. Skutch (1962) found that precipitation also affected incubation behaviour although behaviour varied with precipitation severity and extent. Female-only incubators that experienced rain during a recess usually returned to nests to shield eggs leading to sessions that were longer than normal (Skutch 1962). Ambient temperature can influence the duration of both incubating sessions and recesses (Afton 1980). However, no simple pattern has been shown suggesting factors such as female fat reserves may affect how ambient conditions affect behaviour (Kluivjer 1950, Haftorn 1978, 1984, Afton 1980, Halupka 1994, Conway and Martin 2000). Energy reserves play a key role in the nesting ecology of waterfowl. Blums and Clark (1991) suggested that reliance on endogenous reserves during incubation might be more important in birds that breed in northern areas because of lower ambient temperatures and often unpredictable environmental conditions. Reliance on energy reserves may be particularly high in arctic-nesting species as environmental conditions are often harsh and unpredictable.

Afton and Paulus (1992) found that patterns of nest attendance (incubation constancy) varied widely among North American waterfowl species, and that body size accounted for part of the variation. Larger-bodied waterfowl species such as King Eiders and Common Eiders, (*Somateria mollissima*) may rely more on (stored) endogenous reserves during incubation reducing the time required to feed, thereby leading to high incubation constancy (Afton and Paulus 1992). On the other hand, smaller-bodied waterfowl species have a short fasting endurance and therefore, may rely more heavily on exogenous energy sources to meet incubation requirements (Afton and Paulus 1992). King Eiders (95-99%) and Common Eiders, (96%) have higher incubation constancies and lose between 24 – 30% mass during incubation (Korshgen 1977, Kellett and Alisauskas 2000, Manlove and Hepp 2000, McGuire et al. Unpubl.). Smaller-bodied Spectacled Eider (*Somateria fishcheri*) and Common Goldeneyes (*Bucephala clangula*) had incubation constancies of 90% and 81% respectively (Mallory and Weatherhead 1993, Flint and Grand 1999). Mass loss during breeding was 26% and 7% for Spectacled Eiders and Long-tailed Ducks respectively (Flint and Grand 1999, Kellett et al. 2005). These findings suggest that smaller-bodied Long-tailed Ducks may rely more on exogenous food resources and use an income incubator strategy and larger-bodied King Eiders may rely almost exclusively on endogenous reserves during incubation suggesting they are capital incubators.

Long-tailed Ducks and King Eiders winter and breed in arctic and sub-arctic regions, migrating inland to freshwater and coastal areas during the breeding period (Alison 1976, Kellett and Alisauskas 2000, Suydam 2000, Robertson and Savard 2002, Kellett et al. 2005). Spring migration paths through marine environments suggest that ample opportunities exist for King Eiders and Long-tailed Ducks to feed and acquire endogenous nutrients needed for reproduction on freshwater breeding grounds. Incubation periods of Long-tailed Ducks and King Eiders are 26 and 23 days, respectively. Similar to most arctic-nesting waterfowl, there is likely only one breeding attempt per season; and if the first attempt fails, the nest is abandoned and/or predated (Parmelee 1967, Lamothe 1973, Pehrsson 1986, Alison 1975, Kellett and Alisauskas 1997). Incubating females often are unable to meet their own energy requirements during this period and either abandon nests in favor of their own survival or die on the nest while incubating (Deeming 2002).

The goal of this study was to compare, and describe incubation behavior and the relationship to nest success of Long-tailed Ducks and King Eiders at Karrak Lake, Nunavut. Long-tailed Ducks and King Eiders were particularly appropriate for this study as they are (1) members of the same tribe (2) migrate similar distances to reach freshwater breeding areas, (3) are exposed to the same environmental conditions on arctic breeding areas, (4) nest sympatrically at Karrak and Adventures Lakes, but (5) differ substantially in body size.

3.2.0. METHODS

3.2.1. Measuring nest attendance

Remote temperature probe (Hobo XT, Onset Computer Corporation) data recorded per nest (*n* = 55) ranged from several hours to twenty days of incubation. Temperature probes were place in wooden eggs with the thermistor sensor flush against the wooden egg to ensure the highest probability of contact with the incubating hen without protruding. Wooden eggs were staked in the center of the nest bowl, surrounded by nest eggs and covered with nest down.

Temperature was recorded at three minute intervals. Previous research using remote temperature probes found nest attendance interval recordings should not exceed 5 minutes (Hoover et al. 2004). At this northern latitude, there are 24 hours of daylight during nesting; therefore data was grouped into 60 minute intervals over this period. Incubation constancy is defined as the proportion of the incubation period spent on the nest, number of recesses as the number of departures from the nest, and recess duration as the mean length of time (minutes) for each departure (Mallory and Weatherhead 1993). Incubation constancy, number of recesses and duration of recesses were calculated daily and over the whole incubation period. Recesses and constancy of incubating females were identified as combined drop and an increase in temperature of at least 2.5 ^{0}C over two intervals (6 minutes) (modified from Hoover et al. 2004).

3.3. ANALYSIS

SAS Institute (1996) software was used to perform statistical analyses. Time periods when human disturbance may have influenced recesses were eliminated from analysis. Intervals during egg laying and latter stages of pip and hatch were also removed from analyses because it is difficult to determine recesses and incubation behaviour of females at these times (Hoover et al. 2004). To examine if incubation constancy is affected by the stage of incubation and weather, I used analysis of covariance ANCOVA (PROC GLM) to examine variation in daily incubation constancy, daily number of recesses and duration of recesses between Long-tailed Ducks and King Eiders. Daily constancy, number of recesses and duration of recesses (minutes) were dependent variables and mean daily weather variables of air temperature (^{0}C), wind speed (km/h), wind direction (0 – 360^0) and precipitation (mm/day), incubation stage (day since last egg laid) and incubation stage^2 were covariates. A squared term for stage of incubation (incubation stage^2) (Eichholz and Sedinger 1999) was included in the model to allow for nonlinear relationships between incubation constancy, number of recesses and recess duration. I also used ANCOVA to examine within-species variation of incubation constancy using the same dependent variable. I included all interactions between factor and covariates in each of these ANCOVA analyses, then removed interactions that did not explain a significant amount of variation in the dependent variables based on type III mean square errors. Values presented are means ± standard error (SE). Best approximating models for incubation constancy, recesses and duration of recesses were selected using Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002).

Success of nests with known incubation constancies was estimated using the Mayfield Logistic Regression (PROC LOGISTIC) (Hazler 2004) to investigate relationships between success, nest initiation, incubation constancy and weather variables. Best approximating models for both nest success analyses were selected using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002).

3.4.0 RESULTS

3.4.1. Incubation patterns of Long-tailed Ducks and King Eiders

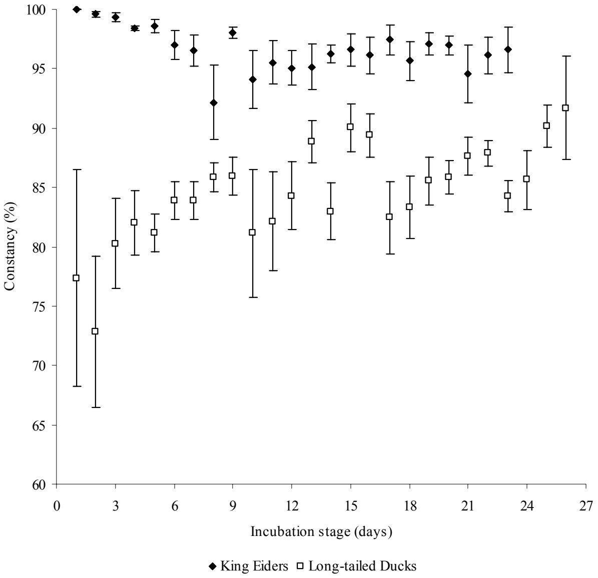
I monitored 26 King Eider and 29 Long-tailed Duck nests with hobo temperature probes for a total of 244 and 351 nest days, respectively. I had sufficient data to estimate from day 2 to day 23 of incubation for King Eiders and day 1 to day 26 of incubation for Long-tailed Ducks. During 2004 King Eider (n = 13) and Long-tailed Ducks (n = 11) nests with hobo temperature probes that successfully completed incubation had an incubation period of 23 ± 0.17 (95% C.I.) and 26 ± 0.69 (95% C.I.) respectively.

During the 2004 breeding season neither dates of arrival nor nest initiation dates differed between species. Incubation constancy ($F_{1,597} = 232.5$, $P < 0.0001$), number of recesses/day ($F_{1,2869} = 166.31$, $P < 0.0001$) and recess duration, minutes/recess, ($F_{1,2869} = 14.26$, $P < 0.0002$) differed significantly between the two species (Figures 3.1, 3.2).

Incubation constancy and recess models that included incubation stage^2 and species had the lowest AIC_c values explaining 63% and 89%, respectively of the variation found in incubation patterns of Long-tailed Ducks and King Eiders ($AIC_c < 2$; Burnham and Anderson 1992; Table 3.1, 3.2). AIC_c model results showed a non-linear relationship between incubation stage, incubation constancy and number of recesses. As incubation progressed, King Eider daily constancy decreased and number of recesses increased (Figure 3.1, 3.2). Long-tailed Duck incubation constancy and the number of recesses increased as incubation progressed. However, the duration of recesses taken by Long-tailed Ducks decreased as hatch approached (Figure 3.2). Models with the lowest AIC_c values for recess duration explained 54% of the variation and showed a linear relationship between incubation stage and recess duration (Table 3.3).

Although Long-tailed Duck incubation constancy and the number of recesses varied over time, recess duration constantly decreased as incubation progressed (Figure 3.1, 3.2). During mid incubation King Eiders and Long-tailed Ducks decreased their daily incubation constancy. This decrease appeared to coincide with changes in weather, specifically a decrease in ambient temperature. However, none of the best fit AIC_c models for each of the response variables included weather variables. Instead variation in each of incubation constancy, number of recesses and recess duration was more a function of the stage of incubation than it was daily weather. Between day 1 and day 26 of incubation Long-tailed Ducks spent 84.4 % ± 0.8 (range 72.8 – 91.7%) incubating clutches (Figure 3.1). One monitored nest included a recess of 12 hours. Allison (1979) described a recess of several days, and therefore this 12-hour recess was not removed from the analysis. King Eiders spent 96.1% ± 0.4 (range 92.2 – 100%) of the day incubating between day 2 and 23 (Figure 3.1). Incubating Long-tailed Ducks took 3.1 ± 0.04 and King Eiders took 2.0 ± 0.06 recesses per day (Figure 3.2). Recesses from incubation by Long-tailed Ducks and King Eiders lasted 26.6 ± 0.3 and 23.7 ± 0.7 minutes, respectively (Figure 3.2). Forty-four percent of variation in daily incubation constancy was among individual King Eider hens ($F_{25,243} = 6.4$, $P < 0.0001$), as was 26% of variation in daily number of recess ($F_{24,523} = 6.5$, $P < 0.0001$), and 15% of variation in recesses duration ($F_{24,519} = 3.7$, $P < 0.0001$). Similarly, much of the variation, 32%, in daily incubation constancy was among Long-tailed Duck females ($F_{29, 346} = 5.0$ $P < 0.0001$). Only 8% of variation in daily number of recess ($F_{29, 2350} = 8.3$, $P < 0.0001$), and 6% of variation in recess duration ($F_{28, 2350} = 6.5$, $P < 0.0001$) was among individual Long-tailed Duck females.

Figure 3.1. Daily percent (mean ± SE) of time spent incubating, constancy, by female King Eiders and Long-tailed Ducks over the incubation period at Karrak and Adventure Lakes, Nunavut 2004. Sample size (*n*) of observed nests were grouped into 4 day intervals during the incubation stage.



				Legend			
Species	0 - 3	4 - 7	8 - 11	12 - 15	16 - 19	20 - 23	24 - 27
King Eiders *n*	9	24	44	53	56	58	0
Long-tailed Ducks *n*	15	47	62	65	63	62	30

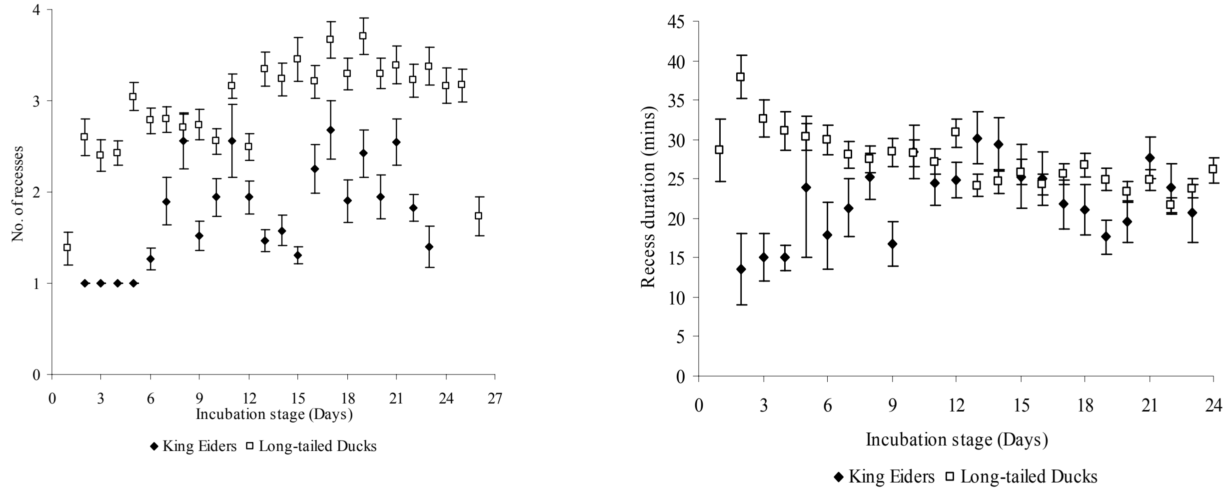
Table 3.1. Akaike's Information Criterion (AIC_c) values for four candidate models for variation in daily incubation constancy (% of day) in Long-tailed Ducks and King Eiders (*n* = 1127) at Karrak and Adventure Lake, Nunavut, Canada in 2004. Models were based on ANCOVA with daily constancy (%), daily recess and duration of recesses as the dependent variables and species, number of incubation days (days), incubation stage (inc), incubation stage^2 (incsq) and mean weather variables per day of temperature ^{0}C (temp), precipitation mm/day (ppt), wind direction 0 - 360^0 (wdir) and wind speed km/hour (wsp) as the independent variables. AIC_c model weight (w_i^c) reflects the relative support of each model given the model set and sum to one; *k* is the number of parameters (* indicate an interaction).

Model	RSS^b	K^a	AIC_c	ΔAIC_c	w_i^c
species inc incsq species*inc species*incsq	39070	10	4016.3	0.0	0.63
species inc species*inc	39320	7	4017.4	1.2	0.37
species inc species*inc temp ppt wdir wsp	39055	11	4017.9	1.6	0.28
Global	38758	19	4025.7	9.0	0.01

^{a} = Number of parameters
^{b} = Residual sum of squares
^{c} = Model weight

Figure 3.2. Mean number of recesses (± SE) and recess duration (minutes) taken by Long-tailed Ducks and King Eiders at Karrak and Adventure Lakes, Nunavut 2004 a) recesses b) duration

during the 2004 breeding season. Sample size (*n*) of observed nests were grouped into 4 day intervals during the incubation stage.



a) b)

			Legend				
Species	0 - 3	4 - 7	8 - 11	12 - 15	16 - 19	20 - 23	24 - 27
King Eiders *n*	9	24	44	53	56	58	0
Long-tailed Ducks *n*	15	47	62	65	63	62	30

Table 3.2. Akaike's Information Criterion (AIC_c) values for five candidate models for variation in number of incubation recesses/day by female Long-tailed Ducks and King Eiders (*n* = 2871) at Karrak and Adventure Lake, Nunavut, Canada in 2004. Models were based on ANCOVA with number of daily recesses as the dependent variable and species, number of incubation days (days), incubation stage (inc), incubation stage^2 (incsq) mean weather variables per day of temperature ^{0}C (temp), precipitation mm/day (ppt), wind direction 0 - 360^0 (wdir) and wind speed km/hour (wsp) as the independent variables. AIC_c model weight (w_i^c) reflects the relative support of each model given the model set and sum to one; *k* is the number of parameters (* indicate an interaction).

Model	RSS^b	K^a	AIC_c	ΔAIC_c	w_i^c
species inc incsq species*inc species*incsq	8279	10	3060.7	0.0	0.89
species inc species*inc temp ppt wdir wsp	8289	11	3066.0	5.3	0.06
Global	8244	19	3066.7	5.9	0.05
species inc	8336	5	3070.4	9.7	0.01
species ppt species*ppt	8455	7	3115.1	54.4	0.00

Table 3.3. Akaike's Information Criterion (AIC_c) values for five candidate models for variation in recess duration (minutes) in female Long-tailed Ducks and King Eiders (*n* = 2871) at Karrak and Adventure Lake, Nunavut, Canada in 2004. Models were based on ANCOVA with number of daily recesses as the dependent variable and species, number of incubation days (days), incubation stage (inc), incubation stage^2 (incsq) and mean weather variables per day of temperature ^{0}C (temp), precipitation mm/day (ppt), wind direction 0 - 360^0 (wdir) and wind speed km/hour (wsp) as the independent variables. AIC_c model weight (w_i^c) reflects the relative support of each model given the model set and sum to one; *k* is the number of parameters (* indicate an interaction).

Model	RSS^b	K^a	AIC_c	ΔAIC_c	w_i^c
species incstage species*incstage	736185	5	15934.9	0.0	0.54
species inc incsq species*inc species*incsq	733702	10	15935.3	0.4	0.45
species incstage species*incstage temp ppt wdir wsp	734987	11	15942.3	7.4	0.01
Global	733109	19	15951.2	16.2	0.00
species temp species*temp	747570	7	15983.0	48.1	0.00

3.4.2. Nest Success Model Selection

Mayfield Logistic Regression (Hazler 2004) and best fit AIC_c models (Burnham and Anderson 2002) suggest relationships between nest success, incubation constancy and weather variables were present during the 2004 breeding season. Models of Long-tailed Duck nest success explained 20% of variation with support for various factors influencing nest success such as incubation constancy, nest initiation date, incubation stage, and weather variables of temperature, precipitation, wind speed and wind direction (Table 3.4). This suggested that weather conditions and incubation constancy are good predictors of nest success for Long-tailed Ducks. Models of King Eider nest success found that variation was not explained by incubation constancy or weather, but rather by incubation stage (Table 3.4). Incubation stage of King Eiders explained only 5% of nest success variation, suggesting that other variables unaccounted for in this study such as body condition and/or available endogenous and exogenous nutrients may be better predictors of nest success. These results suggested that incubation constancy, incubation stage and weather variables are strong predictors of nest success for Long-tailed Ducks but not for King Eiders.

Table 3.4. Akaike's Information Criterion (AIC_c) values for the top three of fifty-one candidate models explaining nest success in Long-tailed Ducks and King Eiders at Karrak and Adventure Lakes, Nunavut, Canada in 2004. Models were based on Mayfield Logistic regression with nest success as the dependent variable and daily incubation constancy (const), number of incubation days (days) (Long-tailed Ducks *n* = 347, King Eiders *n* = 244), nest initiation date (nid) incubation stage (incstage) and mean weather variables per day of temperature ^{0}C (temp), precipitation mm/day (ppt), wind direction 0 - 360^0 (wdir) and wind speed km/hour (wsp) as the independent variables. AIC_c model weight (w_i^c) reflects the relative support of each model given the model set and sum to one; *k* is the number of parameters (* indicates an interaction).

Species	Model	K^a	AIC_c	ΔAIC_c	w_i^c
Long-tailed Duck	const incstage nid temp ppt wsp wdir	9	187.54	0.00	0.203
	ppt*wsp	5	187.96	0.42	0.165
	ppt*wsp*wdir	6	189.53	1.99	0.075
King Eider	incstage	3	148.31	0.00	0.047
	incstage temp	4	149.90	1.60	0.021
	incstage ppt	4	150.20	1.90	0.018

^{a} = Number of parameters
^{c} = Model weight

3.5. DICUSSION

Measurement of incubation behaviour varied among individual nests of both species. As with other waterfowl species, incubating King Eiders and Long-tailed Ducks establish a pattern of daily nest attendance during incubation. Long-tailed Ducks incubation constancy increased as incubation progressed. Long-tailed Duck females took more recesses that were shorter in duration near the end of incubation. Incubation constancy declined slightly in King Eiders as incubation progressed. Incubating King Eiders maintained an incubation constancy of >~95% constancy throughout the incubation period. However, variation in both number and duration of recesses between individual incubating King Eider and Long-tailed Duck females was found. This was consistent with other bird species (Kendiegh 1952, Skutch 1962, Warham 1990, Williams 1996). Long-tailed Duck nest attendance was similar to that described for sea ducks of similar size such as Common Goldeneyes, (81% - Mallory and Weatherhead 1999) and Spectacled Eiders (90% - Flint and Grand 1999). King Eider nest attendance at Karrak Lake was similar to that reported for nesting King Eiders in Alaska 95-99% (McGuire unpubl.) and Common Eiders 96% (Korshgen 1977, Manlove and Hepp 2000).

Weather conditions can have profound effects on incubation constancy by influencing how birds incubate, particularly in species with female-only behaviour patterns (Deeming 2002). Open-nesting birds increase attentiveness during rain, snow and fog (Hawksley 1957, Rittinghous 1961 Willis 1961, Skutch 1962, Drent 1970). Mallory and Weatherhead (1999) found that daily temperature was the main influence on incubation rhythms of Common Goldeneyes. Afton (1980) found that weather variables explained more of the components of incubation rhythm in small ducks than in larger geese and swans. Consistent with these findings, I found weather variables and incubation stage explained 28% and 6% (Table 3.1, 3.2) of the variation in incubation constancy and number of recesses of Long-tailed Ducks and King Eiders, respectively. However, weather conditions were not found to have influenced the duration of recesses. Mallory and Weatherhead (1999) suggested Common Goldeneyes may be able to spend more time off nests later in incubation when ambient temperatures are higher and Flint and Grand (1999) concluded that incubating Spectacled Eider females timed recesses to take advantage of warmer ambient temperatures. This was not consistent with incubation patterns observed in both Long-tailed Ducks and King Eiders. As incubation progressed, ambient temperatures also decreased for a time and incubation patterns suggested that incubating females adjusted incubation behavior accordingly to this change in weather (Figure 3.3).

Incubation stage is critical in determining nest attentiveness. Models for both King Eiders and Long-tailed Ducks suggested 63% of nest attentiveness was explained by incubation stage. Nest attentiveness in several waterfowl species progressively decreases as hatch approaches (Afton 1980, Aldrich and Raveling 1983, Brown and Fredickson 1987 and Yerkes 1998, Mallory and Weatherhead 1999, Eichholz and Sedinger 1999) and data generated here reveal that nest attentiveness by King Eiders followed a similar pattern. This could have resulted from depletion of (stored) nutrient reserves by King Eiders, instead relying more on exogenous nutrients to successfully complete incubation. Conversely, nest attentiveness by Long-tailed Duck did not follow this pattern and increased as hatched approached. Nest attentiveness by Long-tailed Ducks may be influenced by other factors such as reliance upon exogenous nutrients acquired daily and thereby allowing incubating females to increase attentiveness as a result of replenished available nutrients.

Considering the entire breeding cycle, the incubation period may represent a time when females, in the Mergini Tribe, have depleted remaining endogenous reserves and subsequently switched to local food sources (exogenous) to meet the metabolic requirements of incubation (Brown and Fredrickson 1987, Afton and Paulus 1992, Mallory and Weatherhead 1999). Common Goldeneyes (Mallory unpubl. data), White-winged Scoters (Brown and Fredrickson 1987) and Spectacled Eiders, all members of the Mergini Tribe, spend a portion of time feeding on exogenous nutrients during incubation recesses perhaps replenishing nutrients needed to successfully compete incubation (Mallory and Weatherhead 1999).

Results of stable carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$) isotope analysis of nutrients used for egg production of Long-tailed Ducks and King Eiders at Karrak Lake, Nunavut (Chapter 4) suggested that both species relied primarily on breeding ground nutrients for egg production. However, Long-tailed Ducks allocated more nutrients from marine and freshwater wintering grounds to egg production than King Eiders did in 2004. Stable-isotope results of eggs (Chapter 4) suggested that smaller bodied Long-tailed Ducks arrived at breeding grounds with endogenous reserves, and allocated these nutrients to egg production not incubation. Conversely, $\delta^{13}C$ and $\delta^{15}N$ values of larger bodied King Eider eggs suggested these females arrived at breeding grounds with endogenous reserves and allocated these nutrients to incubation not egg production. These results suggest differences between Long-tailed Ducks and King Eider incubation strategies may be due to allocation and use of nutrients during the breeding cycle and not body size, as previously suggested. Average incubation constancy of 98% and mass loss of 30% during incubation (Kellett and Alisauskas 2000) suggested that King Eiders relied primarily on endogenous nutrients to supply metabolic requirements for incubation. Perhaps as hatch approached, increased heat production from developing embryos simultaneously with an increase in air temperature allowed female King Eiders to reduce attentiveness and subsequently increase feeding time. This could help to meet energetic costs of successful incubation (Drent 1990 and Caldwell and Cornwell 1975). Decreases in air temperature, increases in wind speed and shifts of wind direction may have increased rates of egg cooling and influenced an increase in attentiveness in Long-tailed Ducks as incubation progressed. Long-tailed Ducks may have increased attentiveness to maintain a constant thermal environment for developing embryos. Long-tailed Ducks had an incubation constancy of 84% coupled with an incubation mass loss of 7% during incubation (Kellett et al. 2005) suggesting that Long-tailed Ducks relied largely upon exogenous nutrients to maintain metabolic requirements throughout incubation.

Results of this study are consistent with inferences of Kellett et al. (2005) that King Eiders are primarily capital incubators, while Long-tailed Ducks are primarily income incubators. These findings suggest differences between Long-tailed Duck and King Eider incubation strategies may be due to allocation and use of nutrients during the breeding cycle and not body size. Incubation rhythms described here in combination with results from stable-carbon and nitrogen of egg components suggest that both species are combining both capital and income breeding strategies to meet the high energy demands of arctic breeding.

4.0 NUTRIENT ALLOCATION IN LONG-TAILED DUCK AND KING EIDER EGGS AT KARRAK LAKE, NUNAVUT: STABLE ISOTOPE ANALYSIS OF EGG COMPONENTS

4.1 INTRODUCTION

Two main breeding strategies used by migratory birds are those of the “capital breeder”, whereby costs of breeding are met with stored energy (endogenous reserves) transported to breeding and the “income breeder”, whereby birds acquire nutritional requirements from the local diet (exogenous resources) on breeding areas (Drent and Dann 1980). Reliance on energy and nutrient reserves for reproduction is a ubiquitous adaptation by waterfowl to meet high energy demands of breeding and can be crucial to egg-laying processes essential for successful reproduction (Ankney et al. 1991, Alisauskas and Ankney 1992, Afton and Paulus 1992). Energy demands are expected to be particularly high in arctic breeding areas with lower ambient temperatures and harsh unpredictable environmental conditions compared to those in temperature areas. Thomas (1989) reviewed capital and income breeding among waterfowl (Anserinae) and confirmed that many waterfowl species use a capital breeder strategy during reproduction (Drent and Dann 1980 and Jonsson 1997). A re-examination of published data found that only 3 of 12 well-studied species showed a reliance on a capital strategy (Meijer and Drent 1999). All three species breed in cold climates and reliance ranges from 50 - 100% in the Lesser Snow Goose (*Chen caerulescens caerulescens*) and Common Eider (*Somateria mollissima*) respectively (Meijer and Drent 1999). Income and capital breeding strategies are on opposite extremes of a continuum, and several arctic-breeding species use a mixed strategy (Bonnett et al. 1998, Meijer and Drent 1999, Gauthier et al. 2003, Morrison and Hobson 2004).

Many arctic-breeding birds are long-distance migrants that require sufficient energy stores to successfully complete spring migration and then to reproduce. Klaassen (2003) suggested proportions of stores of fat (energy) and protein, required for migration and reproduction most likely differ, as typical fuel stores for migration are deficient in proteins and are not completely adequate for egg synthesis. Meijer and Drent (1999) pointed out proteins and lipids are deposited in the developing eggs, but noted that both nutrients are also required laying females for nitrogen metabolism and as an energy substrate for existence; they suggested that protein rather than fat is the limiting factor for reproduction in several species regardless of their size. Female birds of many species accumulate energy and protein before egg-laying, likely to allow egg production and/or incubation to be performed at the physiologically maximum rate (Andersson and Norberg 1981, Hedenstrom 1992). Capital and income breeding strategies represent options of energy use defined largely by foraging decisions which may have important consequences for an organism’s fitness (Andersson and Norberg 1981, Hedenstrom 1992).

The measurement of naturally occurring stable-isotopic ratios of endogenous nutrients, egg macronutrients and local diet as a means of tracing nutrient allocation to reproduction in birds has been used as an alternative to more conventional methods (Hobson 1995). This approach relies on isotopic differences between endogenous and exogenous sources of nutrients to laying females (Hobson et al. 2004). Stable-isotopic ratios of avian egg components can provide dietary information and permit inferences about contributions of endogenous and exogenous nutrient sources from differing habitats such as, marine or freshwater systems (Hobson 1995, Hobson et al.1997, Hobson et al. 2000, Morrison and Hobson 2004, Hobson et al. 2004). Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are typically enriched in marine versus freshwater systems and these isotopic signatures are incorporated by consumers (Braune et al. 2005). Stable-carbon and nitrogen isotopic analyses of avian eggs are particularly amenable because nutrients required for egg production are either derived from nutrient reserves or directly from the diet of laying females (Hobson et al. 1997).

Research by Gauthier et al. (2003) provided evidence that Greater Snow Geese (*Chen caerulescens atlantica*) used a mixed breeding strategy, of both endogenous and exogenous resource use for reproduction, contrary to earlier suggestions (Ryder 1970, Ankney and MacInnes 1978, McLandress and Raveling 1981) that arctic-nesting geese relied almost solely on endogenous reserves brought with them to the breeding grounds for reproduction. The $\delta^{13}C$ and $\delta^{15}N$ signatures from Gauthier et al. (2003) support findings of intense feeding activities on breeding grounds by pre-laying and laying arctic-nesting geese (Gauthier and Tardif 1991, Prop and deVries 1993, Ganter and Cooke 1996, Carriere et al. 1999). Hobson et al. (2004) used stable-carbon and deuterium to investigate nutrients allocated by female migratory Redhead Ducks (*Aythya americana*) to egg production, and found that females relied mainly on exogenous dietary lipids and proteins for egg production, and endogenous reserves to satisfy body maintenance and energy requirements. Investigations of nutrient allocation to egg production using stable-carbon and nitrogen, in arctic-nesting shorebirds revealed that first-laid eggs of a clutch in some species contain endogenous nutrients and that later laid eggs of the same clutch contain exogenous nutrients (Morrison and Hobson 2004). Bond (2005) investigated exogenous versus endogenous nutrient allocation in Harlequin Ducks and found that females allocated nutrients from freshwater breeding areas to egg production. Results of these studies provide support of mixed breeding strategies, where birds relied on both exogenous and endogenous nutrients (Morrison and Hobson 2004).

Long-tailed Ducks (*Clangula hyemalis*) and King Eiders (*Somateria spectabilis*) winter and breed in arctic and subarctic regions, coming inland to freshwater and coastal areas during the nesting period (Alison 1976, Kellett and Alisauskas 2000, Suydam 2000, Robertson and Savard 2002, Kellett et al. 2005). Both species are predominantly carnivorous. On freshwater breeding grounds they feed on larval and adult aquatic insects (chironmids, trichopterans and larval dipterans), crustaceans (amphipods, fairy and brine (*Polyartemia* spp) shrimp and tadpole shrimp), cladocerans (*Eurycercus lametllatus*), fish roe and some vegetable matter (Cottam 1939, Taylor 1986, Pehrsson and Nyström 1988, Kondratyev 1999, Robertson and Savard 2002 and Suydam 2000). In marine wintering habitats these species feed on epibenthic crustaceans, mollusks, amphipods, mysids, isopods and in some areas bivalves, barnacles, sea anemone, insects, gastropods, brine and fairy shrimp, fish, fish eggs, tubiolous and nereid worms, algae and some plant matter. Long-tailed ducks are found wintering in freshwater habitats, such as the Great Lakes, where their diet consists of amphipods, fish and mollusks (Peterson and Ellarson 1977) and/or Olgochaete worms (Rofritz 1977).

During spring migration to breeding grounds, most Long-tailed Ducks fly within 2km of the coast along shore leads, adjacent to mainland and barrier islands over lagoon ice (Johnson 1985), though offshore migration following open ice leads does occur (Richardson and Johnson 1981, Johnson and Richardson 1982). When ice cover is extensive, birds will migrate over land (Woodby and Divoky 1982). King Eiders migrate over frozen sea, often following open sea ice leads or polynas to get to freshwater breeding areas (Suydam 2000). Spring migration paths through marine environments suggest that ample opportunities exist for King Eiders and Long-tailed Ducks to feed and acquire endogenous stores that could be used for reproduction on freshwater breeding grounds.

Incubating female King and Common Eiders on average lose 30% of pre-incubation body mass during incubation (Parker and Holm 1990, Kellett and Alisauskas 2000) and maintain 95 – 99% daily incubation constancy (Chapter 3, McGuire et al. Unpubl.) suggesting a capital strategy during incubation. Conversely, arctic-nesting Long-tailed Ducks lost ~13% carcass weight between early incubation and brood rearing (Peterson and Ellarson 1979), 7% of pre-incubation body mass during incubation (Kellett et al. 2005) and maintain a daily incubation constancy of 84% (Chapter 3). Long-tailed Ducks acquire considerable protein and fat stores before spring migration (Peterson and Ellarson 1979, Leafloor et al. 1996), but Peterson and Ellarson (1979) found that breeding females lost 69% of fat reserves during the egg-laying period, leaving only 6% of fat at the start of incubation. This suggests Long-tailed Ducks have an income strategy during incubation. However, little information is known about nutrient allocation to egg production in either Long-tailed Ducks or King Eiders.

Capital breeders are typically larger-bodied birds whose body size may be advantageous for storage of sufficient endogenous reserves from wintering grounds required for reproduction on breeding grounds (Drent and Daan 1980). King Eiders are large-bodied birds, and thus may be better adapted to acquiring endogenous reserves required for migration and reproduction. In contrast, Long-tailed Ducks may be limited by small body size from acquiring enough endogenous reserves to fuel migration and meet subsequent energetic demands of reproduction. Therefore, Long-tailed Ducks may rely upon exogenous resources for reproduction. I predicted that King Eiders allocated most if not all endogenous reserves to egg production and Long-tailed Ducks allocated exclusively exogenous resources to egg production.

To test this hypothesis, I collected eggs of Long-tailed Ducks and King Eiders for stable carbon and nitrogen ($\delta^{13}C$ and $\delta^{13}N$, respectively) isotope analysis at three inland freshwater lakes in the Central Canadian Arctic. I collected potential diet items, hereafter referred to as diet items, at Karrak and Adventure Lakes for $\delta^{13}C$ and $\delta^{13}N$ analysis and obtained $\delta^{13}C$ and $\delta^{13}N$ values from published and unpublished sources of diet items from known marine and freshwater wintering areas. These species were particularly appropriate for this study as they are (1) members of the same tribe (2) exposed to the same environmental conditions on wintering and breeding areas, (3) share similar feeding ecology, (4) migrate similar distances to reach freshwater breeding areas, and (5) nest sympatrically at Karrak, Adventure and Simpson lakes.

4.2. METHODS

As laying order was undeterminable egg component (albumen, yolk protein, whole yolk and yolk lipid) $\delta^{15}N$ and $\delta^{13}C$ values from the same nest were averaged to investigate contribution of exogenous versus endogenous nutrient allocation on a per nest basis. Egg component δ^{15}N and δ^{13}C values hereafter refer to the mean δ^{15}N and δ^{13}C values of each nest sampled. Egg components of twenty-nine Long-tailed Duck and forty-four King Eider nests were used in the δ^{15}N and δ^{13}C stable isotope analysis and the multi-source diet mixing model.

4.2.1. Yolk Lipid Values

As yolk lipids were not directly analyzed for δ^{13}C and δ^{15}N, derived yolk lipid δ^{13}C values, hereafter referred to as yolk lipids, for each individual egg was obtained using the below calculation. Due to high discrimination factors and low δ^{15}N values of whole yolk and yolk protein only yolk lipid δ^{13}C values could be calculated.

$$\text{Yolk lipid } \delta^{13}\text{C} = \frac{(\delta^{13}\text{C Whole yolk } - (\delta^{13}\text{ C Yolk protein}^{*}\text{ E}))}{\text{L}} \qquad (4.1)$$

Lipid proportion (L) is the calculated proportion of lipids in whole dry yolk and protein proportion (E) is the calculated proportion of protein in dry whole yolk. Protein proportion e (E) was calculated by subtracting L from 1.00. Lipid proportion (L) was obtained from Table 1.7 in Burley and Vadhehra (1989). Since the lipid and protein proportions of Long-tailed Duck and King Eider egg components is unknown average lipid proportion (L) of the Northern Gannet (*Morus bassanus*), Brown Pelican (*Pelecanus occidentalis*) and Herring Gull (*Larus argentatus*) were used (Burley and Vadhehra 1989). These species share a carnivorous diet similar to Long-tailed Ducks and King Eiders (Mowbray 2002, Sheilds 2002, Pierotti and Good 1994). It was reasonable to assume that egg yolk lipid and protein proportions from these species would reflect those of King Eiders and Long-tailed Ducks. Lipid proportion (L) used was 0.638, and protein value (E) was then 0.362 (1-0.638).

4.3. ANALYSIS

4.3.1. General Linear Models

SAS Institute (1996) was used to perform statistical analysis of egg components and lake effects. Differences between species', and egg component samples (albumen, whole yolk, lipid-free yolk, and yolk lipids) were evaluated using a multivariate analysis of variance, MANOVA, (PROC GLM) with post-hoc Tukey Studentized tests. I tested for an effect among Karrak, Adventure and Simpson Lakes using a general linear model (PROC GLM). Five King Eider eggs where lake assignment was unknown were excluded from lake effect analysis. I used a general linear model (PROC GLM) to test for differences between 1) wintering, marine and freshwater, and breeding ground diet items $\delta^{13}C$ and $\delta^{15}N$ values and 2) egg components and wintering, marine and freshwater, and breeding diet items $\delta^{13}C$ and $\delta^{15}N$ values. Diet item $\delta^{13}C$ and $\delta^{15}N$ values used in analyses were corrected for discrimination using the carnivore model (Hobson 1995, Gauthier et al. 2003).

4.3.2. Multi-source Diet Mixing Model

Isosource is a multi-source mixing model developed by Phillips and Gregg (2003) that uses isotopic ratios to estimate the proportional contribution of various sources to *n*, in this study *n* are eggs and sources are diet items. The proportion of contributions of *n* + 1 different sources can be uniquely determined by the use of *n* different isotope tracers ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$) with linear mixing models based on mass balance equations (Phillips and Gregg 2003). The Isosource (Phillips and Gregg 2003) approach relies on an iterative model that considers all possible solutions to the measured mean consumer's tissue isotope values and the mean values of the potential food endpoints (Phillips and Gregg 2003). The observer chooses the appropriate tissue-diet discrimination factors, the tolerance permitted about the mean consumer tissue values, and the interval increment (in $^{o}/_{oo}$) for the model (Phillips and Gregg 2003). I used Isosource (Phillips and Gregg 2003) to estimate the proportional contributions of wintering and breeding ground diet items to eggs. As King Eiders and Long-tailed Ducks are carnivorous I applied carnivore model (Hobson 1995) discrimination values to diet items. Discrimination values were applied so 1) $\delta^{13}C$ and $\delta^{15}N$ signatures from diet items and egg components could be compared, and 2) to investigate allocation of diet items to egg components of Long-tailed Ducks and King Eiders. Diet items were grouped based on wintering ground (marine and freshwater) and breeding ground biomes, trophic guild, taxon and overlapping means and standard deviations (Phillips and Gregg 2005). Grouping allows inferences about the importance of diet items (Phillips and Gregg 2005) to consumer's tissues. Egg components (albumen, yolk protein and whole yolk) of each species and diet groups (see Table 4.3) mean low and high endpoints $\delta^{13}C$ and $\delta^{15}N$ values were run separately in Isosource. These mean endpoints represented the range of $\delta^{13}C$ and $\delta^{15}N$ diet values found on the wintering and breeding grounds. As I only had $\delta^{13}C$ values of yolk lipids I ran Isosource using $\delta^{13}C$ values for this egg component and diet groups. King Eiders do not winter in freshwater areas as Long-tailed Ducks do, therefore diet groups from these areas (Table 4.3 : groups 5 and 6), were excluded from the King Eider diet mixing model.

4.3.0. RESULTS

4.3.1. Stable-isotope Ratios of Egg Components

Stable-isotope ratios in egg components - Values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of all egg components (albumen, whole yolk, yolk protein yolk lipids) did not differ significantly between Long-tailed Ducks and King Eiders (MANOVA $F_{7,60} = 1.75$ $P > 0.11$) (Figure 4.1 and 4.2).

Carbon-13 - Long-tailed Duck egg component $\delta^{13}C$ values had a wider variation than those of King Eiders (Table 4.1). Long-tailed Duck $\delta^{13}C$ values showed both depleted and enriched $\delta^{13}C$ values. Enriched $\delta^{13}C$ values suggested close associations with $\delta^{13}C$ values from marine wintering grounds and depleted $\delta^{13}C$ values such as those $\leq$ - 29.0 $^{0}/_{00}$ indicated close association with freshwater wintering areas. These $\delta^{13}C$ values indicated some Long-tailed Duck females allocated nutrients from wintering grounds to eggs. King Eider egg component $\delta^{13}C$ values indicated close associations with freshwater breeding grounds. These results suggested King Eiders allocated primarily nutrients to eggs from the breeding grounds.

Nitrogen-15 –The $\delta^{15}N$ values between wintering and breeding grounds were highly variable and close associations between egg components and these areas were not as defined as $\delta^{13}C$ values. $\delta^{15}N$ values of egg components of Long-tailed Duck and King Eiders showed associations to diet source $\delta^{15}N$ values from breeding grounds. Egg component and diet source $\delta^{15}N$ values of this study were similar to shorebird and diet item $\delta^{15}N$ values of high arctic terrestrial areas (Morrison and Hobson 2004).

Table 4.1. Stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) analysis (mean ± SD ($^{o}/_{oo}$), [*n*] and range) of egg components of Long-tailed Ducks and King Eiders. Tukey's studentized post-hoc multiple comparison results indicated egg components did not differ significantly.

		Long-tailed Duck			**King Eider**		
Tissue		*n*	Mean ($^{0}/_{00}$)	Range ($^{0}/_{00}$)	*n*	Mean ($^{0}/_{00}$)	Range ($^{0}/_{00}$)
Albumen	$\delta^{15}N$	*29*	8.49 ± 1.30	5.35 to 11.80	*39*	8.84 ± 1.14	6.39 to 11.94
	$\delta^{13}C$	*29*	-20.95 ± 1.94	-16.72 to -25.27	*39*	-21.19 ± 1.49	-18.01 to -23.67
Yolk Protein	$\delta^{15}N$	*29*	9.74 ± 1.42	6.33 to 13.03	*44*	9.84 ± 1.11	7.03 to 14.00
	$\delta^{13}C$	*29*	-23.64 ± 2.03	-19.39 to -29.27	*44*	-23.78 ± 1.23	-20.57 to -26.62
Whole Yolk	$\delta^{15}N$	*29*	9.53 ± 1.72	5.51 to 14.66	*44*	9.31 ± 1.29	6.67 to 12.67
	$\delta^{13}C$	*29*	-24.31 ± 2.36[a]	-18.20 to -30.94	*44*	-24.86 ± 1.12	-21.32 to -26.67
Yolk lipids	$\delta^{13}C$	*29*	-25.85 ± 2.50	-19.35 to -32.90	*44*	-26.43 ± 1.19	-22.67 to -28.36

Figure 4.1. Stable-carbon (δ^{13}C) and nitrogen (δ^{15}N) values of Long-tailed Duck (n = 29) and King Eider (n = 44) egg components a) albumen b) yolk protein c) whole yolk collected at Simpson, Karrak and Adventure Lakes, Nunavut 2004. Sold circles are King Eiders and empty circles are Long-tailed Ducks.

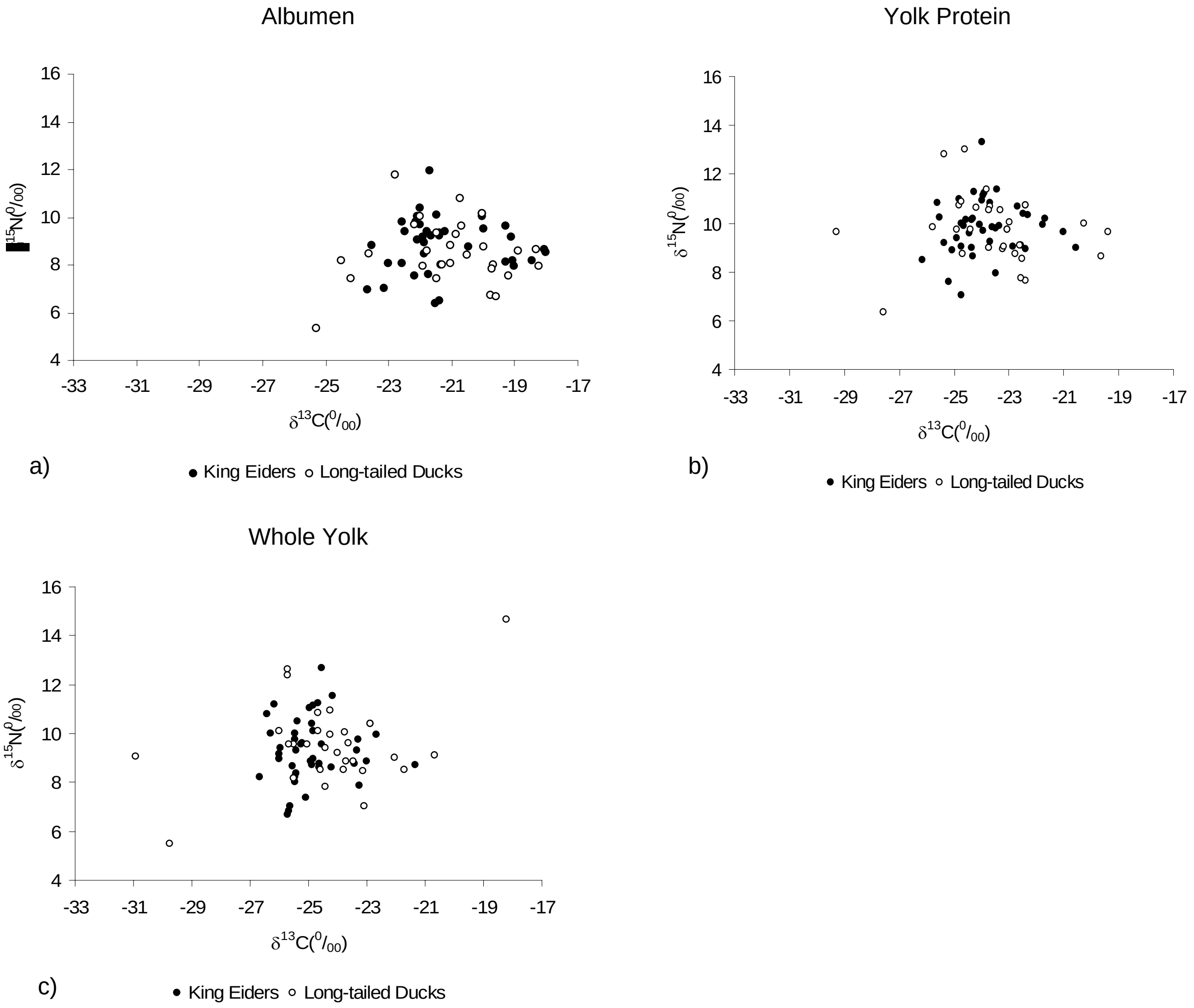
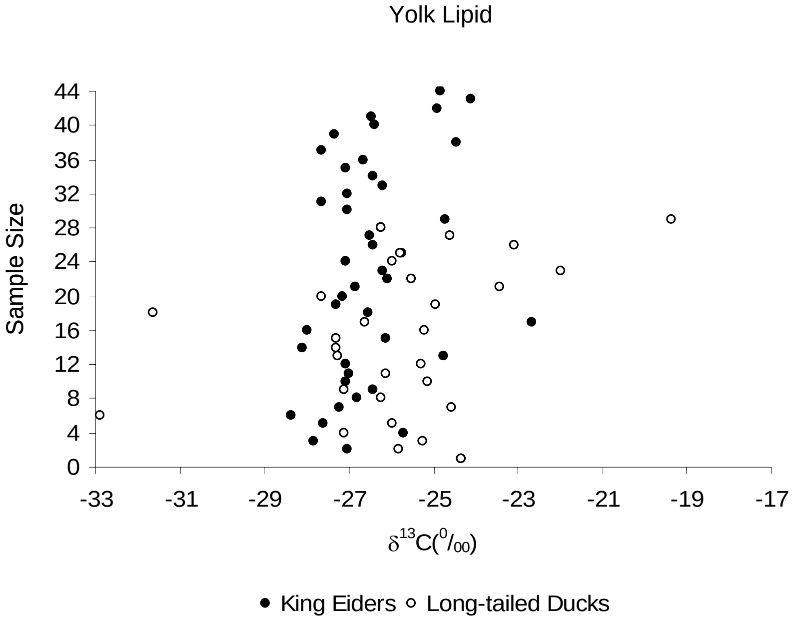


Figure 4.2. Stable-carbon ($\delta^{13}C$) values of Long-tailed Duck (*n* = 29) and King Eider (*n* = 44) yolk lipid collected at Simpson, Karrak and Adventure Lakes, Nunavut 2004. Solid circles are King Eiders and empty circles are Long-tailed Ducks.



4.3.2 Lake Effects

Lake Effects (Carbon-13) – The $\delta^{13}C$ values of nest albumen ($F_{3,65} = 4.71$, $P < 0.01$) and yolk protein ($F_{3,69} = 4.57$, $P < 0.01$) showed significant differences between the three lakes. However, Tukey Post-hoc Studentized tests found only a difference between albumen and yolk protein $\delta^{13}C$ values of Simpson and Adventure Lakes. Yolk protein and albumen $\delta^{13}C$ values of both species in Simpson Lake were depleted in $\delta^{13}C$ compared to $\delta^{13}C$ values of eggs from Adventure Lake. This result suggests that birds nesting at Adventure Lake allocated more carbon enriched nutrients into albumen.

Lake Effects (Nitrogen-15) - The δ^{15} N values of all egg components were not significantly different between the three lakes. No differences in δ^{15} N values were found between egg components of Long-tailed Ducks and King Eiders.

4.3.3. Stable-isotope Ratios in Diet items

Stable-isotope ratios in diet items – The $\delta^{13}C$ signatures from wintering grounds, marine and freshwater, and my study site, a freshwater breeding ground, were significantly different

(ANOVA $F_{5,103}$ = 5.54, $P < 0.0002$) (Figure 4.4 and 4.6). The $\delta^{13}C$ signatures of marine wintering grounds were enriched in carbon, while diet items from freshwater areas were depleted in carbon. Freshwater diet items from the breeding ground were more enriched in $\delta^{13}C$ than those diet items from freshwater winter grounds. There is some overlap between the $\delta^{13}C$ values of fish and shrimp found on freshwater wintering grounds (Table 4.3, Group 5) and freshwater copepods collected at Karrak and Adventure Lakes (Table 4.3, Group 4). Overlapping $\delta^{13}C$ values between these two species could be attributed to their associated trophic position in the ecosystems. The overlap is only applicable to Long-tailed Ducks as King Eiders do not winter in freshwater areas.

Stable-isotope ratios in diet items (Nitrogen -15) - The $\delta^{15}N$ signatures from diet groups on wintering grounds and breeding grounds were different ($F_{5,96}$ = 10.22, $P < 0.0001$) (Figure 4.4). δ^{15} N signatures of diet items in wintering grounds, marine and freshwater, were generally enriched compared to breeding ground diet items.

4.3.4. Stable-isotope Ratios of Diet items and Egg Components

Stable-isotope ratios egg components and diet items (Carbon-13) - $\delta^{13}C$ values of egg components (albumen, yolk protein, whole yolk and yolk lipids) of Long-tailed Ducks and King Eider were significantly different from marine diet items ($F_{\text{albumen } 2,142}$ = 54.9, $P < 0.0001$; $F_{\text{yolk protein } 2,146}$ = 316.2, $P < 0.0001$; $F_{\text{whole yolk } 2,146}$ = 353.4, $P < 0.0001$; $F_{\text{yolk lipid } 2,146}$ = 296.5, $P < 0.0001$) (Figure 4.5 and 4.7). Long-tailed Duck $\delta^{13}C$ values of albumen, yolk protein, and whole yolk were significantly different from freshwater winter ground diet items ($F_{\text{albumen } 1,47}$ = 45.7 $P < 0.0001$; $F_{\text{yolk protein } 1,47}$ = 20.9, $P < 0.0001$; $F_{\text{whole yolk } 1,47}$ = 36.6, $P < 0.0001$; $F_{\text{yolk lipid } 1,47}$ = 31.9, $P < 0.0001$). $\delta^{13}C$ values of albumen, yolk protein, whole yolk and yolk lipids of Long-tailed Ducks and King Eider did not differ significantly from breeding diet items, suggesting nutrients allocated to egg production are being acquired on breeding grounds.

Stable-isotope ratios egg components and diet items (Nitrogen - 15) – The $\delta^{15}N$ values of albumen, yolk protein, and whole yolk of Long-tailed Ducks and King Eider were significantly different from marine diet items ($F_{\text{albumen } 2,142}$ = 118.5, $P < 0.0001$; $F_{\text{yolk protein } 2,146}$ = 91.4, $P < 0.0001$; $F_{\text{whole yolk } 2,146}$ = 92.9, $P < 0.0001$) (Figure 4.5). $\delta^{15}N$ values of albumen, yolk protein, and whole yolk of Long-tailed Ducks were significantly different from freshwater winter ground diet items ($F_{\text{albumen } 1,47}$ = 24.6, $P < 0.0001$; $F_{\text{yolk protein } 1,47}$ = 13.8, $P < 0.0008$; $F_{\text{whole yolk } 1,47}$ = 11.8, $P <$

0.001). $\delta^{15}N$ values of albumen, yolk protein, and whole yolk of Long-tailed Ducks and King Eider did not differ significantly from breeding diet items.

4.3.5. Multi-source Diet Mixing Model

The range and mean of each diet group contribution to each egg component was reported because only reporting the mean misrepresents the unique results of the mixing model (Phillips and Gregg 2003). Results from the Isosource mixing model (Phillips and Gregg 2003) (Table 4.3) suggested freshwater diet items contributed the largest portion of nutrients to egg components. As calculated by Isosource, Long-tailed Ducks (*n* = 55) relied significantly on diet breeding ground group 3, for production of albumen, yolk protein and whole yolk. While King Eiders appear to rely on diet breeding ground group 3 for albumen (*n* = 70) and whole yolk production (*n* = 76), but relied equally on breeding ground groups 3 and 4, for yolk protein (*n* = 76). Isosource calculations suggested that both species relied more on wintering ground diet items than those on breeding grounds for yolk lipids. However, Long-tailed Ducks appear to allocate proportionally larger amounts of wintering ground nutrients to yolk lipids than King Eiders. These results support the wide variation of $\delta^{13}C$ and $\delta^{15}N$ values from wintering and breeding ground areas, seen in egg components of Long-tailed Ducks. King Eider egg component $\delta^{13}C$ and $\delta^{15}N$ values were predominantly associated with breeding ground values and Isosource calculations support those findings.

Table 4.2. Stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (means ± SD $^{0}/_{00}$) of diet items from wintering grounds (marine and freshwater) and breeding grounds. Wintering ground diet items were obtained from literature.

	n	**$\delta^{13}C$**	**$\delta^{15}N$**	**Source**
Wintering Grounds: Marine				
Bivalves	162	-18.1 ± 1.6	10.16 ± 1.6	*Haramis et al. 2001, Hobson et al. 1994, Morrison and Hobson 2004, Lovvorn et al. 2005, Hobson et al. 2004, Ben-David et al. 1997, Hobson et al. 1998, Fry 1998*
Aneome	1	-17.3	7.0	*Fry 1988*
American plaice	1	-16.7	12.9	*Fry 1988*
Cheatnognaths	4	-21.1	14.7	*Lovvorn et al. 2005,*
Echinoderms	53	-15.3 ± 3.9	11.2 ± 3.8	*Hobson et al. 2004, Lovvorn et al. 2005,*
Flounder	1	-16.1	12.0	*Fry 1988*
Herrring	10	-19.0 ± 2.7	12.35 ± 1.6	*Chisholm 1986, Fry 1988, Hobson et al. 1994*
Polycheates	21	-18.0 ± 1.5	12.7 ± 2.6	*Fry 1988, Haramis et al. 2001, Hobson et al. 2004, Lovvorn et al. 2005*
Sculpin	1	-16.6	12.4	*Fry 1988*
Sand Lance	9	-18.4 ± 0.6	12.25 ± 2.9	*Fry 1988,Hobson 1990*
sea worms & sea squirts	8	-19.3 ± 2.8	14.1 ± 4.1	*Fry 1988, Hobson et al. 2004, Lovvorn et al. 2005*
Gastropoda	52	-16.4 ± 3.4	10.82 ± 2.1	*Hobson et al. 1998, Hobson et al. 2004, Lovvorn et al. 2005, Bond 2005*
Crustaceans	362	-18.3 ± 3.1	9.84 ± 1.8	*Fry 1988, Hobson and Sealy 1991, Hobson and Welch 1992, Ben-David et al. 1997*, Hobson et al. 1998, Haramis et al. 2001, Morrison and Hobson 2004, Lovvorn et al. 2005, Bond 2005*
Arctic Cod	1	-20	10.8	*Hobson et al. 2004*
Wintering Grounds: Freshwater				
Alewife	2	-23.2 ± 0.3	11.1 ± 2.7	*Hebert et al. 1999*
Herring	1	-26.2	7.8	*Keough et al. 1996*
Rainbow smelt	3	-24.4 ± 2.3	10.8 ± 3.5	*Hebert et al. 1999*
Carp	1	-29.7	9.3	*Keough et al. 1996*
Perch	5	-26.8 ± 4.7	10.4 ± 2.7	*Keough et al. 1996*
Shrimp	1	-26.5	5.0	*Keough et al. 1996*
Group:Chironomidae, Zooplankton	4	-30.9 ± 1.9	5.6 ± 2.0	*Keough et al. 1996, Mitchell et al. 1996**
Zebra mussel	1	-32.2 ± 0.3	11.1 ± 2.7	*Mitchell et al. 1996**
Breeding Grounds: Freshwater				
Tipulidae	10	-21.8 ± 2.2	4.5 ± 2.5	*This Study*
Chironomidae	10	-21.4 ± 0.5	3.9 ± 1.8	*This Study*
Fish:	5	-23.7 ± 1.3	8.6 ± 1.3	*This Study*
Haliplidae	13	-19.9 ± 0.9	4.5 ± 1.4	*This Study*
Eubranchiopoda	11	-22.0 ± 1.3	5.2 ± 1.2	*This Study*
Copepoda	2	-25.7 ± 0.1	8.0 ± 0.2	*This Study*

* These studies did not remove lipids from potential food sources. Not removing lipids can show a depletion $\delta^{13}C$ value of -2 $^{0}/_{00.}$

Table 4.3. Diet item groups from wintering and breeding grounds used in Isosource (Phillips and Gregg 2003, Phillips and Gregg 2005).

Wintering Grounds: Marine		**Breeding Grounds: Freshwater**		**Wintering Grounds: Freshwater**	
Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Aneome	Herring	Tipulidae	Copepod	Alewife	Chironomids
American plaice	Arctic cod	Chironomids		Herring	zooplankton
Echinoderms	Cheatnognaths	Coleoptera		Rainbow smelt	Zebra mussel
Bivalves	Sea worms & Sea squirts	Fish:Ninespine stickleback & unknowns		Shrimp	
Crustaceans		Eubranchiopoda		Perch	Carp
Flounder					
Polycheates					
Sculpin					
SandLance					
Gastropods					

Figure 4.4. Stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of equivalent diet item means for each egg component: a) albumen b) whole yolk c) yolk protein. Diet items were grouped based on wintering and breeding ground, trophic guild, taxon and overlapping $\delta^{13}C$ and $\delta^{15}N$ values (Phillips and Gregg 2005).

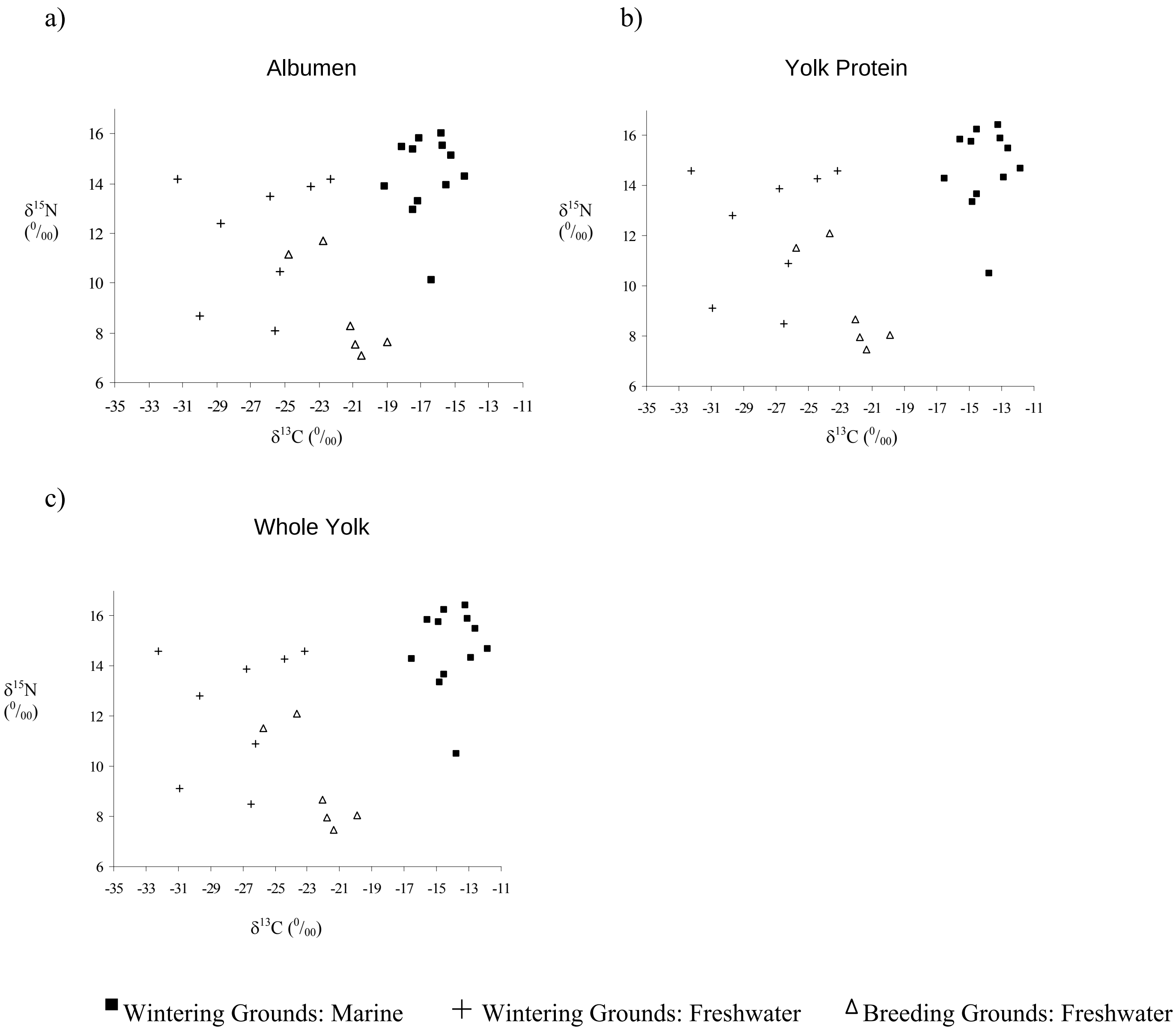


Figure 4.5. Isosource diet polygons of stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of Long-tailed Duck and King Eider egg component means and mean equivalent diet item wintering and breeding ground group $\delta^{13}C$ and $\delta^{15}N$ endpoint values. Solid diamonds are King Eiders and empty diamonds are Long-tailed Duck egg components.

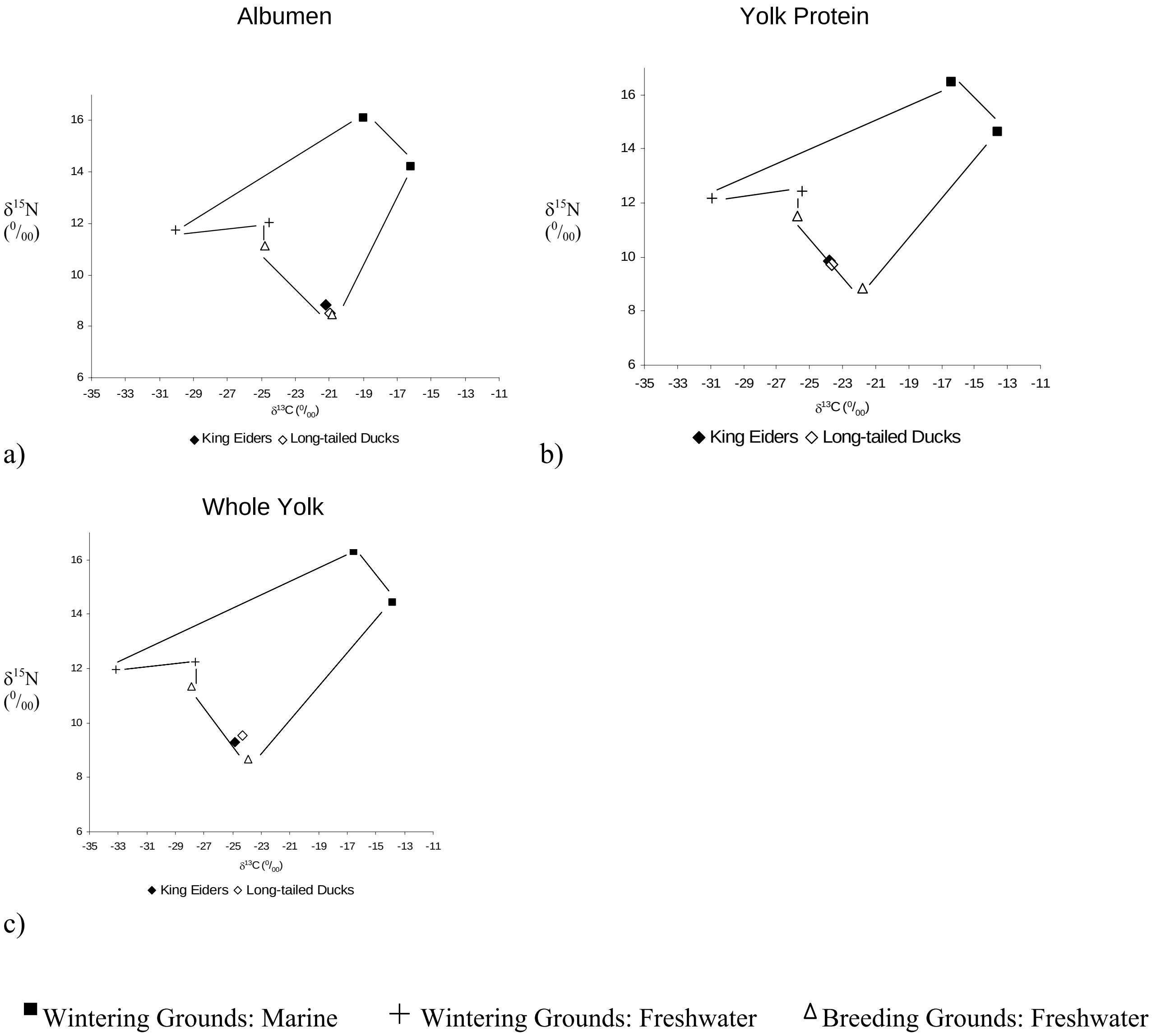


Figure 4.6. Stable-carbon ($\delta^{13}C$) isotope values of equivalent diet item means for yolk lipids. Diet items were grouped based on wintering and breeding ground, trophic guild, taxon and overlapping $\delta^{13}C$ values (Phillips and Gregg 2005).

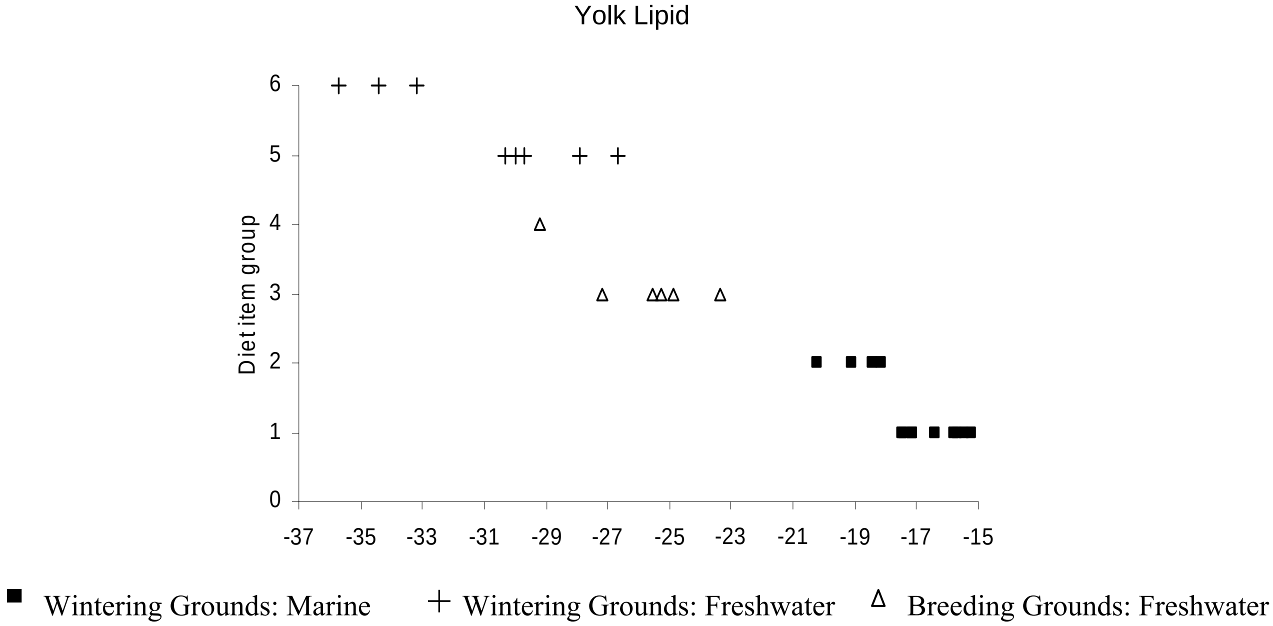


Figure 4.7. Stable-carbon ($\delta^{13}C$) isotope values of Long-tailed Duck and King Eider yolk lipid and equivalent diet item group $\delta^{13}C$ and $\delta^{15}N$ endpoint values. Solid diamonds are King Eiders and empty diamonds are Long-tailed Duck yolk lipid.

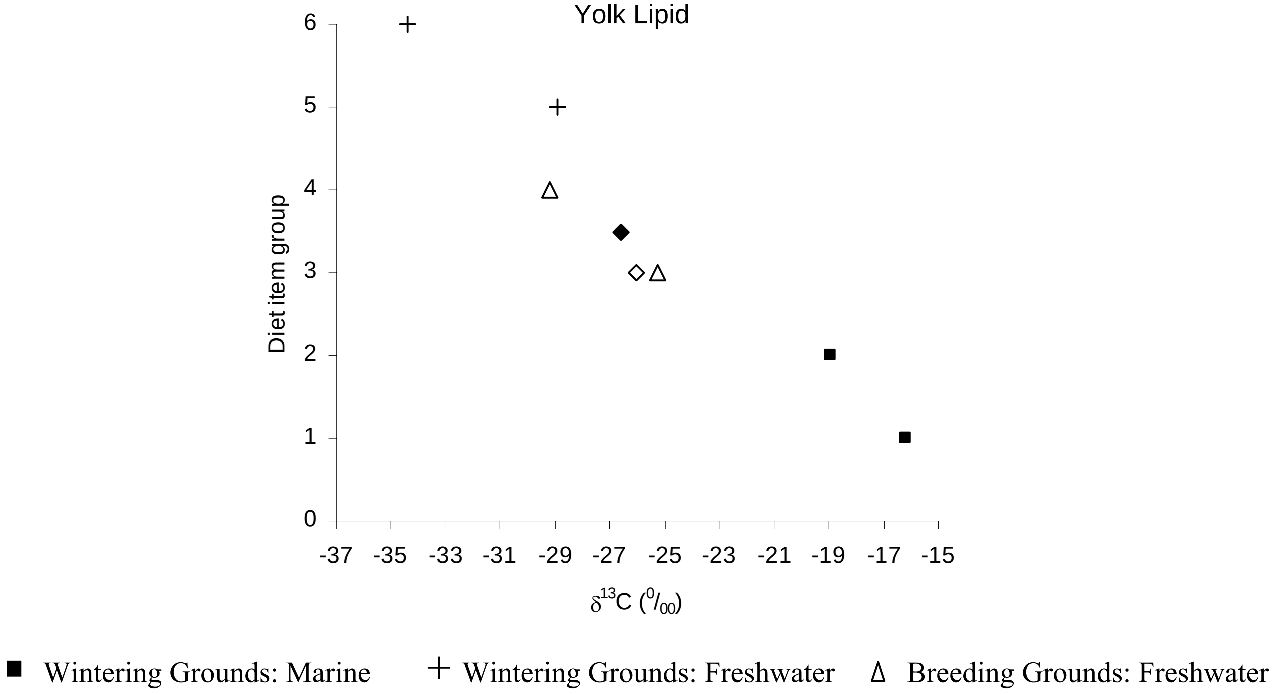


Table 4.4. Isosource (Phillips and Gregg 2003) mean and range (1st and 99th percentile) of marine and freshwater diet source Stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values in egg components of Long-tailed Ducks and King Eiders .

			Marine : Wintering Grounds				**Freshwater: Breeding Grounds**				**Freshwater: Wintering Grounds**			
			Group 1		Group 2		Group 3		Group 4		Group 5		Group 6	
Egg Component	Species	*n*	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Albumen	King Eider	39	1.0	0 - 3	1.0	0 - 3	88.0	85 - 91	10.1	8 -13	NA		NA	
	Long-tailed Duck	29	0.2	0 - 1	0.1	0 - 1	97.5	96 - 100	1.0	0 - 4	0.7	0 - 3	0.5	0 - 2
Whole yolk	King Eider	44	0.8	0 -38	0.8	0 - 3	51.5	51 - 60	46.9	47 – 55	NA		NA	
	Long-tailed Duck	29	3	0 - 7	2.5	0 - 7	78	73 - 83	6.9	0 - 20	5.6	0 - 17	4.1	0 - 11
Yolk Protein	King Eider	44	1.6	0 - 6	1.6	0 - 6	70.7	60 - 86	26.1	13 – 38	NA		NA	
	Long-tailed Duck	29	0.4	0 - 2	0.3	0 - 2	72.8	68 -77	5.5	0 - 19	2.8	0 - 10	18.1	12 - 23
*Yolk lipids**	King Eider	44	7.0	0 - 20	9.0	0 - 25	24.0	0 - 66	60.0	32 – 77	NA		NA	
	Long-tailed Duck	29	13.3	0 -35	15.2	0 - 42	20.0	0 - 69	18.3	0 - 57	18.5	0 - 59	14.7	0 - 41

- Only $\delta^{13}C$ values of yolk lipids were run in Isosource as $\delta^{15}N$ values were not available (Phillips and Gregg 2003).
- NA: King Eiders do not winter in freshwater areas therefore these diet groups were excluded in the King Eider diet mixing model.

4.4. DISCUSSION

When dietary carbon is incorporated into a particular tissue, a characteristic discrimination or change in the isotope value relative to diet is expected (Hobson and Clark 1992). Patterns of stable isotope turnover from diet to bird tissues are tissue-dependant ranging from a few days to over a hundred days (Hobson and Clark 1992a, Hobson and Bairlein 2003). Isotope turnover in captive quail eggs was 3 -5 days for albumen, and 8 days for yolk (Hobson 1995). Each egg-laying is preceded by rapid follicle growth (RFG) during which yolk accumulates in each ovarian follicle (Alisauskas and Ankney 1992). Estimated RFG for King Eiders and Long-tailed Ducks are 6 and 8 days respectively (Alisauskas and Ankney 1992). If yolk is formed rapidly from dietary sources then the contribution of the new isotopic signal in the yolk should be proportional to the additional mass of yolk formed using the new diet (Hobson 1995). Research suggests the time for egg yolk (RFG) to reach a new isotopic equilibrium following a diet switch is estimated to be about 8 days (Gilbert 1971, Bluhm 1992, Hobson 1995). Birds arriving on the breeding grounds with endogenous reserves for egg laying should lay eggs with isotopic signatures representing diet obtained elsewhere such as the wintering grounds (Hobson and Clark 1992). If eggs showed a strong isotopic shift in the direction of the isotopic value of the new diet, then this would indicate a strong dietary component to egg synthesis (Hobson and Clark 1992).

Birds that winter in marine and freshwater biomes and breed in ecosystems that are isotopically distinct from wintering areas encounter foods that differ substantially in their $\delta^{13}C$ values (Hobson and Sealy 1991, Hobson and Clark 1992). Hobson (1995) provided herbivore and carnivore models relating stable-isotope signatures in birds' diets to their egg components. That study provided discrimination values of isotopes between food and eggs that allow predictions of dietary isotope values from those in eggs (Hobson 1995). Differences between predicted values and actual measured values can provide evidence for incorporation of stored endogenous nutrients where they may differ from local dietary endpoints (Hobson et al. 1997a, Hobson et al. 2000, Morrison and Hobson 2004). Stable isotopes have been used to determine relative contributions of diet items from different biomes to birds diets and then as nutrient tracers from diets to tissues (Hobson et al. 1997a, Hobson et al. 2000, Gauthier et al. 2003, Morrison and Hobson 2004, Hobson et al. 2004, Bond 2005). Evidence of an isotopic diet switch during egg-laying has been found in several migratory species (Hobson et al. 1997a, Hobson et al. 2000, Klaassen et al. 2001, Gauthier et al. 2003, Morrison and Hobson 2004, Hobson et al. 2004, Bond 2005).

Values of δ^{13}C and δ^{15}N of King Eider and Long-tailed Duck egg components correspond to δ^{13}C and δ^{15}N values of diet items on breeding grounds. This indicated a dietary shift between wintering grounds, marine and freshwater, and breeding grounds. Results from Isosource models and δ^{13}C and δ^{15}N values of egg components suggest that marine-derived nutrients made up relatively small contributions to King Eider and Long-tailed Duck eggs. However, Long-tailed Duck egg components had a broader variation of δ^{13}C values than those of King Eiders, consistent with higher contributions of wintering ground (both marine and freshwater) nutrients to egg production. Thus, indicating primary nutrients allocated to eggs of Long-tailed Ducks and King Eiders were from breeding grounds. The ability to distinguish between δ^{15}N signatures of nutrients from breeding and wintering grounds in egg components of Long-tailed Ducks and King Eiders although significant was not as clear as it was for δ^{13}C signatures. This was due to a large variation in δ^{15}N values of diet items. Nitrogen (δ^{15}N) values are determined by trophic level in both marine and freshwater biomes (Morrison and Hobson 2004). However, relatively low δ^{15}N values in egg components of both species supports allocation of nutrients from breeding grounds in both Long-tailed Duck and King Eider eggs. Yolk protein, and albumen values of δ^{13}C differed among Simpson and Adventure Lakes but not between species. This suggested that birds nesting on Simpson Lake consumed a diet item(s) not sampled at Adventure Lake.

Past research has suggested that egg-production is much more limited by protein than by energy, and perhaps a breeding females' own protein requirements are temporarily depressed during the egg-lying period to spare protein for the eggs (Meijer and Drent 1999). If egg-laying is energetically costly, timing of breeding may be constrained by the ability to obtain sufficient food (Perrins 1970). Robins (1981) found for 5 groups of birds, with a mean body mass between 25 and 927 g protein costs of egg production were twice as high (201g ± 60g) than during the non-laying period. Long-tailed Duck and King Eider body mass are 500 – 700 g and 1200 – 2100 g respectively (Suydam 2000, Robertson and Savard 2002). Based on body mass smaller bodied female Long-tailed Ducks may require twice as much protein for egg production than female King Eiders. This extra need for protein may account for the variation of δ^{13}C found in egg components of Long-tailed Ducks, as some females may need to allocate nutrients from the wintering grounds to meet protein requirements for egg production.

King Eiders and Long-tailed Ducks winter on both Pacific and Atlantic coasts (Suydam 2000, Robertson and Savard 2002). Long-tailed Ducks are also known to winter in freshwater lakes, such as the Great Lakes (Robertson and Savard 2002). Spring migration of King Eiders and Long-tailed Ducks coincides with break up of arctic sea ice in North America and starts in early June (Suydam 2000, Robertson and Savard 2002). Sea-ice break up begins along the coastlines of the Bering and Beaufort Seas and Hudson Bay. Migratory behavior of King Eiders and Long-tailed Ducks suggests birds prefer to migrate through marine environments on the way to breeding grounds (Richardson and Johnson 1981, Johnson and Richardson 1982, Woodby and Divoky 1982, Johnson 1995, Suydam et al. 1997). King Eiders and Long-tailed Ducks are first seen in the Karrak Lake area early in the second week of June (Kellett and Alisauskas 1997) and the majority of nest initiation is in early July (Kellett and Alisauskas 1997). Birds are observed spending considerable time on the lake between arrival and egg-laying (Lawson per. obs.). Results from stable isotope analysis suggested that breeding females are feeding on local food resources, building up lipid and protein levels for egg production after having migrated to breeding grounds.

Some attention has been called to the problem of forming large amounts of protein in a short period of time (Drent and Daan 1980). Results from this study reveal protein available at breeding grounds is incorporated into eggs. The $\delta^{13}C$ and $\delta^{15}N$ signatures of egg components of both species corresponded with signatures found in local food items. Overall, eggs showed breeding ground stable isotope signatures. However, individual allocation of nutrients likely varied with arrival time (i.e. bird arriving late may have less time to obtain and incorporate local diet items into egg production).

Research suggested King Eiders relied almost exclusively on endogenous reserves during incubation losing ~30% of pre-incubation body mass during incubation (Kellett and Alisauskas 2000) while maintaining a daily incubation constancy of 95 - 99% (McGuire et al. Unpubl, Chapter 3). Incubation constancy, defined as percent time spent on the nest during a 24 hour period, suggests King Eiders are relying upon stored reserves to sustain them through the incubation period. Long-tailed Ducks were found to lose between ~7 – 13% (Peterson and Ellarson 1979, Kellett et al. 2005) of pre-incubating body mass during incubation while maintaining ~84% daily incubation constancy (Chapter 3). These results suggest Long-tailed ducks are relying on local nutrients to maintain their own energetic requirements during incubation. However, $\delta^{13}C$ and $\delta^{15}N$ values of King Eider and Long-tailed Duck egg components suggest a heavy reliance on breeding ground nutrients for egg production, results consistent with other sea duck species, Common Eiders and Harlequin Ducks (Bond 2005, Rigou and Guillemette Unpubl.).

During spring, availability of open water in the Great Lakes (Schummer per. comm.) and open sea leads in combination with knowledge of migratory behavior suggests King Eiders and Long-tailed Ducks had opportunities to acquire nutrients from freshwater and marine wintering grounds for egg production. Few Long-tailed Duck egg components showed correspondence with associated wintering ground freshwater and marine values via stable isotope results. These results suggested some Long-tailed Ducks acquired nutrients allocated for egg production on the wintering grounds.

Long-tailed Duck and King Eider egg component results indicated a dietary shift between winter and breeding areas that are inherent when birds migrate between regions with distinct isotopic abundance, marine versus freshwater (Hobson et al. 1997a, Hobson et al. 2000, Klaassen et al. 2001, Gauthier et al. 2003, Morrison and Hobson 2004, Hobson et al. 2004, Bond 2005). Results from Isosource (Phillips and Gregg 2003) suggested King Eiders and Long-tailed Ducks as in the case of other migratory birds, allocated both wintering and breeding ground nutrients to egg production (Hobson et al. 1997a, Hobson et al. 2000, Klaassen et al. 2001, Gauthier et al. 2003, Morrison and Hobson 2004, Hobson et al. 2004). However, Isosource (Phillips and Gregg 2003) results suggested King Eiders and Long-tailed Ducks allocated a maximum of 8% and 23% of nutrients from wintering grounds to egg production respectively. The $\delta^{13}C$ values of King Eider yolk lipids and breeding ground nutrients did differ, however, the values closely corresponded with freshwater values. This suggested an unknown diet source may have been missed during diet collections on the breeding ground. Bivalve shells and an unidentified gastropod were found in Karrak River and Karrak Lake respectively, however samples were unobtainable. King Eiders may have fed on these or other unknown diet items which may account for the difference found in $\delta^{13}C$ yolk lipid values. King Eiders appeared to use a mixed breeding strategy similar to that of Greater snow geese (Gauthier et al. 2003) and Common Eiders (Parker and Holm 1990, Rigou and Guillemette Unpubl.), allocating endogenous reserves for incubation and breeding ground nutrients, exogenous resources, for egg production. Long-tailed Ducks also appeared to use a mixed capital/income strategy, allocating breeding ground nutrients for incubation. However, Long-tailed Ducks allocated both wintering and breeding ground nutrients to egg production. Results from this study provide further evidence that a continuous breeding strategy gradient is used by migratory and arctic-nesting birds.

5.0 SYNTHESIS

In cold regions, such as the arctic, reproductive activity, egg laying and incubation must be compressed into a short summer of four months or less (Irving 1972). Although preparations for breeding must be synchronized with the environment birds must be able to adjust to unpredictable local variation such as weather (Silverin 1995). Capital and income breeding strategies (Drent and Dann 1980) represent options of energy use (Andersson and Norberg 1981). Apart from organisms that rely exclusively on stored resources for offspring production many species use stores to supply entirely or partially the requirements of particularly demanding stages of reproduction (Andersson and Norberg 1981, Hedenstrom 1992).

King Eiders and Long-tailed Ducks are first seen in the Karrak Lake area in the second week of June, but do not start to initiate egg-laying typically until the 3 or 4th week of June. Birds are observed spending most of the time on the lake at this time (S. Lawson per. obs.), suggesting they are feeding on local food sources. Results from stable-carbon and nitrogen analysis of egg components indicates there is adequate time, between arrival and egg laying, and sufficient local nutrients to allow these birds to obtain the necessary energy and protein requirements to form eggs.

Weather conditions such as temperature and precipitation have a profound affect on the degree of incubation constancy and are major influences on how birds incubate, particularly in those species with female-only incubators (Deeming 2002). Results from this study show that weather conditions did not affect King Eider and Long-tailed Duck incubation constancy but incubation stage did. Incubation constancy in King Eiders and Long-tailed Ducks may not be directly influenced by weather conditions, however nest success is. Nest success models suggested incubation stage is a good predictor for King Eiders and incubation constancy and weather conditions are good predictors of Long-tailed Duck nest success. King Eiders and Long-tailed Ducks breeding at Karrak Lake have been shown to lose ~30% and 7% respectively, of pre-breeding mass during incubation (Peterson and Ellarson 1979, Kellett and Alisauskas 2000, Kellett et al. 2005). Results suggested that incubating female King Eiders and Long-tailed Ducks use different incubation strategies to meet metabolic/physiological/nutritional costs of incubation. King Eiders and Long-tailed Ducks have a daily incubation constancy of 98% and 84% respectively. There was little variation in incubation constancy of King Eiders compared to that of Long-tailed Ducks. Variation in incubation constancy may only play a small role in nest success of Long-tailed Ducks and almost no influence on King Eider nest success. This suggested other factors and/or relationships such as nutrients and/or body condition are influencing nest success of these species. Overall, findings suggested Long-tailed Ducks used an income incubator strategy, and King Eiders used a capital incubator strategy.

Nutrient allocation to egg production has long been a topic of interest to ornithologists. Naturally occurring stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of avian eggs has been successful in providing dietary information and insights into metabolic pathways linking endogenous and exogenous reserves to egg production, gaining considerably interest and application by researchers (Hobson 1995, Hobson et al. 1997a, Hobson et al. 2000, Klaassen et al. 2001, Gauthier et al. 2003, Morrison and Hobson 2004, Hobson et al. 2004, Bond 2005). Stable isotope analysis demonstrates an alternative way to address nutrient allocation in reproduction than conventional methods which may have limitations, as diet items and egg values can be directly compared. Results from this study suggested Long-tailed Ducks and King Eiders relied primarily on nutrients from breeding grounds for egg production.

Results of nutrient allocation in egg production (Chapter 4) combined with incubation constancy and mass loss during incubation provides insight into breeding strategies of Long-tailed Ducks and King Eiders. This study provided evidence that both species rely on endogenous nutrients for egg laying and or incubation. Results from this study suggested that King Eiders and Long-tailed Ducks used a “mixed” strategy to meet energetic demands of reproduction. Breeding female King Eiders may be capital incubators but income egg producers where as breeding female Long-tailed Ducks are income incubators and are both income and capital egg producers.

Future studies could include several breeding seasons as long term data may be able to address weather conditions and body condition of incubating females that may vary from year to year and investigate the influence these conditions may have on incubation constancy, nest success and nutrient allocation for egg production. These findings suggested arctic freshwater areas are extremely important to breeding Long-tailed Ducks and King Eiders as nutrients acquired during the breeding season are required for successful reproduction.

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6.0 APPENDIX: POPULATION DELINATION OF LONG-TAILED DUCKS: MIGRATORY CONNECTIVITY FROM BREEDING GROUNDS TO THE WINTERING GROUNDS

A.1. INTRODUCION

In migratory species, events occurring at different stages of an annual cycle have important consequences on the ecology, evolution and conservation of migratory organisms (Webster et al. 2002). Linking wintering and breeding areas of migratory wildlife can provide important information on population dynamics (Fretwell 1972, Webster et al. 2002). Individuals from the same breeding areas often share wintering areas so entire cohorts could be affected by ecological factors on either of these areas (Mehl et al. 2004, Esler 2000). For many waterfowl species band recovery data can provide inferences about wintering and breeding area connectivity. However, for species such as the Long-tailed Duck (*Clangula hyemalis*) that spends most of the year at arctic and sub-arctic latitudes, band recovery information is sparse making inferences about breeding and wintering ground connectivity difficult**.** For example from 1923 to 2004 4,445 Long-tailed Ducks were banded and only 61 were subsequently encountered (Bird Banding Office, United States Fish and Wildlife Service, Laurel, MD) resulting in a 1.3% recovery rate. Alternative methods such as satellite telemetry are expensive and breeding areas where Long-tailed Ducks are found in sufficient numbers to provide adequate marked birds are limited, compromising the ability to obtain data at a population level that would provide robust inferences about the species movements. On wintering grounds methods such as re-sighting colour banded individuals is difficult given that Long-tailed Ducks are widely distributed, winter in varying sized flocks and can be far offshore (Robertson and Savard 2002). Information regarding known breeding grounds is limited as birds nest across both arctic and sub-arctic areas of North America at low densities (Robertson and Savard 2002) making connectivity between breeding grounds and wintering grounds difficult.

Naturally-occurring stable isotopes in animal tissues reflect local food webs (DeNiro and Epstein 1978, Fry and Sherr 1984, Hobson and Welch 1992, Hobson 2003). Isotopic signatures of food webs, in turn, can vary spatially, based on several possible biogeochemical processes, and these signatures are passed onto animals feeding in those foodwebs (Webster et al. 2002, Hobson 2003). The resulting geographical variation in stable isotope ratios in animal tissues then provides the basis for determining the geographical origins of migratory populations across seasons and space (Webster et al. 2002). Birds that move between isotopically distinct foodwebs can retain information of previous feeding location for periods that depend upon the elemental turnover rates of the tissue of interest (Tiezsen and Boutton 1988, Hobson and Clark 1992, Hobson 2003). Feathers are keratinous tissues that are metabolically inert following synthesis and therefore maintain an isotopic record reflecting the location where the tissue was synthesized (Mizutian et al. 1990). Naturally occurring stable isotopes and values of diet items and consumers tissues can be used in combination to investigate relationships between origins of diet items and associated tissues (Phillips and Gregg 2003). Stable-carbon ($\delta^{13}C$) and ($\delta^{15}N$) isotope analysis has been used successfully to differentiate freshwater and marine habitats used by birds throughout their annual cycles (Mizutian et al. 1990, Hobson et al. 1997a, Bearhop et al. 1999, Hobson et al. 2000, Klaassen et al. 2001, Morrison and Hobson 2004, Hobson et al. 2004).

Information regarding Long-tailed Duck population size and trend estimates has been difficult to obtain (Roberston and Savard 2002). The current population status is unknown however, declines of Long-tailed Ducks on both east and western coasts have been noted (Prairie & Northern Region Sea Duck Team 2000). Presently, it is unknown if Long-tailed Ducks in North America make up one continuous population or whether there are distinct populations, western, eastern and/or a Great Lakes subgroups. Band recoveries from hunter-killed birds suggest that Long-tailed Ducks from western and eastern coasts and Great Lakes region share similar breeding areas (Bird Banding Office, United States Fish and Wildlife Service, Laurel, MD).

Long-tailed Ducks are a circumpolar species that breed in extensive portions of the arctic and sub-arctic areas of Alaska and Northern Canada in freshwater and coastal areas (Robertson and Savard 2002). The winter range of the Long-tailed Duck includes both Western and Eastern coasts, the Great Lakes, and other large inland lakes. These birds often remain in northern areas while open water persists, migrating to wintering areas when open water is no longer available. Long-tailed Ducks are considered a late fall migrant returning to western and eastern wintering grounds in October with numbers peaking in late November to December (Campbell et al. 1990, Viet and Petersen 1993, Walsh et al. 1999, Hess et al. 2000). They are first seen returning to wintering areas in the Great Lakes in mid-October (Peterjohn 1989, Robbins 1991).

Unlike other waterfowl species, Long-tailed Ducks annually undergo 3 molts; basic plumage, alternate plumage and eclipse plumage. The basic plumage is acquired in the fall and alternate (breeding) plumages are thought to be acquired on wintering areas. Body feathers of Long-tailed Ducks should therefore reflect isotopic signatures of food webs associated with regions were they where grown (Mizutani et al. 1990, Hobson and Clark 1992, Hobson et al. 2001). Based on previously reported isotopic gradient in polar waters and an east-west marine delineation of King Eiders (Dutton et al. 1989, Schell et al. 1998, Mehl et al. 2005) I predicted that δ^{15}N and δ^{13}C values for feathers from Long-tailed Ducks wintering in western marine areas would be relative to feathers from Long-tailed Ducks wintering in eastern marine areas and the Great Lakes. Use of stable isotope analysis from feathers should reflect stable isotope composition of wintering areas at the time of feather molt for specific tracts. Feather δ^{15}N and δ^{13}C values should closely correspond to δ^{15}N and δ^{13}C values of potential diet items, hereafter referred to as diet items, from associated areas where grown. The purpose of this study was to use δ^{15}N and δ^{13}C values of Long-tailed Duck feathers and diet items to link the Karrak Lake, NU breeding area to wintering grounds and to delineate the Long-tailed Duck population(s).

A. 2. METHODS

Capturing, Marking and Feather Collection

Mist nets were used to capture and mark adult female Long-tailed Ducks (Alison 1975a, Alison 1975b, Kellett et. al. 2005) at Karrak Lake, NU in mid to late incubation. All birds caught were marked with standard US Fish and Wildlife Service aluminum leg bands. Feathers from three body regions (chest, head and back) and a piece of 9th primary feather of adult female Long-tailed Ducks, were collected from 9, 12 and 7 incubating female Long-tailed Ducks in 2003, 2004 and 2005 respectively. Feathers of male and females, juveniles and adults, were collected in known wintering areas throughout North America in 2003 and 2004 from other researchers and hunter-killed birds. All feathers were placed in 20ml vials and soaked in a 2:1 chloroform methanol mixture to clean feathers and remove any surface oils, feathers were then allowed to air dry under a fume-hood. All feather samples were weighed into tin cups at a weight of 1.0 milligrams and submitted for carbon and nitrogen analysis to the Soil Science Department University of Saskatchewan, combusted in a Roboprep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Europa Scientific, Crewe, UK; Hobson and Schell 1998) at the Department of Soil Science, University of Saskatchewan. We report all stable isotope values in δ notation relative to the Pee Dee Belemnite (PDB) and atmospheric air standards for $\delta^{13}C$ and $\delta^{15}N$ measurements, respectively. Measurement precision is based on thousands of measurements of our albumen lab standard is estimated to be ± 0.1 $^{o}/_{oo}$ for $\delta^{13}C$ measurements and 0.3 $^{o}/_{oo}$ $\delta^{15}N$ measurements (see Hobson 1995). Isotope values are expressed as $\delta^{13}C$ and $\delta^{15}N$ (with units of $^{o}/_{oo}$) according to the following equation:

$$\delta^{13}C, \delta^{15}N = [\ (R_{sample}/R_{standard}) - 1]\ X\ 1000 \quad \text{Where } R = {}^{13}C/{}^{12}C,\ {}^{15}N/{}^{14}N \quad (A.1)$$

Diet items - Long-tailed Ducks winter on both west and east coasts and inland freshwater lakes in southern Canada and the Northern United States. $\delta^{13}C$ and $\delta^{15}N$ signatures of diet items from these wintering grounds were obtained from the literature (Table 4.2). I applied discrimination to diet source $\delta^{13}C$ and $\delta^{15}N$ values using the carnivore model (Hobson and Clark 1992b). Discrimination values were applied so $\delta^{13}C$ and $\delta^{15}N$ signatures from known wintering ground diet items and feathers could be compared. Diet items were grouped based on marine, east and west, and freshwater wintering ground origins overlapping means and standard deviation (Phillips and Gregg 2005). Correspondence of $\delta^{13}C$ and $\delta^{15}N$ signatures between diet items and feathers may provide evidence of population delineation of western, eastern and Lake Ontario Long-tailed Duck populations.

A.3. STATISTICAL ANALYSIS

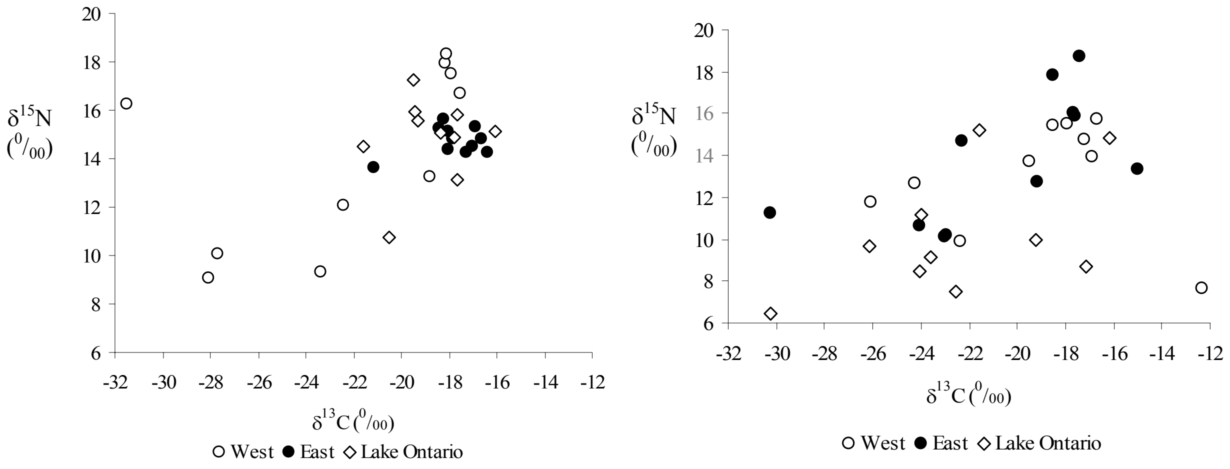
A.3.1. East, West and Lake Ontario Delineation

Statistical analysis was carried out using SAS Version 8.2 (SAS Institute 1996). I plotted $\delta^{13}C$ and $\delta^{15}N$ values from each feather tract to determine the amount of overlap between eastern, western and Lake Ontario populations. Discrimination between the three populations was based on isotopic ratios from one or more feather tract(s), using discriminate function analysis (DFA; SAS Institute 1996, Mehl et al. 2004). Homogeneity of within-covariance matrices was tested using a chi-square test of homogeneity (option within SAS) and used discriminate function analysis (DFA; SAS Institute 1996).

A.4. RESULTS

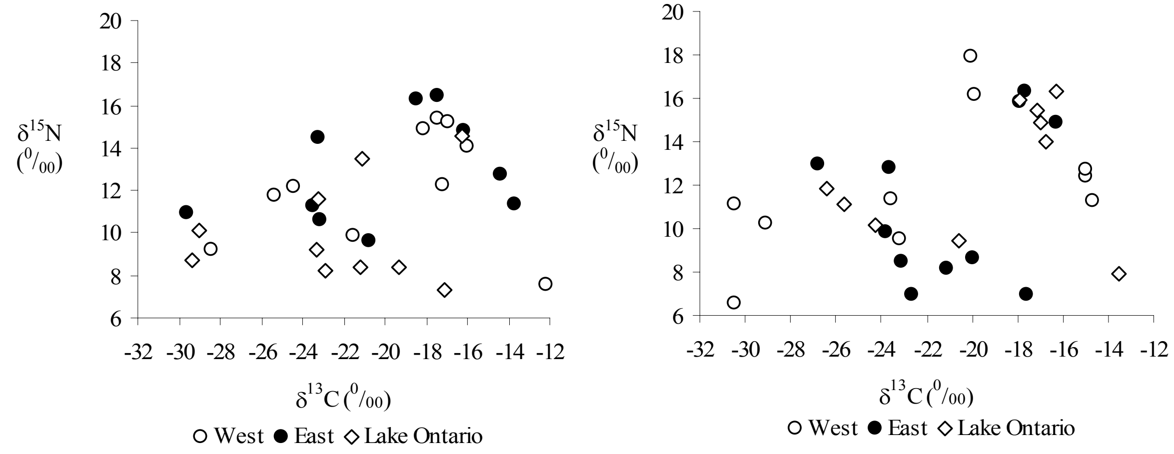
I used a subset of feather samples ($n = 10$) to determine which feather tract (chest, back, belly, head or 9th primary) provided the best discrimination between wintering locations. Results determined that head feathers were significant with the least posterior probability of misclassification by region (X^2= 35.05 P < 0.0001) (FigureA.1). Head feathers from west (*n* = 26) and east (*n* = 31) coasts and Lake Ontario (*n* = 66) were used in predictive equations from Discriminant Function Analysis to classify individuals as wintering in western and eastern marine areas and Lake Ontario.

Figure A.1. Isotopic values from head, back, chest and primary wing feathers of Long-tailed Ducks collected opportunistically by researchers and hunters that wintered on western (*n* = 10), eastern (*n* = 10) coasts and Lake Ontario (*n* = 10). Open circles are western birds, solid circles are eastern birds and triangles are birds from Lake Ontario.



a) Head Feathers

b) Back Feathers



c) Chest Feathers

d) 9th Primary

The δ^{13}C and δ^{15}N head feather values and results from DFA suggest that 14%, 32% and 53% of Long-tailed Duck females breeding at Karrak Lake wintered on the east coast, Lake Ontario and the west coast respectively (Table A.1.). However, results of head feather classification showed a high percentage of misclassification between Lake Ontario and west coast collection and assignments (Table A.1). Head feather δ^{13}C and δ^{15}N signature ranges from all three known wintering areas marine, east and west, overlapped as did some head feathers collected from Lake Ontario (Table A.2). These results suggested Long-tailed Duck classification was not as distinct as it had been for King Eiders and White-winged Scoters (Mehl et al. 2004, Mehl et al. 2005, Swoboda and Alisauskas Unpubl).

Table A.1. Classification of Long-tailed Duck head feathers collected in 2003 and 2004 at known wintering, marine and freshwater, locations and at Karrak Lake 2003, 2004 and 2005. Region collected is the region of feather collection and classified into region is the region that feathers were classified as coming from. Sample size (*n*) is the number of birds classified into the region and percent % is the percentage of classification.

	Classified into Region					
	East		Lake Ontario		West	
Region Collected	*n*	%	*n*	%	*n*	%
East (31)	21	67.7	10	32.3	0	0.0
Lake Ontario (66)	20	30.3	43	65.2	3	4.6
West (27)	4	14.8	16	59.3	7	25.9
Karrak Lake (28)	4	14.3	9	32.1	15	53.6

Diet items - Results of ANOVA show potential marine diet source δ^{13}C and δ^{15}N values from different coasts did not differ (δ^{13}C $F_{2,3}$ = 0.28 P = 0.77; δ^{15}N $F_{2,3}$ = 0.02 P = 0.98) and fall within the same range (Table A.2). Knoche (2004) showed marine δ^{13}C and δ^{15}N values of King Eider wing feathers grown in the Bering and Beaufort seas overlapped, making it difficult to distinguish between these two molting areas. Using δ^{13}C and δ^{15}N values of feathers grown in these associated areas may prove problematic for population delineation. Diet item δ^{13}C and δ^{15}N values from the Great Lakes and tundra lakes did not differ (ANOVA δ^{13}C $F_{1,2}$ = 0.16 P = 0.73; δ^{15}N $F_{1,2}$ = 0.10 P = 0.78) and ranges overlapped (Table A.2). Freshwater and marine diet source $\delta^{13}C$ and $\delta^{15}N$ value ranges do not overlap suggesting $\delta^{13}C$ and $\delta^{15}N$ values can be used to discriminate between feathers grown in freshwater versus marine environments.

Band recovery information (Bird Banding Office, Laurel MD) and $\delta^{13}C$ and $\delta^{15}N$ values of Long-tailed Ducks wintering in the Atlantic Ocean suggest that these birds molt head feathers exclusively in marine environments. Band recovery information and $\delta^{13}C$ and $\delta^{15}N$ values of Long-tailed Ducks wintering in Lake Ontario suggest head feathers of these birds are grown in freshwater, brackish and marine areas. This suggested that these birds may be moving between freshwater and marine areas during molt. The $\delta^{13}C$ and $\delta^{15}N$ values of Long-tailed Ducks collected on marine western wintering areas were either exclusively freshwater or marine. These results suggested that western Long-tailed Ducks are molting head feathers either in marine or freshwater areas and suggested they are not moving between areas during molt. Band recovery and satellite telemetry maps (www.absc.usgs.gov/research/seaducks/sat_telem_ltdu_maps.htm) show these birds wintering in both marine and freshwater environments.

Figure A.2.Wintering ground, marine and freshwater, diet item $\delta^{13}C$ and $\delta^{15}N$ isotopic values (Table 4.2).

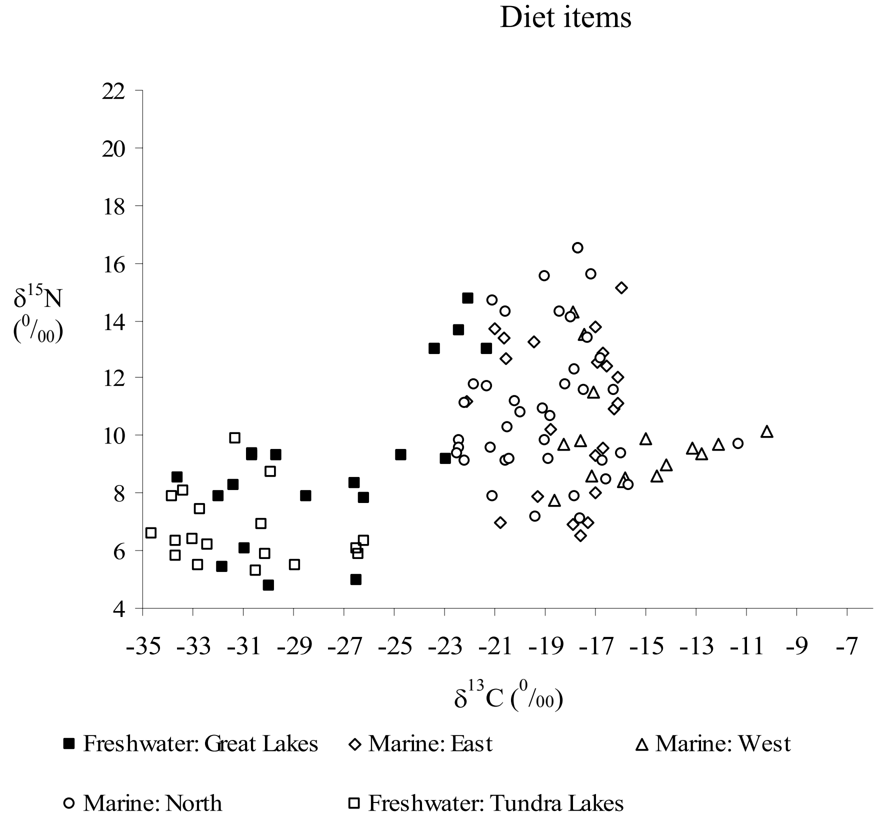


Figure A.3. δ^{13}C and δ^{15}N isotopic values of wintering ground, marine (east and west) and freshwater (Alaskan Lakes and Great Lakes), diet items and Long-tailed Duck head feathers classified as east (*n* = 49), west (*n* = 25), and Lake Ontario (*n* = 78). Diet items were grouped as marine and freshwater.

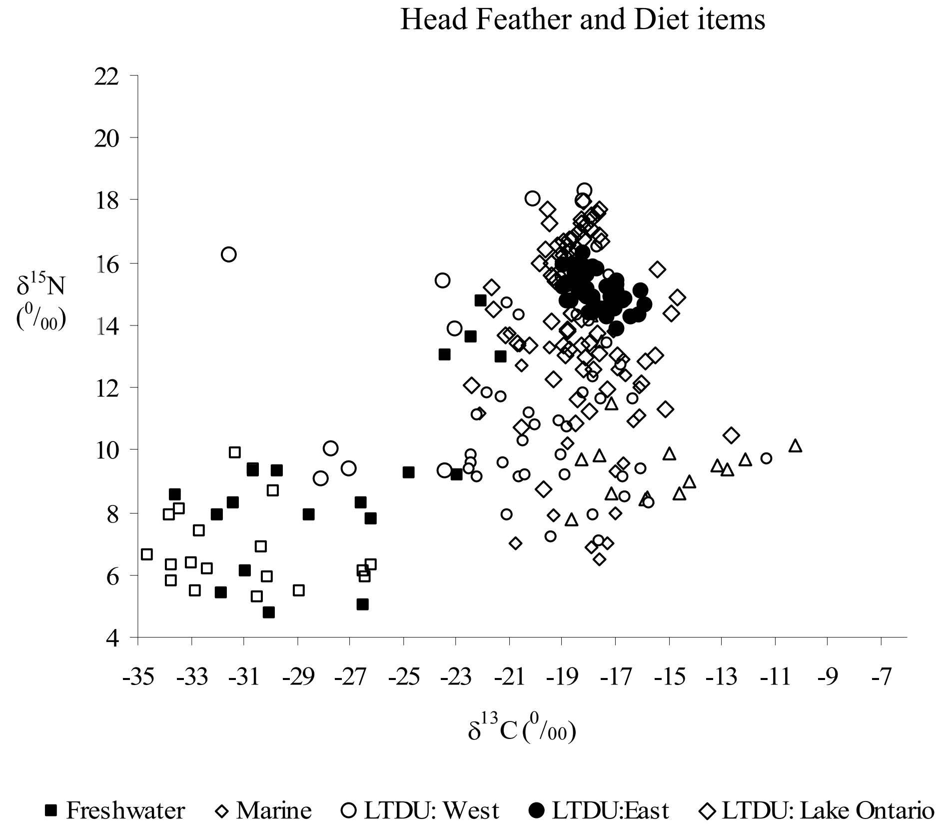


Table A.2. Range of isotopic δ^{13}C and δ^{15}N isotopic values of Long-tailed Duck head feather and wintering ground, marine (east, west and north) and freshwater (Great Lakes, Lake Oneida, and lakes on Alaska's north slope).

	Location	**δ^{13}C**	**δ^{15}N**
Diet items	*Marine*		
	East Coast	-22.1 to -16.0	6.5 to 15.2
	West Coast	-18.6 to -10.2	7.8 to 14.3
	Northern Oceans and Seas	-22.5 to -11.3	7.1 to 16.5
	Freshwater		
	Alaska's North Slopes Lakes	-34.6 to -26.2	3.7 to 9.9
	Great Lakes & Lake Oneida, NY	-33.6 to -21.3	3.0 to 14.8
Head Feathers	East Coast	-21.1 to -14.7	13.6 to 16.8

West Coast	-31.5 to -16.9	9.1 to 18.3
Lake Ontario	-26.9 to -12.6	8.7 to 17.2

A.5 DISCUSSION

Results of this study suggested that there is no clear δ^{13}C and δ^{15}N isotopic gradient between western and eastern oceans and east-west polar areas (Dutton et al. 1989, Schell et al. 1998, Mehl et al 2005, Knoche 2005). The δ^{13}C and δ^{15}N values of Long-tailed Duck head feathers grown in eastern and western oceans of North America overlap, weakening the ability to distinguish between wintering populations of Long-tailed Ducks. Diet source δ^{13}C and δ^{15}N values from marine areas also overlap and therefore, did not aid in Long-tailed Duck wintering delineation. Head feathers collected on Lake Ontario and the west coast δ^{13}C and δ^{15}N values reflected marine and freshwater values and closely corresponded with diet source δ^{13}C and δ^{15}N values from both ecosystems. Results suggested certain Long-tailed Ducks wintering on Lake Ontario moved between freshwater and marine areas such as the Saint Lawrence sea way, therefore acquiring nutrients from both marine and freshwater areas to grow basic head feathers. Results also suggest birds on western wintering grounds spent time in freshwater ecosystems while molting head feathers. These birds may have wintered in inland lakes and/or molted in freshwater and then moved to marine areas. Head feathers from eastern wintering grounds had δ^{13}C and δ^{15}N values that reflected marine signatures and corresponded closely marine diet source δ^{13}C and δ^{15}N values. Eastern wintering Long-tailed Ducks may acquire nutrients and molt in a marine environment.

Band recoveries from 1923 to 2004 (Bird Banding Office, Laurel, MD) and locations of satellite-radio marked Long-tailed Ducks (United States Geological, M. Mallory Unpubl.) found birds banded in western and eastern regions were recovered in these regions. Long-tailed Ducks marked in the Bering Sea with satellite-radios migrated to wintering areas in Alaska, Russia and Asia (United States Geological). Wintering Long-tailed Ducks marked with satellite radios in Ontario migrated in the spring to Hudson’s Bay and returned in the fall. There was no information available showing Long-tailed Ducks switched wintering grounds, east, west or Great Lakes region, from year to year. Data from band recoveries and satellite-radios suggests Long-tailed Ducks are remaining in the regions where they were marked. This information combined with δ^{13}C and δ^{15}N signatures of head feathers suggests there may be separate wintering populations of Long-tailed Ducks. However, precisely where populations separate still remains unclear. Perhaps birds wintering in eastern areas are not exposed to the same harvest pressures or effects as those wintering in the west and are therefore not experiencing declines of the same magnitude.

A wide variety of factors may be held responsible for generating considerable isotopic variability in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ signals of the primary carbon and nitrogen sources in tissue components of individual organisms and different individuals within and between populations and communities (Smit 2001). Variation of $\delta^{15}N$ and $\delta^{13}C$ values of Long-tailed Duck head feathers grown in marine areas in this study support Smit's (2001) findings and provide further evidence by Braune et al. (2004) that $\delta^{13}C$ and $\delta^{15}N$ isotopes are not the best population tracers to delineate western and eastern marine wintering populations of Long-tailed Ducks. Future stable isotope analysis could address seasonality and location of freshwater versus marine molt of Long-tailed Ducks using multiple feather tracts. This approach may be able to answer questions regarding molting areas of Long-tailed Ducks across North America and may be able to address the use of freshwater and/or marine molting areas across seasons.

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