

Postbreeding Ecology of Barrow's Goldeneyes in Northwestern Alberta

by
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of the Requirements for the Degree of
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Abstract

I studied remigial molt phenology, body mass dynamics, foraging effort, and survival of Barrow's Goldeneyes (*Bucephala islandica*) on Cardinal and Leddy Lakes, Alberta to evaluate whether the postbreeding period imposed nutritional or demographic constraints that could affect population dynamics. Adult male Barrow's Goldeneyes, the predominant cohort on the study sites, arrived by mid-June and departed by mid-November. Remigial molt lasted 39 days during which body mass increased despite low foraging effort by adult males; mass and foraging patterns differed between lakes. Cumulative survival of adult males during remigial molt was high (95%). Taken together, these results indicate that remigial molt was not a period of nutritional limitation or high mortality risk for Barrow's Goldeneyes and that molt strategy was responsive to local conditions. Cumulative adult male survival during fall staging (71%) was substantially lower than during remigial molt with at least half of mortalities on Cardinal Lake attributed to hunting.

Keywords: Barrow's Goldeneye; foraging; remigial molt; sea duck; staging; survival

*To the BAGO: I can only strive to ensure that
your alien abduction was for the greater good
of BAGO kind.*

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1. General Introduction

1.1. Background

Feathers serve many functions for birds including temperature regulation, cryptic colouring, mate attraction, epidermal protection, and flight (Stettenheim 1976), thus they must be kept in good repair and require replacement as they become worn and damaged. During replacement of feathers, or molt, synthesis of feathers increases daily energy and nutrient requirements to well above that of maintenance levels (Heitmeyer 1988, Murphy 1996). These increased daily requirements are largely the result of processes related to feather production, such as increases vascularized tissues, blood volume, and protein and bone metabolism, rather than the direct production of the feathers themselves (Murphy and King 1992; Murphy *et al.* 1992; Murphy 1996). In addition, sulphur-containing amino acids, which are used to produce keratin (the substance from which feathers are constructed), may be limiting during molt, as dietary concentrations of these amino acids are typically lower than that of feathers (Murphy and King 1992, Murphy 1996; Newton 2011). Other costs of molt may relate to decreased thermoregulatory efficiency as feathers are replaced (King 1981; Dietz *et al.* 1992), decreased flight efficiency and performance (Chai 1997; Chai *et al.* 1999; Swaddle *et al.* 1999), or decreased foraging efficiency (Bridges 2004). Despite the costs of molt, it is necessary for all birds to undergo this process to retain feather function; however the sequence, timing, duration, and strategies of molt vary considerably among species, reflecting different solutions to accommodating the costs of molt.

Most families of birds molt remiges (flight feathers) gradually and thus retain the ability to fly throughout the annual cycle. However, 11 families, including loons, grebes, coots, auks, and waterfowl, undergo simultaneous remigial molt, resulting in flightlessness as new flight feathers are grown (Hohman *et al.* 1992). One explanation for development simultaneous remigial molt suggests that birds with high wing loading experience decreased flight efficiency or are unable to fly with missing remiges. Thus, simultaneous remigial molt acts to reduce the vulnerable remigial replacement period

and/or reduce energy costs associated with locomotion for birds with high wing loading compared to sequential molt (Hohman *et al.* 1992; Filardi and Rohwer 2001; Guillemette *et al.* 2007). This explanation is unlikely to apply to waterfowl, as many *Anatids* are able to maintain flight capabilities while missing a few remiges. Simultaneous remigial molt also may have developed in certain avian taxa because it allows nutritional costs of remigial molt to be concentrated into a shorter, discrete window of time when exogenous nutrient resources are most abundant and thermoregulatory costs are minimal. This would also allow individuals to complete molt without overlapping other costly stages, such as reproduction and migration. Further, birds with other reliable means of locomotion (e.g. diving, swimming) may be able to redirect energy and nutrients for flight to other activities, such as foraging or feather synthesis, by molting simultaneously (Guillemette *et al.* 2007). Finally, undergoing remigial molt as a distinct annual cycle stage allows birds to select habitats with conditions that are particularly conducive to safely replacing feathers.

Although simultaneous remigial molt may provide the benefits mentioned above, it also might impose costs associated with flightlessness. Flightlessness affects mobility, and thus the ability to escape predators or other risks (Panek and Majewski 1990; Dopfner *et al.* 2009). Flightlessness may also affect an individual's ability to move to different foraging areas in response to changes in forage quality or availability. Further, absence of remiges during molt may decrease foraging efficiency in diving birds (Bridge 2004). Choice of molting location may moderate costs of remigial molt. Many northern hemisphere waterfowl species complete a northward molt-migration to specific habitats before onset of remigial molt (Salomonsen 1968; Van de Wetering and Cooke 2000; Robert *et al.* 2002; Flint *et al.* 2004; Phillips *et al.* 2006; Lewis *et al.* 2010). This movement may ensure food availability and reduce intraspecific competition for food resources that would otherwise be encountered if molt occurred on breeding grounds (Salomonsen 1968; Derksen *et al.* 1982; Madson and Mortensen 1987). High latitude molting locations also may have lower predator diversity and abundance and less anthropogenic disturbance compared to sites used during other periods of the annual cycle (Salomonsen 1968; Zicus 1981; Kahlert 2003).

Other strategies for accommodating nutritional costs and mortality risks of simultaneous remigial molt include altering energy allocation and behavioural patterns

during this time. Some waterfowl use endogenous resources during remigial molt, losing mass throughout the molting period. Female Ring-necked Ducks (*Aythya collaris*) showed a 45% reduction in somatic lipid stores during remigial molt (Hohman *et al.* 1988) and similar decreases have been observed for Mallards (*Anas platyrhynchos*) (Panek and Majewski 1990) and Greylag Geese (*Anser anser*) (Fox and Kahlert 2005). Ruddy Ducks (*Oxyura jamaicensis*) utilize somatic protein, as opposed to lipids, during this time (Hohman 1993). Mass loss associated with remigial molt has been postulated to facilitate an intentional decrease in wing loading for an earlier return to flight, effectively shortening the vulnerable flightless period (Panek and Majewski 1990; Brown and Saunders 1998; Van de Wetering and Cooke 2000; Zimmer *et al.* 2011). However, mass loss in molting waterfowl also may be a function of a deficiency of exogenous resources available to birds on molt sites, adaptive loss of excess, metabolically costly tissue, or decreased foraging effort and increased time allocated to resting or vigilance behaviour. Pochard (*A. ferina*) and Tufted Ducks (*A. fuligula*) lost mass, and increased resting and vigilance behaviour during remigial molt (Fox and King 2011). Alteration of daily activities in this manner may act to reduce daily energetic costs, vulnerability to predators, and damage to growing remiges (Owen and Ogilvie 1979; Panek and Majewski 1990; Adams *et al.* 2000; Dopfner *et al.* 2009; Portugal *et al.* 2010).

Many waterfowl use exogenous, as opposed to endogenous, resources during remigial molt, maintaining or gaining mass and often increasing foraging effort throughout this time period. This has been observed in Lesser Snow Geese (*Chen caerulescens caerulescens*), some Mallard populations, scoters (*Melanitta spp.*), and Canvasbacks (Ankney 1979; Young and Boag 1982; Thompson and Drobney 1996; Fox *et al.* 2008; Dickson 2011). In some species, both sources of nutrients are used at different stages of remigial molt. For instance, male Redheads (*A. americana*) utilize somatic protein stores during early remigial molt, but stores are replenished through uptake of exogenous nutrients later in this stage (Bailey 1985). Similar observations have been made for lipid reserves in Mottled Ducks (*A. fulvigula*) and Canvasbacks (*A. valisineria*) (Moorman *et al.* 1993; Thompson and Drobney 1996). Further, Owen and Ogilvie (1979) suggest that Barnacle Geese (*Branta leucopsis*) utilize difference sources of nutrients depending on body condition (birds with more somatic lipid reserves use those reserves until they reach an optimal body weight, at which time they increase

foraging and rely on exogenous nutrients). Thus, specific strategies for balancing the costs and benefits of remigial molt vary considerably among waterfowl species.

Strategies for coping with costs of remigial molt might also vary with environmental conditions. Blue-winged Teal (*A. discors*) molting at different locations use different energy management strategies, exhibiting different body mass patterns during remigial molt (Dubowy 1985; Brown and Saunders 1998). The same has been observed in Mallards (*A. platyrhynchos*) (Young and Boag 1982; Panek and Majewski 1990) and Barnacle Geese (*Branta leucopsis*) (Owen and Ogilvie 1979; Portugal *et al.* 2007). These observations suggest that remigial molt strategies are flexible within some species, and that strategy is sensitive to local environmental conditions.

Molt strategies might also vary with age and sex cohorts, as the constraints imposed by simultaneous remigial molt may not be the same for all individuals in a population. In many waterfowl species, non-breeding individuals initiate remigial molt earlier than their breeding counterparts (Owen and Ogilvie 1979; Ankney 1979; Gates *et al.* 1993; Hohman and Crawford 1995; Gilliland *et al.* 2002; Savard *et al.* 2007). Given this, breeding individuals, particularly females due to their greater commitment to brood care, may be under greater temporal constraints during remigial molt. As a result of reproductive activities, breeding individuals also may initiate remigial molt with fewer somatic stores than non-breeding individuals, and thus may be more susceptible to nutritional constraints during this time. These constraints could put reproductively active birds at greater risk of mortality during remigial molt, or in subsequent stages of the annual cycle, due to faster feather growth resulting in poorer quality feathers (de la Hera *et al.* 2009), or decreased body condition (Haramis *et al.* 1986; Pehrsson 1987; Boos *et al.* 2002; Inger *et al.* 2008).

The potentially high risk of mortality, as well as temporal and nutritional constraints associated with simultaneous remigial molt, suggest a high potential for demographic constraints during this stage of the annual cycle. Estimated survival rates during remigial molt are varied amongst waterfowl: Harlequin Ducks (*Histrionicus histrionicus*) and scoters (*Melanitta spp.*) had very high survival during remigial molt, while American Black Ducks (*A. rubripes*), Northern Pintails (*A. acuta*), and Mallards showed considerably lower survival rates during this same stage (Kirby and Cowardin

1986; Bowman and Longcore 1989; Miller *et al.* 1992; Iverson and Esler 2007; Fleskes *et al.* 2010; Uher-koch, unpublished data). Thus, understanding variation in demographic constraints imposed upon waterfowl at postbreeding sites is essential for proper management of populations during this time period, and may provide insights into mechanisms behind population trends.

The postbreeding period is much less studied than other life stages in the annual cycle of waterfowl (Hohman *et al.* 1992). Studies focusing on postbreeding ecology are needed to determine whether constraints faced during this potentially vulnerable period could have demographic consequences that limit or regulate populations (Calvert *et al.* 2009). As a result, there is a growing body of literature addressing the gaps in our knowledge of this stage in the annual life cycle, especially for sea ducks, a group for which very little was once known about postbreeding ecology (Adams *et al.* 2000; Flint *et al.* 2000; Van de Wetering and Cooke 2000; Gilliland *et al.* 2002; Robert *et al.* 2002; Flint *et al.* 2004; Petersen *et al.* 2006; Phillips and Powell 2006; Guillemette *et al.* 2007; Iverson and Esler 2007; Craik *et al.* 2009; Craik *et al.* 2011; Dickson 2011). This study will add to that body of work, providing insights into the molting strategies employed by Barrow's Goldeneyes, and sea ducks in general, and the demographic consequences of those strategies. This study is also the first to quantify survival of a sea duck species during the fall staging period.

My primary objective was to investigate if Barrow's Goldeneyes were nutritionally constrained during remigial molt (i.e., were birds able to obtain the nutrients for remigial molt from their environment?). I achieved this by examining: 1) remigial molt phenology and primary feather growth rate, 2) body mass dynamics during the molting period, and 3) foraging effort during the molting period. These data, rarely gathered concurrently, provided insights on possible nutritional constraints on Barrow's Goldeneye during remigial molt, and comparison across sites and years provided information about plasticity of molting strategies.

My second objective was to determine the potential for demographic constraints (i.e., events or processes that negatively impact survival/population growth) to occur during the postbreeding period of Barrow's Goldeneyes. Survival rates during remigial molt and fall staging were determined to evaluate the influence of the postbreeding

period on population dynamics. Both objectives will aid wildlife managers in designing informed conservation plans for this species.

1.2. Study Species

Barrow's Goldeneyes (*Bucephala islandica*) are part of the *Mergini* (sea duck) tribe, which includes Common Goldeneyes (*B. clangula*), Bufflehead (*B. albeola*), eiders (*Somateria* spp., *Polysticta stelleri*), scoters (*Melanitta* spp.), mergansers (*Mergus* spp., *Lophodytes cucullatus*), Harlequin Ducks (*Histrionicus histrionicus*), Long-tailed Ducks (*Clangula hyemalis*) and Smew (*Mergellus albellus*). Most Barrow's Goldeneyes occur west of the North American Continental Divide, with over 90% of the world's population (estimated between 125 000 and 200 000 birds) found west of the Rocky Mountains between Alaska and California (Bellrose 1980; Eadie *et al.* 2000). Small numbers of Barrow's Goldeneyes occur in eastern Canada (primarily Quebec) and the eastern United States (primarily Maine), as well as Iceland.

Barrow's Goldeneyes from the Pacific coast of North America typically undertake three major migration movements annually : 1) spring migration from coastal wintering grounds to freshwater breeding ponds/lakes (March- mid April), 2) molt migration of males, failed breeding females, and sub-adults from breeding ponds to molt sites (mid-June to late-July), and 3) fall migration from molting and/or staging sites to wintering locations (early Sept- mid Nov). Wintering and breeding distributions are generally documented for the western population of Barrow's Goldeneyes; however, the only significant molt sites known prior to the discovery of my study sites (Cardinal and Leddy Lakes) were Old Crow Flats, YT and Ohtig Lake, AK (King 1963; Van de Wetering and Cooke 2000). Thus, the postbreeding ecology of Barrow's Goldeneyes, like many sea ducks, is poorly understood, though some cohorts of this species may spend more than 1/3 of the annual cycle at postbreeding sites (Hogan *et al.* 2011).

The diet of Barrow's Goldeneyes consists mainly of aquatic invertebrates captured from the substrate or on submerged vegetation, with shallow, shoreline habitats void of dense vegetation being preferred for foraging (Eadie *et al.* 2000). Winter diet consists mostly of aquatic insect larvae and molluscs (Vermeer 1982, Fitzner and Gray 1994), while breeding diet items are mainly insects such as dragonfly and

damselfly (*Odonata spp.*) nymphs, and *Dipteran* larvae (Thompson and Ankney 2002). Diving is the primary means of foraging.

1.3. Study Site

Cardinal Lake (56° 14'N, 117° 44'W; also known as Lac Cardinal) is a large (50km²) lake located in the Boreal Transition Zone of northwestern Alberta. The basin is shallow (<2m), with a primarily sand and gravel substrate. Substantial groundwater discharge is received in the basin from the Grimshaw Gravel Bed Aquifer, and the system drains into the Peace River via Cardinal Creek and the Whitemud River. Leddy Lake is a small (4km²) shallow lake located ~25km northeast of Cardinal Lake. Leddy Lake has a muddy substrate and dense submerged vegetation mat throughout most of the basin. Both systems are highly productive, supporting a diverse and abundant aquatic macroinvertebrate community (D.Hogan, unpublished data).

A large number of waterfowl use Cardinal Lake during the breeding, molting, and staging periods of the annual cycle. Scaup (*Aythya spp.*), goldeneyes, Buffleheads and Mallards (*A. platyrhynchos*) are the most abundant waterfowl using the lake. Fixed-wing waterfowl surveys conducted by Ducks Unlimited Canada from 2004-2007 indicated that this basin annually supports 16-18,000 molting ducks and at least 22-27,000 ducks during fall staging (Thompson, unpublished data). Recent satellite telemetry research and aerial waterfowl surveys revealed the lake to be a major molting and staging site for Barrow's Goldeneyes breeding in the intermountain region of British Columbia (Hogan *et al.* 2011). Molting goldeneye counts from 2004 to 2010 ranged from 2 300 to 6 000 birds, while fall staging counts from 2009 to 2010 ranged from 1 200 to 5 200 birds (Hogan *et al.* 2011). This makes Cardinal Lake comparable in importance to other known Barrow's Goldeneye molting sites such as Ohtig Lake (~5 000 molting birds) and Old Crow Flats (~ 7 000 molting birds) (King 1963; Van de Wetering 1997).

Historically, Leddy Lake has supported fewer than 500 molting and staging Barrow's Goldeneyes, however, surveys conducted in 2009 revealed approximately 2000 molting birds on this water body (Hogan *et al.* 2011). As a result of the large number of birds using Leddy during the molting period, and the opportunity to evaluate habitat-specific molt strategies, it was included in this study.

1.4. Thesis Outline

My thesis consists of four sections following this introductory chapter: three data chapters, each exploring one aspect of Barrow's Goldeneye post-breeding ecology, and a concluding chapter that summarizes the findings of my thesis and puts them in the context of broader ecological and conservation implications.

In my first data chapter, Chapter 2, I documented phenology of Barrow's Goldeneye remigial molt, including remigial growth rate, duration of remigial molt and the flightless period, and timing of molt initiation as a function of lake, year, and age and sex cohort. I provided three methods for estimating the time period between shedding of old primaries and emergence of new feathers, a stage of molt rarely quantified in previous studies. I concluded this chapter with inferences about temporal and nutritional constraints and mortality risk that can be drawn from these data.

My third chapter focused on body mass and foraging dynamics of Barrow's Goldeneyes during remigial molt to identify strategies used to accommodate nutritional constraints and mortality risks during this annual cycle stage. Mass variation was evaluated as a function of sex, age, lake, year, molt stage, molt initiation date, and body size. Mass of adult males during remigial molt was also put in the context of the annual cycle. Foraging effort of radio-marked adult male birds was modelled as a function of lake, year, molt initiation date, molt stage, mass, and time of day. Nocturnal and diurnal foraging effort were modelled separately. I concluded this chapter with a discussion about the implications of my findings relative to the nutritional constraints and risk of mortality Barrow's Goldeneyes experience during remigial molt, as well as consideration of the plasticity of molt strategy in this species.

My final data chapter explored potential for demographic constraints during the postbreeding period of Barrow's Goldeneyes. I estimated daily and period survival rates for adult males during remigial molt and fall staging, and discussed sources of mortality throughout these times periods. I concluded with a discussion of the conservation issues that emerge from my findings.

In my concluding chapter, I highlighted the major findings of my research and recommended conservation actions for Barrow's Goldeneyes at my study sites. I

finished with suggestions for future studies that will expand our knowledge of the postbreeding ecology of waterfowl.

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2. Remigial Molt Phenology and Remigial Growth Rates of Barrow's Goldeneyes

2.1. Introduction

Remigial molt, commonly called wing molt, is essential to maintenance and function of flight feathers in birds. Timing and duration of remigial molt varies, lasting from a few weeks to multiple years depending upon species (Howell 2010). Waterfowl (Family *Anatidae*) are one of 11 bird families that undergo simultaneous remigial molt, during which all flight feathers are shed and replaced at once (Hohman *et al.* 1992). As a result, waterfowl are rendered flightless during remigial molt for a period of 20 to 40 days (Hohman *et al.* 1992) on an annual basis. Typically, remigial molt of ducks occurs after the breeding season at the end of pre-basic molt (a complete molt of all feather tracts) and, in males, pre-alternate molt (an incomplete molt of contour feathers only) occurs towards the end of remigial molt (Hohman *et al.* 1992).

During the flightless period, waterfowl may be more vulnerable than at other periods in the annual cycle to deleterious factors including predation, inclement climate, limited food availability, and disruptive stochastic events. Waterfowl are known to adopt an array of strategies to reduce risks incurred during remigial molt. For example, birds may choose specific molting locations that differ from habitats used during other stages in the annual cycle in order to minimize nutritional or mortality risks associated with flightlessness. Waterfowl in the northern hemisphere often undertake a molt migration to specific molt sites (Salomonsen 1968), which usually takes them to higher latitudes than they occupied during the breeding season. These movements are thought to provide benefits such as access to large, permanent wetlands with high food availability, reduced human disturbance, increased day length, and lower predator densities relative to lower latitude sites (Madsen and Mortensen 1987; Derksen *et al.* 1982; Zicus 1981). Also, timing of remigial molt is such that it does not interfere with other activities that require substantial commitment of time and resources such as courtship and breeding

(Howell 2010). Remigial molt also occurs during warm parts of the year (late summer, early fall), perhaps in order to reduce thermoregulatory costs associated with incomplete contour feather coverage during pre-alternate and pre-basic molts.

Phenology and duration of remigial molt may reflect optimization of the costs and benefits of different molt strategies. The production of a large number of feathers requires energy and nutrients above that of general maintenance levels (Murphy 1996; Panek and Majewski 1990). If nutritional constraints are highly influential on molt strategy, birds may decrease their daily nutritional requirements by growing feathers slowly to extend the duration of remigial molt over a longer period of time (Thompson and Drobney 1996; Guillemette *et al.* 2007). In cases where birds are strongly influenced by high mortality risks associated with remigial molt, the flightless period may be completed as quickly as possible to minimize the duration of this vulnerable state (Bailey 1985; Sjorberg 1998; Panek and Majewski 1990). Further, temporal constraints (e.g. weather) may cause synchronous timing in remigial molt, as has been observed in some high-latitude molting geese (Owen and Ogilvie 1979; Taylor 1995).

Within waterfowl species, timing of remigial molt often varies by age, sex, and reproductive status. Immature and non-breeding individuals of some species tend to initiate remigial molt earlier than breeding individuals (Salomonsen 1968; Gates *et al.* 1993). Further, breeding females tend to initiate remigial molt later than their male conspecifics as a result of brood rearing obligations. For example, Savard *et al.* (2007) found that failed breeding, female Surf Scoters (*Melanitta perspicillata*) migrated to molt sites 6 weeks later, on average, than male scoters but still arrived earlier than successfully breeding females. When males had completed remigial molt, some females had not, suggesting that sex cohorts initiated molt at different times.

Unfortunately, remigial molt remains poorly studied for many waterfowl species, particularly those belonging to the sea duck tribe (*Mergini*). Barrow's Goldeneye (*Bucephala islandica*), a mid-sized sea duck primarily occurring on the Pacific coast of North America from Alaska to Oregon, is no exception to this knowledge gap. While this Pacific population of Barrow's Goldeneye is estimated between 125 000 – 200 000 (Bellrose 1980; Eadie *et al.* 2000), only 5 locations have been identified as remigial molting sites for < 20% of individuals (King 1963; Van de Wetering 1997; Hogan *et al.*

2011). A single study of the phenology and mass dynamics of remigial molt of the northern portion of Pacific Barrow's Goldeneyes was conducted on the Old Crow Flats, YT in the late 1990s (Van de Wetering and Cooke 2000). All band recoveries from birds marked at Old Crow Flats have been reported from Alaska, suggesting that the majority of these molting birds occur at the northern extent of the species range (Van de Wetering 1997). Aerial surveys and satellite telemetry recently revealed two molting locations in northwestern Alberta for the large, southern portion of Pacific Barrow's Goldeneyes (Hogan *et al.* 2011); however molting ecology of these birds has never been studied.

We characterized molt phenology of Barrow's Goldeneyes belonging to the southern portion of the Pacific population of this species to facilitate a better understanding of constraints of this stage in the annual cycle, and its ability to influence population dynamics. We expected that sub-adult birds (i.e. birds in their second year after hatch, SY) would initiate remigial molt before adult birds (i.e. birds more than 2 years old, ASY) and that male Barrow's Goldeneyes would initiate remigial molt earlier than females, who generally stay at breeding sites longer to look for future breeding sites and care for broods (Eadie and Gauthier 1985; Eadie *et al.* 2000). Assuming that remigial growth rate can be influenced by proximate environmental factors, we predicted that remigial growth would be slow and that remigial molt would be extended over a long period of time relative to other waterfowl species if nutritional constraints were strongly influencing molt strategy of birds at Cardinal and Leddy Lakes. If high risk of mortality (e.g., predation risk, anthropogenic and/or natural disturbances) had a strong influence on molt strategy, we expected that the flightless period would be short relative to other waterfowl species. Asynchronous timing of remigial molt was expected if temporal constraints were absent at our study sites.

2.2. Methods

2.2.1. Study Area

Cardinal Lake (56° 14'N, 117° 44'W) is a large (50 km²) wetland located in the Boreal Transition Zone (BTZ) of northwestern Alberta. The basin rarely exceeds a depth of 2 m, has a primarily sand and gravel substrate, and is hypereutrophic. Leddy Lake

(56° 23'N, 117° 27'W) is a small (4 km²), open fen located approximately 25 km NE of Cardinal Lake. This basin is shallow (< 2 m), has a primarily muddy substrate, dense submerged vegetation mat throughout most of the lake, and is mesotrophic. Combined, these lakes support 5 000- 7 000 molting Barrow's Goldeneyes annually, the majority of which are adult males (Hogan *et al.* 2011).

2.2.2. Captures and Collections

Barrow's Goldeneyes were captured using drive trapping techniques (Van de Wetering 1997) on Cardinal and Leddy Lakes, Alberta in 2009 and 2010. Captures started as soon as flightless birds were observed (end of July) and ended when nearly all birds had regained flight (early September). Upon capture, each bird was fitted with a uniquely numbered US Fish and Wildlife Service stainless steel tarsal band. We recorded morphological measurements, including 9th primary length measured to the nearest 1 mm. Sex of each bird was determined by cloacal and plumage characteristics (Hochbaum 1942; Carney 1983). Age class was estimated by plumage characteristics (Thompson, unpublished data) in conjunction with bursal depth (Mather and Esler 1999; Iverson *et al.* 2003). Birds with a bursa >10 mm were classified as second year (SY; i.e., hatched the previous year) and those with bursal depth of 0-10 mm were classified as after second year (ASY). In addition, adult male Barrow's Goldeneyes on Cardinal Lake were collected by shooting in the falls of 2008- 2010 and the spring of 2010 as part of a study of mass dynamics of postbreeding birds. Morphometric measurements described above also were taken from collected birds.

2.2.3. Data Analysis

2.2.3.1. Remigial Growth Rate (RGR)

The remigial growth rate (RGR) for individuals captured twice in the same year was calculated by dividing the difference between 9th primary length of first and second captures, by the number of days between captures:

$$\text{RGR} = \frac{\Delta 9^{\text{th}} \text{ length (mm)}}{\# \text{ days}}$$

Calculation of average RGR for males and females excluded individuals that were first captured with no visible new 9th primary growth. These birds were excluded either because they were functionally flightless but had not yet shed their 9th primary feathers, or their stage in the pre-emergence interval was unknown and inclusion may have biased the average RGR estimates low. An information theoretic approach was used to determine if RGR differed between sexes. The null model was best supported (AIC_c weight= 0.51), suggesting that remigial growth rate did not differ between sexes. This has also been observed in other sea ducks (Dickson 2011). As such, a RGR was estimated for all individuals, regardless of sex.

2.2.3.2. Emergence Date

We refer to “emergence date” as the date that a new feather becomes visible as it emerges from the skin of the wing. This date traditionally has been deemed the start of remigial molt and the total length of molt estimated as the time it takes a newly erupted feather to reach maturity (Sjoberg 1988; Van de Wetering and Cooke 2000; Iverson and Esler 2007). However, very few studies have considered the time it takes for a new feather to erupt from the skin once an old feather has been dropped (Owen and Ogilvie 1979; Panek and Majewski 1990; Miller *et al.* 1992; Dickson 2011), which we refer to as the “pre-emergence interval”. The start of remigial molt and the flightless period in this study refers to the time at which an old feather is dropped. Thus, the entire remigial molt period encompasses both the pre-emergence interval and the time it takes a newly erupted feather to reach maturity.

Emergence date for all captured individuals was calculated by dividing the 9th primary length at 1st capture by the average RGR for all individuals, and subtracting this from the capture date:

$$\text{Emergence Date} = \text{Date 1}^{\text{st}} \text{ capture} - (9^{\text{th}} \text{ length 1}^{\text{st}} \text{ capture} / \text{RGR}) \text{ day}$$

Birds first captured with a 9th primary length of zero were assigned an emergence date the same as their capture date.

Multiple linear regression models were used to examine variation in emergence dates as a function of explanatory parameters including cohort (a 4-level categorization of a combination of age and sex), lake, and year (Table 1). We used an information-

theoretic approach to data analysis to evaluate support from the data for a suite of 17 candidate models (Table 1). We included a null model to test the hypothesis that emergence date was not influenced by any of the variables we examined. All models in the candidate set, excluding the null, included a variable pertaining to cohort, as the effect of this variable was assumed given the information known regarding breeding phenology of Barrow's Goldeneyes (i.e. males and females spend different amounts of time in the breeding stage of the annual cycle). However, we categorized cohort in 2 ways to discern if differences among cohorts were primarily driven by the difference between adult (breeding) females and all other cohorts or if all cohorts had unique timing. One cohort categorization included all 4 cohorts as different categories, whereas another lumped males of all ages with SY females and contrasted those with a category for adult females (FASY). Two models including each of the cohort variables separately were incorporated in the candidate set. Two models included one of the cohort variables and the additive effect of lake, two more included one of the cohort variables and the additive effect of year, and two models included one of the cohort variables and the additive effects of both lake and year. Finally, 8 models investigating the interactive effects of each of the cohort variables and lake and year also were included in the candidate set (Table1). Akaike's Information Criterion, corrected for small sample size (AIC_c ; Burnham and Anderson 2002) was used to indicate the most parsimonious models. The difference between each model and the most parsimonious model (ΔAIC_c) and AIC_c weights (ω_i) were used to evaluate the relative support for each model. Parameter likelihood values ($\Sigma\omega_i$) were calculated for each variable to evaluate the level of support for the variable within the candidate model set. Weighted parameter estimates (with 95% CIs) also were calculated for each variable. Analyses were performed in R 2.12.1 (R Core Development Team 2010).

2.2.3.3. Pre-emergence Interval

Due to lack of a strong precedent for calculating the pre-emergence interval (see above), this was estimated using three methods, and an average pre-emergence interval was calculated across methods. As the variance surrounding the average of each of the three methods was independent, propagation of variance was used to calculate the error surrounding the average across methods.

2.2.3.3.1. Method 1: Collected birds

The shaft of the right 9th primary of birds with fully grown remiges collected from Cardinal Lake in 2008-2010 was marked where it emerged from the skin. The feather was then plucked and the distance between the base of the feather to the mark was measured. The number of days required to grow this amount of feather was calculated using the estimated average RGR. Assuming that RGR was constant over the entire molt period, the average of all individuals represented an average value of the pre-emergence interval.

2.2.3.3.2. Method 2: Panek and Majewski 1990

Birds first captured with 9th primary = 0 mm, and captured again in the same year were used to estimate the pre-emergence interval. The emergence date of each bird was calculated (as above) using the second capture date. The number of days between the calculated emergence date and the first capture date (when 9th primary = 0 mm) was determined and doubled to give the length of the pre-emergence interval. This assumes that, on average, birds were first captured in the middle of the pre-emergence period.

$$\text{Pre-emergence} = 2 ((\text{Date 2}^{\text{nd}} \text{ capture} - (9^{\text{th}} \text{ length } 2^{\text{nd}} \text{ capture}/\text{RGR})) - \text{Date } 1^{\text{st}} \text{ capture})$$

The average of all individuals was calculated to give an estimate of the length of the pre-emergence interval.

2.2.3.3.3. Method 3: Ratios

The ratio of birds captured with 9th primary = 0 mm to total birds captured was assumed to be equal to the ratio of days that birds have 9th primary = 0 mm to days that birds are flightless and available to capture. This assumes the following: 1) capture effort was consistent over time, 2) captures took place over the entire flightless period and 3) all flightless individuals were equally trappable.

Given these assumptions, the length of the pre-emergence period in days was calculated by solving for x in the following equation:

$$\frac{\# \text{ birds } 9^{\text{th}} = 0 \text{ mm}}{\text{Total birds captured}} = \frac{X}{(\text{Length of flightless period} + X)}$$

2.2.3.4. Length of the Flightless and Molt Period

We assumed that most birds captured at Cardinal and Leddy lakes in 2009 and 2010 were flightless, although a small number may have had primaries long enough to be flight capable but were still captured; as such, the 97.5 percentile of the 9th primary length of birds captured during remigial molt was used to represent the minimum 9th primary length required to re-gain flight. The length of the flightless period was calculated as the number of days to grow the 9th primary to the 97.5 percentile length from 0 mm, plus the number of days in the pre-emergence interval:

$$\text{Flightless period} = (97.5 \text{ percentile } 9^{\text{th}} \text{ length} / \text{RGR}) + \text{average pre-emergence}$$

The length of the total molt period, including the period in which 9th primary was not fully grown but birds were flight capable, was calculated using the same equation, but we substituted the estimated mature 9th primary length in place of the 97.5 percentile length of molt-captured birds. The average length of a mature 9th primary feather was estimated for male and female BAGO using data collected from birds captured between February and May in Alaska and BC between 2005 and 2011, as well as collected birds with fully grown primaries from Cardinal Lake in 2008- 2010.

2.3. Results

2.3.1. Remigial Growth Rates (RGR)

Average remigial growth rates of males and females did not differ, thus a combined average (\pm SE) RGR of 3.94 ± 0.13 mm/day was estimated ($n=38$).

2.3.2. Pre-emergence Interval

Average length of the pre-emergence interval (\pm SE) was similar across all methods of calculation (collected birds = 6.0 ± 0.56 days, Panek and Majewski = 4.5 ± 0.93 days, ratio = 9.1 ± 3.0 days). Length of the pre-emergence interval averaged over all three estimation methods was 6.5 ± 1.2 days.

2.3.3. Length of the Flightless and Molt Period

Average lengths of mature 9th primaries (\pm SE) of non-molting BAGO caught in BC, AK and AB were 155 ± 0.4 mm (n= 247) for males and 141 ± 0.7 mm (n=65) for females. Based on the 97.5 percentile of 9th primary lengths of male birds captured during remigial molt, 77% (120 mm) of the total 9th primary length was required for males to re-gain flight capabilities. Because females molt later than males and males are the dominant sex cohort using Cardinal and Leddy Lakes, trapping efforts became inefficient before the end of female remigial molt. As a result, we did not capture females late enough in remigial molt to ascertain the minimum percentage of 9th primary growth required for flight. This percentage was found to be similar for male and female scoters (Dickson 2011), so we assumed that 77% (109 mm) of the total 9th primary length was required for female Barrow's Goldeneye as well. The number of days necessary for males and females to have sufficient 9th primary growth to re-gain flight was 30 days and 28 days since emergence, respectively. The total duration of the flightless period, including the pre-emergence interval, was 36.5 days and 34.5 days respectively.

Based on the average RGR, the number of days required to grow the full 9th primary from the time of emergence was 39 days for males and 36 days for females. The overall duration of remigial molt, including the pre-emergence interval, was 45.5 days and 42.5 days for males and females, respectively.

2.3.4. Emergence Date

Average 9th primary emergence date of each cohort is summarized in Figure 1 for Cardinal and Leddy Lakes in 2009 and 2010. The model containing cohort as 4 separate combinations of sex and age, lake and year as main effects received most support for explaining variation in emergence dates (AIC_c weight = 0.72, r²= 0.31, Table 1). The model containing cohort, lake and year as main effects, and a lake x year interaction was the next best supported model (AIC_c weight = 0.27, r²= 0.31, Table 1). All other cohort models received very poor support from the data (AIC_c weight \leq 0.01, Table 1) relative to the two best-supported models.

Parameter likelihoods also supported cohort, lake and year variables as the best variables for explaining variation in emergence dates (likelihood values= 1). Model

averaged parameter estimates for cohort indicate that 9th primaries of ASY females emerged an average (\pm SE) of 5 ± 1.2 days later than SY females, 12 ± 0.8 days later than ASY males, and 17 ± 1.0 days later than SY males (Figure 1). Emergence dates for each cohort were 2 ± 0.5 days earlier on Cardinal Lake than Leddy Lake, and 3 ± 0.4 days earlier in 2010 than 2009. The lake x year interaction received some degree of support with a parameter likelihood of 0.27, though the parameter estimate was small (0.03 ± 0.19 days) and 95% confidence intervals for this parameter estimate overlapped zero, indicating that the effect of this parameter was weak.

2.4. Discussion

Based on a relatively slow remigial growth rate, long flightless period, and high degree of variation in timing of molt both between and within age and sex cohorts, it is unlikely that molting Barrow's Goldeneyes at Cardinal and Leddy Lakes are subject to high risk of mortality (e.g., predation/disturbance) or temporal constraints. In contrast, temporal optima exist at other stages of the annual cycle for many waterfowl: Timing of nest initiation of Wood Ducks (*Aix sponsa*) is constrained by the cost of incubation at cooler temperatures early in the breeding season (Hepp and Kennamer 2011); Common Eider (*S. mollissima*) nest initiation must be timed to ensure plenty of ice-free foraging for ducklings (Love *et al.* 2010); Pink-footed Goose (*Anser brachyrhynchus*) migration is timed to follow availability of food resources along migration pathways (Duriez *et al.* 2009); Barnacle Geese (*Branta leucopsis*) appear to time spring migration with the onset of warmer temperatures and increased day length at wintering grounds (Tombre *et al.* 2008). Further, synchronous timing of remigial molt of some other waterfowl suggest temporal optima associate with this stage (Barnacle Geese; Owen and Ogilvie 1979; Black Brant (*Branta bernicula nigricans*), Taylor 1995; Red-breasted Mergansers (*Mergus serrator*), Craik *et al.* 2009). Thus, while the lack of temporal constraints associated with remigial molt in this study concur with observations of molting scoters (Dickson 2011), this may be rare within the waterfowl community.

Barrow's Goldeneyes in the BTZ grew their primaries at an average rate of 3.94mm/day (\pm 0.13mm SE), which is similar to the 4.04mm/day growth rate observed for Barrow's Goldeneyes molting at higher latitudes (Van de Wetering and Cooke 2000).

These rates are similar to, or slightly slower than, those estimated for other species of ducks (Green-winged Teal (*Anas carolinensis*), 4.8mm/day, Sjoberg 1988; Mallard (*A. platyrhynchos*), 5.5mm/day, Panek and Majewski 1990; Northern Pintail (*A. acuta*), 4.2mm/day, Miller *et al.* 1992; Harlequin Duck (*Histrionicus histrionicus*), 3.5mm/day, Iverson and Esler 2007; Surf Scoter (*Melanitta perspicillata*), 3.9mm/day, Dickson 2011; White-winged Scoter (*M. fusca*), 4.3mm/day, Dickson 2011). The rate at which feathers are grown can have a significant impact on quality of feathers produced, with feathers grown faster being lighter, and therefore less durable, than feathers grown slower (de la Hera *et al.* 2009). Barrow's Goldeneyes, and other sea ducks, may grow their primaries at a slightly slower rate than similarly sized dabbling ducks to ensure growth of high quality feathers. This may be of greater importance to diving ducks than other non-diving waterfowl, as wing feathers may need to withstand greater abuse when used in underwater propulsion, especially in saltwater. Alternatively, relatively slow feather growth rates of Barrow's Goldeneyes could act to reduce daily nutritional demands of remigial molt by spreading costs of feather growth over a longer period of time. This might be expected if molt were a nutritionally challenging stage for Barrow's Goldeneye, however information about mass dynamics and foraging effort during remigial molt (Chapter 3) strongly indicate that this is not the case for Barrow's goldeneyes.

Male and female Barrow's Goldeneyes had estimated flightless periods (excluding the pre-emergence interval) of 30 and 28 days, respectively, which is a relatively long period of time compared with other duck species (Green-winged Teal, 19 days, Sjoberg 1988; Mallard, 20-27 days, Panek and Majewski 1990; Northern Pintail, 25 days, Miller *et al.* 1992; Canvasback (*Aythya valisineria*), 21-28 days, Thompson and Drobney 1995; Long-tailed Duck (*Clangula hyemalis*), 21-28 days, Flint *et al.* 2004). Barrow's Goldeneyes molting on the Old Crow Flats, YT also had a relatively long flightless period of 31 days. While the longer flightless period experienced by Barrow's Goldeneyes could be interpreted to reflect nutritional constraints on feather growth (but see Chapter 3), it could also be an artifact of greater wing loading in this species compared to other ducks. If this were the case, Barrow's Goldeneyes would be expected to require a greater percentage of the 9th primary feather to be grown before re-gaining flight capability. We estimated that Barrow's Goldeneyes achieved flight at approximately 77% 9th primary growth, which falls within the upper range for waterfowl described by Hohman *et al.* (1992) (55%-85%). A high percentage of primary growth for

flight has also been documented in White-winged and Surf Scoters (Dickson 2011). Thus, the longer flightless period of Barrow's Goldeneyes compared to non-sea duck waterfowl may simply be a function of having higher wing loading. In any case, it appears that Barrow's Goldeneyes are not under selective pressure to shorten the duration of the flightless period, indicating that they are probably not under intense risk of mortality (e.g. high predation risk, anthropogenic and/or natural disturbances) during remigial molt at Cardinal and Leddy Lakes. This also is supported by high survival rates that have been documented during remigial molt at these sites (Chapter 4).

Average length of the pre-emergence interval estimated in this study was 6.5 days, which is similar to estimates of the pre-emergence interval for Surf Scoters and White-winged Scoters (Dickson 2011). This is considerably longer than has been assumed or calculated for other waterfowl species on the few occasions that this time period has been considered (2 days, Owen and Ogilvie 1979; 2 days, Sjoberg 1988; 2 days, Panek and Majewski 1990). Even the lowest estimate of the pre-emergence interval in this study (4.5 days) was over twice as long as has been calculated using the same method for Mallards (Panek and Majewski 1990). This may indicate that the pre-emergence interval varies from species to species. Also, estimates of the total duration of the flightless and remigial molt periods for many waterfowl species may be underestimated by almost a week through failure to account for this stage of remigial molt. Perhaps the most reliable method of calculation for the pre-emergence interval results from measuring the length of feather shaft that is sheathed in the skin of the wing, as this makes only a single assumption i.e. that feather growth rate remains constant throughout molt. Future studies of remigial molt in any bird species should incorporate the pre-emergence interval into estimates of the length of remigial molt.

We found that emergence date of Barrow's Goldeneyes differed among all of the age and sex cohorts. Differential timing of molt among age and sex cohorts has been observed in many species of waterfowl (Owen and Ogilvie 1979, Gates *et al.* 1993, Gilliland *et al.* 2002, Savard *et al.* 2007, Oppel *et al.* 2008). Differences have been attributed to breeding status, breeding success, and differences in parental duties between sexes. The estimated difference between average emergence dates of the earliest molting Barrow's Goldeneye cohort, SY males, and the latest molting cohort, ASY females, was about 2.5 weeks. Males generally molted earlier than females, and

sub-adult cohorts generally molted earlier than adult cohorts. These differences are likely due to differences in breeding activity. Adult females may molt later than other cohorts because they stay on breeding grounds longer to attend to broods (Eadie *et al.* 2000). Sub-adult females may molt later than either sub-adult or adult males because they stay at breeding sites longer to prospect for future nest sites (Eadie and Gauthier 1985).

Variation in emergence dates among individuals within cohorts was high. Variation was greatest in male cohorts, with some individuals initiating remigial molt over 42 days earlier than others (M ASY CL 2009, Figure 1). This asynchrony suggests that optimal molt initiation dates fall within a relatively large period of time, perhaps indicating that Barrow's Goldeneyes molting at Cardinal and Leddy Lakes are not strongly constrained by seasonal factors such as prey abundance or weather. Females may be more synchronous than males because they initiate molt later in the year and are perhaps more constrained by seasonal factors as a result.

Timing of initiation of remigial molt also varied by lake and year. The estimated difference in emergence dates between Cardinal and Leddy Lakes was 2 days, while the difference between years was 3 days. It is unlikely that these differences are biologically significant given the range of emergence dates within cohorts. The difference in emergence dates between years could be due to any number of environmental variables that influence breeding or molt migration phenology, and subsequently cause differential timing of molt (e.g., weather, food availability).

The apparent absence of temporal constraints and low risk of mortality of Barrow's Goldeneyes at our study sites highlights the importance of both Cardinal and Leddy Lakes as molting locations, as they appear to provide ideal habitats during a stage in the annual cycle that has been identified as potentially stressful for birds. Concerted effort should be made to protect these areas from anthropogenic degradation or major disturbances in the future. Small-scale anthropogenic disturbances, such as boating, should also be kept to a minimum for the duration of the remigial molting period of Barrow's Goldeneyes at these sites. Information regarding mass dynamics and foraging effort of Barrow's Goldeneyes molting at Cardinal and Leddy Lakes, in

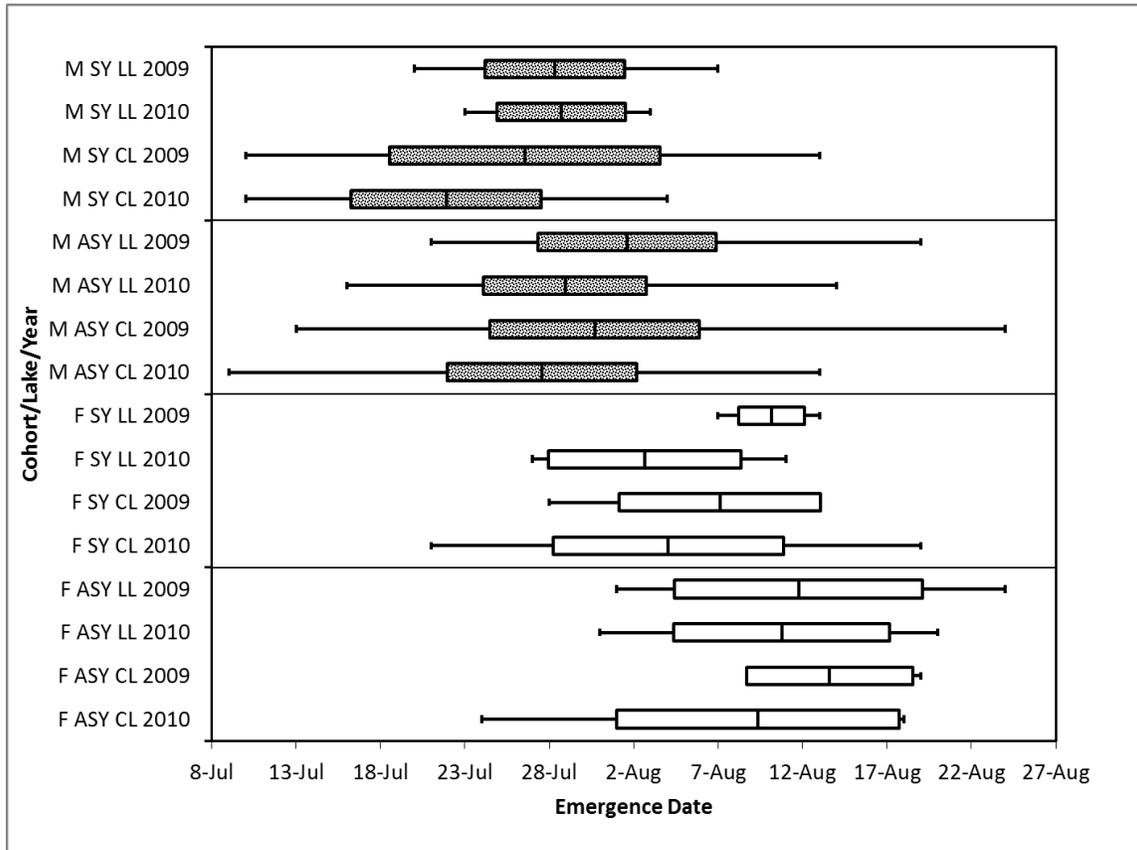
conjunction with the phenological results presented here, are needed to infer more about potential nutritional constraints faced by birds during this stage of the annual cycle.

2.5. Tables and Figures

Table 1: Linear model selection results for models explaining variation in emergence dates among Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB in 2009 and 2010. Variable interactions are denoted by 'x'.

Response Variable	Model	K	$\Delta AICc$	AICc weight (w_i)
Emergence Date	cohort + lake + year	7	0.00	0.72
	cohort + lake + year + lake x year	8	1.99	0.27
	cohort + lake + year + cohort x lake x year	17	8.61	0.01
	cohort + year	6	21.50	0.00
	cohort + year + cohort x year	9	26.25	0.00
	cohort + lake	6	86.68	0.00
	cohort + lake + cohort x lake	9	86.92	0.00
	FASY + lake + year	5	122.79	0.00
	FASY + lake + year + lake x year	6	124.75	0.00
	FASY + lake + year + FASY x lake x year	9	128.59	0.00
	cohort	5	137.94	0.00
	FASY + year	4	143.73	0.00
	FASY + year + FASY x year	5	145.09	0.00
	FASY + lake	4	199.70	0.00
	FASY + lake + FASY x lake	5	200.86	0.00
	FASY	3	248.89	0.00
	null	2	425.77	0.00

Figure 1: Emergence dates of 9th primary feathers during remigial molt of Barrow's Goldeneye age and sex cohorts on Cardinal and Leddy Lakes, AB in 2009 and 2010 (bars are average \pm SD). Whiskers represent earliest and latest dates for each cohort. Filled bars represent male cohorts. Y-axis abbreviations include M = male; F = female; SY = second-year age class; ASY = after-second-year; LL = Leddy Lake; CL = Cardinal Lake, followed by the year (2009 or 2010).



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3. Body Mass Variation and Foraging Effort of Barrow's Goldeneyes: Strategies for Managing Risks of Simultaneous Remigial Molt

3.1. Introduction

Waterfowl replace remiges simultaneously, becoming flightless for approximately 20-40 days depending upon species (Hohman *et al.* 1992). While simultaneous remigial molt reduces the overall duration of remigial molt compared to sequential molt (Filardi and Rohwer 2001; Guillemette *et al.* 2007), it also represents a potentially vulnerable stage in the annual cycle (Dopfner *et al.* 2009) when the ability to acquire food and escape predators or other risks may be diminished by reduced mobility associated with loss of flight. As such, waterfowl have developed an array of molting strategies to accommodate risks of simultaneous remigial molt, which can vary widely among species.

One strategy that many waterfowl employ to reduce risks associated with loss of flight during remigial molt is to undergo molt migrations to predictable environments that typically provide abundant food resources and reduce risks of predation and disturbance compared to habitats used during the rest of the annual cycle (Salomonsen 1968; Madsen and Mortensen 1987; Derksen *et al.* 1982; Zicus 1981). In the northern hemisphere, molting habitats often are large, high latitude wetlands or coastal habitats with little human disturbance and relatively low predator abundance (Van de Wetering and Cooke 2000; Robert *et al.* 2002; Flint *et al.* 2004; Phillips *et al.* 2006; Lewis *et al.* 2010). In addition to selection of molting habitats, waterfowl can strategically vary when and where they acquire nutrients and energy required for feather growth, as well as associated foraging behavior on molt sites, to optimize the balance between food acquisition and avoidance of predation risk.

Remigial molt requires protein and energy (Heitmeyer 1988, Murphy 1996, Thompson and Drobney 1997) beyond that of maintenance requirements (Murphy 1996). Nutritional and energetic needs during remigial molt can be met using endogenous reserves and/or exogenous resources. The degree to which each source is relied upon varies widely by species. Some waterfowl primarily meet their energy and nutrient requirements for remigial molt through their diet, often increasing foraging effort and maintaining or gaining mass throughout this time period (Ankney 1979; Young and Boag 1982; Thompson and Drobney 1996; Fox *et al.* 2008). Others rely primarily on somatic reserves of lipids and proteins to fuel feather growth, catabolizing body tissues, often foraging very little and losing mass (Panek and Majewski 1990; Hohman 1993; Brown and Saunders 1998; Fox and Kalhert 2005; Portugal *et al.* 2007; Fox and King 2011). A few species rely on both approaches to meet their energetic and nutritional demands during different stages of remigial molt (Owen and Ogilvie 1979; Bailey 1985; Moorman *et al.* 1993; Fox *et al.* 2009).

Predation risk may play a part in determining nutritional sources and foraging strategies used by waterfowl during remigial molt. High risk of predation may lead to decreased foraging effort and use of somatic reserves in an attempt to do one or both of two things: 1) decrease detection by predators or increase vigilance by decreasing other activities during remigial molt (Panek and Majewski 1990; Adams *et al.* 2000; Dopfner *et al.* 2009; Portugal *et al.* 2010) or 2) reduce mass over the molting period to decrease wing loading and re-gain ability to fly earlier (Panek and Majewski 1990; Brown and Saunders 1998; Van de Wetering and Cooke 2000). High perceived risk of predation might also lead to nocturnal foraging (Evans and Day 2001), though this behaviour has seldom been observed in sea ducks (Systad and Bustnes 2001; Lewis *et al.* 2005) and is more often attributed to nutritional requirements (Systad and Bustnes 2001; Lane and Hassall 1996). Hence, mass and foraging strategies can be used to infer nutritional and predation pressures influencing waterfowl during remigial molt, though these have rarely been measured concurrently. Concurrent evaluation of mass and foraging dynamics allows for a more complete understanding of pressures imposed on birds during remigial molt by giving insight into the potential causes of mass change (i.e. concurrent foraging effort data allows for a better interpretation of mass change).

Some species appear to utilize different molt strategies at different locations (Owen and Ogilvie 1979; Young and Boag 1982; Dubowy 1985; Panek and Majewski 1990; Brown and Saunders 1998; Dopfner *et al.* 2009; Portugal *et al.* 2007; Fox and King 2011). This suggests that strategies used to meet costs of remigial molt may be plastic within species, and may be environmentally mediated. Furthermore, for some species, molting strategy may be influenced by individual traits or condition, such as mass or structural size (Ndlovu *et al.* 2010; Portugal *et al.* 2011).

Mass and foraging dynamics of sea ducks during remigial molt have rarely been studied, and the few studies available do not address both of these aspects concurrently (Adams *et al.* 2000; Van de Wetering and Cooke 2000; Guillemette *et al.* 2007; Fox *et al.* 2008). The objective of this study was to quantify foraging effort and mass dynamics of molting Barrow's Goldeneye to evaluate strategies by which they accommodate risks associated with remigial molt. If Barrow's Goldeneyes are primarily limited by nutritional demands of remigial molt, we would expect high foraging effort and declining body mass throughout this period as birds struggle to meet costs of molt with both exogenous and endogenous resources. This assumes that mass loss is due to catabolism of tissues, and that birds are more influenced by the need to obtain energy and nutrients for feather growth than by the risk of predation. If risk of predation is primarily limiting Barrow's Goldeneyes during remigial molt, we would expect body mass to decline and foraging effort to be low, indicating that birds are actively losing mass to regain flight sooner and/or modifying foraging behavior to allow for increased vigilance. Constant or increased mass during remigial molt would indicate that the birds are not nutritionally limited, particularly if associated with low or moderate levels of foraging effort. If mass loss at the beginning of remigial molt is accompanied by mass gain towards the end of this period, then mass loss may be the result of shedding potentially costly somatic reserves during a time when high-quality foraging conditions and high temperatures make them superfluous.

3.2. Methods

3.2.1. Study Areas

Cardinal Lake (56° 14'N, 117° 44'W), also known as Lac Cardinal, is a large (50 km²) wetland located in the Boreal Transition Zone of northwestern Alberta. The basin rarely exceeds a depth of 2 m, has a primarily sand and gravel substrate, and is hypereutrophic. Leddy Lake (56° 23'N, 117° 27'W) is a small (4 km²), lake located approximately 25 km NE of Cardinal Lake. This basin is shallow (< 2 m), has a primarily muddy substrate, dense submerged vegetation mat throughout most of the lake, and is mesotrophic. Combined, these lakes support 5 000- 7 000 molting Barrow's Goldeneyes, the majority of which are adult males (Hogan *et al.* 2011). Cardinal and Leddy Lakes were only recently recognized as important molting areas for Barrow's goldeneyes and are two of only five known molting sites for large numbers of the species in North America (Hogan *et al.* 2011).

3.2.2. Captures and Foraging Effort

Barrow's Goldeneyes were captured during remigial molt (late July-early September) using drive trapping techniques (Van de Wetering 1997) on Cardinal and Leddy Lakes in 2009 and 2010. Each bird was fitted with a uniquely numbered US Fish and Wildlife Service stainless steel tarsal band and mass of each bird was measured to the nearest gram. Morphometric measurements were taken, including 9th primary length measured to the nearest millimeter as an indicator of stage of remigial molt. Sex was determined by cloacal and plumage characteristics (Hochbaum 1942; Carney 1983) and age class was indicated by bursal depth (Mather and Esler 1999; Iverson *et al.* 2003). Age class was categorized as either second-year (SY; i.e., ~2 months beyond the first year after hatching, bursa >10 mm) or after-second-year (ASY, bursa ≤ 10 mm).

A subset of 25 ASY male Barrow's Goldeneyes was marked with radio transmitters on each lake in both 2009 and 2010 to monitor foraging effort during the molting period (total 100 transmitters). Small VHF radio transmitters weighing less than 12g (~1% of average molting body mass) were attached using subcutaneous prongs and superglue (Iverson *et al.* 2006). Foraging effort of each radio-tagged individual was monitored multiple times throughout remigial molt for one hour intervals during different

parts of the day. Observations were classified as diurnal if the majority of the observation period occurred between sunrise and sunset. Nocturnal observations occurred between sunset and sunrise. Dives were indicated by temporary disappearance of the radio signal, and duration of each signal disappearance was recorded to estimate the total time spent underwater per hour (Lewis *et al.* 2005). Disappearances of less than 4 seconds were discarded as they were likely due to belly preening/rolling behaviour (Lewis *et al.* 2005). Twenty hours of daytime visual observations of unmarked Barrow's Goldeneyes confirmed that diving constituted the principal method of foraging used by birds on both lakes, as other foraging behaviors (e.g., dabbling) were not observed.

Average masses of ASY male Barrow's Goldeneye during other stages of the annual cycle were determined from birds captured in Alaska, the Yukon Territory, British Columbia and Alberta during other studies (Esler, unpublished data; Thompson, unpublished data; Van de Wetering 1997). Mass estimates from other periods in the annual cycle were compared to those during remigial molt to better understand how remigial molting mass fits into the annual mass cycle.

3.2.3. Data Analysis

3.2.3.1. Mass Dynamics during Remigial Molt

Multiple linear models were used to evaluate variation in mass as a function of age, lake, year, emergence date, molt stage and structural size. Emergence date referred to the date at which the new 9th primary erupted from the skin of the wing (Chapter 2). Molt stage (days since emergence) was calculated by dividing the 9th primary length at capture by the average remigial growth rate determined for Barrow's Goldeneyes recaptured while this primary was still growing (3.94mm/day; Chapter 2). Separate analyses of sources of variation in body mass were performed for males and females because of distinct sexual dimorphism in this trait for Barrow's Goldeneyes (Eadie *et al.* 2000, Schamber *et al.* 2009). The effect of structural size on mass was investigated through PC1 scores generated for each bird by a principle components analysis based on diagonal tarsus, head and culmen length. PC1 accounted for 57% of

variation in male measurements ($PC1 = -0.43 \cdot \text{tarsus} - 0.61 \cdot \text{culmen} - 0.66 \cdot \text{head}$) and 49% in female measurements ($PC1 = 0.30 \cdot \text{tarsus} + 0.65 \cdot \text{culmen} + 0.70 \cdot \text{head}$) with positive values indicating smaller birds in males and larger birds in females.

An information-theoretic approach to data analysis was used to evaluate support for a suite of candidate models. 12 models were included in each of our candidate sets (Table 2, Table 3). A null model was included to represent the hypothesis that variation in mass was unrelated to any of the explanatory variables we investigated. We were primarily interested in whether mass changed with molt stage, so we included a model that specifically addressed this hypothesis. Mass could vary with age, as sub-adult birds may have yet to achieve their full adult mass, and structural size, as structurally larger birds might be heavier than smaller birds. Environmental/food conditions (lake and year) also could account for some variation in mass. Age, size, lake and year were grouped as a set of covariates and included in all models (excluding the null and molt stage models) to account for potential variation caused by these factors. Interactions between the covariates and molt stage were included in some models to investigate whether the effect of molt stage on mass was influenced by other factors. Emergence date also could influence mass, as birds starting molt later could have more time to gain weight before initiating molt and thus have different starting masses and mass trajectories through remigial molt, so emergence date and its interactions with covariates were included in some models. Two models in addition to the null excluded molt stage (with and without two-way interactions among other variables) to explicitly test whether body mass remained constant through the wing molt phase. A global model was included in the candidate set to test the complex hypothesis that all variables and their biologically plausible interactions best explained variation in mass.

Akaike's Information Criterion corrected for small samples sizes (AIC_c ; Burnham and Anderson 2002) was used to identify the most parsimonious model in the candidate set. The difference between each model and the most parsimonious model (ΔAIC_c) and AIC_c weights (ω_i) were used to evaluate the relative support for each model. Parameter likelihood values ($\sum \omega_i$) were calculated for each variable to evaluate the level of support for the variable within the candidate model set. Weighted parameter estimates (with unconditional 95% CIs) also were calculated for each variable across the entire candidate model set.

3.2.3.2. Foraging Effort during Remigial Molt

Thirty-nine days are required for an ASY male Barrow's Goldeneye to grow a full 9th primary feather after it emerges (Chapter 2). Foraging observations that occurred < 39 days after the estimated emergence date of radio-marked birds were considered to occur during remigial molt. We modeled variation in foraging effort (min/hr) during remigial molt as a function of lake, year, emergence date, molt stage (days since emergence), residual mass and time since diurnal/nocturnal transition (hours). Residual mass was calculated by subtracting the predicted mass of each individual (obtained using the model averaged parameter estimates from the mass analysis above) from the actual mass recorded at capture. This provided an estimate of how much heavier/lighter each individual was compared to the average individual. Time since transition referred to the time since sunrise for diurnal observations, and the time since sunset for nocturnal observation. Separate analyses were performed for diurnal and nocturnal observations to simplify the candidate model set. Squared terms for emergence date, molt stage, residual mass, and time since transition were included in models to allow for non-linear relationships with foraging effort. A non-linear relationship with emergence date might be expected if birds initiating molt earlier or later had to forage harder due to seasonal variation in environment/prey availability. Also, birds may be inclined to forage less/more during different stages of molt (e.g., birds that have regained flight may forage more because of increased metabolic demands/decreased risk of predation). Lighter birds may forage more than average to gain weight to achieve an optimal mass, while heavier birds may forage more due to increased metabolic costs. Also, foraging effort may peak at certain times of the day. Lake and year were combined into a single categorical variable (LKYR) with four levels to represent differences in environmental conditions and prey availability on each lake each year. Because observations included repeated measures of individuals, we examined whether using a mixed modeling approach to accommodate the repeated measures structure and lack of independence among observations on the same individual improved model fit. We used the 'step-up' approach described by Zuur *et al.* 2009 to determine the ideal structure for models within our candidate set by comparing AIC_c values of the global model including a random term for individual bird (mixed model) to the same model without random effects. Heterogeneity of residuals resulting from unequal variances among the levels of LKYR was an issue for both models, so a model variance structure accounting for unequal

residual variances between levels of LKYR was applied to both models. This structure provided better model fit in both models, and after its application the Generalized Least Squares (GLS) global model without random effects was found to provide the best fit for both the nocturnal (AIC_c weight= 0.88) and diurnal (AIC_c weight= 0.78) data (i.e., individual bird effects did not matter).

We included 20 models in our candidate set (Table 6, Table 7). We included a null model to test the hypothesis that variation in foraging effort was not related to any of the variables we investigated. We treated LKYR and time since transition variables as a set of covariates to account for potential variation in foraging effort caused by environmental factors, though their specific effects were not our primary interest. We were most interested in the relationship between foraging effort and residual mass, molt stage, and emergence date and included models for each relationship separately, as well as models investigating the interactive effect of the covariates on the relationship between foraging effort and each variable. We also included a model containing residual mass, molt stage and emergence date together as a way to investigate the overall effects of molt on foraging effort. Some models contained covariates and their interactions alone, while other included covariates as well as all other variables and their interactions to test whether environmental or molt-related factors best explained variation in foraging effort. A global model was included to represent a situation where all main effects and their interactions best described variation in foraging effort. Akaike's Information Criterion (AIC_c ; Burnham and Anderson 2002) was used to identify the most parsimonious models. The difference between each model and the most parsimonious model (ΔAIC_c) and AIC_c weights (ω_i) were used to evaluate the relative support for each model. Parameter likelihoods ($\sum \omega_i$) were calculated for each variable to evaluate the support for the variable within the candidate model set. Weighted parameter estimates (and 95% CIs) were calculated for each variable across the entire candidate model set. All analyses were performed in R 2.12.1 (R Core Development Team 2010) and foraging analyses were performed using the nlme package in R (Pinheiro *et al.* 2010).

3.3. Results

3.3.1. *Male Mass Dynamics during Remigial Molt*

The global model, containing all main effects and biologically plausible interactions of variables received almost all of the support for explaining variation in mass of male Barrow's Goldeneyes (AIC_c weight= 0.99, $r^2= 0.45$, Table 2). As such, model averaging was not necessary and parameter estimates and associated SE are those generated by the best-supported model (Table 4).

Both male age classes on both lakes in both years exhibited increased mass through the period of remigial growth (Figure 2a). Mass at initiation of remigial growth varied considerably by lake, year, and age class (Figure 2a; Table 4), although rate of mass gain was similar across these groups. Similarly, average body mass at initiation of remigial molt progressively increased with increasingly later emergence dates, with considerable variation in both intercepts and slopes across lakes, years, and age classes (Figure 3a). Taken together, these findings indicate a general, progressive increase in male Barrow's Goldeneye body mass through the remigial molt season. Also, while mass differences by age class were expected (with ASY consistently heavier than SY) as a common phenomenon in waterfowl, we were surprised by persistent and large differences in mass by lake. Average body mass at Leddy Lake was consistently higher than at Cardinal Lake, accounting for molt stage, emergence dates and size (Figures 2 and 3; Table 4), at biologically meaningful levels, e.g., over 100 g in some cases. Average mass varied to a smaller degree across years, with mass tending to be higher in 2010 than 2009 after accounting for other effects, generally in the 10s of grams.

3.3.2. *Female Mass Dynamics during Remigial Molt*

The model containing molt stage, emergence date, age, lake, year and size main effects was best at explaining variation in body mass of female Barrow's Goldeneyes (AIC_c weight= 0.38, $r^2= 0.29$, Table 3). The model containing all main effects and a molt stage x age interaction was next best supported (AIC_c weight= 0.16, $r^2= 0.29$, Table 3). The models containing all main effects and molt stage x year (AIC_c weight= 0.13, $r^2= 0.29$, Table 3), molt stage x lake (AIC_c weight= 0.12, $r^2= 0.29$, Table 3),

molt stage x emergence date (AIC_c weight= 0.12, $r^2= 0.29$, Table 3) and all main effects excluding molt stage (AIC_c weight= 0.08, $r^2= 0.26$, Table 3) received similar levels of support. All other models received little support (Table 3). Despite the model uncertainty, there was consistent support for all main effects, with high parameter likelihoods for emergence date, lake, year, age, PC1 and molt stage (Table 5).

As with males, average body mass of female Barrow's goldeneyes consistently increased through remigial molt (Figure 2b), as well as with increasing emergence dates (Figure 3b), indicating persistent seasonal mass increases. Also similar to males, females showed dramatic inter-annual and inter-lake variation in average mass levels (Figures 2b and 3b; Table 5), though not in trajectories. Differences related to age class were minor (Table 5).

3.3.3. *Remigial Molt Mass in the Annual Cycle of Barrow's Goldeneye*

Average mass of ASY male Barrow's Goldeneyes captured in Alaska, the Yukon Territory, British Columbia and Alberta were contrasted across different stages in the annual cycle (Figure 4). Increasing mass observed during remigial molt appeared to be part of a general increasing trend throughout the entire postbreeding period. Mass decreased over winter, reaching levels similar to those during remigial molt by early spring.

3.3.4. *Foraging Effort during Remigial Molt*

Average foraging effort of radio-marked ASY male Barrow's Goldeneyes on Cardinal and Leddy Lakes was ~120-140 min/hr during remigial molt (Figure 5). Cardinal Lake birds foraged mostly diurnally, while Leddy Lake birds foraged mostly nocturnally, however, birds on both lakes, in both years, foraged similar average amounts per day (~8-9% of day, Figure 5, Figure 6, Figure 7).

The best supported model explaining variation in diurnal foraging effort included LKYR, time since transition, and molt stage variables and the LKYR x molt stage interaction (AIC_c weight= 0.94, Table 6). All other models were weakly supported (AIC_c

weight ≤ 0.03 , Table 6). Diurnal foraging effort varied substantially by lake and year, as well as time since transition (Figure 6).

The best supported model to explain nocturnal foraging effort included LKYR, time since transition, and molt stage variables as well as the LKYR x time since transition interaction (AIC_c weight= 0.50, Table 7). The models containing LKYR, time since transition and their interactions (AIC_c weight= 0.18, Table 7) and LKYR, time since transition, and molt stage variables (AIC_c weight= 0.16, Table 7) were the next best supported models. All other models received little support (AIC_c weight ≤ 0.06 , Table 7). The LKYR (likelihood=1), time since transition (likelihood=0.99), molt stage (likelihood=0.68), and LKYR x time since transition interaction (likelihood=0.74) variables best explained variation in nocturnal foraging. These results, along with the diurnal foraging model results suggest a strong environmental influence on foraging effort during remigial molt.

3.4. Discussion

The combination of mass variation and foraging effort, which are rarely measured concurrently, provided strong inference that molting Barrow's Goldeneyes at our study sites were constrained neither by mortality risks nor nutritional constraints. Thus, remigial molt does not appear to be a period of demographic or nutritional limitation in the annual cycle of this population of Barrow's Goldeneyes, indicating that a key component of their strategy for completing remigial molt was selection of appropriate molt sites. Remigial molt marked the start of a period of mass gain in the annual cycle of Barrow's Goldeneyes at our study sites (Figure 4). Further, foraging effort of ASY males during remigial molt was low, indicating that mass gains could be supported with much less than maximal foraging, suggesting that (1) our study areas were highly productive, and (2) mass levels and trajectories were not constrained by food availability, indicating that these attributes were strategically optimized for the local conditions. Similar conclusions regarding constraints during remigial molt have been made about other waterfowl species (Ankney 1979; Young and Boag 1982; Hohman *et al.* 1993; Hohman and Crawford 1995; Thompson and Drobney 1996; Fox *et al.* 2008; Dickson 2011),

which suggests that remigial molt is not necessarily a period of increased risks for all waterfowl, but that molt site quality is a key factor in determining this.

3.4.1. Mass and Foraging Dynamics during Remigial Molt

Male and female Barrow's Goldeneyes on Cardinal and Leddy Lakes gained mass throughout remigial molt (Figure 2, Figure 3). Similar increasing or constant mass throughout remigial molt also has been found for other diving duck species (Hohman *et al.* 1988; Hohman *et al.* 1992; Thompson and Drobney 1996; Fox *et al.* 2008; Dickson 2011). However, mass declines have been observed for many dabbling ducks, as well as some of the smaller diving ducks, during remigial molt (Bailey 1985; Panek and Majewski 1990; Moorman *et al.* 1993; Brown and Saunders 1998; Fox and King 2011). Diving ducks, and sea ducks in particular, may be less influenced by predation risk during remigial molt than dabbling ducks because they tend to forage in off-shore habitats where they are less susceptible to land-based predators and are able to escape predators by diving. As a result, there may be little advantage for diving species to lose mass to re-gain flight compared to dabbling species, resulting in different remigial molt mass strategies between the two.

Barrow's Goldeneyes molting at Cardinal and Leddy Lakes foraged at similar rates as, or less than, other molting ducks of similar size (Adams *et al.* 2000; Dopfner *et al.* 2009; Dickson 2011; Craik *et al.* 2011). They also foraged similar amounts or less than other ducks at other stages of the annual cycle (Custer *et al.* 1996; Fischer and Griffin 2000; Systad and Bustnes 2001; Kirk *et al.* 2007; Lewis *et al.* 2007). Thus, Barrow's Goldeneye molting on our study sites were foraging at relatively low rates compared to that observed for other waterfowl. Combined with observed increases in mass, this observation suggests that Barrow's Goldeneyes in Alberta were obtaining the nutrients/energy they required for remigial molt easily, which could be achieved by 1) reducing daily energy expenditure by reducing activity or prolonging molt over an extended period of time (Thompson and Drobney 1995; Dopfner *et al.* 2009) and/or 2) choosing molting habitats that provide high quality food resources.

3.4.2. Remigial Molt Mass in the Annual Cycle of Barrow's Goldeneye

Average masses of ASY male Barrow's Goldeneyes at the beginning of remigial molt were amongst the lowest of the annual cycle (Figure 4). While traditionally remigial molt has been viewed as a constraining time in the annual cycle of waterfowl, our data indicate that this is not the case for Barrow's Goldeneyes at our study sites. Birds gained somatic stores during remigial molt, and continued to do so throughout the fall staging period. Also, the dramatic decrease in mass over winter suggests that postbreeding mass gain may not only ensure adequate energy for fall migration, but is possibly relied upon to sustain individuals throughout the wintering period and/or ensure adequate resources during an unpredictable stage in the annual cycle. This lends support to the idea that postbreeding habitat quality can have cross-seasonal effects on Barrow's Goldeneyes, and that these areas should be carefully protected to sustain stable populations of this species.

3.4.3. Plasticity of Molting Strategies

3.4.3.1. Cohort Variation in Mass Strategy

Accounting for size differences, male Barrow's Goldeneyes showed a large difference in mass between age classes (~83g). This is a common trend in many species, and could result from sub-adult birds having yet to achieve their full adult mass. If this is the case, differences observed in remigial molt mass gain between age classes is unsurprising, as SY birds may be trying to achieve both their threshold migration mass (Salomonsen 1968) and full adult mass, meaning that they may have to gain more weight/day than ASY birds, who are already at their adult mass. Female Barrow's Goldeneyes exhibited a small, biologically insignificant difference in mass between age classes (~3g) and SY and ASY females gained approximately the same amount of weight/day throughout remigial molt. The similarity between SY and ASY female mass might be attributed to differences in breeding status. Although no structural size differences have been observed between female age classes on Cardinal and Leddy Lakes, SY birds might be expected to be lighter than ASY birds as a result of not having reached their full adult mass. However, sub-adult birds do not expend energy breeding (Eadie *et al.* 2000), a costly stage in the annual cycle during which adult females typically rely on somatic reserves for egg production and incubation (Afton and Paulus

1992; Hobson *et al.* 2005). Thus, ASY female mass might be expected to be most similar to SY female mass just after breeding due to the high nutritional/energetic costs experienced by adult females during the breeding period.

The effect of emergence date on mass was similar to the effect of molt stage on mass for both male and female Barrow's Goldeneyes. The postbreeding period, in general, is a period of mass gain for Barrow's Goldeneyes (Figure 4), thus it is likely that these increases are related in that they represent separate portions of the same daily increase in mass over the post-breeding period. A plausible explanation for a larger effect of emergence date on mass for SY males than ASY males is the same as the explanation for why SY males gain more weight per day during remigial molt than ASY males (i.e., SY males are striving to obtain both their full adult mass and an optimal migration mass).

3.4.3.2. Lake and Year Variation in Mass Strategy

Male and female Barrow's Goldeneyes were heavier in 2010 than 2009, although differences observed between years may not be biologically significant (38g and 17g respectively). These differences could be attributed to annual variation in environmental conditions or habitat quality of sites used prior to the molting period. Male and female Barrow's Goldeneyes were heavier on Leddy Lake than Cardinal Lake in both 2009 and 2010 (Table 4, Table 5). Satellite telemetry (S. Boyd, unpublished data) indicates that it is unlikely that birds on each lake are coming from different breeding areas, and Leddy and Cardinal Lakes are close to one another geographically (~25km), thus it is unlikely that the differences observed result from birds expending more/less energy during migration to molt sites. It is more likely that optimal mass during remigial molt differs between lakes, and that birds account for this accordingly. Perhaps, as a smaller lake, Leddy is a less predictable molting habitat so birds molting there accumulate greater somatic nutrient reserves than birds on Cardinal Lake in case food resources deplete before the end of molt. This notion is supported by birds radio-marked on Leddy Lake during remigial molt that move to Cardinal Lake soon after they regain flight (Chapter 4), perhaps indicating that habitat conditions on Leddy Lake deteriorate over time. This begs the question of why molt on Leddy Lake in the first place? Birds molting on Leddy Lake may do so out of tradition. Perhaps in the past, Leddy Lake provided a more reliable molt site than it does presently. Indeed, studies suggest that the geographic

region surrounding Leddy Lake has experienced greater annual evaporation than precipitation over the last 40-50 years, resulting in many shallow lakes becoming wetlands (J. Thompson, unpublished data). However, recent surveys of molting birds on Leddy Lake suggest that use of this lake by Barrow's Goldeneyes fluctuates dramatically (Hogan *et al.* 2011), perhaps dispelling the notion of traditional use.

3.4.3.3. Variation in Foraging Strategy

Cardinal Lake birds foraged primarily diurnally during remigial molt, while Leddy Lake birds foraged primarily at night. This suggests that foraging behavior was being influenced by either daily activity patterns of prey organisms or a perceived risk from diurnal predators that caused birds to be more vigilant on Leddy Lake. Survival of molting birds on both Cardinal and Leddy Lake was high (Chapter 4) and avian predators were rarely observed on either lake during remigial molt (D. Hogan, per.obs.), so predation risk should, in theory, be perceived as low. However, the small size and almost continuous forest cover of Leddy Lake compared to Cardinal Lake (4 km² vs. 50 km²) may have caused birds to perceive a higher risk of predation on Leddy as a result of being in closer proximity to shore. Also, although invertebrate sampling of the lakes suggests that invertebrate communities are similar (D. Hogan, unpublished data), dense aggregations of *gammarid* amphipods were observed along the shoreline of Leddy Lake during nocturnal sampling. This amphipod behavior was not observed on Cardinal Lake. While a study of breeding Barrow's Goldeneye in BC showed that birds actively avoided amphipods (Thompson and Ankney 2002), amphipod remnants were found in the upper digestive tracts of three birds collected during spring and fall staging on Cardinal Lake in 2009 and 2010. Thus, the nocturnal foraging habits of Leddy Lake birds could be the result of the nocturnal habits of their prey organisms rather than a higher perceived risk of predation. More information regarding potential predator communities and Barrow's Goldeneye prey dynamics on Cardinal and Leddy Lakes is required before any conclusions can be drawn regarding proximate causes of nocturnal foraging behaviour at Leddy Lake.

Differences in starting mass and mass gain throughout remigial molt, as well as the differences in foraging activity of Barrow's Goldeneyes at Cardinal and Leddy Lakes suggest that while the over-all molting strategy was the same at each lake for each year and age cohort (gain mass and forage little), the mass and foraging strategies used to

realize this differed between lakes, years and age classes. In contrast, Barrow's Goldeneyes molting on the Old Crow Flats (YT), appear to employ an entirely different molting strategy which involved mass loss over the molting period. Foraging effort for these birds was not measured, thus whether mass loss represented a response to nutritional constraints or predation pressure is unknown (Van de Wetering and Cooke 2000). Descriptions of molting habitat at Old Crow Flats (Van de Wetering 1997) suggests that it is similar in productivity to Cardinal and Leddy Lakes, so mass loss there may more directly relate to predation or time constraints than nutritional limitations. Regardless of the proximate causes for this variation, molt strategy appears to show some degree of plasticity within Barrow's Goldeneyes, which is mediated by environmental conditions at the molt site and individual traits. Similar plasticity has been observed in breeding female Barrow's Goldeneyes with regards to nutrient sources used for egg production (Hobson *et al.* 2005). This realization has important implications with regards to constraints of remigial molt and the conservation strategies used to mitigate these potential limitations.

3.4.4. Conservation Implications

Results of this study suggest that the long-held assumption that remigial molt is nutritionally demanding and a period of increased risk of mortality is not necessarily true for all species of waterfowl, but rather that the degree to which this is true of a species depends on characteristics and quality of molting habitats. The molting strategy of Barrow's Goldeneyes appears to be somewhat flexible in response to varying environmental conditions, and remigial molt can be a period of low risk in the annual cycle of this species. Further, postbreeding period mass gain may provide cross-seasonal benefits to birds from Cardinal and Leddy Lakes by allowing individuals to build somatic stores for use during fall migration and winter. A productive molt site and increase in mass during the postbreeding period may be essential for adult females that deplete somatic stores of protein and lipids for egg production and brood-rearing during the breeding period (Hobson *et al.* 2005). Cardinal and Leddy Lakes are two of only five sites in North America known to sustain large aggregations of postbreeding Barrow's Goldeneye, and are the only sites at which postbreeding increases in mass are known to occur. As such, conservation efforts at Cardinal and Leddy Lakes should strive to keep

these valuable postbreeding habitats intact by protecting them from future industrial and agricultural development, as well as minimizing anthropogenic disturbances.

3.5. Tables and Figures

Table 2: Linear model selection results for models explaining variation in body mass (g) of male Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB in 2009 and 2010. Molt refers to stage of molt (days since emergence of the 9th primary, emergence date=0). Emergence refers to emergence date (earliest day in study = 0). Size is a structural size variable (PC1). Age is a categorical variable with two levels, second-year (SY) or after-second-year (ASY). Lake is a categorical variable with two levels (Cardinal Lake or Leddy Lake). Year is a categorical variable with two levels (2009 or 2010). Interactions between variables are denoted by 'x'.

Response Variable	Model	K	ΔAICc	AICc weight (w_i)
Mass (g)	molt + emergence + age + lake + year + size + emergence x age + emergence x lake + emergence x year + age x lake + age x year + lake x year + molt x emergence + molt x age + molt x lake + molt x year	18	0.00	0.99
	molt + emergence + age + lake + year + size + emergence x age + emergence x lake + emergence x year + age x lake + age x year + lake x year	14	14.42	0.01
	molt + emergence + age + lake + year + size + molt x age	9	45.44	0.00
	molt + emergence + age + lake + year + size + molt x emergence + molt x age + molt x lake + molt x year	12	46.12	0.00
	molt + emergence + age + lake + year + size + molt x emergence	9	58.13	0.00
	molt + emergence + age + lake + year + size	8	60.70	0.00
	molt + emergence + age + lake + year + size + molt x lake	9	61.56	0.00
	molt + emergence + age + lake + year + size + molt x year	9	62.73	0.00
	emergence + age + lake + year + size + emergence x age + emergence x lake + emergence x year + age x lake + age x year + lake x year	13	92.56	0.00
	emergence + age + lake + year + size	7	143.36	0.00
	molt	3	547.04	0.00
NULL	2	617.72	0.00	

Table 3: Linear model selection results for models explaining variation in body mass (g) of female Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB in 2009 and 2010. Molt refers to stage of molt (days since emergence of the 9th primary, emergence date=0). Emergence refers to emergence date (earliest day in study = 0). Size is a structural size variable (PC1). Age is a categorical variable with two levels, second-year (SY) or after-second-year (ASY). Lake is a categorical variable with two levels (Cardinal Lake or Leddy Lake). Year is a categorical variable with two levels (2009 or 2010). Interactions between variables are denoted by 'x'.

Response Variable	Model	K	$\Delta AICc$	AICc weight (w_i)
Mass (g)	molt + emergence + age + lake + year + size	8	0.00	0.38
	molt + emergence + age + lake + year + size + molt x age	9	1.74	0.16
	molt + emergence + age + lake + year + size + molt x year	9	2.24	0.13
	molt + emergence + age + lake + year + size + molt x lake	9	2.29	0.12
	molt + emergence + age + lake + year + size + molt x emergence	9	2.42	0.12
	emergence + age + lake + year + size	7	3.24	0.08
	molt + emergence + age + lake + year + size + emergence x age + emergence x lake + emergence x year + age x lake + age x year + lake x year	14	8.32	0.01
	molt + emergence + age + lake + year + size + molt x emergence + molt x age + molt x lake + molt x year	12	8.69	0.00
	emergence + age + lake + year + size + emergence x age + emergence x lake + emergence x year + age x lake + age x year + lake x year	13	10.11	0.00
	molt + emergence + age + lake + year + size + emergence x age + emergence x lake + emergence x year + age x lake + age x year + lake x year + molt x emergence + molt x age + molt x lake + molt x year	18	15.92	0.00
	molt	3	23.23	0.00
NULL	2	26.20	0.00	

Table 4: Parameter estimates (\pm SE) for the best supported model (global model) explaining variation in body mass of male Barrow's Goldeneyes during remigial molt at Cardinal and Leddy Lakes, AB in 2009 and 2010. Intercept value refers to average mass (g) of ASY males on Cardinal Lake in 2009 on the earliest remigial emergence date. Remaining parameter estimates denote the effect of each parameter on the change in mass. Molt and emergence estimates are in g/day format. Molt refers to stage of molt (days since emergence of the 9th primary, emergence date=0). Emergence refers to emergence date (earliest day in study = 0). Age is a categorical variable with two levels, second-year (SY) or after-second-year (ASY). Lake is a categorical variable with two levels (Cardinal Lake or Leddy Lake). Year is a categorical variable with two levels (2009 or 2010). PC1 estimate denotes the rate at which mass changes with decreasing size (increasingly positive PC1 scores). Interactions between variables are denoted by '*'. All parameter likelihoods are 0.99.

Parameter	Parameter Estimate	SE
(Intercept)	977.11	16.45
Molt	1.94	0.88
Emergence	0.81	0.62
Age	-82.69	28.89
Lake	35.14	19.06
Year	38.52	17.20
Molt * Emergence	-0.04	0.03
Molt * Age	2.46	0.70
Molt * Lake	1.21	0.41
Molt * Year	-0.19	0.41
Emergence * Age	2.64	1.13
Emergence * Lake	1.98	0.67
Emergence * Year	0.37	0.66
Age * Lake	-29.01	13.12
Age * Year	17.61	12.53
Lake * Year	-41.26	7.66
PC1 (size)	-17.40	1.36

Table 5: Model-averaged parameter estimates (\pm SE) for variables explaining variation in body mass of female Barrow's Goldeneyes during remigial molt at Cardinal and Leddy Lakes, AB in 2009 and 2010. Intercept value refers to average mass (g) of ASY females on Cardinal Lake in 2009 on the earliest emergence date. Remaining parameter estimates denote the effect of each parameter on the change in mass. Molt and emergence estimates are in g/day format. Molt refers to stage of molt (days since emergence of the 9th primary, emergence date=0). Emergence refers to emergence date (earliest day in study = 0). Age is a categorical variable with two levels, second-year (SY) or after-second-year (ASY). Lake is a categorical variable with two levels (Cardinal Lake or Leddy Lake). Year is a categorical variable with two levels (2009 or 2010). PC1 estimate denotes the rate at which mass changes with increasing size (increasingly positive PC1 scores). Interactions between variables are denoted by ").**

Parameter	Model Averaged Estimate	Unconditional SE	Parameter Likelihood
(Intercept)	706.41	21.71	1.00
Molt	1.44	1.02	0.92
Emergence	1.75	0.76	1.00
Age	2.83	11.09	1.00
Lake	34.81	10.84	1.00
Year	17.03	10.77	1.00
Molt * Emergence	0.00	0.02	0.12
Molt * Age	0.20	0.29	0.17
Molt * Lake	0.07	0.19	0.13
Molt * Year	0.08	0.21	0.13
Emergence * Age	0.02	0.02	0.01
Emergence * Lake	0.00	0.01	0.01
Emergence * Year	-0.02	0.02	0.01
Age * Lake	0.17	0.26	0.01
Age * Year	-0.14	0.25	0.01
Lake * Year	-0.12	0.22	0.01
PC1 (size)	11.26	3.71	1.00

Table 6: Generalized Least Squares (GLS) model selection results for models explaining variation in diurnal foraging effort (min/hr) of radio-marked ASY male Barrow's Goldeneyes molting on Cardinal (CL) and Leddy Lakes (LL), AB in 2009 and 2010. Variance structure accounted for unequal residual variation between lakes and years. A random effect of individual was not included in models, as this did not improve model fit (i.e. observations from one individual were not more correlated with each other than with observations from other birds). LKYR is a 4-level categorical variable (CL2009, CL2010, LL2009, LL2010). Molt refers to stage of molt (days since emergence of 9th primary). Time refers to time since sunrise. Mass variables relate to residual mass of each individual (actual mass- mass predicted by best supported model).

Response Variable	Model	K	$\Delta AICc$	AICc weight (w_i)
Foraging effort (min/hr)	LKYR + time + time ² + molt + molt ² + LKYR x molt + LKYR x molt ²	18	0.00	0.94
	LKYR + time + time ² + molt + molt ² + LKYR x time + LKYR x time ²	18	6.81	0.03
	LKYR + time + time ² + molt + molt ²	12	7.18	0.03
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ²	16	12.57	0.00
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ² + LKYR x time + LKYR x time ²	22	12.71	0.00
	LKYR + time + time ² + LKYR x time + LKYR x time ²	16	15.19	0.00
	LKYR + time + time ² + emergence + emergence ² + LKYR x time + LKYR x time ²	18	15.36	0.00
	LKYR + time + time ²	10	16.48	0.00
	LKYR + time + time ² + emergence + emergence ²	12	16.60	0.00
	LKYR + time + time ² + mass + mass ² + LKYR x time + LKYR x time ²	18	19.26	0.00
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ² + LKYR x time + LKYR x time ² + LKYR x molt + LKYR x molt ² + LKYR x emergence + LKYR x emergence ²	34	20.12	0.00
	LKYR + time + time ² + mass + mass ²	12	20.62	0.00
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ² + LKYR x time + LKYR x time ² + LKYR x molt + LKYR x molt ² + LKYR x emergence + LKYR x emergence ² + emergence x mass + emergence x mass ² + emergence ² x mass + emergence ² x mass ²	38	26.00	0.00
	LKYR + time + time ² + emergence + emergence ² + LKYR x emergence + LKYR x emergence ²	18	27.18	0.00
	molt + molt ² + emergence + emergence ² + mass + mass ²	11	46.59	0.00
	molt + molt ²	7	47.57	0.00
	molt + molt ² + emergence + emergence ² + mass + mass ² + emergence x mass + emergence x mass ² + emergence ² x mass + emergence ² x mass ²	15	53.04	0.00
	emergence + emergence ²	7	56.55	0.00
	mass + mass ²	7	57.33	0.00
	NULL	5	58.47	0.00

Table 7: Generalized Least Squares (GLS) model selection results for models explaining variation in nocturnal foraging effort (min/hr) of radio-marked ASY male Barrow's Goldeneyes molting on Cardinal (CL) and Leddy Lakes (LL), AB in 2009 and 2010. Variance structure accounted for unequal residual variation between lakes and years. A random effect of individual was not included in models, as this did not improve model fit (i.e. observations from one individual were not more correlated with each other than with observations from other birds). LKYR is a 4-level categorical variable (CL2009, CL2010, LL2009, LL2010). Molt refers to stage of molt (days since emergence of 9th primary). Time refers to time since sunrise. Mass variables relate to residual mass of each individual (actual mass- mass predicted by best supported model).

Response Variable	Model	K	$\Delta AICc$	AICc weight (w_i)
Foraging effort (min/hr)	LKYR + time + time ² + molt + molt ² + LKYR x time + LKYR x time ²	18	0.00	0.50
	LKYR + time + time ² + LKYR x time + LKYR x time ²	16	2.02	0.18
	LKYR + time + time ² + molt + molt ²	12	2.24	0.16
	LKYR + time + time ²	10	4.14	0.06
	LKYR + time + time ² + emergence + emergence ² + LKYR x time + LKYR x time ²	18	5.41	0.03
	LKYR + time + time ² + mass + mass ² + LKYR x time + LKYR x time ²	18	6.59	0.02
	LKYR + time + time ² + molt + molt ² + LKYR x molt + LKYR x molt ²	18	7.11	0.01
	LKYR + time + time ² + emergence + emergence ²	12	7.15	0.01
	LKYR + time + time ² + mass + mass ²	12	8.20	0.01
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ² + LKYR x time + LKYR x time ²	22	8.37	0.01
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ²	16	10.33	0.01
	LKYR + time + time ² + emergence + emergence ² + LKYR x emergence + LKYR x emergence ²	18	14.95	0.00
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ² + LKYR x time + LKYR x time ² + LKYR x molt + LKYR x molt ² + LKYR x emergence + LKYR x emergence ²	34	19.22	0.00
	LKYR + time + time ² + molt + molt ² + emergence + emergence ² + mass + mass ² + LKYR x time + LKYR x time ² + LKYR x molt + LKYR x molt ² + LKYR x emergence + LKYR x emergence ² + emergence x mass + emergence x mass ² + emergence ² x mass + emergence ² x mass ²	38	19.23	0.00
	molt + molt ² + emergence + emergence ² + mass + mass ² + emergence x mass + emergence x mass ² + emergence ² x mass + emergence ² x mass ²	15	34.39	0.00
	NULL	5	35.07	0.00
	mass + mass ²	7	35.52	0.00
molt + molt ²	7	35.54	0.00	
emergence + emergence ²	7	36.74	0.00	
molt + molt ² + emergence + emergence ² + mass + mass ²	11	41.16	0.00	

Figure 2a: Relationship between predicted body mass (g) and stage of molt (days since emergence of 9th primary) for male Barrow's Goldeneyes molting on Cardinal (CL) and Leddy (LL) Lakes, AB in 2009 and 2010. Predicted mass was calculated using the model- averaged parameter estimates and holding emergence date and PC1 constant at the average value.

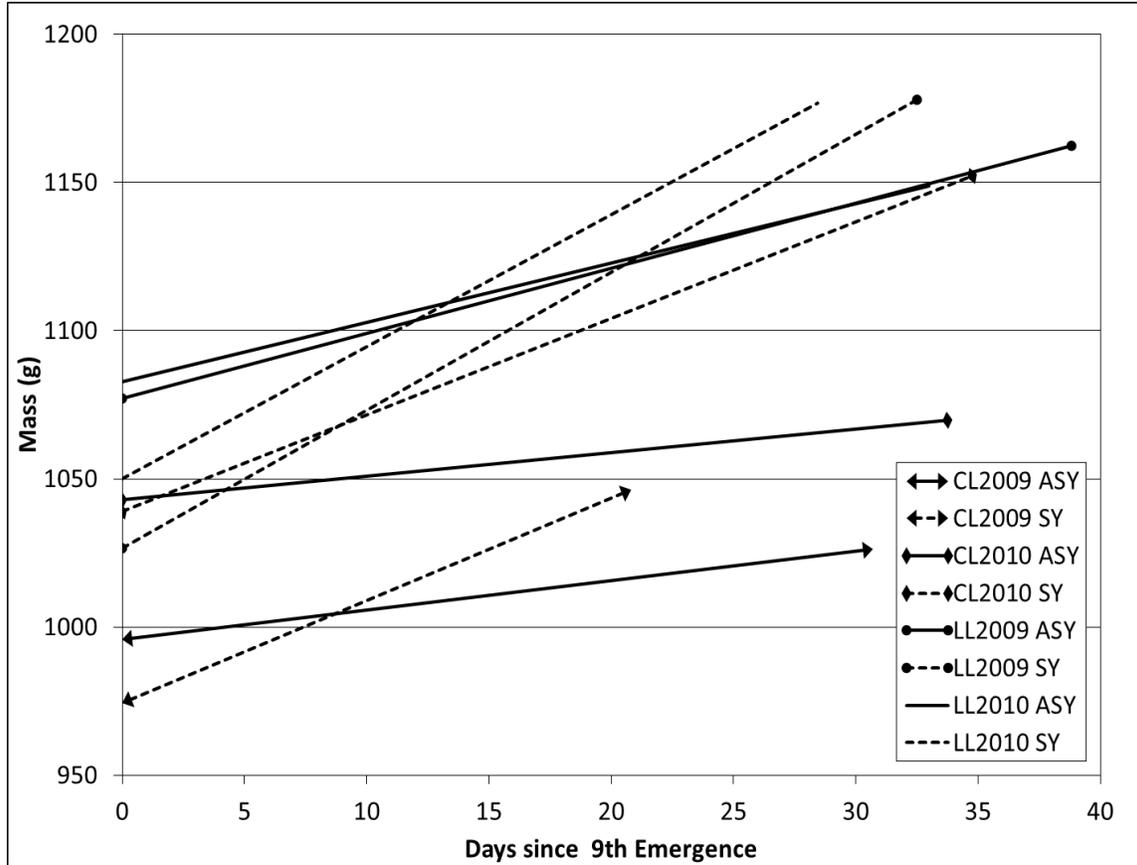


Figure 2b: Relationship between predicted body mass (g) and stage of molt (days since emergence of 9th primary) for female Barrow's Goldeneyes molting on Cardinal (CL) and Leddy (LL) Lakes, AB in 2009 and 2010. Predicted mass was calculated using the model- averaged parameter estimates and holding emergence date and PC1 constant at the average value.

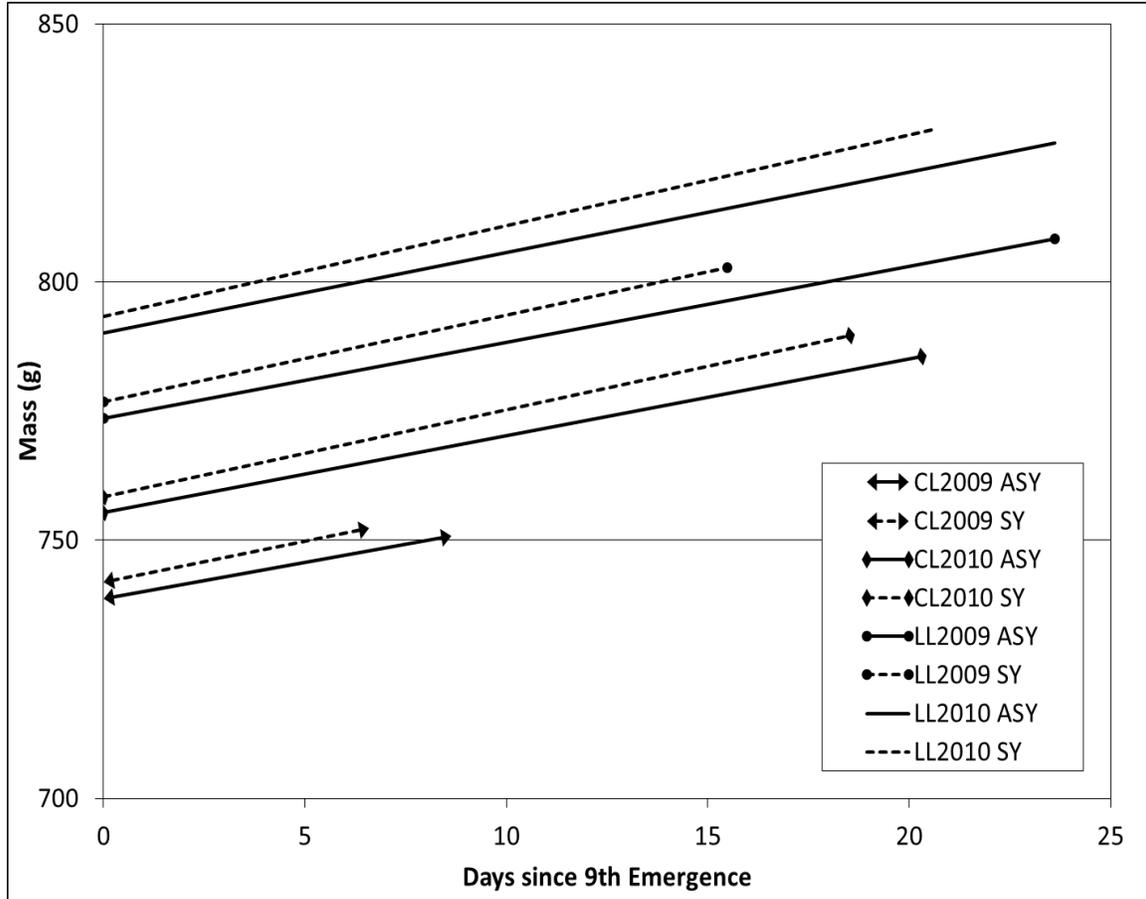


Figure 3a: Relationship between predicted body mass (g) and emergence date for male Barrow's Goldeneyes molting on Cardinal (CL) and Leddy (LL) Lakes, AB in 2009 and 2010. Predicted mass was calculated using model-averaged parameter estimates and holding molt stage and PC1 constant at the average value.

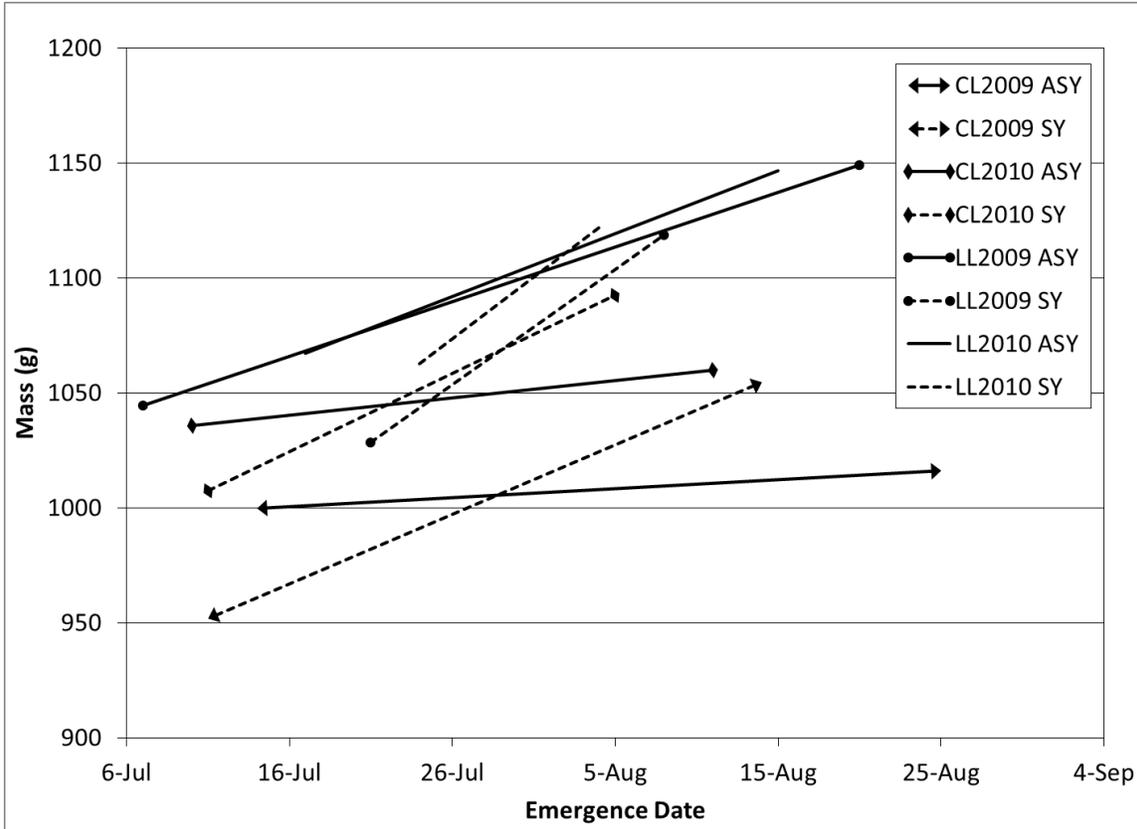


Figure 3b: Relationship between predicted body mass (g) and emergence date for female Barrow's Goldeneyes molting on Cardinal (CL) and Leddy (LL) Lakes, AB in 2009 and 2010. Predicted mass was calculated using model-averaged parameter estimates and holding molt stage and PC1 constant at the average value.

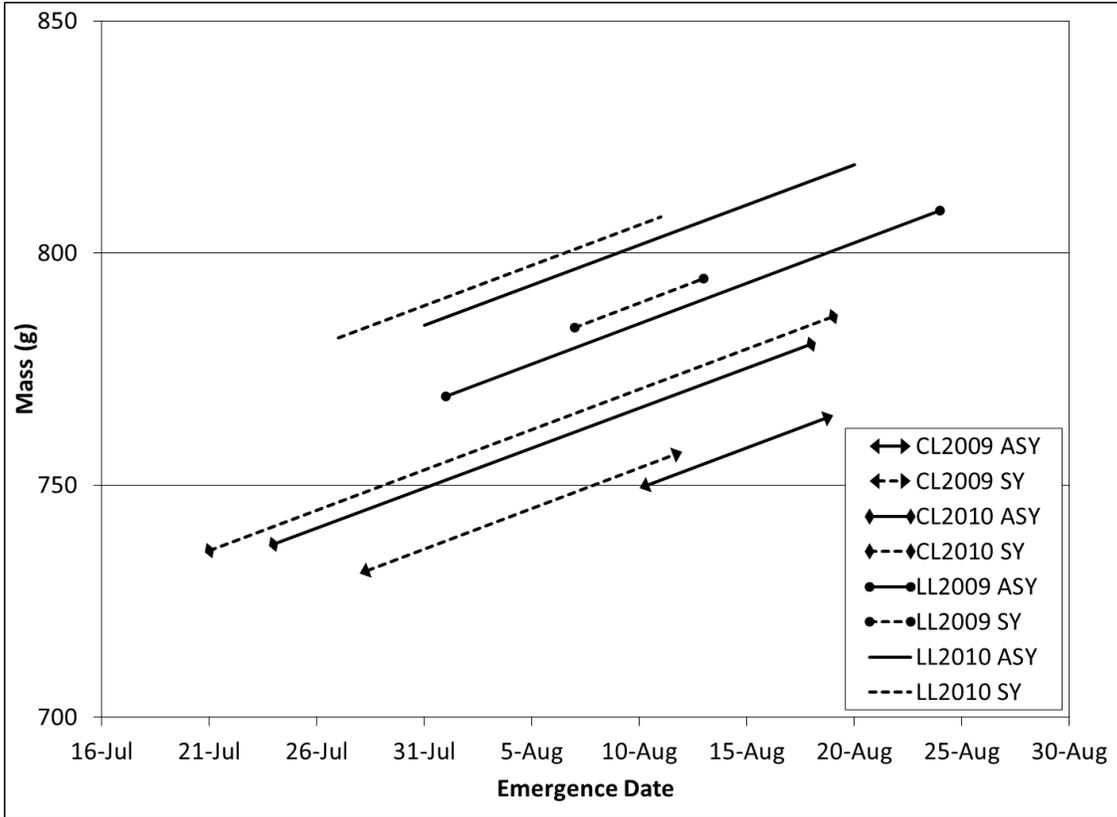


Figure 4: Average body mass \pm SE (g) of ASY male Barrow's Goldeneyes captured in Alaska (AK), Yukon Territory (YT), British Columbia (BC), and Alberta (CL, LL) from 1995 to 2011 at various stages of the annual cycle. Mass for Yukon Territory birds was taken from Van de Wetering (1997). Trend lines in remigial molting stage represent mass gain of birds from Cardinal (solid lines) and Leddy (hashed lines) Lakes, AB.

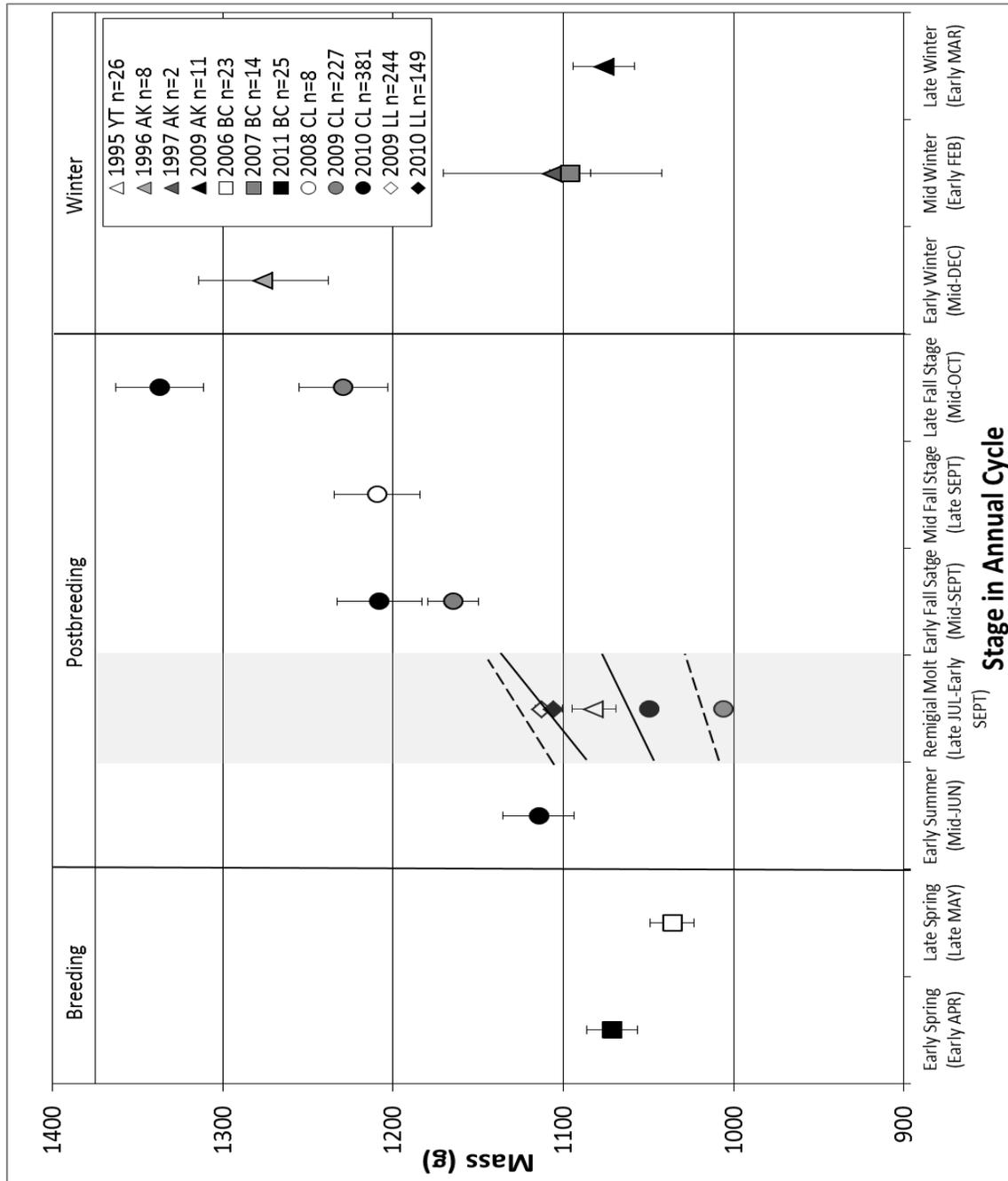


Figure 5: Average foraging effort (min/day \pm SE) of radio-marked ASY male Barrow's Goldeneyes molting on Cardinal (CL) and Leddy Lakes (LL), AB in 2009 and 2010. Averages were estimated by multiplying nocturnal and diurnal hourly foraging rates by the number of nocturnal and diurnal hours in a day. Filled portions of bars represent the amount of daily foraging effort conducted nocturnally. Percentages above each bar indicate the proportion of total time spent foraging per day.

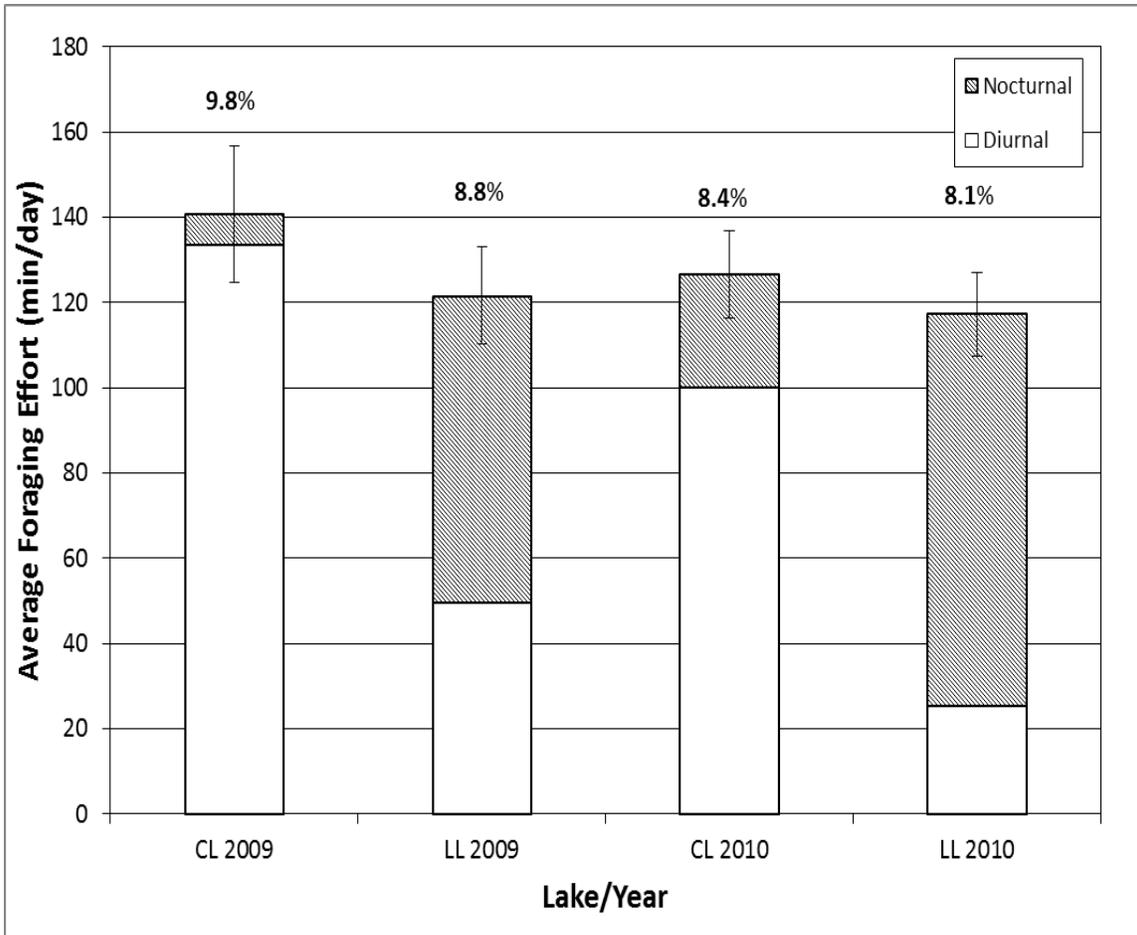


Figure 6: Model-predicted diurnal foraging effort (min/hr) over time (hours since sunrise) for adult male Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB in 2009 and 2010. All continuous model variables were held constant at mean values.

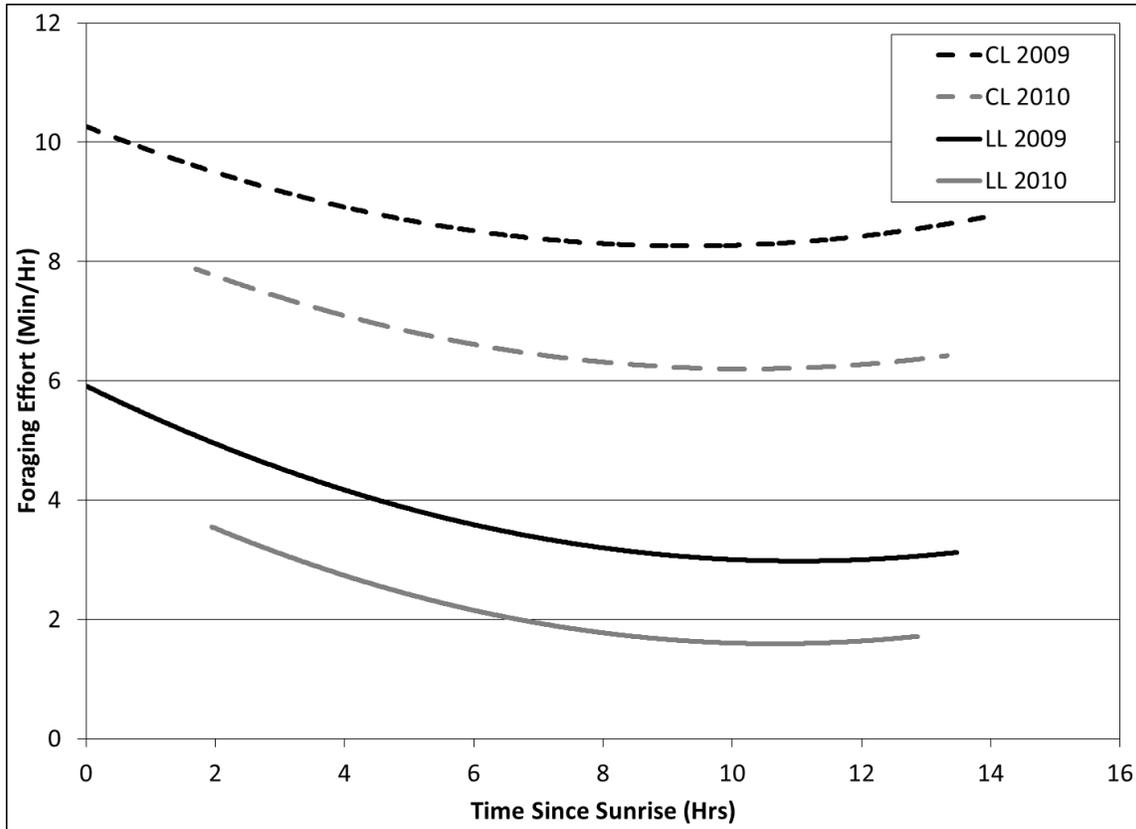
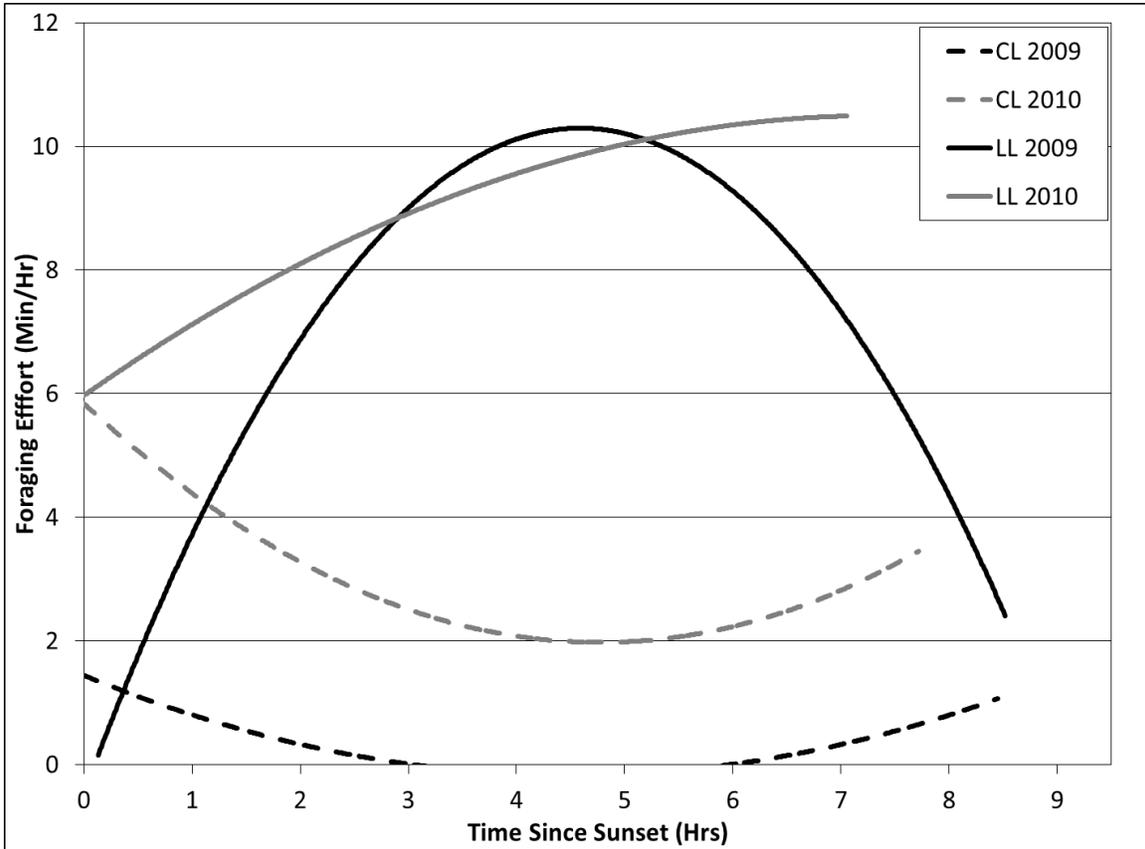


Figure 7: Model-predicted nocturnal foraging effort (min/hr) over time (hours since sunset) for adult male Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB in 2009 and 2010. All continuous model variables were held constant at mean values.



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4. Postbreeding Survival of Barrow's Goldeneyes during Remigial Molt and Fall Staging

4.1. Introduction

Population dynamics of birds that are long-lived and exhibit delayed reproductive maturity are more sensitive to variation in adult survival than reproductive output or juvenile survival (Schmutz *et al.* 1997; Saether and Bakke 2000; Stahl and Oli 2006). Sea ducks (*Mergini*) are long-lived ducks (*Anatinae*) that typically reproduce at two or three years of age, thus variation in adult survival potentially has strong influences on population dynamics for this tribe (Goudie *et al.* 1994) relative to other ducks. However, despite conservation concern about many sea duck populations (Sea Duck Joint Venture Management Board 2008), the contribution of variation in adult survival to population dynamics is unknown, as survival rates of sea ducks have seldom been investigated. Further, direct measures of survival at specific annual cycle stages are rare for sea ducks, which constrains understanding about when and where demographic bottlenecks might occur, and subsequently limits the ability of managers to target those bottlenecks for conservation action.

The postbreeding period represents a potentially risky stage in the annual cycle of waterfowl, which could lead to demographic constraints (i.e., events or processes that negatively impact survival/population growth). This stage encompasses the period between arrival on molting sites to departure for wintering areas. Remigial molt typically occurs within this stage, rendering birds flightless for 20-40 days (Hohman *et al.* 1992). Costs associated with simultaneous remigial molt potentially include reduced foraging efficiency (Bridge 2004), reduced ability to escape predators/anthropogenic disturbances, and increased daily nutritional demands that may require catabolism of

somatic stores (Hohman 1993; Murphy 1996; Brown and Saunders 1998; Fox and Kahlert 2005; Portugal *et al.* 2007; Fox and King 2011). A number of studies have quantified strategies that waterfowl have developed to accommodate constraints imposed by simultaneous remigial molt, including adaptive loss of mass for an earlier return to flight and/or greater chance of evading predators (Panek and Majewski 1990; Brown and Saunders 1998; Van de Wetering and Cooke 2000, Zimmer *et al.* 2011), reduced foraging activity to decrease detection by predators (Panek and Majewski 1990; Adams *et al.* 2000; Dopfner *et al.* 2009), and selection of molt sites with abundant food, low predator density, and low anthropogenic disturbance (Salomonsen 1968; Zicus 1981; Derksen *et al.* 1982; Madsen and Mortensen 1987; Thompson and Drobney 1997; Kahlert 2003). However, few studies have quantified survival rates of waterfowl during remigial molt to assess the potential of this stage to act as a demographic bottleneck (Kirby and Cowardin 1986; Bowman and Longcore 1989; Miller *et al.* 1992; Iverson and Esler 2007; Evelsizer *et al.* 2010; Fleskes *et al.* 2010). Survival rates have never been quantified for sea ducks during fall staging (post- remigial molt). Some species of ducks remain at molt sites beyond remigial molt and into fall staging, which in some cases results in occurrence on postbreeding areas for over 1/3 of the annual cycle (Gilliland *et al.* 2002; Iverson and Esler 2006; Savard *et al.* 2007; Oppel *et al.* 2008; Hogan *et al.* 2011). Understanding demographic rates at postbreeding sites is essential for assessing the potential of this period to influence population dynamics, and can aid in identifying stages in the annual cycle upon which conservation efforts should focus.

Barrow's Goldeneyes (*Bucephala islandica*) are mid-sized sea ducks primarily distributed along the western coast of North America (Eadie *et al.* 2000). The postbreeding period of Barrow's Goldeneyes encompasses prebasic molt (including remigial molt) and most of pre-alternate molt. Studies at two newly discovered postbreeding sites for the Pacific Population of Barrow's Goldeneye in the Boreal Transition Zone of Alberta (i.e., Cardinal and Leddy Lakes; Hogan *et al.* 2010) indicate that birds are neither nutritionally constrained nor likely under strong predation pressure at these sites (Chapter 3). These findings suggest that these lakes currently provide high- quality postbreeding habitat for Barrow's Goldeneyes. However, demographic consequences of selecting these sites as postbreeding sites, is unknown. The objective

of this study was to quantify survival rates of postbreeding adult male Barrow's Goldeneyes at Cardinal and Leddy Lakes, AB to determine if remigial molt and fall staging were periods of demographic constraint for this species.

4.2. Methods

4.2.1. Study Area

Cardinal Lake (56° 14'N, 117° 44'W, also Lac Cardinal) is a large lake (50km²) in the Boreal Transition Zone of northwestern Alberta. The lake is shallow (<2m) and hypereutrophic with a gravel and mud substrate, and dense submergent vegetation. Leddy Lake (56° 23'N, 117° 27'W) is a small (4km²) lake located ~25km northeast of Cardinal Lake. It is also shallow, eutrophic, and has a dense submerged vegetation mat throughout most of the lake. Neither basin supports populations of sport-fish. These sites are two of only five postbreeding sites known for large aggregations of the Pacific population of Barrow's Goldeneyes, with 5 000- 7 000 birds (primarily adult males) using the lakes during remigial molt and fall staging annually (Hogan *et al.* 2011). Barrow's Goldeneyes have been observed using these sites for approximately five months, from mid-June to November, or almost half of their annual cycle (Hogan *et al.* 2011). The fall waterfowl hunting season at Cardinal and Leddy Lakes opens September 1st and encompasses the entire fall staging (post-molt) period of Barrow's Goldeneyes.

4.2.2. Captures and Monitoring Survival

Adult male Barrow's Goldeneyes were captured on Cardinal and Leddy Lakes using drive trapping techniques during remigial molt (late July-early September) in 2009 and 2010. Morphometric measurements, including 9th primary length (mm) and mass (g) were taken for each individual and each bird was fitted with a uniquely numbered US Fish and Wildlife Service stainless steel tarsal band. Sex was determined by cloacal and plumage characteristics (Hochbaum 1942; Carney 1983) and age class was determined by bursal depth (Mather and Esler 1999; Iverson *et al.* 2003; Hogan *et al.*

2011). Individuals with bursal depths <10mm were classified as after-second-year (ASY), i.e., more than 2 years since hatching.

Each year, 25 ASY males from each lake were marked with VHF radio transmitters (<12g) from Advanced Telemetry Systems (100 transmitters total). Transmitters were attached using subcutaneous prongs and super glue (Iverson *et al.* 2006). Survival of each radio-marked individual was monitored by listening for its radio signal approximately every 10 days during remigial molt (late July- early September) and every 5 days during fall staging (mid-September- early November). Transmitters were equipped with a mortality sensor that doubled the signal pulse-rate after 12 hours of inactivity. All mortality signals were confirmed by recovery of a carcass or location of transmitters in upland habitats (farm field/forest) that are never normally used by Barrow's Goldeneyes. Mortalities also were identified from reports of radio-marked birds by hunters. In the case of harvested birds, the date of death was assigned as the day the hunter reported shooting the bird. Disappearance of a bird without detection of a mortality signal or harvest report from a hunter was assumed to be due to either radio failure, shedding of the radio over water during remigial molt, or emigration during fall staging.

4.2.3. Data Analysis

4.2.3.1. Survival during Remigial Molt

A 7-day censor period following radio attachment was applied to each bird before inclusion in survival data analyses (Kirby and Cowardin 1986) to account for any influence of capture and handling. Birds that died during the censor period, or were found dead upon first observation following the censor period, were not included in the analysis (n=1). Daily survival rate (DSR) was calculated using a modified Mayfield method of nest survival analysis (Bart and Robson 1982; Dinsmore *et al.* 2002) for ragged telemetry data in Program MARK 6.1 (White and Burnham 1999). The calculation of DSR using this model required four pieces of information from each radio-marked bird: 1) first day observed (in this case, first day post-censor period), 2) last day

the bird was known alive, 3) last day the bird was checked, and 4) the fate of the bird (0=alive, 1=dead).

Multiple linear logistic regression models were used to investigate variation in DSR during remigial molt as a function of lake, year, molt stage (time) and body mass. Lake and year were combined into a single categorical variable (LK YR) with four levels to represent different environmental conditions on each lake each year. Molt stage was a time variable that encompassed the period of remigial molt (39 days, Chapter 2) and was based on number of days since eruption of the new 9th primary feather from the skin of the wing (emergence date = day 1). Mass was indexed by two calculations of residual mass for each bird: overall residual mass (MASSALL) and lake/year-specific residual mass (MASSLK YR). MASSALL was calculated by subtracting the average mass of all ASY males captured during remigial molt from the observed mass of each individual at first capture. MASSLK YR was calculated by subtracting the average mass of all flightless ASY males captured on a given lake in a given year from the observed mass of each individual on that lake in that year at first capture. MASSALL was used to investigate the general effects of mass on survival of Barrow's Goldeneyes. MASSLK YR was used to investigate the effect of mass on survival of birds at each lake in each year, accounting for known differences in mass by LK YR (Chapter 3). This allowed for the evaluation of models that included the additive effects of LK YR and mass on DSR without known mass differences between lakes and years confounding other LK YR effects (i.e. once known differences in mass were accounted for, the individual effects of mass and other LK YR effects on DSR could be evaluated).

An information theoretic approach was used to contrast support for a suite of models in a candidate set. Ten models were included in the candidate set (Table 8), including a null model that tested the hypothesis that survival was constant over remigial molt and across lakes, years, and masses. Survival also might vary only with environmental conditions, so we also included a model with only the LK YR parameter to address this hypothesis. Mass could affect survival in multiple ways: lighter birds may gain flight earlier and thus evade predators better than heavier birds, resulting in improved survival; conversely, heavier birds with more reserves may be better able to

meet nutritional costs of remigial molt or they may require less foraging effort, either of which could improve survival. As such, models with MASSALL only and MASSLK YR only were included in the candidate set. Survival also may vary through stages of molt (as environmental conditions change or birds re-gain flight) and we included a model that addressed this possibility explicitly. Additionally, we included models that explored the additive effects of LKYR and molt stage, LKYR and MASSLK YR, molt stage and MASSALL, and molt stage and MASSLK YR. The global model included LKYR, MASSLK YR and molt stage variables. Interaction terms were not included in the candidate set as the data could not adequately address such complex hypotheses.

Akaike's Information Criterion corrected for small samples sizes (AIC_c ; Burnham and Anderson 2002) was used to identify the most parsimonious model in the candidate set. The difference between each model and the most parsimonious model (ΔAIC_c) and AIC_c weights (ω_i) were used to evaluate the relative support for each model. Parameter likelihood values ($\Sigma \omega_i$) were calculated for each variable to evaluate the level of support for the variable within the candidate model set. Model averaged estimates of DSR (with unconditional 95% CIs) also were calculated. Period survival rate (PSR) was calculated for the entire remigial molt period as DSR^n where n = days in the period, in this case 39 days. Confidence intervals for PSR were calculated by raising the 95% confidence intervals of DSR to the power of n .

4.2.3.2. Survival during Fall Staging

An information theoretic approach also was used to investigate support for a candidate set of linear models evaluating variation in DSR during the fall staging period (mid-September to mid-November; 62 days) as a function of LKYR and time. DSR was calculated using the same modified Mayfield method for ragged telemetry data described above. LKYR was the same 4- level categorical variable used to model DSR during remigial molt and time corresponded to the number of days since the end of remigial molt for each individual (first day after remigial molt=1). A model explicitly testing the hypothesis of constant DSR over the fall staging period was included in the candidate set. LKYR, time, and LKYR+ time models also were included to investigate if DSR varied with environmental conditions and/or time. Some birds that started the fall

staging period on Leddy Lake moved to Cardinal Lake during the course of the fall staging period. These birds were treated as Leddy Lake birds until they were observed on Cardinal Lake, at which time they were treated as Cardinal Lake birds. We conducted an a priori evaluation of whether switching lakes affected the survival of birds. The constant survival model (AIC_c weight= 0.70) was better supported than the model containing a variable for switching (AIC_c weight= 0.30), suggesting that where a bird stayed previously did not affect whether it lived or died when it was on Cardinal Lake, thus we did not include a switching variable in our candidate set of models. Akaike's Information Criterion corrected for small samples sizes (AIC_c ; Burnham and Anderson 2002) was used to identify the most parsimonious models in the candidate set, and support for each model and parameter in the candidate set was evaluated by using values of ΔAIC_c , AIC_c weights (ω_i), and parameter likelihoods, as described above. The model averaged estimates of DSR and PSR (with unconditional 95% CIs) were calculated using the same methods as for remigial molt, with the exception that $n= 62$ for PSR.

4.3. Results

4.3.1. *Survival during Remigial Molt*

We monitored survival of 100 radio-marked ASY male Barrow's Goldeneyes during the remigial molting period in 2009 and 2010, however only 99 were included for analysis in our Mayfield models, as one individual on Leddy Lake died before the end of the 7-day censor period in 2010. One of 25 birds died during the 39-day remigial molt period on Cardinal Lake in 2009, one of 25 birds died on Leddy Lake in 2009 and two of 24 birds died on Leddy Lake in 2010. No birds died during remigial molt on Cardinal Lake in 2010. Carcasses and mortality signals of all dead birds were found in upland habitats never used by Barrow's Goldeneyes, however, it could not be determined if birds had died as a result of predation or if the carcass had been scavenged after death due to some other factor.

The constant survival model received most support from the data (AIC_c weight= 0.70, Table 8). While the MASSLK YR model (AIC_c weight= 0.11), MASSALL model (AIC_c weight= 0.10) and LKYR model (AIC_c weight= 0.07) received similar support from the data (Table 8), all were substantially less supported than the constant survival model. All other models received almost no support (AIC_c weight \leq 0.02). Consistent with support of the constant survival model, none of the explanatory variables had a strong effect on DSR (parameter likelihoods \leq 0.15). The model-averaged estimate of DSR was 0.999 (95% CI: 0.997-1.000), which corresponded to a PSR of 0.95 (95% CI: 0.88-1.00) over the 39-day remigial molt period (Figure 8).

4.3.2. Survival during Fall Staging

Two radio-marked birds on Cardinal Lake, and one on Leddy Lake, went missing before the end of remigial molt, presumably due to radio failure or shedding. Thus, we monitored 92 birds during the fall staging period (mid-September to mid-November) on Cardinal and Leddy Lakes in 2009 and 2010. 16 birds moved from Leddy to Cardinal Lake during the course of fall staging in 2009, and 19 birds made the same move in 2010. Birds that underwent remigial molt on Cardinal Lake never moved to Leddy Lake. Four birds died during fall staging on Cardinal Lake in 2009 and 10 died in 2010. Two birds died on Leddy Lake during fall staging in 2009 and none during 2010. Seven of 14 mortalities on Cardinal Lake were directly attributable to hunting. The remaining Cardinal and Leddy Lake mortality signals were found in upland habitats never used by Barrow's Goldeneyes; one carcass was inside a mink den, and one carcass had been eaten in a field. Whether birds had been killed by predators or scavenged after death due to some other factor (e.g., wounding by hunters) could not be determined.

The constant survival model received the most support from the data (AIC_c weight= 0.72), followed by the LKYR model (AIC_c weight= 0.28, Table 9). Neither of the time-dependent models received virtually any support, suggesting that daily survival did not vary over the staging period. Model-averaged DSR of adult male Barrow's Goldeneyes over the fall staging period was 0.994 (95% CI: 0.993-0.996), which corresponded to a 62-day PSR of 0.71 (95% CI: 0.66-0.77) (Figure 8). The point estimate of the 2-month PSR on Cardinal Lake was lower than on Leddy Lake by 4% in

2009 and 9% in 2010 (Table 10). Fall staging estimates of DSR and PSR were substantially lower than the estimates of DSR and PSR during remigial molt (Table 10, Figure 8).

4.4. Discussion

Postbreeding survival of ASY male Barrow's Goldeneyes was high during remigial molt, with a cumulative survival estimate of 95% for the 39-day period. Survival during the fall staging period was substantially lower, and half of the observed mortality on Cardinal Lake was directly attributable to hunting. Furthermore, given relatively high wounding rates for many species of waterfowl (Whitlock and Miller 1947; Perry and Geissler 1980; Norton and Thomas 1994; Madsen and Noer 1996; Tavecchia *et al.* 2001), and particularly sea ducks (Goudie *et al.* 2000; Byers and Dickson 2001; Hicklin and Barrow 2004; Merkel *et al.* 2006), it is likely that hunting was responsible for an even larger fraction of the observed mortality during fall staging.

Simultaneous remigial molt can impose elevated nutritional costs and increase risk of predation on waterfowl (Hohman 1993; Murphy 1996; Brown and Saunders 1998; Bridge 2004; Fox and Kahlert 2005; Portugal *et al.* 2007; Dopfner *et al.* 2009; Fox and King 2011). However, ASY male Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB were not nutritionally constrained nor were they subject to high predation pressure (Chapter 3). Our estimates of high daily survival rate (DSR) and period survival rate (PSR) during remigial molt further support the conclusion that males are not experiencing demographic bottlenecks during this stage of the annual cycle. The average DSR of 0.999 corresponded to a 95% survival rate over the 39-day molting period, which is similar to rates estimated for other sea duck species during molt (Iverson and Esler 2007; Uher-Koch, unpublished data) and higher than estimates for some dabbling ducks (Bowman and Longcore 1989; Miller *et al.* 1992; Fleskes *et al.* 2010).

High survival rates of molting males observed on Cardinal and Leddy Lakes indicate that these sites provide high-quality molting habitat and that Barrow's

Goldeneyes employ successful strategies to accommodate risks associated with the flightless period. Previous, associated studies (Chapter 3) found that mass and foraging dynamics varied considerably between lakes and years, which was interpreted to represent optimized strategies based on variation in local conditions. Our survival findings reinforce the conclusion that these strategies, while different, are all tenable and result in completion of molt without nutritional or demographic constraints.

Average DSR and PSR were somewhat lower during fall staging at Cardinal and Leddy Lakes than during remigial molt (Table 10, Figure 8). Seven of the 14 mortalities reported on Cardinal Lake during fall staging were attributed to hunting. The remaining mortalities on Cardinal and Leddy Lakes were due to unknown causes, though some could have been due to hunting related wounds/crippling or unreported hunting. The PSR of 0.71 during fall staging was lower than PSR for other duck species during fall staging and winter periods (Kirby and Cowardin 1986; Esler *et al.* 2000; Mittelhauser 2008; Fleskes *et al.* 2010). If winter survival of adult males is similar to that of other sea duck species (Esler *et al.* 2000; Mittelhauser 2008), then fall staging at Cardinal and Leddy Lakes could represent the period of lowest survival in the annual cycle of adult male Barrow's Goldeneyes. Annual apparent survival of adult male Barrow's Goldeneyes has been estimated at 58-60% at a breeding site for the southern portion of the Pacific population of this species, though these estimates are likely lower than true survival (Savard and Eadie 1989; Boyd *et al.* 2009). While adult survival is likely a strong driver of population growth for Barrow's Goldeneye, it is unclear how adult male survival at these sites may influence population growth of Barrow's Goldeneye on a larger scale.

Some potential consequences of high fall staging mortality of adult male Barrow's Goldeneyes include disruption of population sex ratios and long-term pair bonds. Sex ratios of Barrow's Goldeneyes on breeding and wintering grounds are male biased (by a factor of ~1.2-1.5) suggesting intraspecific competition between males for females (Bellrose 1980; Savard and Eadie 1989). If high adult male fall staging mortality skewed sex ratios in favour of females on breeding grounds, population growth could be negatively affected. As an annually monogamous sea duck, Barrow's Goldeneyes might

be particularly sensitive to unequal sex ratios (Lehikoinen *et al.* 2008), especially as extra-pair copulations have never been documented and thus some reproductively active females may not find a mate if there are too few males in the population. Also, Savard (1985) documented the existence of long-term pair bonds in some Barrow's Goldeneyes breeding at Riske Creek, BC, which could increase the influence of adult male survival on population dynamics. Long-term Barrow's Goldeneye pairs reunite on the wintering grounds in multiple seasons (Savard 1985). This has also been observed in other sea duck species, such as Harlequin Ducks and Common Eiders (Spurr and Milne 1976; Smith *et al.* 2000). Inter-annual monogamy is generally thought to increase overall fitness of individuals by decreasing time spent on courtship behaviour, and increasing the probability of securing a territory, time spent feeding, and reproductive success (Spurr and Milne 1976, Coulson and Thomas 1983, Black 2001). Further, loss of long-term male mates has been shown to decrease subsequent female survival (Nicolai *et al.* 2012). Thus disruption of long-term pair bonds might negatively affect population growth.

4.4.1. Conservation Implications

Propensity of waterfowl to aggregate during remigial molt suggests that degradation of postbreeding sites might have wide reaching implications for waterfowl populations. This study and concurrently collected mass and foraging data (Chapter 3) indicate that Cardinal and Leddy Lakes provided high quality habitat for large numbers of molting Barrow's Goldeneyes. Cardinal Lake supported consistently large numbers of molting Barrow's Goldeneyes (Hogan *et al.* 2011) and its importance likely increases in years of drought because of its large size in relation to surrounding water bodies. Additionally, postbreeding Barrow's Goldeneyes use Cardinal and Leddy Lakes for over 1/3 of their annual cycle, with some birds staying for both remigial molt and fall staging (Hogan *et al.* 2011). Given the small number of sites in western North America that have been identified to support substantial numbers of molting Barrow's Goldeneyes (Hogan *et al.* 2011), conservation of those sites and assurance of protection during this sensitive stage in the annual cycle is warranted. Identification and protection of additional Barrow's Goldeneye molting sites in the Boreal Transition Zone of Alberta is

also warranted so that rapid industrial/agricultural development of this area (Mills 1994; Hobson *et al.* 2002) does not force birds to concentrate at unsustainable levels that can lead to catastrophic outbreaks of disease, especially botulism.

There was some evidence that fall staging survival on Cardinal Lake was lower than on Leddy Lake, particularly in 2010 (Δ PSR= 9%). Of 14 radio-marked birds that died on Cardinal Lake during fall staging, seven were reported by hunters, while neither of the Leddy Lake mortalities was due to hunting. Hunting activity was never observed on Leddy Lake, but was observed nearly daily on Cardinal Lake during the fall staging period. The proportion of banded (but not radio-marked) birds reported by hunters was lower than that of radio-marked birds, however 95% confidence intervals overlapped, suggesting no statistical difference. We suspect that band return rates at Cardinal Lake are low, as hunters that phoned to report radio-marked birds did not report banded birds unless prompted. Thus, we are confident that our survival estimates of fall staging survival are un-biased and that hunting pressure on radio-marked birds accurately reflects hunting pressure on Cardinal Lake, generally. While it is uncertain how hunting mortality on Cardinal Lake is affecting dynamics of the Pacific population of Barrow's Goldeneyes, the evidence from this study suggests that it is a significant cause of mortality of fall staging birds from the inter-mountain breeding portion of this population. Further, other sites used by substantial numbers of postbreeding Barrow's Goldeneyes in the Boreal Transition Zone of Alberta (e.g., Chip Lake) also support hunting activities. Efforts should be made to understand the intricacies of how fall staging harvest at these sites is influencing Barrow's Goldeneye population dynamics so that appropriate management plans can be implemented.

Until the population level effects of fall staging mortality on Cardinal Lake are better understood, conservative measures for moderating hunting mortality at this site should be implemented. Barrow's Goldeneyes are extremely susceptible to decoying (J.Thompson, per.obs.), and extensive guiding activity on the lake, particularly on the large northeastern peninsula, may artificially inflate overwater hunting at this site. I recommend the following measures to moderate hunting mortality at Cardinal Lake: 1) decrease the liberal bag limit on Barrow's Goldeneyes (currently 8 birds/day), 2) restrict

boating activity to the eastern half of the lake, minimizing access to the northwestern peninsula, and 3) decrease number of days that goldeneye hunting is permitted on the lake. These measures will act to decrease the hunting-related mortality of Barrow's Goldeneyes on Cardinal Lake, and can be re-assessed as we obtain more information on the impact of the goldeneye hunt at this site on population dynamics.

4.5. Tables and Figures

Table 8: AICc model selection results for variation in survival (S) of adult male Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, AB in 2009 and 2010. LKYR is a categorical variable with 4 levels (Cardinal Lake or Leddy Lake in 2009 or 2010). MASSALL is residual mass of individuals calculated as difference between mass at capture and average mass of all individuals captured during the study. MASSLKYR is residual mass of individuals calculated as difference between mass at capture and average mass of all individuals captured on the same lake in the same year. Time dependent (molt stage) models were not supported by the data.

Model	$\Delta AICc$	AICc weight (w_i)	K
S _{CONSTANT}	0	0.70	2
S _{MASSLKYR}	3.77	0.11	3
S _{MASSALL}	3.79	0.10	3
S _{LKYR}	4.65	0.07	5
S _{LKYR + MASSLKYR}	6.63	0.02	6
S _{MOLT STAGE}	57.94	0.00	32
S _{MOLT STAGE + MASSLKYR}	59.74	0.00	33
S _{MOLT STAGE + MASSALL}	59.76	0.00	33
S _{MOLT STAGE + LKYR}	60.68	0.00	35
S _{MOLT STAGE + LKYR + MASSLKYR}	62.69	0.00	36

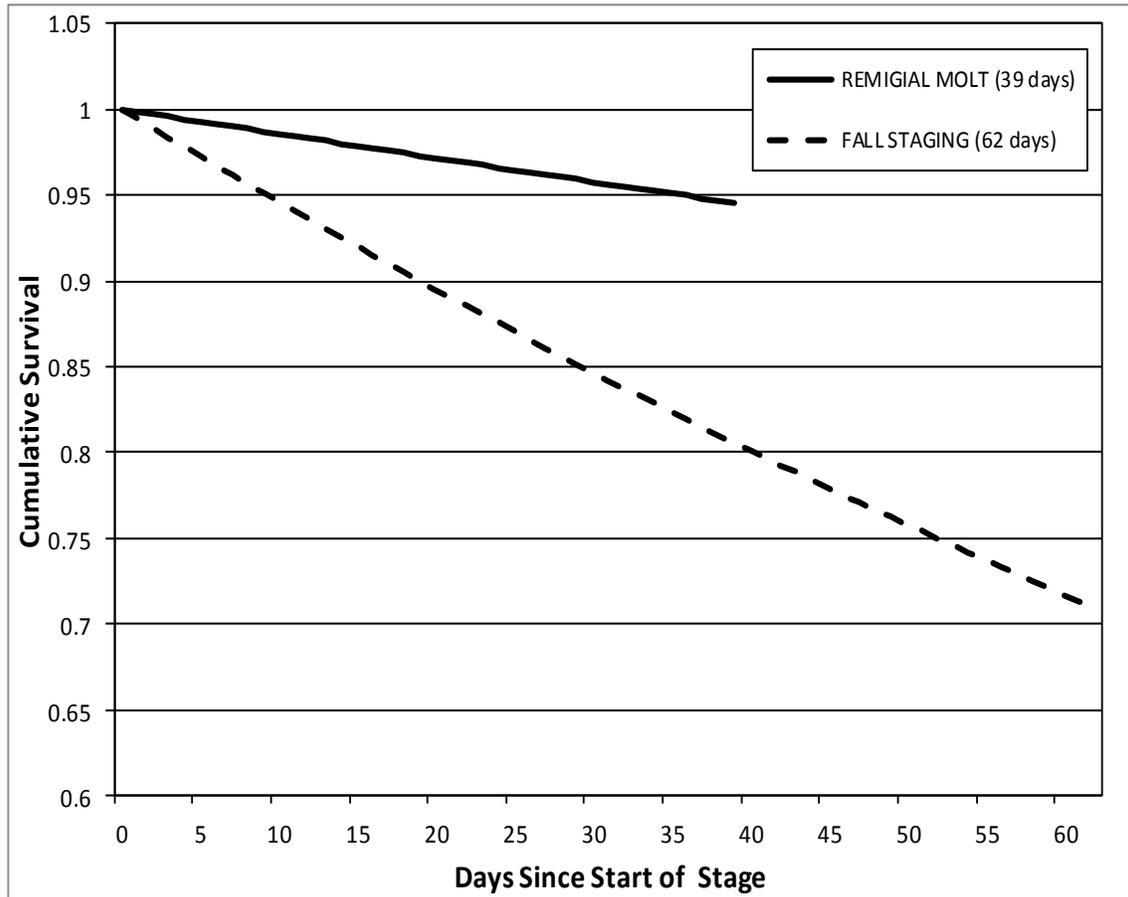
Table 9: AICc model selection results explaining variation in survival (S) of adult male Barrow's Goldeneyes during fall staging on Cardinal and Leddy Lakes, AB in 2009 and 2010. LKYR is a categorical variable with 4 levels (Cardinal Lake or Leddy Lake in 2009 or 2010). Time dependent models were not supported by the data.

Model	$\Delta AICc$	AICc weight (w_i)	K
$S_{CONSTANT}$	0	0.72	2
S_{LKYR}	4.65	0.28	5
S_{TIME}	90.86	0.00	63
$S_{TIME + LKYR}$	93.52	0.00	66

Table 10: Model-averaged estimates of daily survival rate (DSR) and period survival rate (PSR) of adult male Barrow's Goldeneyes during remigial molt (39days) and fall staging (62 days) on Cardinal and Leddy Lakes, AB in 2009 and 2010.

	Remigial Molt		Fall Staging	
Cardinal Lake	2009	2010	2009	2010
DSR (95%CI)	0.999 (0.997-1.000)	0.999 (0.997-1.000)	0.994 (0.990-0.997)	0.994 (0.990-0.998)
PSR (95% CI)	0.95 (0.89-1.00)	0.95 (0.90-1.00)	0.68 (0.52-0.89)	0.68 (0.54-0.85)
Leddy Lake				
DSR (95%CI)	0.999 (0.997-1.000)	0.998 (0.996-1.000)	0.995 (0.990-0.999)	0.996 (0.990-1.000)
PSR (95% CI)	0.95 (0.89-1.00)	0.94 (0.86-1.00)	0.72 (0.55-0.92)	0.77 (0.54-1.000)

Figure 8: Cumulative survival of ASY male Barrow's Goldeneyes on Cardinal and Leddy Lakes, AB during remigial molt and fall staging based on model- averaged daily survival rates (DSR). Survival rates were calculated using a modified Mayfield method. Remigial molt DSR= 0.999, fall staging DSR= 0.994. Remigial molt and fall staging are 39 and 62 days, respectively.



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5. General Conclusions

Based on my findings, I conclude that remigial molt was not a period of nutritional or demographic constraint for Barrow's Goldeneyes at Cardinal and Leddy Lakes in the Boreal Transition Zone (BTZ) of Alberta. Duration of remigial molt was protracted relative to many other waterfowl species (Chapter 2; Hohman *et al.* 1992), indicating that birds were not under strong temporal constraints to complete molt, which might be expected under scenarios with high predation risk, risk of freeze-up, or timing optima related to migration or arrival on wintering sites. Also, initiation of remigial molt occurred over multiple weeks across individuals, further indicating that molting birds were not strongly influenced by temporal constraints.

All cohorts gained mass during remigial molt (Figure 2, Chapter 3), and radio-marked birds foraged little throughout this period (~8-9% of day, Chapter 3), indicating that individuals were meeting energetic and nutritional demands of molt without difficulty. Stable mass and/or mass gain also has been observed for molting scoters (*Melanitta spp.*) (Fox *et al.* 2008; Dickson 2011), Canvasbacks (*Aythya valisineria*) (Thompson and Drobney 1996), male Ring-necked Ducks (*A. collaris*) (Hohman *et al.* 1988), and female Lesser Scaup (*A. affinis*) (Hohman *et al.* 1992). In contrast, Redheads (*A. americana*), Mallards (*Anas platyrhynchos*), Mottled Ducks (*A. fulvigula*), Blue-winged Teal (*A. discors*), Pochard (*A. ferina*), Tufted Ducks (*A. fulvigula*), and Barrow's Goldeneyes in the Yukon Territory decreased mass during remigial molt (Bailey 1985; Panek and Majewski 1990; Moorman *et al.* 1993; Brown and Saunders 1998; Van de Wetering and Cooke 2000; Fox and King 2011). Mass loss in these species has been attributed to one, or a combination, of three things: 1) a deliberate reduction of wing loading for an earlier return to flight, 2) reduction in foraging activity as a result of secretive behaviour and/or increased resting or vigilance behaviour, or 3) inability to acquire adequate resources through foraging efforts (i.e. demands of molt exceed what can be acquired from the

environment). The first explanation suggests that birds could obtain nutrients required for remigial molt through exogenous sources but do not, due to selective pressure to regain flight. The second explanation suggests that birds trade-off benefits of exploiting exogenous nutrient sources against risks associated with foraging. The third explanation suggests that birds select molting habitats that have food quantity or quality that is too low to fully fuel costs of remigial growth. Alternatively, mass loss might also arise if somatic reserves are not required (due to abundant food) and costly to maintain during remigial molt. Unfortunately, most studies that have quantified mass dynamics of molting ducks have not concurrently quantified foraging effort, so interpretation of mass loss during remigial molt as it relates to nutritional constraints is limited (i.e. the ability to distinguish among the 4 hypotheses is limited). One exception was a study of White-winged and Surf Scoters on the Pacific coast of North America, which indicated that scoters gained mass during remigial molt while foraging at moderate levels, suggesting that birds were not nutritionally constrained (Dickson 2011). The same conclusion can be made for Barrow's Goldeneyes at Cardinal and Leddy Lakes, as foraging effort of these birds was similar to or less than that of other molting waterfowl of similar size (Adams *et al.* 2000; Dopfner *et al.* 2009; Dickson 2011; Craik *et al.* 2011) and less than that of other waterfowl during different stages of the annual cycle (Custer *et al.* 1996; Fischer and Griffin 2000; Systad and Bustnes 2001; Kirk *et al.* 2007; Lewis *et al.* 2007).

Mass and foraging dynamics of molting Barrow's Goldeneyes at Cardinal and Leddy Lakes indicated that although birds from both lakes utilized the same overall molt strategy (gain mass, forage little), there appeared to be some flexibility regarding the execution of this strategy. In addition to being heavier throughout molt, Leddy Lake birds foraged primarily at night, while Cardinal Lake birds foraged primarily diurnally. In contrast, Barrow's Goldeneyes molting on Old Crow Flats, Yukon Territory used a different strategy, losing mass throughout remigial molt (Van de Wetering and Cooke 2000). A recent study of characteristics of wetlands in the BTZ suggests that lake productivity is strongly correlated with waterfowl use, and that molting diving ducks, such as Barrow's Goldeneyes, prefer highly productive lakes (Wong *et al.*, in review). Evidence of this preference also has been documented on Old Crow Flats (Van de Wetering 1997). Wetlands in the Old Crow Flats have lower total phosphorus and

chlorophyll A concentrations than those in the BTZ (Van de Wetering 1997; Thompson *et al.*, unpublished data). Thus, differences in productivity of molting habitat at these sites may explain some of the observed differences in mass patterns of Barrow's Goldeneyes; Barrow's Goldeneyes at Old Crow Flats may rely more heavily on somatic nutrient reserves during remigial molt. The differences in molt strategy employed by birds on different lakes suggest that molt strategy is optimized for local environmental conditions (i.e. that molting strategy is plastic within species). This notion is supported by contrasting results from studies of other waterfowl species (Owen and Ogilvie 1979; Young and Boag 1982; Dubowy 1985; Panek and Majewski 1990; Brown and Saunders 1998; Dopfner *et al.* 2009; Portugal *et al.* 2007; Fox and King 2011) and could be further investigated through experimental manipulation of captive and free-living birds.

Survival of radio-marked, adult male Barrow's Goldeneyes during remigial molt was high (DSR= 0.999, PSR= 0.95, Chapter 4). Estimated survival was similar to that of other molting sea duck species (Iverson and Esler 2007; Uher-Koch, unpublished data), and higher than for some dabbling ducks (Bowman and Longcore 1989; Miller *et al.* 1992; Fleskes *et al.* 2010). This suggests that remigial molt is not a period of demographic constraint for Barrow's Goldeneyes in the BTZ of Alberta.

Survival of fall staging adult male Barrow's Goldeneyes on Cardinal and Leddy Lakes was substantially lower than survival during remigial molt at these sites, and lower than fall staging and winter survival of many other duck species (Kirby and Cowardin 1986; Esler *et al.* 2000; Mittelhauser 2008; Fleskes *et al.* 2010). This stage could be the period of lowest survival in the annual cycle of adult males. Half of the mortalities on Cardinal Lake during the fall staging period were directly attributed to hunting activity; however, given the high rate of crippling described for sea ducks (Goudie *et al.* 2000; Byers and Dickson 2001; Hicklin and Barrow 2004; Merkel *et al.* 2006), the proportion of deaths related to hunting activities is likely even higher. Effects of low adult male survival at these sites on population dynamics of Barrow's Goldeneyes in the Pacific population are unknown, but this high localized mortality could have important consequences for the inter-mountain breeding portion of this population. Because of this species' propensity for strong seasonal pair bonds (Savard 1985), a negative effect

on population growth might be expected if sex ratios were biased against males, as evidence for extra-pair copulations in this species does not exist. Population growth also might be negatively affected by high adult male mortality through disruption of long-term pair bonds that are sometimes observed in this species (Savard 1985), especially if long-term pairs are more productive than their seasonally monogamous counter-parts.

The lack of constraints experienced by molting Barrow's Goldeneyes in this study agrees with findings from studies of other molting sea ducks; sea ducks, generally, do not appear to be constrained during remigial molt. Concurrently collected molt phenology, mass, foraging, and survival data do not exist for most *Mergini* species, however, the few existing studies of molting scoters (Savard *et al.* 2007; Fox *et al.* 2008, Dickson 2011, Uher-Koch, unpublished data), Common Eiders (*Somateria mollissima*) (Guillemette *et al.* 2007), Red-breasted Mergansers (*Mergus serrator*) (Craik *et al.* 2009; Craik *et al.* 2011), and Harlequin Ducks (*Histrionicus histrionicus*) (Adams *et al.* 2000; Iverson and Esler 2007) suggest that birds are not temporally constrained, do not rely on somatic reserves or forage excessively to meet the nutritional demands of remigial molt, and have high survival. These conclusions appear to be applicable to all *Mergini* species studied to date, including those that molt in both freshwater and marine environments, and lead me to suggest that large-scale declines of sea duck populations are not likely due to demographic constraints experienced during remigial molt. Additional study of other sea duck species would be useful for evaluating the ubiquity of this conclusion. Interestingly, the lack of constraints on molting sea ducks observed to date is not necessarily shared by other ducks species, even other diving ducks. Sea ducks may be better suited than other ducks to simultaneous remigial molt because they are better adapted to coping with the loss of flight. Sea ducks rely on highly developed diving abilities throughout the year and are accustomed to inhabiting offshore habitats, thus they may naturally be less affected by the loss of flight with regards to foraging behaviour and risk of predation. This line of reasoning lends support to the hypothesis that simultaneous remigial molt, and its associated flightlessness, most commonly developed in birds that had alternative means of locomotion, such as species that were strong swimmers/divers. The advantage of this molt strategy may be that it condenses feather replacement into a discrete stage in the annual cycle so that 1) the costs of

feather synthesis do not overlap with other costly stages in the annual cycle and 2) habitats specifically conducive to molt, but perhaps not ideal at other stages in the annual cycle, can be utilized without fitness consequences. Examination of constraints experienced by other strong swimming, non-waterfowl species that undergo simultaneous remigial molt (e.g. auks, loons, grebes) would be an informative test of this hypothesis, as one might expect these species to experience a similar lack of constraints during remigial molt as sea ducks.

5.1. Conservation Implications

High survival and lack of nutritional and temporal constraints observed for Barrow's Goldeneyes molting on Cardinal and Leddy Lakes suggest that these molt sites provide high-quality habitat for this species during a potentially risky period in the annual cycle. Degradation of these sites could have far-reaching implications for population dynamics of this species as a result of the propensity of birds to aggregate in large numbers at a few sites during remigial molt. Indeed, Cardinal and Leddy Lakes consistently host between 5 000 – 7 000 postbreeding Barrow's Goldeneyes annually, and are two of only five known postbreeding sites that are heavily used by this species in western North America (Hogan *et al.* 2011), where over 90% of the world population resides (Eadie *et al.* 2000). Conservation efforts should focus on protecting these molting sites from further agricultural and industrial development, such as the nuclear reactor that was recently proposed to be built on the shores of Cardinal Lake (Bruce Power 2009). Though the proposal has since been withdrawn, had the project been completed, the ecology of the lake, which was to be used as a cooling pond for up to four reactors, would have changed dramatically, possibly with severe consequences to waterfowl using this site. For example, thermal pollution could alter seasonal ice formation, allowing birds to winter on Cardinal Lake. As food resources dwindle throughout winter, birds may become too weak to leave this sub-optimal habitat, which could lead to death or severe emaciation. This highlights the importance of securing land adjacent to the lakes for conservation purposes, whether this is accomplished through purchase of private land or conservation easements on crown and/or private

land. Two such easements and a land purchase have already been secured by Ducks Unlimited Canada on the southeastern shore and northeastern peninsula of Cardinal Lake, and other landowners surrounding the lake have expressed interest in similar agreements. Based on this local interest in conservation efforts, I suggest further development of conservation plans involving landowner participation. Actively engaging landowners to consider easements may be the best way to approach this, as many landowners are aware of the existence of easements, but unclear about the details of such agreements. Another option to ensure minimal anthropogenic disturbance at Cardinal Lake in the future would be to identify it as an internationally important wetland under the Ramsar Convention (Ramsar Convention Secretariat 2011). This lake qualifies for Ramsar status under the criteria indicated for waterbirds as it 1) regularly supports $\geq 20\,000$ waterfowl during remigial molt (J.Thompson, unpublished data), a particularly vulnerable stage of the annual cycle and 2) supports greater than 1% of the global population of Barrow's Goldeneyes during the remigial molt and fall staging periods (Hogan *et al.* 2011).

Given the low rate of survival of adult male Barrow's Goldeneyes during the fall staging period, and the high proportion of Cardinal Lake mortalities attributed to hunting activities, efforts should be made to determine the population level effects of this source of mortality. Because vital rates of Barrow's Goldeneyes are relatively understudied, models that evaluate effects of adult male mortality on population growth may take years to develop. Meanwhile, I suggest that management plans for this species at Cardinal and Leddy Lakes err on the side of caution, closely regulating hunting activity at these sites until implications of the hunt can be determined. The majority of hunting-related mortalities of Barrow's Goldeneyes on Cardinal Lake have been reported by a single hunting outfitter (D. Hogan, unpublished data). This source of mortality could be reduced by regulating outfitter activities on the lake, perhaps by decreasing the number of days goldeneye hunting is permitted or reducing bag limits for goldeneyes at this site. Furthermore, goldeneye harvest on Cardinal Lake appears to take place mainly on the large northeastern peninsula (D.Hogan, pers. obs.). Restricting boating activity to the eastern basin of the lake during the fall staging period may decrease hunting pressure at this site by discouraging hunting from this peninsula. While the effects of male mortality

at Cardinal and Leddy Lakes on overall population dynamics of Barrow's Goldeneyes on the Pacific coast are unknown, male mortality at these sites could potentially influence the subset of this population that breeds in southwestern British Columbia, where it is thought most of the Cardinal and Leddy Lake birds originate (S. Boyd *et al.*, unpublished data).

5.2. Future Directions

While this study has increased our understanding of the strategies that Barrow's Goldeneyes use to accommodate potential costs and risks of remigial molt, the scope of this research does not address reasons for choice of molt site in this species. Cardinal and Leddy Lakes share some similar characteristics with each other and other known Barrow's Goldeneye molting sites, e.g. shallow, highly productive, absence of large fish (King 1963; Van de Wetering and Cooke 2000; Hogan *et al.* 2011), yet it is unclear why other lakes in the Boreal Transition Zone with similar characteristics are not heavily utilized. Furthermore, Barrow's Goldeneyes in eastern North America sometimes use estuarine habitats during remigial molt (Robert *et al.* 2002), which has not been observed in the Pacific. Thus, a more complete study of characteristics of Barrow's Goldeneye molt sites should be conducted to help focus efforts to conserve other postbreeding habitats for this species. Diet analysis and patterns of prey availability at known molt sites also could be examined to determine if certain invertebrate communities are preferred by molting Barrow's Goldeneyes over others. Conservation of potential, though not currently heavily used, molting sites may become important for this species as environmental conditions become less predictable at known molting sites through global climate change.

Understanding a species' resilience to change can help inform conservation management plans and priorities. This study suggests that molting Barrow's Goldeneyes modify their molt strategy for local environmental conditions, yet the limits of this plasticity, and its prevalence in the waterfowl community, are unknown. I suggest that multiple experiments manipulating availability of food resources, risk of predation, and rate of disturbance of captive molting birds of a variety of species could allow for a

better understanding of the physiological and behavioural flexibility of molt strategies. Differences in plasticity between dabbling and diving ducks may be of particular interest, as these potential differences may provide insight as to how habitat preferences affect molt strategy and flexibility. These experiments would also help to parse out the importance of choice of molting habitat vs. flexibility of strategy (i.e. can birds molt on many different sites, but choose only the best when possible, or are known molt sites chosen because birds are unable to complete molt elsewhere?). Alternatively, repeating the study outlined in this thesis with wild Barrow's Goldeneyes at other molt sites, and perhaps even re-locating molting individuals to different sites, also would shed light on the degree of plasticity of molt strategy within a species. Ultimately, understanding the ability of waterfowl to adapt molt strategy to changes in environmental conditions will allow managers to better predict waterfowl reactions to climate change as well as localized anthropogenic activities at molt sites.

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