Nutrient Acquisition and Allocation Strategies for Reproduction by Female Harlequin Ducks

by

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THESIS
SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the
Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

Fall 2005

APPROVAL

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Degree: Master of Science

Title of Thesis:

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ABSTRACT

I analysed body mass variation and stable isotope signatures ($\delta^{15}N$, $\delta^{13}C$) of adult female Harlequin Ducks (*Histrionicus histrionicus*) on marine wintering areas and freshwater breeding streams in southern British Columbia to investigate when and where they acquire nutrients prior to reproduction and the sources of nutrients allocated to clutch formation. I found that female body mass on wintering grounds increased by 7% in the weeks before migration, irrespective of whether they were consuming their usual winter diet of intertidal invertebrates or superabundant spawn of Pacific herring (*Clupea pallasi*). However, stable isotope analyses revealed that freshwater nutrients, not marine, were allocated to eggs, and therefore, stored marine nutrients were likely used during other reproductive stages. I also estimated breeding propensity of Harlequin Ducks using a novel method combining yolk precursor analyses and radio telemetry, and estimated that 92% of females on streams initiated egg formation.

Keywords: Harlequin Duck, stored nutrient reserves, body mass, herring spawn, income breeding, reproductive investment, stable isotopes, breeding propensity, yolk precursors

DEDICATION

For Joel

Thanks for your love and support throughout this process

... I know it hasn't always been easy...

ACKNOWLEDGEMENTS

I would first like to thank my supervisory committee: Dan Esler, Tony Williams and Ron Ydenberg. They acted as my scientific mentors and were generous with sharing their breadth of knowledge. I am particularly indebted to Dan, for it was his guidance that made this thesis possible. He has been supportive and kind while encouraging me to think for myself and believing in my ability to face challenges. I also thank Kathy Martin for serving as my public examiner during my thesis defence and for contributing valuable comments to the final product.

I had many people assist in data collection including Chester Alec, Eric Anderson, Joan and Ken Bond (aka Mom and Dad), Sean Boyd, Sam Copeland, Shawn Freeman, Delphine Jacob, Joel Harding, Joel Heath, Sam Iverson, Sunny LeBourdais, Erica McClaren, Bobbie Vinnie, Josh Weisner, Ken Wright, and Ramunas Žydelis. We were lucky enough to be able to work in some beautiful locations around British Columbia and I would like to thank Joan and Ken Bond, Hamish Nichol, and Erdman Tuemp for helping to put a roof over our heads during those times. Thank you to the Stl'atl'imx Nation for allowing us to work in their traditional territory and to Bonnie Adolph and Larry Casper for aiding in our search for field assistants.

I have had a wonderful experience in the Centre for Wildlife Ecology at Simon Fraser University. Connie Smith always seems to do an amazing job of keeping the lab organized (especially using her computer prowess) and up-to-date with permits. Judy Higham is invaluable with her skills for managing budgets. As well, many fellow grad students have provided knowledgeable assistance and friendship over the last couple years including BriAnne Addison, Courtney Albert, Lilly Cesh, Kristen Gorman, Joel Heath, Allison Henderson, Sarah Jamieson, Iain Jones, Jamie Kenyon, Kim Mathot, Molly Kirk, Sunny LeBourdais, Tyler Lewis, Erika Lok, Josh Malt, Holly Middleton, and Andrea Pomeroy.

Tony Williams provided laboratory space and advice at Simon Fraser University, and many others assisted with laboratory analyses. Kristen Gorman and Kat Salvante were extremely helpful with my yolk precursor analyses. For stable isotope analyses, Keith Hobson provided valuable suggestions and counsel, and Mano Benjamin, Patricia Healy, and Myles Stocki assisted with determining final isotope results.

Primary funding for this work was provided by BC Hydro Bridge-Coastal Restoration Program. I thank Environment Canada Science Horizons Program for their contribution. Also, the Centre for Wildlife Ecology contributed some conference funding as well as logistical support.

Finally, I am extremely grateful to Joel Harding and to my family for their support and for reminding me that there is more to life than graduate work. Thanks to Joel for keeping our lives in order, for keeping a sense of humour, and for ungrudgingly making the sacrifices necessary to see this degree to completion. I really appreciate it.

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CHAPTER 1
GENERAL INTRODUCTION

1.1 Thesis Background

Birds have evolved various life history strategies to maximize lifetime fitness. A central tenet of life history theory is that trade-offs exist between components of fitness (Stearns 1992). Physiological trade-offs are thought to result through the allocation of a limited amount of energy among competing functions within an individual, such as reproduction and survival (Cam et al. 1998; Figure 1.1). Reproduction in birds requires a large investment of energy and nutrients (Carey 1996). Within the broad range of avian taxa, strategies for acquiring and allocating energy and nutrients for reproduction are variable, interspecifically and intraspecifically, and are likely influenced by factors such as body size, mode of development, predation pressure, climate, diet, and food availability (Moreno 1989). Further, these strategies affect migration strategies (Alerstram and Lindström 1990) and reproductive attributes including timing of breeding (Lack 1968), clutch size (King 1973), and incubation behaviour (Moreno 1989).

Nutrient acquisition strategies for meeting the nutritional requirements of reproduction can involve building stored nutrient reserves or increasing foraging in the local environment. The strategy of allocating stored nutrients, also termed endogenous reserves, to reproduction is known as 'capital' breeding, while using locally available food sources, also termed exogenous nutrients, to acquire energy without reliance on stored reserves is known as 'income' breeding (Thomas 1989, Jönsson 1997). Drent and

Daan (1980) originated the concepts of capital and income breeding when considering clutch size determination. According to their definition, a capital breeder would base the decision to lay an additional egg on the absolute level of available capital relative to a critical threshold, whereas an income breeder would base the decision on the rate of nutrient accumulation from the local environment. The original and contemporary definitions of capital and income strategies differ in that Drent and Daan (1980) discuss the origin of *information* for decisions in a specific aspect of reproduction (clutch size) while more recent interpretations focus on the origin of *resources* in general for offspring production (Jönsson 1997).

Capital and income breeding have been considered extremes of a continuum ranging from high to low reliance on stored nutrients (Thomas 1989), although recent evidence suggests that sole reliance on stored nutrients for reproduction is rare (Meijer and Drent 1999). One example of a capital breeder is the Adelie Penguin (*Pygoscelis adelie*), which uses mostly endogenous reserves during reproduction, whereas the American Kestrel (*Falco tinnunculus*) is an example of an income breeders, using only nutrients available in the local environment (Meijer and Drent 1999). Many studies have also found intermediate approaches by various species (Meijer and Drent 1999, Gauthier et al. 2003). Jönsson (1997) considered the costs and benefits of each strategy from energetic and demographic perspectives. Income breeding can be considered beneficial when the energetic costs of nutrient storage are high, and when stores negatively influence flight performance and predator avoidance in such a way as to reduce survival or fitness. Capital breeding is considered beneficial when resources on breeding grounds are unpredictable or scarce, when predation risk on breeding grounds during foraging is high, or when time for reproduction is limited.

Many studies have investigated the role of nutrient reserves for reproduction, and therefore the extent of capital breeding, in waterfowl (see Alisauskas and Ankney 1992 for review). Most of these studies were initiated to consider nutritional effects on clutch size determination and timing of reproduction. For waterfowl, egg production is an energetically demanding stage because it involves the formation of many, large, energy-dense eggs in a short period of time (Alisauskas and Ankney 1992). Because waterfowl are diverse in morphology, distribution, behaviour, and diet, considerable interspecific variation exists in the degree of reliance on endogenous reserves for clutch formation (Alisauskas and Ankney 1992). For example, Common Eiders (*Somateria mollisma*) have been reported to rely heavily on endogenous reserves (Parker and Holm 1990) while Northern Shovelers (*Anas clypeata*) in Alaska use very little (MacCluskie and Sedinger 2000). Many waterfowl species appear to use moderate amounts of endogenous reserves, including Lesser Scaup (*Aythya affinis*; Esler et al. 2001), Canvasbacks (*Aythya valisineria*; Barzen and Serie 1990), and Ruddy Ducks (*Oxyura jamaicensis*; Tome 1984, Alisauskas and Ankney 1994). Esler and Grand (1994) demonstrated that the use of nutrient reserves also can vary intraspecifically. These studies have provided insights into the constraints on waterfowl reproduction and strategies for meeting those constraints, although these questions have seldom been addressed for sea ducks.

Sea ducks are thought to employ a life history strategy in which adult survival is emphasized and annual reproductive effort is low and variable relative to other waterfowl (Goudie et al. 1994). Based on this strategy, sea ducks would be expected to defer reproduction under scenarios of poor food availability or habitat quality (Goudie and Jones in press). However, this has been poorly documented in sea ducks, in part because of the difficulties associated with quantifying breeding propensity. Rates of nonbreeding, and the mediating role of nutrition, are significant data gaps that constrain understanding of sea duck productivity and population dynamics.

Population monitoring data indicate that, of the 17 sea duck species in the north Pacific Rim, at least 13 are reported to be declining (Goudie et al. 1994). Therefore, it is important to identify reproductive strategies of sea duck species to ascertain mechanisms by which productivity and recruitment may be limited. Further, knowledge of breeding strategies allows for informed population and habitat management.

1.2 Harlequin Duck Background

Harlequin Ducks (*Histrionicus histrionicus*) have a holarctic distribution, and on the west coast of North America, they range from Alaska to northern California. Pacific populations of Harlequin Ducks are of conservation concern, and there is evidence to suggest that recruitment in southern British Columbia is not compensating for annual adult mortality, and thus, productivity may be too low to sustain populations (Robertson and Goudie 1999, Smith et al. 2001, Rodway et al. 2003). Because of this concern, further investigation is needed to address knowledge gaps regarding reproduction in Harlequin Ducks.

Harlequin Ducks are small sea ducks that winter in marine environments and feed on a varied diet including amphipods, limpets, small crabs, fish roe, and other marine invertebrates (Vermeer 1983, Goudie and Ankney 1986). They are unusual among North

American waterfowl because they use fast-flowing streams for breeding (Robertson and Goudie 1999). On these breeding streams, they are able to move swiftly in turbulent, white water and dive for invertebrate prey on rocky substrates (Robertson and Goudie 1999). The breeding range for those that winter in British Columbia extends inland to the Rocky Mountains. Like many other sea ducks, they exhibit low productivity, long lifespans, and delayed maturation (Goudie et al. 1994).

1.3 Study Area

The study area for this project included breeding sites on streams near the towns of Pemberton (50° 19'N, 122° 48'W) and Lillooet (50° 41'N, 121° 56'W) in the southern Coast Mountains of British Columbia, Canada (Figure 1.2). Specific study streams included sections of Cayoosh Creek, Seton River, Bridge River, Yalakom River, Ryan River, Rutherford Creek, Brandywine Creek, and Cheakamus River. Study sites on wintering areas were situated around the Strait of Georgia (49° 40'N, 124° 24'W) between Vancouver Island and the southern coast of mainland British Columbia (Figure 1.3). Specific study sites were located around Denman Island, Hornby Island, southern Quadra Island, Williams Beach, and Qualicum Bay.

1.4 Thesis Purpose and Outline

The purpose of this thesis was to investigate nutrient acquisition and allocation strategies used by Harlequin Ducks for reproduction, particularly clutch formation. These issues have never been addressed for this species and have important implications for understanding factors limiting productivity, and subsequently, have important population and habitat management ramifications. This thesis also contributes general knowledge about breeding propensity in Harlequin Ducks and appropriate methodology for quantifying this reproductive attribute. The chapters are written and organized in preparation for journal submission, and therefore, include some repetition. Co-authors are acknowledged in each of the data chapters while introductory and concluding chapters are written in the first person.

The first data chapter, Chapter Two, addresses nutrient acquisition prior to reproduction for Harlequin Ducks wintering in the Strait of Georgia, British Columbia. If Harlequin Ducks store endogenous reserves for subsequent investment in reproduction and especially clutch formation, it is important to determine where and when they build these nutrient stores in order to fully understand their nutrient acquisition strategy, and therefore, elucidate potential sources of constraints to nutrient acquisition. I use body mass measurements of adult females to determine the timing of nutrient acquisition and the relationship to Pacific Herring (*Clupea pallasi*) spawn events.

In Chapter Three, I investigate the sources of nutrients allocated to clutch formation. I use stable isotope analysis to determine whether Harlequin Duck eggs were composed of marine-derived nutrients, freshwater nutrients, or some combination of the two sources. By documenting the relative contribution of breeding and wintering site resources for meeting the nutritional and energetic demands of clutch formation, this chapter lends insight into the relative importance of breeding stream and coastal wintering site quality for Harlequin Duck productivity.

In Chapter Four, I investigate breeding propensity (the proportion of adult females on breeding streams that initiate egg production) and methodological influences on breeding propensity estimates. I employ a new technique combining yolk precursor analysis with radio telemetry to obtain accurate estimates of breeding propensity for Harlequin Ducks in southern British Columbia.

Finally, in Chapter Five, I draw conclusions and consider future directions, and then supplement the thesis with an appendix investigating migration costs between wintering and breeding study sites.

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Figure 1.1 Schematic demonstration of competing demands for allocation of nutrients in adult female birds.

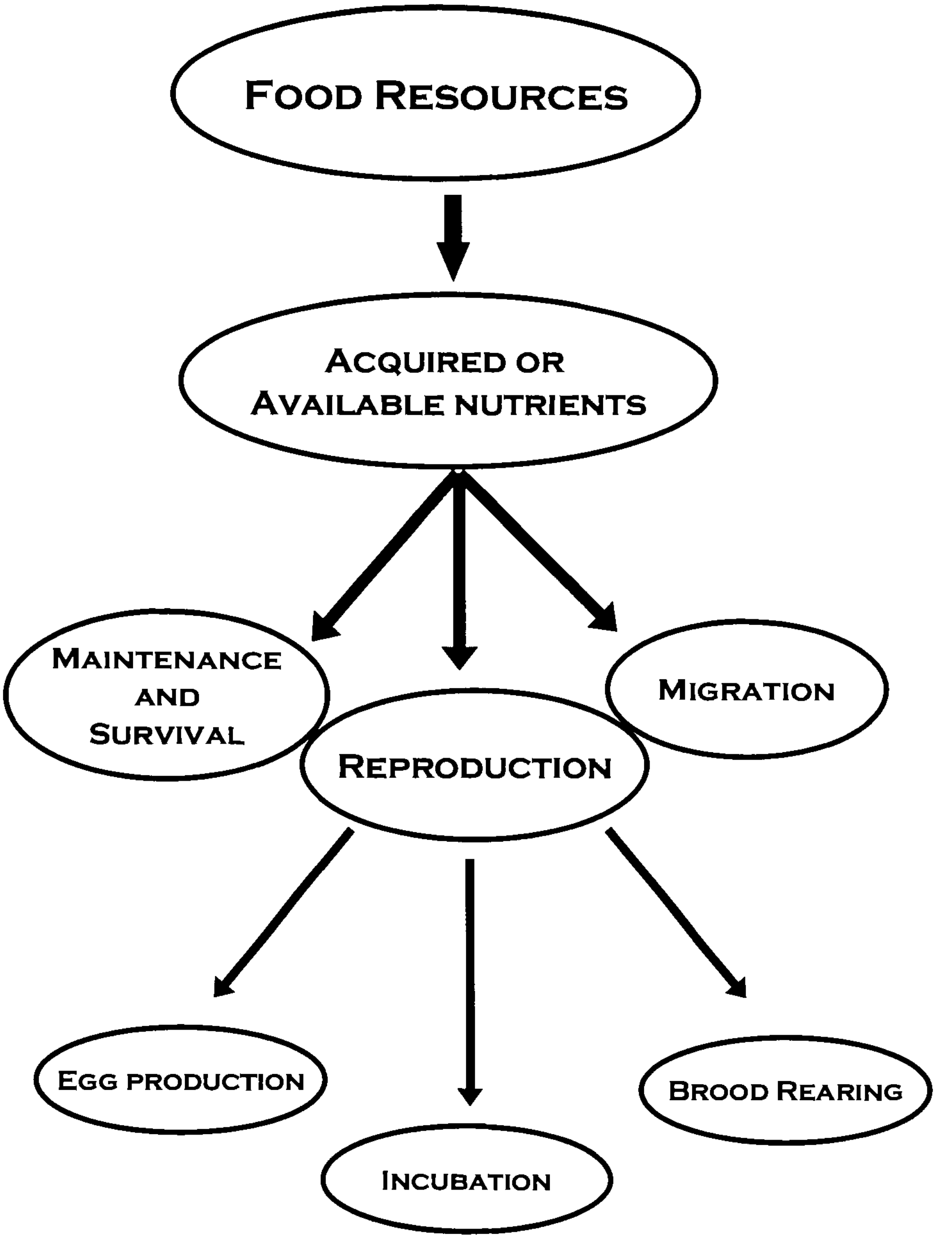


Figure 1.2 Map of breeding area study sites.

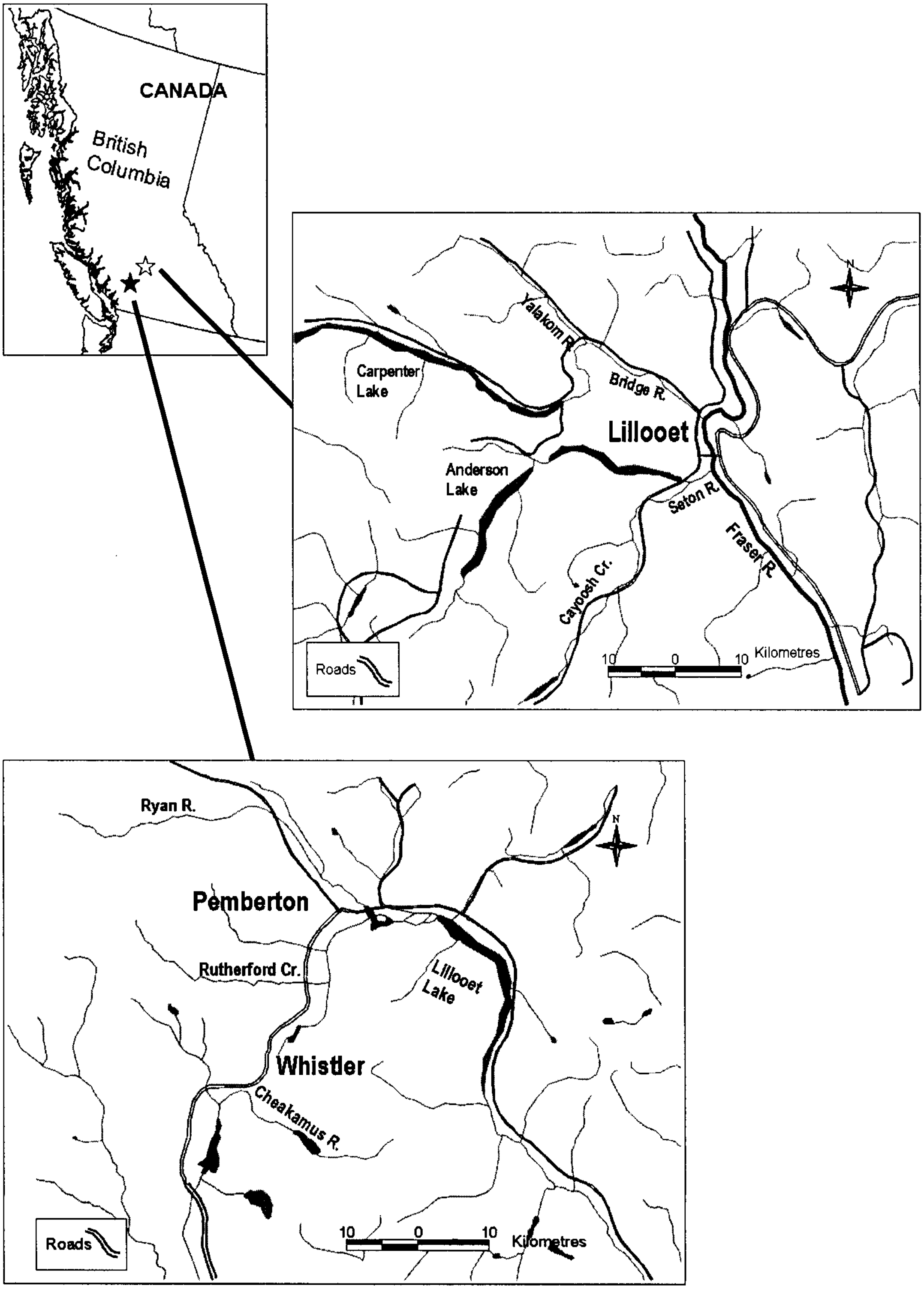
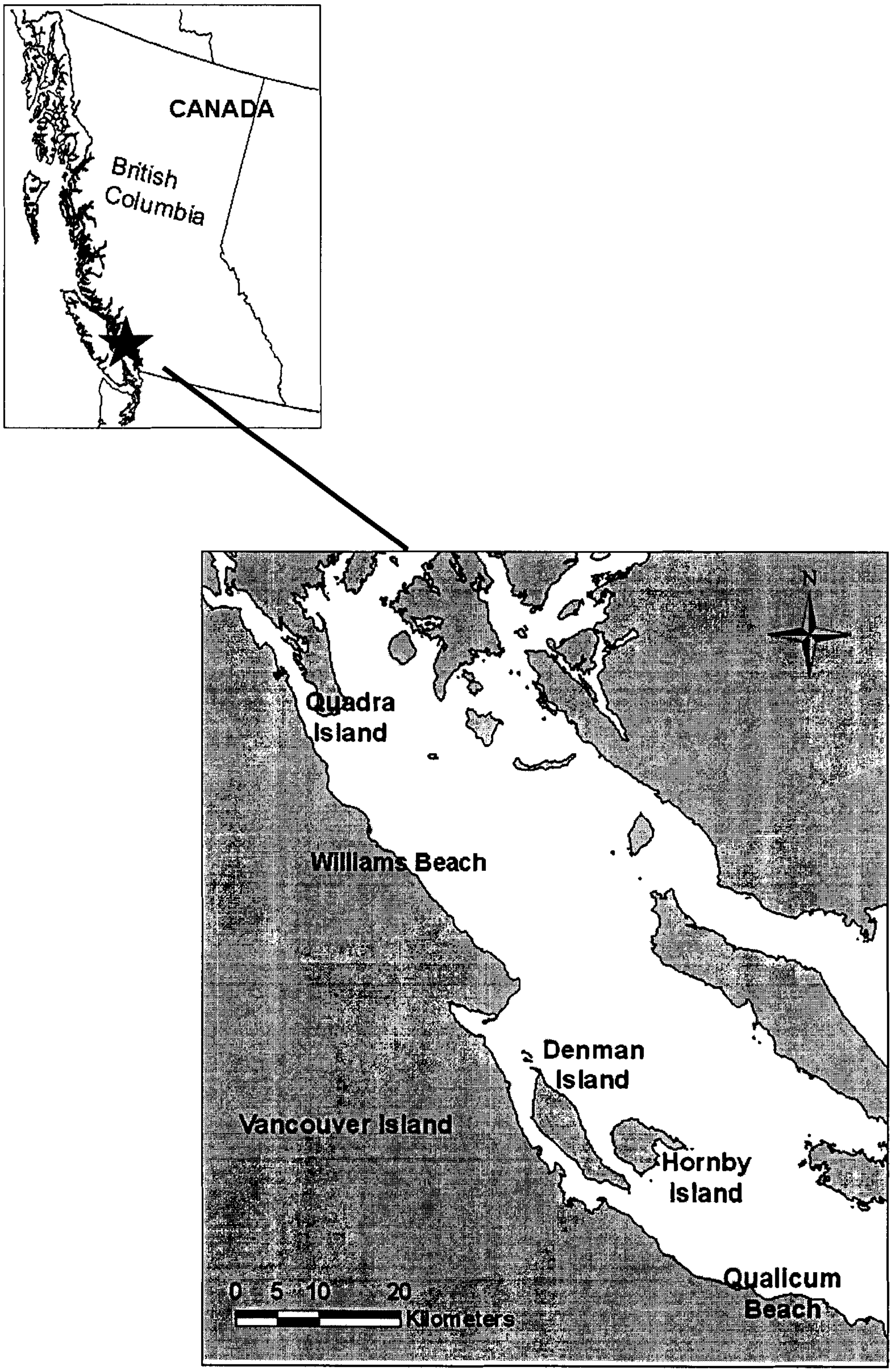


Figure 1.3 Map of wintering area study sites.



CHAPTER 2
NUTRIENT ACQUISITION BY FEMALE HARLEQUIN DUCKS PRIOR TO SPRING MIGRATION AND REPRODUCTION: EVIDENCE FOR BODY MASS OPTIMIZATION

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2.1 Abstract

We analysed variation in body mass of adult female Harlequin Ducks (*Histrionicus histrionicus*) on wintering sites in southern British Columbia, Canada, to investigate the chronology and location of nutrient acquisition prior to migration and reproduction. We found that female mass increased on average by 7% on coastal sites from late-winter to premigration; however, the chronology of mass gain varied depending on prey type. Females feeding on superabundant roe from spawning Pacific Herring (*Clupea pallasi*) became considerably heavier than prespawn measures and appeared to be heavier than females eating marine invertebrates, such as crabs, limpets, and snails, during the herring spawn period (March). By mid-April, prior to migration, females at all sites had similar body masses, with birds at sites without spawn increasing and those at spawn sites maintaining their earlier mass gain. Stable isotope analyses confirmed that birds at these different sites consumed very different diets. These results suggest that female Harlequin

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Ducks target an optimal premigratory body mass, regardless of access to a superabundant food source, and this body mass is likely shaped by the costs and benefits of nutrient storage for migration and reproduction.

2.2 Introduction

There is increasing recognition that cross-seasonal effects should be considered when investigating life history strategies and trade-offs (Tamisier et al. 1995, Gates et al. 2001, Boos et al. 2002, Webster et al. 2002), including those related to nutrient acquisition and allocation. Individuals carry over effects on condition from one season to the next, and these residual effects can influence demographic attributes such as reproductive success and annual survival (Webster et al. 2002). Seasonal variation in nutrient acquisition and allocation is commonly observed in birds as a result of differing energetic demands throughout the year. The relative use of stored nutrients (i.e., endogenous reserves) or dietary sources (i.e., exogenous nutrients) varies interspecifically during demanding stages such as migration and reproduction. The degree to which birds store energy and nutrients presumably reflects an adaptive strategy in which individuals maximize their fitness in relation to different selective pressures (Blem 1976, Moreno 1989, Stearns 1992).

Throughout the annual cycle, birds are thought to maintain optimal levels of endogenous reserves, not necessarily maximum, and this is considered a trade-off based on the costs and benefits of building and storing reserves (Lima 1986, Witter and Cuthill 1993). Benefits of storing nutrients include insulation, mechanical support, buoyancy, and most of all, access to energy (Witter and Cuthill 1993, Biebach 1996), while the costs of storing nutrients include mass-dependent predation risk from reduced flight agility

(Lima 1986, Rogers 1987), mass-dependent foraging costs, and energy conversion inefficiencies (Witter and Cuthill 1993, Jönsson 1997). Decisions on how to balance these costs and benefits are further influenced by the environment in which the species resides.

In waterfowl, strategies of nutrient acquisition for migration and reproduction differ spatially and temporally for various species. For example, McLandress and Raveling (1981) found that Giant Canada Geese (*Branta canadensis maxima*) undergo considerable fattening before they leave wintering sites while Gauthier et al. (1992) determined that Greater Snow Geese (*Chen caerulescens atlantica*) store nutrients while on spring staging areas. Other species such as Ruddy Ducks (*Oxyura jamaicensis*; Tome 1984) and Greater Scaup (*Aythya marila*; Gorman 2005) appear to store nutrients after arrival on nesting areas. These temporal and spatial patterns of nutrient storage are likely affected by predictability and accessibility of exogenous food sources where predictable food supplies may reduce the need for endogenous stores (Jönsson 1997).

The extent to which Harlequin Ducks (*Histrionicus histrionicus*) build and use endogenous stores for migration and reproduction is unknown. If Harlequin Ducks store endogenous reserves for migration and subsequent investment in reproduction, it is important to determine where and when they build these nutrient stores in order to fully understand their nutrient acquisition strategy, and therefore, reveal potential sources of constraints to nutrient acquisition. Harlequin Ducks spend the winter in the marine environment generally consuming intertidal invertebrates such as snails, crabs, and limpets, and in spring, migrate to freshwater streams for nesting where they consume freshwater invertebrates (Robertson and Goudie 1999). Pacific Herring (*Clupea pallasi*) spawn is a key feature of the wintering habitat of Harlequin Ducks on the Pacific coast that could influence nutrient stores. For three to four weeks in late winter-early spring, herring roe is superabundant and some Harlequin Ducks are known to aggregate at herring spawn sites (Vermeer et al. 1997, Rodway et al. 2003). Rodway and Cooke (2002) determined that herring eggs are the principal prey for these aggregated ducks throughout the spawn period. The ecological implications of this food source have received little investigation, although there has been speculation on benefits to survival and/or reproductive potential (Rodway et al. 2003, Žydelis and Esler 2005).

To investigate timing of nutrient storage in Harlequin Ducks, as well as mediating effects of forage type, we measured body mass of captured adult female Harlequin Ducks in winter prior to spring migration. We also used stable isotope analyses to document diets of individuals in order to appropriately interpret the mass data. Our specific objectives were to determine (1) if females store nutrients on the wintering grounds prior to migration, and (2) the relative difference in amount or chronology of nutrient storage between females on herring spawn sites and those on nonspawn sites. For a species of concern like the Harlequin Duck (Robertson and Goudie 1999, Smith et al. 2001), strategies of nutrient acquisition for migration and reproduction can have important implications for understanding factors limiting productivity, and subsequently, can have important population and habitat management ramifications.

2.3 Methods

2.3.1 Study Locations and Capture Techniques

To evaluate body mass variation in relation to timing and occurrence of herring spawn, Harlequin Ducks were captured on marine wintering areas in the Strait of Georgia, British Columbia, at sites with and without spawn during three periods in 2004: prespawn (February 27 to March 5), midspawn (March 19 to 27), and postspawn (April 2 to 11). Capture locations were determined based on historical records of herring spawn occurrence (Fisheries and Oceans Canada 2004), and capture sites with spawn included locations around Hornby Island (49° 31'N, 124° 42'W), Denman Island (49° 32'N, 124° 49'W), and Qualicum Bay (49° 24'N, 124° 38'W) while nonspawn capture sites included locations around southeast Quadra Island (50° 12'N, 129° 15'W) and Williams Beach (49° 52'N, 125° 07'W).

We used a floating mist-net capture method modified for inshore use (Kaiser et al. 1995). Captured birds were immediately removed from the net, and then banded and weighed on an electronic balance (±1 g). We measured morphometric features including exposed culmen length and diagonal tarsal length to the nearest 0.01 mm, as well as wing chord (flattened and straightened) to the nearest mm. Age classes of females were determined by the depth of the Bursa of Fabricius (Mather and Esler 1999), and all females included in further analyses were after-third year (i.e., adults).

2.3.2 Sampling Methods and Laboratory Techniques

Some Harlequin Ducks move from their wintering sites to herring spawn sites and then return to their original wintering site, and because of this, we selected nonspawn sites at which few birds exhibited this movement (Rodway et al. 2003). However, to be sure that birds captured in nonspawn sites had not consumed any herring roe, we used stable isotope analysis to evaluate recent prey composition. The isotopic signatures of consumer tissues are related to their diets (DeNiro and Epstein 1978), and therefore, the stable isotope technique is ideal for identifying individuals that consume different food types. The heavy isotope of nitrogen (^{15}N) is preferentially incorporated into tissues of the consumer from the diet, which results in a systematic enrichment in the nitrogen ratio with each trophic level (Kelly 2000). For this study, we expected herring roe to have a more enriched nitrogen stable isotope value than marine intertidal invertebrates depredated by Harlequin Ducks, and we predicted that this difference would be reflected in the tissues of Harlequin Ducks consuming the different prey. We analysed female plasma because it indicates short-term diet information, i.e., within a few days, rather than cellular blood which may take up to a month to isotopically reflect a dietary change (Hobson and Clark 1992a; Hobson and Clark 1993, Bearhop et al. 2002).

A 1.5 ml blood sample was taken from the jugular veins of captured females using a heparinized 5.0 ml syringe with a 21-gauge needle. For a small number of females, a 1.0 ml syringe with a 24-gauge needle was used to take 0.5 ml of blood from the tarsal vein instead. Collected blood was transferred to a heparinized vial and stored on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 h). These samples were transferred to separate vials and stored frozen. Also, following information provided by Rodway and Cooke (2002), we collected intertidal crabs, snails, limpets, and amphipods as food items making up the majority of Harlequin Duck winter diet, as well as herring roe for comparison.

Samples for stable isotope analyses were prepared at Simon Fraser University and then sent to the Department of Soil Sciences at the University of Saskatchewan for isotope ratio determination. The samples analysed in this study included plasma and marine diet items. Plasma samples were dried in a 60°C oven and ground to a fine powder with a mortar and pestle. The marine diet samples were rinsed with distilled water, removed from shells (for limpets and snails), dried and then powdered in the same fashion. Lipids were removed from the diet samples using a 2:1 chloroform:methanol solution (Bligh and Dyer 1959) and retrieved by evaporating off the solvent in a fume hood. The lipid-free, powdered invertebrate samples were treated with a few drops of a 0.1N HCl solution without rinsing to remove carbonates.

The nitrogen stable isotope signatures of samples were determined by loading 1 mg of each sample into tin cups and combusting them at 1800°C. Then the isotopic ratios were measured using continuous-flow isotope ratio mass spectrometry (CFIRMS). Analytical error for nitrogen isotope measurement was estimated to be 0.3 ‰. All isotope values per sample are expressed in delta (δ) notation, a ratio of the heavier to lighter isotope relative to a standard in parts per thousand. This ratio is written as:

$$\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the corresponding ratio $^{15}N/^{14}N$. The standard for nitrogen is atmospheric nitrogen.

2.3.3 Statistical Methods

We used general linear models to evaluate variation in body mass of adult female Harlequin Ducks on marine areas in relation to spawn site status (spawn vs. nonspawn), period (prespawn, midspawn, and postspawn), and body size. A principal component analysis was conducted to create an index of body size for each individual based on tarsus, wing chord, and culmen measurements. This index, the PC_1 score, showed positive relationships with all morphometric variables and had an eigenvalue of 1.27, explaining 42.5% of the total original variance. PC_1 was included in a subset of candidate models (described below) to consider effects of body size on body mass and, if necessary, account for size-related variation when evaluating effects of sites and periods.

We employed an information-theoretic approach to model selection (Burnham and Anderson 2002), applying a set of biologically plausible combinations of explanatory variables as candidate models (Table 2.1). The assorted models represent different ways of grouping site status and period combinations, which is analogous to a two-way ANOVA with pairwise post-tests in a hypothesis testing statistical paradigm. We used the same model sets with and without PC_1 to allow consideration of body size effects. Because our dataset consisted of 80 females, Akaike's Information Criterion for small sample sizes (AIC_c) was calculated for each model (Table 2.1), which indicates the fit of the model given the data and set of models considered. We also calculated the differences between these values for each model in relation to the best-fitting model (ΔAIC_c) and the AIC_c weights (AIC_cW) for each model, which convey the relative support for each model in the candidate model set.

2.4 Results

2.4.1 Stable Isotope Results

We determined that nitrogen stable isotope values for herring roe and marine invertebrates were, as predicted, different and that after herring spawn commenced, birds captured on spawn sites had plasma isotope values that were more enriched than those at sites where spawn was unavailable (Figure 2.1). We estimated expected plasma values based solely on herring roe diet and mixed marine invertebrate diet by taking an average value for each diet and accounting for changes in isotope signature between prey and duck body tissues (i.e., discrimination or fractionation factors). The discrimination factor between Harlequin Duck plasma and diet has not been experimentally determined, so we applied a literature value of +3.3 ‰ determined for carnivorous species (Peregrine Falcon (*Falco peregrinus*), Hobson and Clark 1992b; Dunlin (*Calidris alpina pacifica*), Evans-Ogden et al. 2004). There was not perfect correspondence between the measured plasma isotope values and the predicted plasma values. This may have been a result of the applied discrimination factor or because we did not sample every possible invertebrate prey type, nor did we know the proportions of different invertebrate prey in the diet. Also, birds feeding primarily on herring spawn may also have consumed some marine invertebrates.

Despite these uncertainties, clear patterns are evident in the data. Plasma stable isotope values were similar for females on both sites prior to the occurrence of herring spawn. Once spawn commenced, stable isotope signatures changed dramatically at spawn sites, consistent with a switch to a more isotopically enriched diet, while isotope signatures on nonspawn sites did not change. Most importantly, there was no isotopic evidence that birds captured at nonspawn areas consumed spawn at any period, and therefore, we are confident that our body mass data accurately represent birds consuming roe and those consuming marine invertebrates. The isotope signatures for some females captured at spawn sites during the postspawn period are decreasing, which presumably is a reflection of birds switching back to consuming marine invertebrates as herring roe becomes less available.

2.4.2 Body Mass Analysis

We captured and measured 80 adult female Harlequin Ducks on wintering sites and found that period, site status, and body size had important effects on body mass. From our candidate set of models evaluating mass variation, the model best supported by the data (model 1, Table 2.1) was that which indicated that body mass differed between the following two groups: birds at both prespawn sites and at nonspawn sites during the midspawn period were in one group, and birds at midspawn spawn sites and both postspawn sites. An examination of the data (Figure 2.2) supports this model structure. This model, which included the body size parameter, was strongly supported with an AIC_cW of 0.628 and an R^2 of 0.41. The second best supported model (model 2) had a similar model structure, with the only difference being that data from the midspawn period at spawn sites were treated as a separate group; this model received less than half the support ($AIC_cW = 0.253$) of model 1. None of the remaining models received substantial support, including global models in which all periods and sites were treated as separate groups (models 6 and 14, with and without PC_1, respectively) and null models in which all data were treated as one group (models 10 and 17, with and without PC_1, respectively). These results strongly support the conclusions that body size explained important variation in the data and that body mass of females differed between prespawn and postspawn periods, but not between sites during those periods. There was more uncertainty surrounding mass dynamics during the midspawn period, although the high AIC_cW for models 1 and 2 combined (summed $AIC_cW = 0.881$) indicates that masses differed between sites during midspawn. Also, models in which midspawn data from both sites were together and either lumped with postspawn (model 4) data or alone (model 5), were not well supported with AIC_cW of 0.045 and 0.015, respectively.

To summarize, our analysis provided strong support for the conclusions that body mass (after accounting for body size) was similar between sites prior to spawn, birds on spawn sites increased mass substantially during the midspawn period while those on nonspawn sites seemed to maintain their prespawn mass, and masses were similar between sites during the postspawn period, due to increases in mass of birds from nonspawn sites and maintenance of previously gained mass by birds from spawn sites. The change in average body mass (± SE) between prespawn and postspawn periods, for both sites, was 40 ± 10 g, an increase of 7 ± 1.8 % (Figure 2.2). Although fewer females were captured during midspawn on nonspawn sites, there is an indication that the chronology of mass gain may depend on prey consumed (i.e., herring roe or marine invertebrates).

2.5 Discussion

Like many waterfowl, adult female Harlequin Ducks store endogenous nutrients on wintering areas prior to spring migration. Our data indicate that, despite differences in forage type and availability on herring spawn sites relative to nonspawn sites, females from both areas achieved a similar body mass prior to departure from wintering areas.

This result suggests that females target an optimal premigratory body mass that balances the costs and benefits of nutrient storage, irrespective of exogenous nutrient availability.

Nutrient acquisition and storage prior to migration and reproduction can have significant fitness benefits. Storing energy for migration is important for sustained flights and reduces the need for stop-overs, which increases the speed of migration, and can buffer against food shortage in low quality stop-over sites (Biebach 1996). For reproduction, a growing body of evidence indicates that female waterfowl must attain some minimum threshold level of nutrient reserves to initiate egg production (Drent and Daan 1980, Alisauskas and Ankney 1994, Esler et al. 2001, Gorman 2005). Hence, arrival on breeding areas with higher levels of energy and nutrients can allow females to attain this breeding threshold faster, and therefore, nest earlier (Schultz 1991, Alisauskas and Ankney 1992). Numerous studies demonstrate that earlier nesting results in higher reproductive success, through larger clutch sizes, increased opportunity for renesting, and/or more favourable environmental conditions for broods (Perrins 1966, Rowe et al. 1994, Lepage et al. 2000).

These benefits of nutrient storage are countered by costs. Predation risk may be higher for heavier birds because of reduced manoeuvrability and ability to escape predators (Lima 1986, Rogers 1987). As well, heavier birds incur higher flight costs through increased wing loading, which is important for migrating birds (Kullberg et al. 2005). This may be especially prominent for ducks, which have relatively high wing loading. Also, for diving birds like the Harlequin Duck, higher fat levels associated with increased mass could increase buoyancy, and therefore, increase costs of foraging (Witter and Cuthill 1993). In light of these potential costs, Harlequin Ducks likely face a trade-off with the potential benefits of nutrient storage.

Our findings indicate that access to Pacific Herring spawn events may influence the chronology of nutrient storage, but it does not affect the absolute amount of nutrients acquired on wintering sites. Herring roe provides a superabundant food source on which Harlequin Ducks are known to aggregate and feed (Rodway and Cooke 2002, Rodway et al. 2003), and fish eggs are a high energy, lipid-rich diet item (Paul and Paul 1999). However, because female Harlequin Ducks can achieve the same premigratory body mass when feeding on intertidal invertebrates, we speculate that there may be benefits to aggregating on spawn sites beyond nutrient acquisition. These may include important social interactions as suggested by Rodway et al. (2003) or an increase in time spent in non-foraging behaviours due to reductions in feeding time (Rodway and Cooke 2001, Žydelis and Esler 2005). Also, Rodway and Cooke (2001) suggested that Harlequin Ducks foraging on herring spawn sites would face less predation risk because they tend to move to safer offshore roosting sites earlier than birds foraging on invertebrates. Therefore, although there are not direct advantages to consuming herring roe and aggregating on spawn sites in terms of nutrient storage, birds may benefit in other ways, and this requires further investigation.

Many other seabirds are known to aggregate and feed at herring spawn sites (Haegele 1993, Vermeer et al. 1997, Sullivan et al. 2002), and it is unknown how their mass dynamics are influenced by herring spawn. Some species may rely more heavily on herring spawn for nutrient acquisition, such as species like scoters that deplete winter foods (Lacroix 2001), and hence may require spawn as a source of nutrients for spring hyperphagia. Also, high arctic nesting species such as the Steller's Eider (*Polysticta stelleri*) that aggregate on herring spawn prior to migration (Žydelis and Esler 2005) may depend on this food source for breeding on potentially food-limited sites. The proportion of a population that aggregates on herring spawn sites may be indicative of the population's dependence on spawn for meeting energetic costs (Vermeer et al. 1997), as illustrated by the fact that not all Harlequin Ducks in the Strait of Georgia aggregated during spawning events. Elucidating strategies for meeting the demands of migration and reproduction, including the role of herring spawn, are critical for informed management and conservation of bird species. As well, these strategies highlight the importance of considering cross-seasonal effects when managing populations.

2.6 Acknowledgements

We acknowledge BC Hydro Bridge Coastal Restoration Program and Environment Canada Science Horizons Program for financial support and the Centre for Wildlife Ecology at Simon Fraser University for logistical support. For assistance in the field, we thank E. Anderson, J. Bond, K. Bond, J. Harding, J. Heath, S. Iverson, S. LeBourdais, E. McClaren, K. Wright, and R. Žydelis. T.D. Williams, R.C. Ydenberg, and S.E. Jamieson provided useful comments on earlier drafts. Also, T.D. Williams provided laboratory facilities at Simon Fraser University. Thanks to K.A. Hobson, P. Healy, M. Benjamin, and M. Stocki for assistance with stable isotope analysis.

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Table 2.1 Candidate models describing variation in female Harlequin Duck body mass in relation to period (before herring spawn [pre], during herring spawn [mid], and following herring spawn [post]), site status (herring spawn site [S] and nonspawn site [N]), and a principal component score of morphometrics that indexes body size (PC_1).

K is the number of parameters estimated in the model, AIC_c is Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c is the difference in AIC_c relative to the best-fitting model, and AIC_cW is the AIC_c weight or model likelihood.

Model Rank	**Candidate Model Structure**	**K**	**AIC_c**	**ΔAIC_c**	**AIC_cW**
model 1	preN = preS = midN, midS = postN = postS + PC_1	4	551.64	0.00	**0.628**
model 2	preN = preS = midN, midS, postN = postS + PC_1	5	553.45	1.81	**0.253**
model 3	preN = preS = midN = postN, midS = postS + PC_1	4	556.89	5.25	0.046
model 4	preN = preS, midN = midS = postN = postS + PC_1	4	556.91	5.27	0.045
model 5	preN = preS, midS = midN, postS = postN + PC_1	5	559.16	7.52	0.015
model 6	preN, preS, midN, midS, postN, postS + PC_1	8	559.48	7.84	0.012
model 7	preN = preS = midN = postN = postS, midS + PC_1	4	564.80	13.16	0.001
model 8	preN = midN = postN, preS = midS = postS + PC_1	4	567.39	15.75	0.000
model 9	preN = preS = midN, midS = postN = postS	3	568.43	16.79	0.000
model 10	PC_1	3	568.72	17.09	0.000
model 11	preN = preS = midN, midS, postN = postS	4	570.28	18.64	0.000
model 12	preN = preS, midN = midS = postN = postS	3	572.31	20.67	0.000
model 13	preN = preS, midS = midN, postS = postN	4	574.52	22.88	0.000
model 14	preN, preS, midN, midS, postN, postS	7	577.12	25.48	0.000
model 15	preN = preS = midN = postN, midS = postS	3	577.75	26.11	0.000
model 16	preN = preS = midN = postN = postS, midS	3	584.77	33.13	0.000
model 17	preN = preS = midN = midS = postN = postS	2	589.46	37.82	0.000
model 18	preN = midN = postN, preS = midS = postS	3	590.05	38.41	0.000

Figure 2.1 Plasma nitrogen isotope ratios of female Harlequin Ducks captured on Pacific Herring spawn sites and nonspawn sites during the three periods corresponding to before, during, and after spawn.
Dotted line = expected plasma values based solely on herring roe. Dashed line = expected plasma values based solely on equal portions of several marine invertebrates (snail, crab, amphipod, and limpet). Discrimination factors were applied to create expected plasma values (see results).

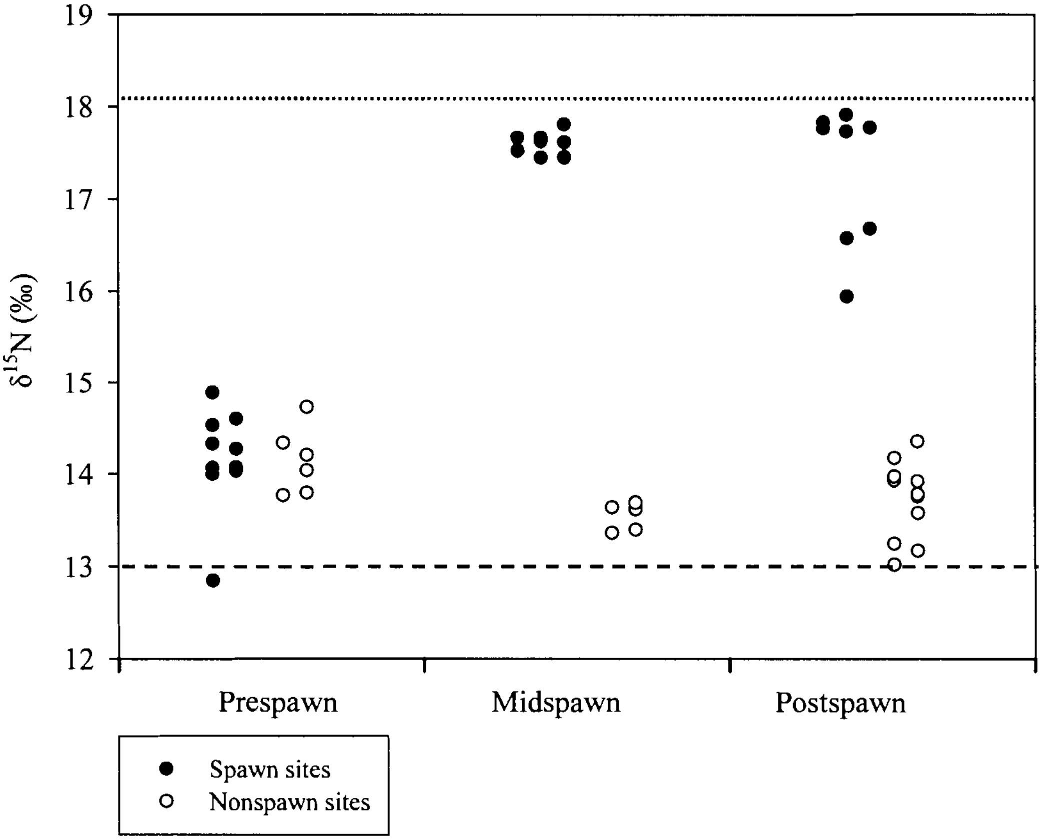
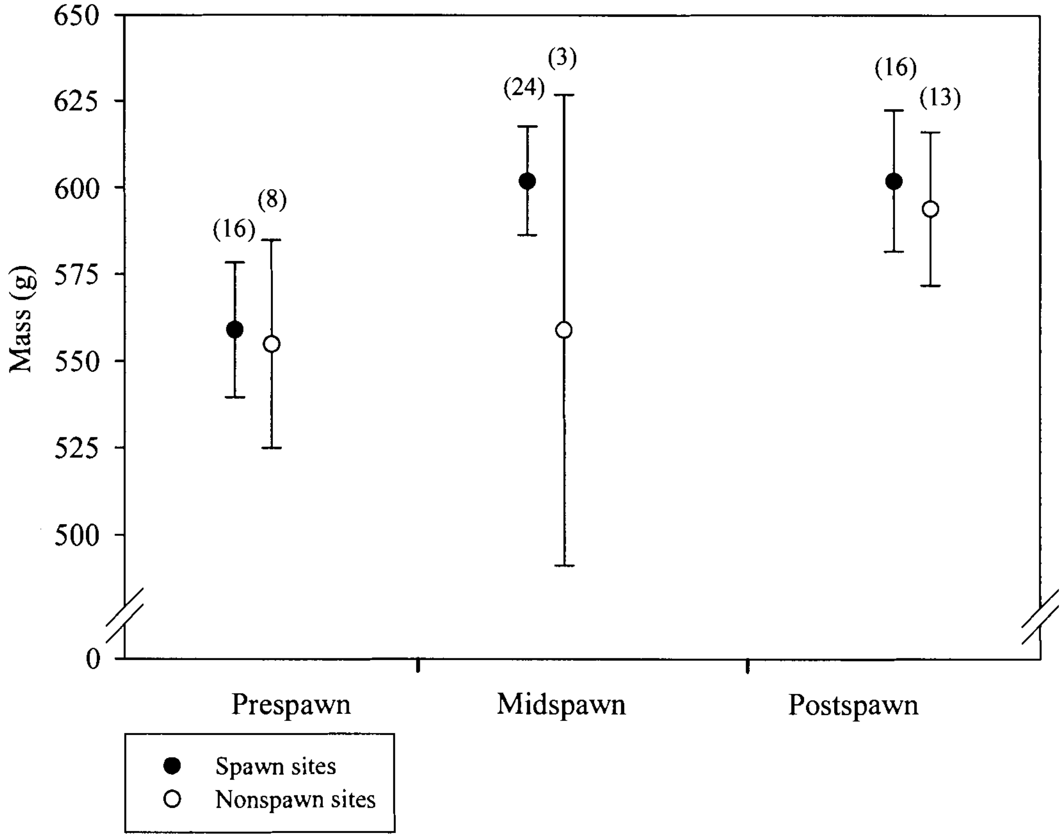


Figure 2.2 Mass (mean ± 95% CI) of adult female Harlequin Ducks on wintering sites with and without spawning Pacific Herring during prespawn, midspawn, and postspawn periods in the Strait of Georgia, BC. Sample sizes for each group are indicated in parentheses.



CHAPTER 3
ISOTOPIC EVIDENCE FOR SOURCES OF NUTRIENTS ALLOCATED TO CLUTCH FORMATION BY HARLEQUIN DUCKS

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3.1 Abstract

Waterfowl employ a broad array of strategies for acquiring energy and nutrients needed for egg formation, ranging from storage of endogenous reserves prior to arrival on breeding areas to complete reliance on exogenous food sources available at breeding sites. We used stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to quantify the relative nutrient inputs to Harlequin Duck (*Histrionicus histrionicus*) eggs, and therefore, identify the strategy of nutrient acquisition and allocation used by females to meet demands of egg production. Harlequin Ducks migrate between isotopically distinct marine wintering grounds and freshwater breeding grounds, which facilitates the use of stable isotope signatures to track origins of nutrients. We found little evidence that endogenous reserves stored on marine wintering areas were allocated to clutch formation, with egg isotope signatures reflecting mostly freshwater nutrient sources. Therefore, Harlequin Ducks relied on food available on breeding streams for egg formation, and any reserves stored

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on marine areas were likely used during other energetically and nutritionally demanding stages.

3.2 Introduction

Animals maximize fitness through optimal resource use, which involves employing various strategies of nutrient acquisition and allocation throughout the annual cycle (Calow and Townsend 1981, Jönsson 1997). Egg production in birds can be an energetically and nutritionally demanding stage, particularly for precocial breeders like waterfowl that lay large clutches of energy-dense eggs (Alisauskas and Ankney 1992). Waterfowl exhibit an array of strategies for meeting demands of clutch formation. One strategy is to build nutrient stores prior to breeding that can be subsequently invested in reproduction. These stores are known as endogenous reserves, and use of these reserves for reproduction has been referred to as 'capital' breeding (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999). Alternatively, reliance on locally available food sources, also known as exogenous resources, to acquire energy and nutrients for reproduction has been termed 'income' breeding (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999).

Nutrient acquisition and allocation for clutch formation by waterfowl spans a continuum of capital to income strategies, and can even be variable within species. Although strict capital breeding is now considered rare (Meijer and Drent 1999), some species such as Common Eiders (*Somateria mollisma*) have been reported to rely heavily on endogenous reserves for egg production (Parker and Holm 1990). Alternatively, Northern Shovelers (*Anas clypeata*) and Greater Scaup (*Aythya marila*) in Alaska rely almost entirely on dietary intake (MacCluskie and Sedinger 2000, Gorman 2005), and many species apparently use intermediate proportions of endogenous reserves for clutch formation, including Lesser Scaup (*Aythya affinis*; Esler et al. 2001), Canvasbacks (*Aythya valisineria*; Barzen and Serie 1990), and Ruddy Ducks (*Oxyura jamaicensis*; Tome 1984, Alisauskas and Ankney 1994). Also, Esler and Grand (1994) demonstrated that there can be intraspecific variation in endogenous reserve use. Identifying the nutrient allocation strategy for different species and populations offers insight into resource use and the suitability of differing habitats for meeting the requirements of reproduction. As well, in a conservation context, this information allows recognition of when and where nutritional constraints might be expressed, which can lead to important population and habitat management ramifications (Anteau and Afton 2004).

Traditionally, energetic strategies used by waterfowl during egg production have been inferred from carcass analysis of collected females (Alisauskas and Ankney 1992). With this method, the change in endogenous reserves relative to investment of nutrients into reproductive tissue can be interpreted as the maximum proportion of the clutch that could be derived from endogenous reserves. For example, if endogenous lipid reserves decline 0.5 of a gram for every gram of lipid used for egg production, no more than 50% of the egg lipid could be derived from endogenous reserves. However, it is unclear how much of the female's reserves actually go into eggs, and how much are used for meeting her own energy requirements (Meijer and Drent 1999, Hobson et al. in press). This could result in an overestimation of nutrients transferred from endogenous reserves to eggs (Meijer and Drent 1999).

More recently, stable isotope analysis has been employed to directly trace nutrient allocation for reproduction (Hobson et al. 2000, Klassen et al. 2001, Gauthier et al. 2003, Hobson et al. in press). This method uses naturally occurring stable isotope signatures in the environment as a means of identifying nutrient sources for egg formation. The isotopic signatures of consumer tissues are related to their diets (DeNiro and Epstein 1978), and therefore, the stable isotope technique is ideal for identifying nutrients acquired from differing environments, either directly through diet or through tissues of laying females. Marine ecosystems are typically enriched in ^{13}C and ^{15}N relative to terrestrial or freshwater ecosystems (Michener and Schell 1994). Birds that migrate between wintering and breeding grounds that differ in isotopic composition, such as marine and freshwater, will have stored nutrients that differ isotopically from locally available nutrient sources (Hobson in press).

In this study, our objective was to identify the nutrient allocation strategy for clutch formation in Harlequin Ducks (*Histrionicus histrionicus*) by quantifying the relative inputs of nutrients from wintering sites and breeding sites into eggs using stable isotope analyses. Stable isotopes are particularly useful for addressing these issues because Harlequin Ducks winter in marine environments and breed along freshwater streams. In both areas, they feed on invertebrate prey (Robertson and Goudie 1999). On wintering areas, immediately prior to migration and reproduction, adult females increase in mass by 7% (Chapter Two), but it is unknown if these acquired nutrients are allocated to egg formation. We investigated the extent to which these acquired nutrients might be allocated to migration, and determined that only 2.6% of their wintering endogenous reserves would be used to fly to the breeding study site (Appendix). Hence, it is possible that females allocate some marine nutrients to egg production, and this information is important for understanding factors influencing reproductive performance.

3.3 Methods

3.3.1 Study Area and Capture Techniques

Harlequin Ducks were captured on breeding streams using mist nets from May 9 to 20, 2003, and from April 21 to May 20, 2004, in the southern Coast Mountains of British Columbia, Canada. The study area included streams near the towns of Pemberton (50° 19'N, 122° 48'W) and Lillooet (50° 41'N, 121° 56'W). Wintering ducks also were captured from February 27 to April 11, 2004, in the Strait of Georgia, British Columbia, using a floating mist-net capture method adapted for inshore ocean use (Kaiser et al. 1995). Captured birds were immediately removed from the net, and then weighed, banded, and assigned to an age class based on the depth of the Bursa of Fabricius (Mather and Esler 1999).

3.3.2 Sample Collection

Samples of blood were taken from captured wintering females for stable isotope analyses to represent endogenous marine nutrients. A 1.5 ml blood sample was taken from the jugular vein using a heparinized 5.0 ml syringe with a 21-gauge needle. For a small number of females, a 1.0 ml syringe with a 24-gauge needle was used to take 0.5 ml of blood from the tarsal vein instead. Collected blood was transferred to a heparinized vial and stored on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 h). These samples were transferred to separate vials and stored frozen.

Also, a subcutaneous lipid biopsy was taken from each wintering female. Feathers in the area of lipid depots on the belly were parted using isopropyl alcohol and the site was prepped with Betadine solution. Using forceps, the skin was lifted and a small (~ 5 mm) incision in the skin was made with surgical scissors. Several milligrams of lipid in the region of the incision were removed with forceps. The incision site was sealed with veterinary-grade adhesive. Lipid samples were kept frozen until analysis.

In order to find nests for egg collection, each female captured on breeding streams was attached with a radio transmitter using a subcutaneous anchor and glue. The transmitters, made by Holohil Systems Ltd, were a six-gram RI-2B model with a motion-sensitive mortality sensor and a battery life of three to nine months. The transmitter was located in the small depression between the scapulae, dorsal to the approximate junction of the cervical and thoracic vertebrae. We monitored radio-tagged females at least once a week to locate nests, and we removed one egg at random from each discovered clutch. Clutches ranged from five to seven eggs. One egg was provided (by S. Freeman) for our study from the Skagit River (49° 00'N, 121° 05'W) in southern British Columbia. We also opportunistically collected two full clutches; in 2003, one female abandoned her nest due to rain and flooding, and in 2004, a female was depredated, leaving her clutch unattended. All collected eggs were hard boiled and then frozen (Gloutney and Hobson 1998).

Prey samples were collected from breeding streams to represent freshwater nutrient sources. Freshwater invertebrate larvae such as stoneflies, mayflies, and caddisflies were collected from each stream in the study area; these are the major diet items of Harlequin Ducks on streams (Wallen 1987, Wright et al. 2000). These samples were frozen in vials until analysis.

3.3.3 Laboratory Techniques

Samples for carbon and nitrogen stable isotope ratio analyses were prepared at Simon Fraser University and then sent to the Department of Soil Sciences at the University of Saskatchewan for isotope ratio determination. Samples were separated into lipids and nonlipid components, if necessary, because of potential differences in allocation of these nutrients to eggs. Samples analysed for this study included abdominal lipid ($n = 18$), cellular fraction of blood ($n = 60$), freshwater invertebrates (lipid [$n = 5$] and nonlipid [$n = 9$] components), lipid-free egg yolk ($n = 23$), egg yolk lipid ($n = 23$), and egg albumen ($n = 23$). Cellular blood samples were dried in a 60°C oven and homogenized by grinding to a fine powder with a mortar and pestle. Freshwater diet samples were rinsed with distilled water, dried, and then homogenized. Lipids were removed from the diet samples using a 2:1 chloroform:methanol solution (Bligh and Dyer 1959) and retrieved by evaporating off the solvent in a fume hood. The lipid-free, homogenized samples were treated with a few drops of a 0.1N HCl solution without rinsing to remove carbonates. Abdominal fat was subsampled and analysed directly. Eggs were separated into yolk and albumen easily because they were previously hard boiled. Albumen was dried and ground into a fine powder. The egg yolk was dried, and yolk lipid and lipid-free yolk were separated using the same extraction methods described above.

The carbon and nitrogen stable isotope signatures of samples were determined by loading 1 mg of each sample into tin cups and combusting them at 1800°C. Then the isotopic ratios were measured using continuous-flow isotope ratio mass spectrometry (CFIRMS). Analytical error for each isotope measurement was estimated to be 0.1 ‰ and

0.3 ‰ for carbon and nitrogen isotope measurements, respectively. All isotope values per sample are expressed in delta (δ) notation, a ratio of the heavier to lighter isotope relative to standards in parts per thousand. This ratio is written as:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard for carbon is PeeDee Belemnite (PDB) and for nitrogen the standard is atmospheric nitrogen.

3.3.4 Statistical Methods

To evaluate the relative contributions of source nutrients (marine or freshwater) to eggs, we used a single-isotope linear mixing model for carbon and for nitrogen (Phillips and Gregg 2001). We were only interested in considering two nutrient sources for the eggs so we did not look at both isotopes simultaneously, i.e., in a dual-isotope mixing model. Also, because lipid contains very little nitrogen, only carbon isotope values were used to model origins of this macronutrient. The two-endpoint linear mixing model can be formulated from the following mass balance equations for a mixture (M) and two sources (A and B) (Phillips and Gregg 2001):

$$\delta_M = f_A\delta_A + f_B\delta_B \qquad 1 = f_A + f_B$$

where δ is the mean isotopic signature and f is the proportion of the source found in the mixture. Then the mean proportion of source A in the mixture can be calculated as (Phillips and Gregg 2001):

$$f_A = \frac{\delta_M - \delta_B}{\delta_A - \delta_B}$$

For freshwater food sources, we used the mean lipid and nonlipid isotopic values (± SE) from the freshwater invertebrate samples collected in our study area (nonlipid: $\delta^{13}C$ = -25.4 ± 0.8 ‰, $\delta^{15}N$ = 2.2 ± 0.4 ‰; lipid: $\delta^{13}C$ = -29.7 ± 1.4 ‰). For endogenous marine sources, we used wintering tissues of cellular blood ($\delta^{13}C$ = -13.9 ± 0.1 ‰, $\delta^{15}N$ = 14.0 ± 0.2 ‰) for nonlipid samples and abdominal lipid ($\delta^{13}C$ = -19.7 ± 0.3 ‰) for lipid samples collected from the captured females. These body tissues do not appear to turnover quickly, and therefore, they represent an average winter diet (Hobson and Clark 1992a, Hobson 2005). We then investigated the relative contributions of these marine and freshwater sources to egg albumen, lipid-free yolk, and yolk lipid tissues.

A critical assumption implicit in the application of the stable isotope technique is that stable isotope concentrations of consumer diets can be related to those of consumer tissues in a predictable fashion (Hobson and Clark 1992b). The changes in isotope values from diet to tissue, also known as isotopic discrimination (or fractionation) factors, have been experimentally determined for various somatic tissues (Hobson and Clark 1992b, Bearhop et al. 2002) and for egg components (Hobson 1995). Although there is debate regarding the applicability of discrimination factors between species and between different tissues (Dalerum and Angerbjörn 2005), it has been recommended to use tissue-specific factors determined for closely related species with similar diets and habitats, in order to minimize errors associated with incorrect discrimination factors (Vanderklift and Ponsard 2003). Because Hobson (1995) is the only published report of discrimination factors between diet and egg tissues, we used his estimates for the carnivore model as being most similar to Harlequin Ducks. For exogenous sources, we used discrimination factors where carbon fractionates by 0 ‰ for yolk lipid and nonlipid and by +0.9 ‰ for albumen, and nitrogen fractionates by +3.4 ‰ for egg yolk nonlipid and albumen from diet to tissues. Discrimination factors for endogenous sources to eggs have not been experimentally determined, and so we followed Gauthier et al. (2003) and Schmutz et al. (in press) in using discrimination factors from the same carnivore model (Hobson 1995), assuming that mobilization of nutrients from somatic tissues is similar to a carnivorous diet.

The mixing model analyses calculated the mean contribution to eggs over the entire clutch because only one randomly chosen egg was analysed from each clutch. However, because we opportunistically collected two full clutches, we were also able to calculate intraclutch variation using a coefficient of variation and compare this to the variation between clutches.

3.4 Results

Of the 34 female Harlequin Ducks captured on breeding streams in the southern Coast Mountains of British Columbia, 22 were discovered on nests. We collected single eggs from 20 of those nests, complete clutches from the remaining two, and received a single egg from a nest on the Skagit River.

Female Harlequin Ducks allocated almost entirely freshwater nutrients to egg formation. From the carbon mixing model, we estimated that 100% (95% confidence interval = 83-100%) of the nutrients for egg albumen and lipid-free yolk were derived from breeding stream sources, and that 100% (95% confidence interval = 60-100%) of the nutrients for yolk lipid also came from freshwater nutrients (Figure 3.1). The nitrogen mixing model produced similar results but indicated a slight transfer of endogenous marine nutrients, especially for lipid-free yolk (89%; 95% confidence interval = 81-98%).

The conclusion that Harlequin Duck eggs are produced almost entirely from freshwater nutrients is supported by examination of plots showing isotopic signatures from the marine and freshwater biomes. Carbon and nitrogen isotope values for nonlipid components of eggs were clearly clustered with the values for freshwater invertebrates, and were distinct from the cluster of values for blood collected on wintering sites (Figure 3.2). Similarly, carbon values for yolk lipid matched those of lipid in freshwater invertebrates and were dissimilar from carbon isotope values of abdominal lipid collected from Harlequin Ducks on wintering areas (Figure 3.3).

We contrasted interclutch and intraclutch variation in stable isotope signatures, and found that variation within clutches was considerably smaller than variation between clutches (Figures 3.4 and 3.5). The interclutch coefficient of variation (CV) for egg yolk nonlipid was 18% and 9% for nitrogen and carbon, respectively. In contrast, intraclutch CVs for nitrogen and carbon were 4% and 3%, respectively, for clutch #1 and 2% and 1%, respectively, for clutch #2 (Figure 3.4). Similarly, the interclutch CV for carbon in egg yolk lipid was 8%, compared to intraclutch CVs of 1% for each complete clutch (Figure 3.5). Even with the higher variation between clutches, the results are still strongly indicative of freshwater rather than marine contributions.

3.5 Discussion

Our stable isotope data indicate that Harlequin Ducks allocated little to no nutrients acquired on marine wintering areas to egg formation, and these results are similar for both protein and lipid components. Therefore, freshwater breeding site nutrient allocation is the predominant strategy of Harlequin Ducks for clutch formation in the southern Coast Mountains of British Columbia.

Because our results were based on a randomly chosen egg from each clutch, they represent the average strategy of nutrient allocation to egg production. There is some evidence to suggest, however, that there can be significant intraclutch variation in sources of egg nutrients. Both Barrow's Goldeneye (*Bucephala islandica*; Hobson et al. in press) and Redhead Duck (*Aythya americana*; Hobson et al. 2004) females allocated more endogenous stores to eggs laid early in the sequence than to later laid eggs. It has been speculated that endogenous nutrients unused during migration are invested in egg formation (Rohwer 1992, Hobson et al. in press) or that females can start egg production earlier if supplemented by some endogenous stores (Schultz 1991, Alisauskas and Ankney 1992). Our data do not support hypotheses of opportunistic marine endogenous transfer to eggs by Harlequin Ducks because variation within clutches is small and entirely within the freshwater range of isotope values. This suggests that values from a single egg per clutch for Harlequin Ducks are representative of each individual's strategy, and when pooled, allow appropriate inference about the average strategy of the population.

Some differences in isotope values were evident among clutches in our data. We suggest that this is not related to variation in strategies of nutrient acquisition and allocation among females, but rather, is due to differences in isotopic signatures across streams and freshwater diets. Other studies have found a lack of precision in freshwater endpoints (Hobson et al. 2004, Hobson et al. in press), and this is likely caused by different processes affecting each of the freshwater sources. In the study system, isotopic signatures between streams differed slightly and the exact prey composition of females' diets also likely differed, and these dissimilarities would lead to variation among eggs laid by different individuals. Despite variation in signatures among clutches, the egg components fall almost entirely within the isotopic range of freshwater stream invertebrates.

If female Harlequin Ducks use freshwater nutrients to form eggs, why do they store endogenous reserves on wintering grounds prior to migration (Chapter Two)? As shown in the Appendix, flights costs for Harlequin Ducks from the Strait of Georgia to our breeding study site near Lillooet are slight and would result in only a 2-3% reduction in body mass. It has been suggested that females may store nutrients to hedge against unfavourable conditions on breeding grounds when they arrive or they could be strategically storing limiting nutrients required for the physiological changes associated with reproduction (Rohwer 1992, Morrison and Hobson 2004). Another possibility is that stored nutrients could be used for the female's own maintenance during clutch formation or during subsequent stages of reproduction, such as incubation. Incubation in waterfowl can be a demanding stage of reproduction, especially because of reduced feeding associated with many incubation strategies (Afton and Paulus 1992). Nesting success has been related to body condition, where the depletion of endogenous reserves may lead to nest failure through nest abandonment or decreased nest attentiveness (Gloutney and Clark 1991, Arnold et al. 1995). Decreased nest constancy can leave the nest vulnerable to predation, and may also result in suboptimal egg temperatures for egg survival (Afton and Paulus 1992, Schmutz et al. in press). Therefore, the condition of females prior to incubation can be very influential to breeding success. In Harlequin Ducks, females are the sole incubators and are thought to take an abeyance from the nest once a day to feed and preen (Robertson and Goudie 1999). Hunt (1997) found that female Harlequin Duck mass decreased by 11% from laying to brood rearing, which indicates significant energy demands during incubation. Thus, it may be beneficial for females to store endogenous marine nutrients in order to meet these high energy requirements.

Harlequin Ducks may be simultaneously balancing demands of clutch formation and benefits of nutrient stores for incubation. Physiologically, it may be more efficient for females to convert exogenous, dietary nutrients directly to eggs rather than mobilizing endogenous reserves. The basis for this is that it would take more processing, with associated decreases in physiological efficiency, to allocate endogenous nutrients into eggs as opposed to currently ingested nutrients. If sufficient nutrients are available locally, then endogenous reserves built on wintering grounds could be used for female maintenance during laying and during incubation. Schmutz et al. (in press) determined that arctic-nesting geese used a mixed strategy of endogenous and exogenous resources for egg production, but also found isotopic evidence of significant endogenous marine reserve use during incubation. This suggests that these geese are 'saving' some endogenous resources for incubation and supplementing egg production with exogenous sources.

The capital/income classification would put Harlequin Ducks in the income breeder category because they use exogenous reserves for egg formation. However, the capital and income strategies, as they have become known, are in need of some clarification. The definitions have changed from their original meaning proposed by

Drent and Daan (1980), which were related to timing of reproduction and clutch size determination. Now these terms are generally used to investigate energy and nutrient storage for reproduction (Stearns 1992, Jönsson 1997). In recent literature, reproduction has been replaced in this definition with egg production, with the justification that this is the most demanding stage especially for precocial birds. However, nutrients required for reproduction are those necessary for egg production and female maintenance (Meijer and Drent 1999, Schmutz et al. in press), and endogenous reserves may be used to varying degrees for the different stages of reproduction, not just egg formation. Meijer and Drent (1999) alluded to this by pointing out that it would be more correct to distinguish between ‘capital layers’ and ‘capital breeders’ because these breeding strategies are quite different. In the case of the Harlequin Ducks, they may be using marine endogenous reserves for incubation, but not egg formation. Therefore, when considering capital and income strategies, it is important to investigate how endogenous reserves may be used during the entire reproductive period.

We have demonstrated that the nutrient allocation strategy for clutch formation by Harlequin Ducks in the southern Coast Mountains of British Columbia involves mostly freshwater sources. Therefore, they are highly dependent on stream productivity and access to invertebrate food items for egg production, and this should be taken into consideration when altering or managing stream habitats. If females have reduced food levels on streams during the clutch formation stage, this may impede their ability to produce viable eggs, which could lead to consequences for population demographics. Because of current concerns regarding low productivity for Harlequin Ducks in southern British Columbia (Smith et al. 2001, Rodway et al. 2003), future research could investigate how food limitation on breeding streams may influence egg production. Previous work has linked diving duck productivity and food availability (Gardarsson and Einarsson 2004, but see Goudie and Jones in press), but more research is required to address the issue of food limitation and resultant effects on productivity in Harlequin Ducks.

3.6 Acknowledgments

We acknowledge BC Hydro Bridge Coastal Restoration Program and Environment Canada Science Horizons Program for financial support and the Centre for Wildlife Ecology at Simon Fraser University for logistical support. For assistance in the field, we thank C. Alec, E. Anderson, J. Bond, K. Bond, S. Boyd, S. Copeland, S. Freeman, J. Harding, J. Heath, S. Iverson, S. LeBourdais, E. McClaren, S. Smith, K. Wright, and R. Žydelis. Also, H. Nichol generously provided field housing near Pemberton. T.D. Williams, R.C. Ydenberg and S.E. Jamieson provided useful comments on earlier drafts. T.D. Williams provided laboratory facilities at Simon Fraser University. Thanks to P. Healy, M. Benjamin, and M. Stocki at the University of Saskatchewan assistance with stable isotope analysis.

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Figure 3.1 Percentage of Harlequin Duck egg components derived from nutrients acquired on freshwater breeding streams (± SE) based on mixing models analyses of carbon (C) and nitrogen (N) stable isotopes.

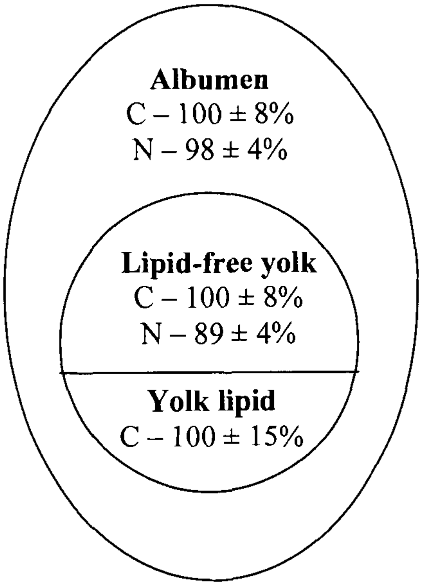


Figure 3.2 Lipid-free carbon and nitrogen stable isotope values for wintering blood, freshwater invertebrates, egg yolk, and egg albumen of Harlequin Ducks. Note: discrimination factors applied to egg components (see methods).

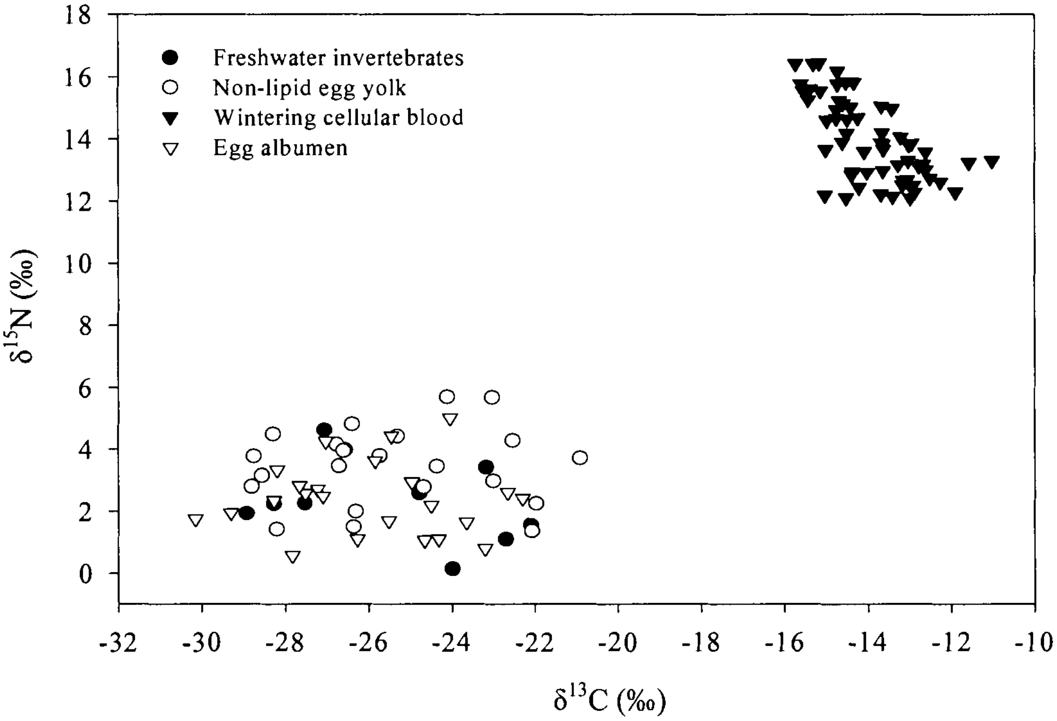


Figure 3.3 Carbon stable isotope values for lipid from freshwater stream invertebrates, and yolk lipid and winter abdominal lipid of Harlequin Ducks.

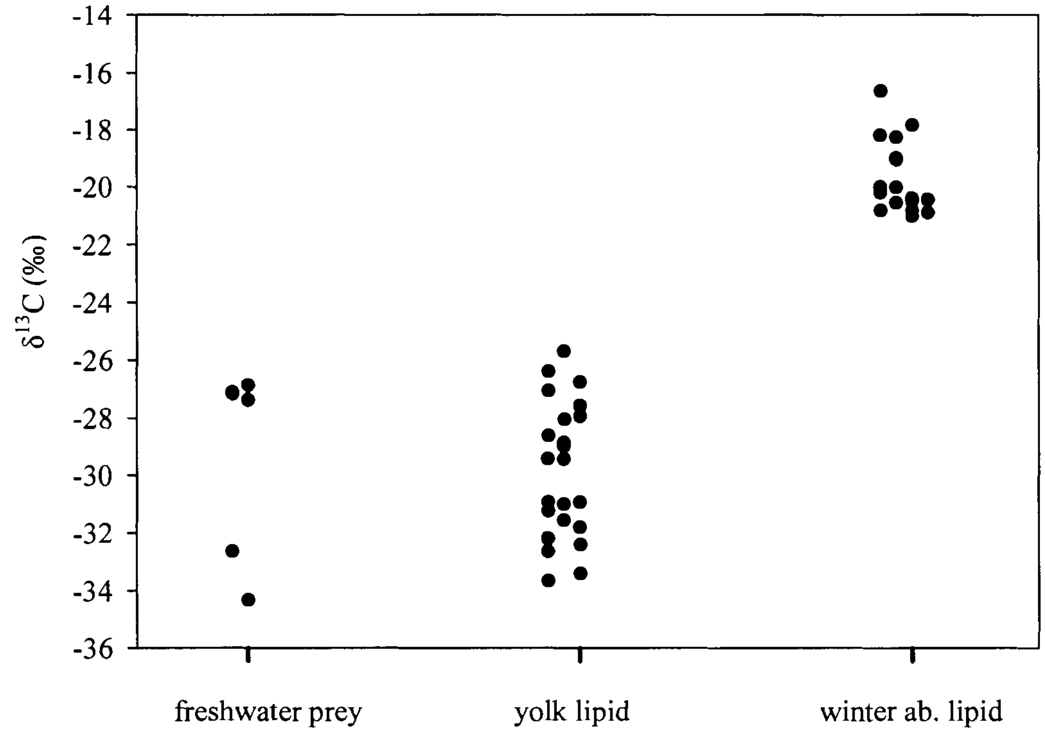


Figure 3.4 Interclutch and intraclutch variation in carbon and nitrogen stable isotope values for lipid-free egg yolk.
The approximate marine stable isotope values for carbon and nitrogen are also shown (from wintering female blood samples).

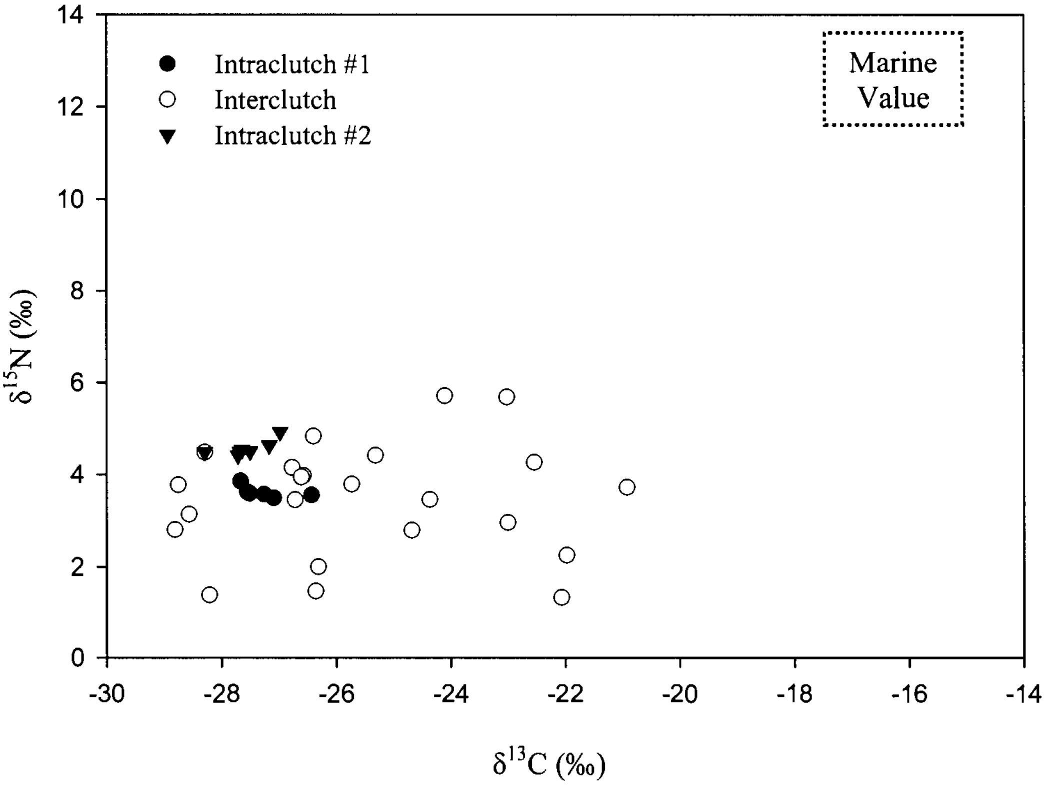
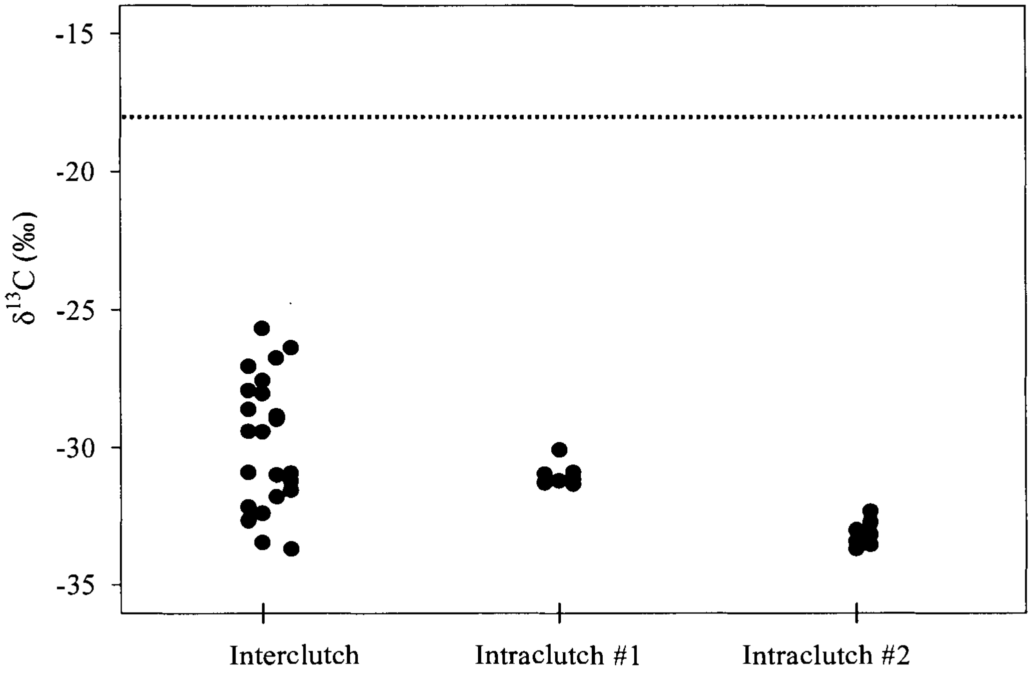


Figure 3.5 Interclutch and intraclutch variation for carbon stable isotope values of egg yolk lipid.
Dashed line indicates approximate value of a marine signature from our samples of female abdominal lipid in winter.



CHAPTER 4
ESTIMATES OF BREEDING PROPENSITY FOR HARLEQUIN DUCKS: A NOVEL APPROACH USING YOLK PRECURSORS AND RADIO TELEMETRY

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4.1 Abstract

Breeding propensity, the proportion of reproductively capable females that initiate egg production, is an important trait when considering reproductive performance in birds. Unfortunately, appropriate methods for quantifying breeding propensity have not been available for many systems. A persistent problem when attempting to document rates of breeding propensity is that failed breeders, especially those that fail early, are difficult to distinguish from nonbreeders, and this can lead to underestimates of breeding propensity. Female Harlequin Ducks (*Histrionicus histrionicus*) have been speculated to show high rates of deferred breeding, although no study of this species has been able to apply an appropriate method to address this issue. We employed a novel approach combining information from radio telemetry and yolk precursor (vitellogenin and very-low-density lipoprotein) analyses to quantify breeding propensity of adult female Harlequin Ducks. Using both methods, we estimated that breeding propensity of females that migrated to

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breeding streams was 92%, the highest estimate reported to date. In our study, telemetry misclassified breeders that failed early (21%), and yolk precursor analyses misclassified breeders captured outside of the egg formation period, although this was rare (3%). These data can lend insight into life history strategies and potential sources of constraints on productivity of Harlequin Ducks. Further, these methods can be applied to other species to derive accurate estimates of reproductive effort.

4.2 Introduction

Intermittent or deferred breeding in birds is a widespread phenomenon, and estimates of nonbreeding rates have indicated that this behaviour can be extensive in some populations, especially in seabirds (Coulson 1984, Cam et al. 1998). This nonbreeding by sexually mature individuals is often viewed in the context of life history theory as a trade-off between current and future reproductive potential (Stearns 1992, Chastel et al. 1995, Golet et al. 1998). In this way, nonbreeding has been proposed as an adaptive strategy for long-lived species under certain conditions (Wooller et al. 1989). Proximate factors suggested to influence rates of nonbreeding include body condition (Drent and Daan 1980, Coulson 1984, Johnson et al. 1992) and inter-individual variation in quality (Mills 1989, Cam et al. 1998). It is likely that rates of nonbreeding are affected by multiple causes, and that individual state, as well as external factors such as food shortage or severe environmental fluctuations, are both influential (Cam et al. 1998).

Overall reproductive success is the product of success across a series of reproductive stages including breeding propensity, which we define as the proportion of females that initiate the egg formation process (the inverse of nonbreeding). The literature is replete with studies of rates of avian reproductive performance at most stages, such as nesting success and brood survival; however, relatively speaking, breeding propensity has been poorly documented. This data gap represents a significant shortcoming in our understanding of avian breeding biology. Without adequate estimates of breeding propensity, overall reproductive performance cannot be determined. Also, documentation of breeding propensity allows consideration of the stages and mechanisms by which reproductive effort may be constrained (Cam et al. 1998). For example, low rates of breeding propensity may indicate poor habitat conditions, such as poor food availability or low nest site availability, while poor nesting or brood success may be a result of high predation rates or inclement weather. We argue that breeding propensity is an important attribute to quantify when investigating avian reproductive success, and unfortunately, studies of breeding propensity have been constrained in part by a lack of appropriate tools.

Sea ducks have been hypothesized to be an avian taxon that exhibits relatively high rates of nonbreeding (Goudie et al. 1994); however, research in this area has been limited and has focused mainly on eiders (Coulson 1984, Quakenbush and Suydam 1999). For Harlequin Ducks (*Histrionicus histrionicus*), a cryptic-nesting sea duck, there has been a general assumption that some proportion of females on breeding streams are nonbreeders, although data to support or refute that assumption are few and, we argue, methodologically flawed. Reported rates of breeding propensity are highly variable (18-88%), as are the methods employed to obtain them (Table 4.1). For example, Bengtson (1971) and Bruner (1997) defined nonbreeders as those females seen in flocks on streams during the nesting period. Hunt (1997) classified nonbreeders as those females active midday when breeding hens were presumed to be on their nests; he also inferred breeding status of captured females based on the presence of a brood patch, wide pelvis, or egg in the abdomen. Crowley (1999) classified captured females as breeders or nonbreeders based on brood patch and cloacal attributes. Most recently, MacCallum and Godslave (2000) and Smith (2000) used telemetry to follow radio-marked birds to determine nesting status. All of these approaches have methodological constraints, a primary one being that most of these cannot distinguish between true nonbreeders, i.e., those females that do not initiate clutch formation, and females that fail early in the egg production or incubation stages. Also, attributes such as brood patches and oviductal eggs may not be apparent if females are captured early in reproduction (McFarlane Tranquilla et al. 2003b). Thus, estimates of proportions of nonbreeding females likely include some proportion of failed nesters and late nesters, and hence breeding propensity can be underestimated (Robertson and Goudie 1999, McFarlane Tranquilla et al. 2003a).

In this study, we apply a novel approach combining radio telemetry and yolk precursor analyses to quantify breeding propensity in Harlequin Ducks. Plasma yolk precursors, vitellogenin (VTG) and yolk-targeted, very-low-density lipoprotein (VLDLy), are produced in the avian liver and become elevated as estrogen concentrations increase during reproduction (Deeley et al. 1975, Chan et al. 1976). VTG and VLDLy are the primary sources of egg yolk protein and lipid, respectively (Wallace 1985, Walzem 1996), and therefore, are highly correlated with egg production. Yolk precursors have been demonstrated to be reliable indices of reproductive status in European Starlings (*Sturnus vulgaris*; Challenger et al. 2001), Marbled Murrelets (*Brachyramphus marmoratus*; Vanderkist et al. 2000, McFarlane Tranquilla et al. 2003a), and Greater Scaup (*Aythya marila*; Gorman 2005). Using a blood sample, it is possible to nondestructively determine if individual females are in the process of egg formation at the time of capture. Radio telemetry allows us to infer breeding propensity by monitoring behaviour to determine the proportion of females found on nests. By using both these methods on the same set of female Harlequin Ducks, we were able to compare the efficiency of each for estimating breeding propensity and to derive an overall estimate of breeding propensity that accounts for misclassification of breeding status by both methods.

4.3 Methods

4.3.1 Study Area and Captures

Harlequin Ducks were captured on breeding streams using mist nets from May 9 to 20, 2003, and from April 21 to May 20, 2004, in the southern Coast Mountains of British Columbia, Canada. The study area included streams near the towns of Pemberton (50° 19'N, 122° 48'W) and Lillooet (50° 41'N, 121° 56'W). Captured birds were immediately removed from the net, and then weighed, banded, and assigned to an age class based on the depth of the Bursa of Fabricius (Mather and Esler 1999).

4.3.2 Radio Telemetry

Each captured female had a radio transmitter attached using a subcutaneous anchor and glue. The transmitters, made by Holohil Systems Ltd, were a six-gram RI-2B model with a motion-sensitive mortality sensor and a battery life of three to nine months. The transmitter was located in the small depression between the scapulae, dorsal to the approximate junction of the cervical and thoracic vertebrae. We monitored radio-tagged females at least once a week (usually several times a week) to determine if each female was detected on a nest. We classified those on nests as breeders, and those not on nests as putative nonbreeders. Some individuals were also categorized as unknown, if their radio signal was lost during the nesting period.

4.3.3 Yolk Precursor Analyses

A 1.5 ml blood sample was taken from the jugular veins of captured females using a heparinized 5.0 ml syringe with a 21-gauge needle. For a small number of females, a 1.0 ml syringe with a 24-gauge needle was used to take 0.5 ml of blood from the tarsal vein instead. Collected blood was transferred to a heparinized vial and stored on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 h). Plasma from the blood samples was analysed for yolk precursor concentrations of vitellogenin (VTG) and total very-low-density lipoprotein (VLDL – both generic and yolk-targeted). Following Mitchell and Carlisle (1991), diagnostic kits for vitellogenic zinc and total triglycerides were used as indices of concentrations of VTG and VLDL, respectively. Intra-assay and inter-assay coefficients of variation for VTG were 3.2% and 13.0% (n = 6), and for VLDL were 5.1% and 4.3% (n = 5), respectively. Also, blood samples were analysed from females captured on wintering grounds in the Strait of Georgia, British Columbia, to determine a baseline, nonbreeding value for the yolk precursors (n = 16).

Although both yolk precursors are correlated with egg production, VTG has been shown to be a more accurate and reliable indicator of reproductive status than VLDL (Vanderkist et al. 2000, Gorman 2005). Therefore, VTG was considered first for determining whether or not females were captured during egg production. Because threshold or cut-off levels for this determination have been variable (see discussion), we categorized individual females into one of three categories based on VTG results: egg-producing, non-egg-producing, and unknown. The unknown category included those females whose VTG concentration fell within a range that we considered uncertain. The lower limit of this uncertain zone was the mean VTG + 3SD of our wintering females (0.44 µg/mL; recommended by McFarlane Tranquilla et al. 2003a), which is low compared to other values in the literature. The upper limit for the unknown category was the highest cut-off value reported in the literature (Gorman 2005, 1.4 µg/mL; Figure 4.1). Any individuals with VTG values higher than 1.4 µg/mL were considered egg producers (and hence breeders) and those below 0.44 µg/mL were categorized as non-egg producers and putative nonbreeders. If an individual was categorized as unknown based on VTG level, the VLDL value was then used to evaluate status. As with VTG, VLDL values also were used to categorize these birds as egg producers, non-egg producers, or unknown with the lower limit defined as mean VLDL + 3SD for our wintering females (3.66 mg/mL) and the upper limit of 5.2 mg/mL from published literature (Gorman 2005). If a female was classified as unknown for both VTG and VLDL, then her overall status using yolk precursors was considered unknown.

4.3.4 Breeding Propensity Determination

Our summary dataset for estimation of breeding propensity consisted of classifications of breeder, putative nonbreeder, or unknown for each individual for each of our two methods, using yolk precursors as a direct measure of egg production and radio telemetry to infer egg production from birds detected on nests. We estimated a putative breeding propensity for each method individually as simply the proportion of individuals that were classified as breeders, excluding those classified as unknown from the calculation. Because we were using two methods to estimate breeding propensity, we also calculated a misclassification rate for each method, which was the proportion of birds that were incorrectly classified as a putative nonbreeder when it was known to produce eggs based on the other method. We then estimated the probability of incorrectly designating an individual as a nonbreeder when using both methods, by multiplying the misclassification rates for each method. This estimated the proportion of birds that were truly breeders, but that were captured before the onset of rapid follicle growth and their nest failed before telemetry methods confirmed incubation. An overall estimate of breeding propensity was the proportion of individuals confirmed as a breeder by either method plus the estimate for the proportion misclassified as a nonbreeder by both methods.

4.4 Results

Over the two years of this study, 34 female Harlequin Ducks were captured and attached with radio transmitters. We determined that the age class of all captured females was after-third year (i.e., breeding age adults). Five females were captured and monitored in both years.

The two methods we applied produced different estimates for breeding propensity. Yolk precursor analyses showed that of the 34 females, 25 were producing eggs when they were captured (Figure 4.1). Five were not producing eggs, two were classified as unknown because their values fell within the uncertain zone for both yolk precursors, and two had blood samples that were unusable for analyses. Therefore, we estimated a putative breeding propensity based solely on yolk precursors to be 83% (95% confidence interval = 69 - 97%; Table 4.2). Our telemetry efforts resulted in detection of

22 females on nests, eight females that were never found on nests, and four whose status was unknown (due to loss of radio signal or mortality); therefore, putative breeding propensity using telemetry was 73% (95% confidence interval = 57 – 89%). Using both data types combined, three females on breeding streams were designated as putative nonbreeders, one was unknown, and 30 (91%; 95% confidence interval = 81 – 100%) were confirmed to have initiated egg production. However, this estimate does not include those breeding females that could have been missed by both methods.

Misclassification rates differed by method. If using telemetry alone, we would have misclassified 17% of egg producers as nonbreeders (Table 4.2). Of the 30 females categorized by telemetry, five putative nonbreeders were known to be breeders based on yolk precursors (Figure 4.2). These five egg producers presumably failed early during the nesting phase, before they could be detected via telemetry. Yolk precursor analysis was less likely to misclassify breeders as putative nonbreeders. Of the 30 birds with yolk precursor data indicating their breeding status, only one (3%) was classified as a putative nonbreeder based on yolk precursors but was subsequently confirmed to produce eggs based on telemetry (Figure 4.2). This was a late-nesting bird that presumably was captured prior to rapid follicle growth. Our estimate of the proportion of individuals misclassified by both methods, derived by multiplying misclassification rates of each method used independently, was low (1%), indicating that it was unlikely for both methods to miss a breeding bird. Our final estimate of breeding propensity (proportion of known breeders by either method plus the estimate of misclassification by both methods) was 92%.

4.5 Discussion

By applying a new approach, we estimated breeding propensity of adult female Harlequin Ducks in southern British Columbia to be 92%. This result is surprisingly high considering that these ducks are long-lived species that have many potential breeding attempts, and are thought to be quick to defer breeding in order to increase survival and lifetime reproductive success (Stearns 1992, Goudie et al. 1994). The Common Eider (*Somateria mollissima*), another long-lived sea duck, has estimates of breeding propensity averaging around 75% with incidents of as low as 45% (Coulson 1984). As well, the breeding propensity of Greater Snow Geese (*Chen caerulescens atlantica*) has been reported to be around 57% on average (Reed et al. 2004). Our data, showing over 90% of adult female Harlequin Ducks on breeding streams initiating clutch formation, possibly indicates that their life history strategy is not as extreme as previously suggested or that the years of this study were favourable for reproduction. We note that our estimate does not include those females that may decide to defer breeding prior to migration and remain on wintering areas. Applying these methods across a range of conditions for Harlequin Ducks will give a clearer, more accurate view of breeding propensity, and hence, life history strategies.

As discussed by Cam et al. (1998), the criterion used to distinguish between breeding and nonbreeding individuals is an important methodological choice that is likely to influence study results and conclusions. Although our comparatively high estimate of breeding propensity could be a site or year effect, we suggest that it is more likely a function of the methods used. Yolk precursor analysis is a direct measure of egg production while most other methods, including radio telemetry, attempt to infer breeding status from behaviour later in the breeding cycle. Yolk precursors, however, can also misclassify individuals and we suggest that it is the combination of this method with another confirming incubation that provides the best estimates of breeding propensity.

Using two methods directed at different phases of the reproductive cycle is also useful in that it allows estimation of misclassification rates by each method, and calculation of an estimate of overall misclassification. It should be recognized that when using yolk precursor analyses, the blood sample is only a snapshot of the condition of a female at the time she was caught. If the female is caught during ovarian follicle development, her status as an egg producer will be evident because yolk precursor levels increase quickly in association with onset of rapid follicle growth and remain high until laying is complete (Challenger et al. 2001, Gorman 2005). However, if a female is caught outside of the egg production stage, yolk precursors will not distinguish nonbreeders from those that will initiate egg formation later or have already completed egg laying. Therefore, captures for yolk precursor sampling should be targeted for the period when females are expected to be producing eggs. Our estimate of misclassification when using yolk precursors was surprisingly low (3%), indicating that our captures were well timed. In most situations, we would expect higher rates of misclassification using yolk precursors, as it seems unlikely to catch all females during the egg production phase; in these situations, a second method for estimating misclassification rates using yolk precursors would be particularly important.

One aspect of the yolk precursor analyses that could be refined is the definition of cut-off levels to distinguish egg-producing from non-egg-producing females. These have been defined by various authors in different ways. For example, McFarlane Tranquilla et al. (2003a) and Peery et al. (2004) used the mean of their known nonbreeding samples plus three standard deviations as the maximum non-egg-producing concentration of VTG in the plasma of Marbled Murrelets (0.96 μg/ml and 0.64 μg/ml, respectively), while Vanderkist et al. (2000) used two times the highest known nonbreeding value for the same species (0.52 μg/ml for VTG). These intraspecific differences in cut-off levels could create different estimates of breeding propensity, although presumably not dramatically different because yolk precursor dynamics, especially those of VTG, generally lead to a clear signal differentiating birds at different stages. Gorman (2005) determined that a VTG value of 1.4 μg/ml correctly classified the most female Greater Scaup as egg-producing or non-egg-producing individuals. This indicates that there are also interspecific differences in appropriate cut-off levels to consider. The physiological causes of this interspecific variation have not been formally investigated and leads to questions about applicability of broad threshold values. Because determination of a distinct cut-off level can be somewhat arbitrary, we recommend using similar methods to ours, in which intermediate values can be categorized as uncertain with respect to breeding status.

Another potentially important factor when estimating breeding propensity, which has been overlooked by some investigators, is determination of age class. Our estimate applies strictly to after-third-year females because ample evidence exists to suggest that young birds are more likely to defer breeding within a given year than older, more experienced birds and young birds are also known to prospect (Johnson et al. 1992). Therefore, inclusion of young birds can lead to underestimates of breeding propensity. For example, Perfito (1998) estimated Harlequin Duck breeding propensity to be 50% but when she removed subadults from the calculation, the estimate became 74%. Although this is presumably still an underestimate due to methodological constraints, it illustrates the importance of accounting for age class when considering mechanisms affecting breeding propensity and applying estimates to population models.

We reiterate that accurate estimates of breeding propensity are important for determining factors that influence reproductive success and productivity. Knowledge of the factors influencing reproduction is vital to managing populations. A high proportion of females that do not initiate egg formation may be indicative of a physiological influence such as poor food availability while a high proportion of females that do not complete incubation may indicate external factors such as high predation pressure. Peery et al. (2004) included the proportion of breeders when considering limiting factors, such as food, nest sites, or predation, on Marbled Murrelet populations. Also, Gardarsson and Einarsson (2004) have linked food availability with productivity of several diving ducks in Iceland. Goudie and Jones (in press) recently suggested that productivity of Harlequin Ducks is limited by predation rather than food based on activity budgets and breeding propensity estimates. Monitoring breeding propensity could indicate chronic or sporadic influences on reproductive success, and if we had an indication of the proportion of birds committing to each stage in the breeding chronology, we may be able to identify mechanisms responsible for low productivity and recruitment.

4.6 Acknowledgements

We acknowledge BC Hydro Bridge Coastal Restoration Program and Environment Canada Science Horizons Program for financial support and the Centre for Wildlife Ecology at Simon Fraser University for logistical support. For assistance in the field, we thank C. Alec, E. Anderson, J. Bond, K. Bond, S. Boyd, S. Copeland, J. Harding, J. Heath, S. Iverson, S. LeBourdais, E. McClaren, S. Smith, K. Wright, and R. Žydelis. Also, H. Nichol generously provided field housing near Pemberton. R.C. Ydenberg and S.E. Jamieson provided useful comments on earlier drafts. Thanks to K. Gorman and K. Salvante for assistance with laboratory analysis.

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Table 4.1 Historical Harlequin Duck breeding propensity estimates and methods.

Region	Year of Study	Breeding Propensity (%)	Method	Reference
Iceland	1965-1969	**70-85**	Proportion of females in flocks during June and July	Bengtson and Ulfstrand 1971
Iceland	1970	**18**	Proportion of females in flocks during June and July	Bengtson and Ulfstrand 1971
Alaska	1979-1980	**50-53**	Brood patch and behavioural observations	Dzinbal 1982
Alaska	1991-1992	**74-86**	Examination of cloaca and brood patch; egg in abdomen	Crowley 1999
Wyoming	1985-1986	**38**	Mass of captured females	Wallen 1987
Oregon	1995-1996	**49**	Repeat observations of females in single or mixed-sex groups	Bruner 1997
Washington	1996-1997	**74**	Multiple captures checking for brood patch presence	Perfito 1998
Alberta	1997-1999	**52**	Telemetry and observational data	MacCallum and Godslave 2000
Alberta	1997-1999	**88**	Telemetry	Smith 2000

Table 4.2 Breeding propensity (with 95% confidence intervals) as determined using yolk precursor analyses and radio telemetry, and the probability of misclassification using each method (see methods).

Method	Breeding Propensity	n	Misclassification Rate
Yolk Precursors (YP)	83% (69 – 97%)	30	3%
Telemetry (T)	73% (57 – 89%)	30	17%
Both (YP & T)	91% (81 – 100%)	33	1%

Figure 4.1 Yolk precursor data for breeding propensity determination. The symbols on this figure show how each individual is classified based on the yolk precursor cut-off criteria and grey areas are zones of uncertainty (see methods). Note two individuals only had values for VTG, and therefore, are not shown.

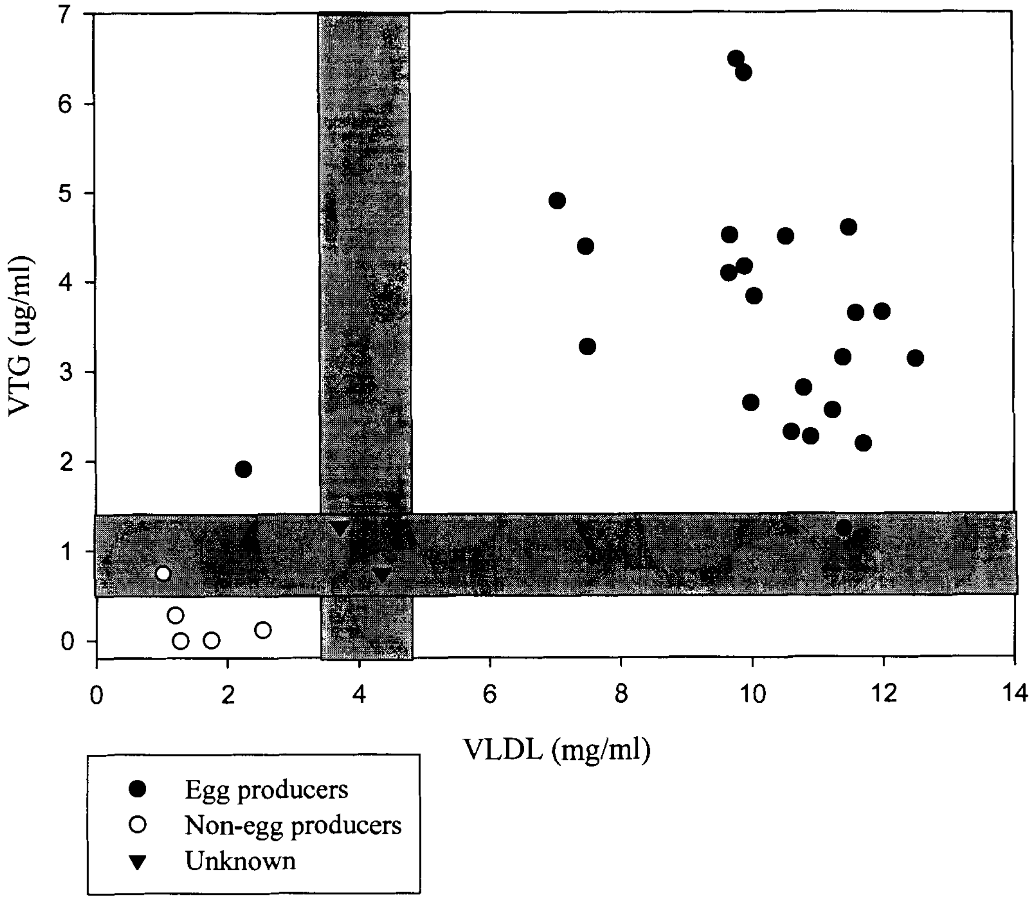
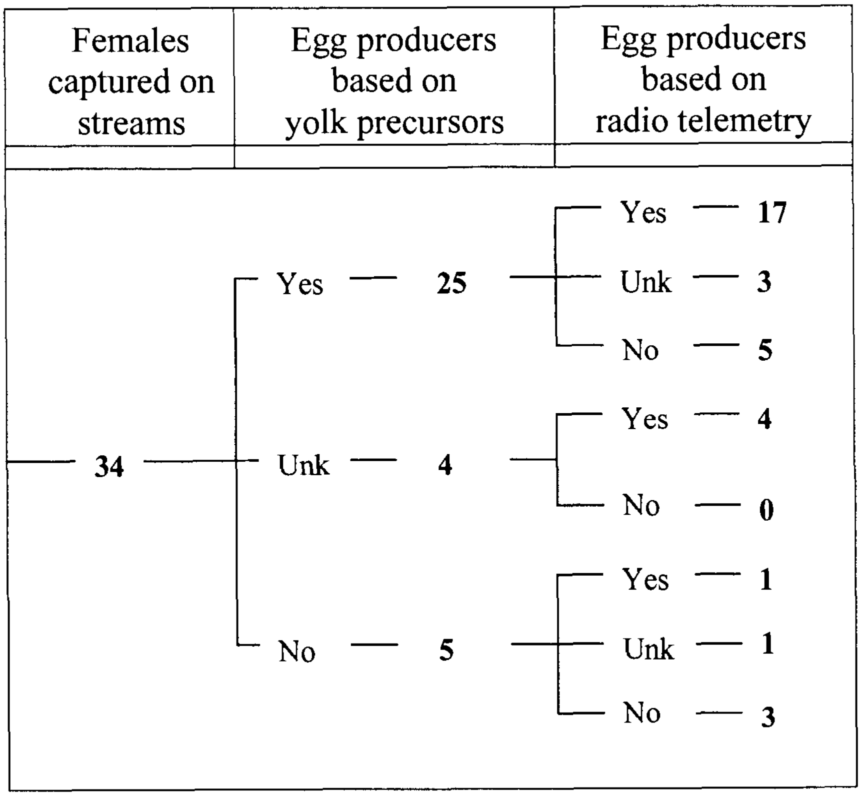


Figure 4.2 Of the 34 females captured on breeding streams, this figure shows the distribution of samples indicating breeding activity at two different points in the reproductive cycle (i.e., yolk precursors measure egg production and radio telemetry measure incubation), and how these two methods work in conjunction to determine the number of females that commit to clutch formation.



CHAPTER 5
GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

5.1 Conclusions

Reproduction in waterfowl is considered an energetically demanding stage and strategies for acquiring and allocating nutrients to meet these demands varies. Current concerns regarding low productivity and recruitment of Harlequin Ducks (*Histrionicus histrionicus*) in southern British Columbia (Smith et al. 2001, Rodway et al. 2003) highlight the need for research improving our knowledge of breeding requirements for this species. In this thesis, I investigated nutrient acquisition and allocation strategies of adult female Harlequin Ducks, and specifically examined (1) nutrient storage on wintering grounds prior to migration and reproduction, with particular focus on the role of herring spawn, (2) nutrient allocation to clutch formation and the relative contributions from marine and freshwater sources to egg components, and (3) breeding propensity of females on freshwater breeding streams in southern British Columbia. These studies provide novel insights into Harlequin Duck reproductive ecology, which have important implications for addressing conservation concerns surrounding low productivity.

I found that body mass of adult female Harlequin Ducks in the southern Strait of Georgia, British Columbia, increased by 7% prior to migration on wintering grounds (Chapter Two). This mass gain occurred regardless of whether females were consuming intertidal invertebrates or herring spawn, although there was a suggestion that diet did correspond to differences in chronology of mass gain. Those females consuming herring roe increased in mass several weeks before those that were feeding on a mixed intertidal invertebrate diet. Females on all sites had similar body masses prior to migration, which suggests that there was a targeted, optimal premigratory body mass, presumably shaped by the costs and benefits of nutrient storage. Therefore, consumption of herring roe rather than marine invertebrates does not necessarily confer advantages in terms of nutrient storage although there may be other aspects of aggregating at spawn sites that are important such as social interactions (Rodway et al. 2003).

I examined allocation of these endogenous marine nutrients by using stable isotope analyses to identify sources of nutrients for clutch formation (Chapter Three). By analysing Harlequin Duck eggs, I determined that freshwater, not marine, nutrients were allocated to eggs for both protein and lipid. This indicates that Harlequin Ducks are highly dependent on stream invertebrates during egg formation. Therefore, in a conservation context, factors that influence availability of invertebrates might be expected to have effects on Harlequin Duck reproductive performance. Although marine nutrients are not used for egg production, they are likely used for migration (Appendix) and potentially during other stages of reproduction. This offers a novel perspective on classification of species along a capital to income breeding continuum (Drent and Daan 1980, Meijer and Drent 1999). If considering egg production (the reproductive phase for which the 'capital' and 'income' labels have usually been applied for waterfowl), these females would be considered strict income breeders. However, my work demonstrates that female Harlequin Ducks store nutrients that may be subsequently invested in other reproductive phases – a capital strategy, but at an unexpected point in the reproductive cycle. These findings corroborate those of other waterfowl studies (e.g., Gorman 2005) that indicate that pre-reproductive nutrient acquisition is important and even limiting, irrespective of the strategy of nutrient acquisition and allocation for clutch formation.

In Chapter Four, I estimate breeding propensity of adult females on breeding streams using yolk precursor analysis and radio telemetry. Yolk precursors (vitellogenin and yolk-targeted, very-low-density lipoprotein) are highly correlated with egg production, and have been demonstrated to be reliable indices of reproductive status in birds (European Starlings (*Sturnus vulgaris*), Challenger et al. 2001; Marbled Murrelets (*Brachyramphus marmoratus*), Vanderkist et al. 2000; Greater Scaup (*Aythya marila*), Gorman 2005). The combination of yolk precursors and radio telemetry is a novel approach that avoids biases associated with using these methods singly, and I estimated that 92% of females on streams produced eggs. This is the highest estimate reported to date for Harlequin Ducks, presumably due in part to methodological limitations of other studies. Breeding propensity estimates are important for assessing reproductive effort and the approach that I employed offers a useful, noninvasive method that can be applied to other species.

5.2 Future Directions

This information on reproductive strategies of Harlequin Ducks can be an impetus for future research. One important avenue would be to address specific mechanisms that may limit productivity, especially the possibility of food limitation (Gardarsson and Einarsson 2004, Goudie and Jones in press). Because my thesis research has demonstrated that females rely almost exclusively on freshwater nutrients for egg production, directed research evaluating how limitation of these freshwater nutrients may influence productivity would be useful. Also, with the improved methods of assessing breeding propensity, investigators may directly consider how food limitation affects a female's probability of producing eggs.

While conducting this research, I found that the stable isotope signatures of adipose tissue in breeding females were highly variable, but tended to declined toward more freshwater values with time spent on breeding streams. This relationship is hard to interpret because the change toward more freshwater signatures could represent (1) use of marine nutrients and storage of freshwater nutrients, (2) simply storage of freshwater nutrients without using stored marine lipid, or (3) turnover. Further research investigating the mechanism responsible for changes in adipose tissue isotope values would be useful for interpretation of endogenous and exogenous lipid allocation to female maintenance and egg formation.

Another fruitful area of investigation could be to evaluate how nutrient acquisition and allocation strategies vary depending on migration strategy and breeding location. Harlequin Ducks winter in fairly large congregations and then disperse to breeding sites that range from just a few kilometres to hundreds of kilometres away from wintering areas (Robertson and Goudie 1999). Migration distance and geographic variation in breeding sites may influence an individual female's strategy for storing and allocating nutrients, and this information would provide a more complete picture of population-level strategies for nutrient acquisition and allocation. Also, comparative studies could be developed to investigate these relationships for Harlequin Ducks on the East Coast of North America as well as Greenland and Iceland.

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APPENDIX*: FLIGHT COSTS FOR HARLEQUIN DUCK MIGRATION

Purpose

The goal for this appendix was to evaluate how much of the acquired endogenous marine nutrients (Chapter Two) female Harlequin Ducks (*Histrionicus histrionicus*) would allocate to migrate from wintering grounds in the Strait of Georgia (49° 40'N, 124° 24'W) to breeding streams near Lillooet (50° 41'N, 121° 56'W) in the southern Coast Mountains of British Columbia, Canada. I investigated this by estimating flight costs and comparing those costs to the estimated level of endogenous stores that females acquired prior to migration.

Methods and Results

I estimated costs of migration using Flight Program 1.15 available at http://www.bio.bristol.ac.uk./people/pennycuick.htm. As per the instructions, I input required variables, and let the program set the default values for most other variables. I entered body mass as the average premigratory (i.e., postspawn) female mass (0.6 kg) from my data (Chapter Two). Wing span (0.685 m) and wing area (0.0295 m^2) were calculated from photographs of extended wings of female Harlequin Ducks (D.Esler, unpublished data) using one-centimetre grids (Pennycuick 1989) and then standardized using the average wing chord measurement from my captured birds. Great-circle distances, which include earth curvature, were used between Hornby Island, in the Strait of Georgia, and Lillooet (235 km) to approximate migration distances from wintering

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* This appendix was created to publish important findings that supplement interpretation of results and conclusions of this thesis, but that do not clearly fit in the established chapters.

grounds to breeding grounds in this study. Based on these input values, I used the Flight Program to calculate change in overall body mass.

These migration flight cost calculations revealed that a female travelling from Hornby Island to Lillooet would lose approximately 16 grams or 2.6% body mass. This is an approximate value although this result is not particularly sensitive to reasonable changes of input values (i.e., changes in initial mass +/- 20 g produces similar flight cost results). Given the migration distance, estimated changes in body mass were fairly consistent across a range of input values.

Conclusions

In general, Harlequin Ducks are comparatively short-distance migrants (Smith and Smith 2003) and are presumed to make fast, direct flights between wintering and breeding grounds (Robertson and Goudie 1999). It appears that females travelling to the Lillooet area to breed only use 2-3% of their body mass to fly from the Strait of Georgia to this breeding site, and that they store more marine endogenous nutrients during spring hyperphagia (7% increase in body mass; Chapter Two) than they need for migration. Therefore, one might predict that females travelling to Lillooet to breed may allocate some marine nutrients to reproduction (see Chapter Three).

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