# Variation in Body Mass and Foraging Effort of Barrow's Goldeneyes (*Bucephala islandica*) During Remigial Molt

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# VARIATION IN BODY MASS AND FORAGING EFFORT OF BARROW'S GOLDENEYES (*BUCEPHALA ISLANDICA*) DURING REMIGIAL MOLT

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Abstract.—Molt is a metabolically demanding process in the annual cycle of birds, particularly for species that undergo simultaneous remigial molt because nutritional and energetic costs occur during a short period. Birds that molt remiges simultaneously utilize many different body-mass and foraging strategies to meet the nutritional and energetic costs of remigial molt, and documentation of interspecific variation has contributed to understanding species-specific risks associated with molt. However, little is known about intraspecific variation in body-mass and foraging strategies among birds that molt remiges simultaneously. We documented body-mass dynamics and foraging effort of Barrow's Goldeneyes (*Bucephala islandica*) during simultaneous remigial molt at two important postbreeding sites, including a large, hypereuthrophic lake and a small, mesotrophic lake in Alberta, to determine whether strategies for meeting nutritional costs of remigial molt varied across sites, years, and cohorts. Average body mass of all age and sex cohorts on both lakes increased during remigial molt in both 2009 and 2010. Birds were heavier on the smaller lake, and heavier in 2010 than in 2009, and adult males were heavier than subadult males. Radiomarked adult males exhibited similar foraging effort on each lake in each year (approximately 120–140 min day$^{-1}$); however, birds foraged primarily diurnally on the large lake and nocturnally on the small lake. We conclude that Barrow's Goldeneyes exhibit considerable intraspecific variation in body-mass and foraging dynamics during remigial molt across sites, years, and cohorts, which suggests that these components of molt strategy are plastic and responsive to local environmental conditions. *Received 20 March 2012, accepted 26 December 2012.*

Key words: Alberta, Barrow's Goldeneye, body mass, *Bucephala islandica*, foraging effort, remigial molt.

## Variation de la masse corporelle et de l'effort d'alimentation de *Bucephala islandica* lors de la mue des rémiges

Résumé.—La mue est un processus du cycle annuel des oiseaux qui est exigeant sur le plan métabolique, particulièrement chez les espèces qui subissent une mue simultanée des rémiges car les coûts nutritionnels et énergétiques se produisent sur une courte période. Les oiseaux dont les rémiges muent simultanément utilisent diverses stratégies de masse corporelle et alimentaires afin d'assumer les coûts nutritionnels et énergétiques de la mue des rémiges. La documentation sur la variation interspécifique a contribué à la compréhension des risques spécifiques associés à la mue. Toutefois, on en sait peu sur la variation intraspécifique de la masse corporelle et les stratégies alimentaires chez les oiseaux qui subissent une mue simultanée des rémiges. Nous avons documenté la dynamique de la masse corporelle et l'effort d'alimentation de *Bucephala islandica* au cours de la mue simultanée des rémiges à deux importants sites de mue postnuptiale, soit un grand lac hypereuthrophe et un petit lac mésotrophe en Alberta, afin de déterminer si les stratégies pour assumer les coûts nutritionnels de la mue des rémiges varient entre les sites, les années et les cohortes. La masse corporelle moyenne de toutes les cohortes d'âge et de sexe sur les deux lacs a augmenté au cours de la mue des rémiges en 2009 et 2010. Les oiseaux étaient plus lourds sur le petit lac, plus lourds en 2010 qu'en 2009, et les mâles adultes étaient plus lourds que les mâles immatures. Les mâles adultes porteurs d'émetteurs présentaient un effort d'alimentation similaire sur chaque lac et à chaque année (environ 120–140 min jour$^{-1}$); cependant, les oiseaux s'alimentaient surtout durant le jour sur le grand lac et durant la nuit sur le petit lac. Nous concluons que *B. islandica* présente une variation intraspécifique considérable de la dynamique de la masse corporelle et d'alimentation au cours de la mue des rémiges entre les sites, les années et les cohortes, ce qui suggère que ces composantes de la stratégie de mue sont flexibles et sensibles aux conditions environnementales locales.

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Feathers serve many functions for birds, including temperature regulation, cryptic coloration, mate attraction, epidermal protection, and flight (Stettenheim 1976). As feathers become worn or damaged, they are replaced through the process of molt. Molt increases daily energy and nutrient requirements because of direct costs of feather production (Murphy and King 1992, Murphy 1996), decreased thermoregulatory efficiency (King 1981, Dietz et al. 1992), and decreased flight efficiency and performance (Chai 1997, Chai et al. 1999, Swaddle et al. 1999). Although most families of birds replace remiges (flight feathers) sequentially, retaining the ability to fly throughout remigial molt, 11 families of birds, including waterfowl, replace remiges simultaneously, resulting in loss of flight for several weeks (Hohman et al. 1992). Strategies for meeting energetic and nutritional costs of remigial molt vary considerably across waterfowl species (Hohman et al. 1992), suggesting variability in environmental constraints experienced by species during this stage of the annual cycle.

Interspecific variation in mass and foraging strategies of waterfowl during remigial molt is widely observed. Some waterfowl meet nutritional requirements of remigial molt through exogenous resources, increasing foraging effort and maintaining or gaining mass during molt (Ankney 1979, Young and Boag 1982, Fox et al. 2008). Other species deplete endogenous (somatic) resources during molt and lose body mass as a result (Panek and Majewski 1990, Hohman 1993, Brown and Saunders 1998, Fox and Kahlert 2005, Portugal et al. 2007, Fox and King 2011). Other species rely on both strategies to meet nutritional demands during different stages of remigial molt (Owen and Ogilvie 1979, Bailey 1985, Moorman et al. 1993, Thompson and Drobney 1996, Fox et al. 2009). Variation in energy and nutrient acquisition and allocation across species presumably reflects different solutions for meeting costs of simultaneous remigial molt based on environmental conditions (e.g., weather, predation risk, and food availability) faced by different species during this stage.

Although interspecific variation in body-mass dynamics and foraging effort during remigial molt is well documented among waterfowl, intraspecific variation in these components of molt strategy is rarely studied. Further, body-mass and foraging dynamics during remigial molt have rarely been studied concurrently, which limits our ability to understand strategies of energy management, as well as sources of variation in strategies. Concurrent investigation of mass and foraging dynamics allows for better examination of energy management strategies by both indicating whether birds are depleting or accumulating somatic nutrients or lipids, and providing information about the amount of effort exerted to acquire exogenous resources. For example, birds that are losing mass (i.e., depleting somatic resources) and foraging little may be adaptively losing mass, possibly to enhance predator evasion (Panek and Majewski 1990, Brown and Saunders 1998, Zimmer et al. 2010). Birds that are losing mass and foraging laboriously may be nutritionally limited (Fox and Kalhert 2005, Portugal et al. 2007, Fox and King 2011), whereas birds that maintain or gain mass and forage little are likely able to acquire exogenous nutrients easily during remigial molt.

Intraspecific variation in energy management strategies has been observed in many waterfowl species at other stages of the annual cycle. For example, breeding Northern Pintails (*Anas acuta*) primarily use endogenous nutrients to lay early clutches, whereas later-nesting females rely more on exogenous nutrients (Esler and Grand 1994). Similarly, Ruddy Ducks (*Oxyura jamaicensis*), and Canvasbacks (*Aythya valisineria*) that nest later in the breeding season rely more on exogenous nutrients for egg production than earlier-nesting conspecifics (Barzen and Serie 1990, Alisauskas and Ankney 1994). Lesser Snow Geese (*Chen caerulescens caerulescens*) and Barrow's Goldeneyes (*Bucephala islandica*) show a large degree of variation among individuals in allocation of endogenous resources to egg formation both within and between sites and years (Hobson et al. 2005, 2011).

Intraspecific variation in energy management strategies has also been observed between age and sex cohorts, and across sites and years, in many wintering and staging waterfowl species (Morton et al. 1990, Thompson and Baldassarre 1990, Loesch et al. 1992, Badzinski and Petrie 2006, Rhodes et al. 2006). For example, Rhodes et al. (2006) found that the rate of use of endogenous reserves over winter was highest in adult American Wigeons (*Anas americana*) and lowest in juvenile males. Badzinski and Petrie (2006) observed constant lipid reserves in male Lesser Scaup (*Aythya affinis*) at one spring staging site, and increasing lipid reserves in males at another site, as well as greater lipid reserves in males than in females at all sites. Female Harlequin Ducks (*Histrionicus histrionicus*) spent 19% more time foraging than males during winter (Fischer and Griffin 2000). Wintering Surf Scoters (*Melanitta perspicillata)* foraged twice as much in California as in Alaska, and they foraged nocturnally in California but only diurnally in Alaska (VanStratt 2011). Also, dive duration of foraging goldeneyes wintering in the Gulf of St. Lawrence differed between foraging sites (Bourget et al. 2007).

Our objective was to concurrently quantify body mass dynamics and foraging effort of molting Barrow's Goldeneyes (hereafter "goldeneyes") in northwestern Alberta to determine the degree of intraspecific variation in energy management strategy during this poorly studied stage of the annual cycle. Goldeneyes are diving ducks that feed on benthic invertebrates (Eadie et al. 2000). We were specifically interested in differences in strategies among sites, years, and age and sex cohorts. We expected that body-mass dynamics would differ between sex and age cohorts because sexual dimorphism in mass is well documented in this species (Eadie et al. 2000, Schamber et al. 2009), and age differences in mass have been documented in other duck species (Peterson and Ellarson 1979, Morton et al. 1990, Rhodes et al. 2006). Further, because environmental conditions likely varied between sites and years, we also expected mass dynamics and foraging effort to vary between sites and years.

## Methods

*Study area.*—Cardinal Lake (56°14′N, 117°44′W), also known as Lac Cardinal, is a large (~50 km$^2$) shallow lake 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 km$^2$) lake located ~25 km northeast of Cardinal Lake. This basin is shallow (<2 m), has a primarily muddy substrate, has a dense submerged vegetation mat throughout most of the lake, and is mesotrophic. Combined, these lakes annually support 5,000–7,000 molting goldeneyes, the majority of which are adult males (for details, see Hogan et al. 2011). Cardinal and Leddy lakes were only recently recognized as important molting areas for goldeneyes and are two of only five known molting sites with large numbers of the species in North America (Hogan et al. 2011).

*Captures and foraging effort.*—In total, 1,149 goldeneyes were captured during remigial molt (late July–early September, 2009 and 2010) using drive-trapping techniques (van de Wetering 1997) on Cardinal and Leddy lakes. Each bird was fitted with a uniquely numbered federal tarsal band, and the mass of each bird was measured to the nearest gram on an electronic scale. Morphometric measurements were taken, including ninth primary length and wing chord measured with a ruler (±1 mm), and diagonal tarsus, culmen, bill width, and head length measured with electronic calipers (±0.01 mm). Ninth primary was measured 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 depth of the bursa of Fabricius, which was measured to the nearest millimeter by insertion of a mall probe (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). Over both years and both lakes, we captured 40 SY females, 56 ASY females, 111 SY males, and 942 ASY males.

A subset of 25 ASY male goldeneyes was marked with radiotransmitters on each lake in both 2009 and 2010 to monitor foraging effort during the molting period (total 100 radiomarked birds). The VHF radiotransmitters, weighing <12 g (~1% of average molting body mass), were attached using subcutaneous prongs and superglue (Iverson et al. 2006). The foraging effort of each radiomarked individual was monitored multiple times throughout remigial molt for 1-h intervals during different parts of the day, including nocturnal observations. Dives were indicated by temporary disappearance of the radio signal, and the duration of each signal loss was recorded to estimate the total time spent underwater per hour (Lewis et al. 2005). Losses of signal for <4 s were discarded because they were likely attributable to belly preening or rolling behavior (Lewis et al. 2005). Twenty hours of daytime visual observations of unmarked goldeneyes confirmed that diving constituted the principal method of foraging used by birds on both lakes, because other foraging behaviors (e.g., dabbling) were not observed.

*Data analysis: Body mass.*—Average masses (± SE) of ASY male goldeneyes during other stages of the annual cycle were determined previously from birds captured in Alaska, the Yukon Territory, British Columbia, and Alberta (van de Wetering 1997, D. Esler unpubl. data, J. E. Thompson unpubl. data). These estimates were compared with those measured during remigial molt to better understand how molting mass fits into the annual mass cycle.

Multiple linear models were used to evaluate variation in mass as a function of molt stage, age, lake, year, emergence date, and structural size. Sex was not included in models because sexual dimorphism in mass is well established for goldeneyes (Eadie et al. 2000, Schamber et al. 2009) and, thus, males and females were analyzed separately. "Emergence date" referred to the date at which the new ninth primary erupted from the skin of the wing. Molt stage (days since emergence) was calculated by dividing the ninth primary length at capture by the average remigial growth rate determined for goldeneyes (3.94 mm day$^{-1}$; Hogan 2012). The effect of structural size on mass was investigated through inclusion of PC1 scores generated for each bird by a principal component analysis based on diagonal tarsus, head length, and culmen length. PC1 accounted for 57% of variation in male measurements and 49% in female measurements, with positive values indicating larger birds.

An information-theoretic approach to data analysis was used to evaluate support for a suite of candidate models. Twelve models were included in each of our candidate sets. In addition to the models shown in Table 1, we included a null model and a global model that included all main effects and all two-way interactions between all variables except size. We also included a model with all main effects and all two-way interactions between molt stage and all other variables except size, a model with all main-effects and all two-way interactions between variables, excluding molt stage and size, the same model excluding molt stage as a main effect, and a model containing molt stage as a main effect by itself. Akaike's information criterion corrected for small sample size (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 ($\Delta$AIC$_c$) and AIC$_c$ weights ($w_i$) were used to evaluate the relative support for each model. Parameter likelihood values ($\Sigma\, w_i$) were calculated for each variable to evaluate the level of support for the variable within the candidate model set. Weighted parameter estimates (± unconditional SE) also were calculated for each variable across the entire candidate model set.

*Data analysis: Foraging effort.*—Thirty-nine days are required for an ASY male goldeneye to grow a full ninth primary feather after it emerges (Hogan 2012). Foraging observations that occurred <39 days after the estimated emergence date of radiomarked birds were considered to occur during remigial molt and were included in analyses. We modeled variation in foraging effort (min h$^{-1}$) during remigial molt as a function of lake and year (LKYR), emergence

Table 1. Linear model-selection results for models explaining variation in body mass of female Barrow's Goldeneyes molting on Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. "Molt" refers to stage of molt (days since emergence of ninth primary). "Emergence" refers to emergence date (earliest day in study; 26 July = 0). Size is a structural size variable (PC1). "Age" is a categorical variable with two levels: second-year or after-second-year. "Lake" is a categorical variable with two levels: CL or LL. "Year" is a categorical variable with two levels: 2009 or 2010. Models with Akaike weights <0.03 were not included in the table.

| Response variable | Model | $k$ | $\Delta$AIC$_c$ | $w_i$ |
|---|---|---|---|---|
| Mass (g) | Molt + emergence + age + lake + year + size | 8 | 0.00 | 0.38 |
| | Molt + emergence + age + lake + year + size + molt * age | 9 | 1.74 | 0.16 |
| | Molt + emergence + age + lake + year + size + molt * year | 9 | 2.24 | 0.13 |
| | Molt + emergence + age + lake + year + size + molt * lake | 9 | 2.29 | 0.12 |
| | Molt + emergence + age + lake + year + size + molt * emergence | 9 | 2.42 | 0.12 |
| | Emergence + age + lake + year + size | 7 | 3.24 | 0.08 |

TABLE 2. Generalized least-squares model-selection results to explain variation in diurnal foraging effort of radiomarked after-second-year male Barrow's Goldeneyes molting on Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. "LKYR" is a four-level categorical variable (CL2009, CL2010, LL2009, LL2010). "Molt" refers to stage of molt (days since emergence of ninth primary). "Time" refers to time since sunrise. Models with Akaike weights <0.03 were not included in the table.

| Response variable | Model | *k* | $\Delta\text{AIC}_c$ | $w_i$ |
|---|---|---|---|---|
| Foraging effort (min $h^{-1}$) | LKYR + time + $\text{time}^2$ + molt + $\text{molt}^2$ + LKYR * molt + LKYR * $\text{molt}^2$ | 18 | 0.00 | 0.94 |
| | LKYR + time + $\text{time}^2$ + molt + $\text{molt}^2$ + LKYR * time + LKYR * $\text{time}^2$ | 18 | 6.81 | 0.03 |
| | LKYR + time + $\text{time}^2$ + molt + $\text{molt}^2$ | 12 | 7.18 | 0.03 |

date, molt stage, residual mass, and time since sunrise or sunset (h). 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 or lighter each individual was in comparison to the average individual. Time since sunrise was used for diurnal observations, and time since sunset for nocturnal observations. 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 sunrise or sunset were included in models to allow for nonlinear relationships with foraging effort. Because foraging data were collected as repeated measures on radiomarked birds, we used the "step-up" approach described by Zuur et al. (2009) to determine the appropriate structure for models within our candidate set by comparing $\text{AIC}_c$ values of the global model, which included a random term for individual birds, to the global model without this random effect. A generalized least-squares (GLS) global model without random effects, and accounting for unequal LKYR variances, provided the best fit for both the nocturnal ($\text{AIC}_c$ weight = 0.88) and the diurnal ($\text{AIC}_c$ weight = 0.78) data (i.e., individual bird effects did not matter).

We included 20 models in our candidate set (Tables 2 and 3). In addition to the models shown in Tables 2 and 3, we included a null model and a global model that contained all main effects and two-way interactions between LKYR and time, molt stage and emergence date, and interactions between emergence date and mass. Molt stage, mass, and emergence date were included in models alone, as well as together. One model included all main effects, one included all main effects and two-way LKYR and time interactions, and another included all main effects and all two-way interactions between LKYR and time, molt stage, and emergence date. Two models included the additive effects of LKYR, time, and emergence date alone and with two-way LKYR and emergence-date interactions. Two models included the additive effects of LKYR, and time and mass alone, with two-way LKYR and time interactions. One model contained molt stage, emergence date, and mass main effects with two-way interactions between emergence date and mass. $\text{AIC}_c$ was used, as described above, to identify the most parsimonious models and determine support for each variable within the candidate set of models. All analyses were performed in R, version 2.12.1 (R Core Development Team 2010), and foraging analyses were performed using the nlme package in R (Pinheiro et al. 2010).

## RESULTS

*Male mass dynamics during remigial molt.*—The global model, containing all main effects and biologically plausible interactions, received almost all the support for explaining variation in mass of male goldeneyes ($\text{AIC}_c$ weight = 0.99, $r^2 = 0.45$). As such, model averaging was not necessary, and parameter estimates and associated variances are those generated by the best-supported model (Table 4).

Average body mass at initiation of remigial growth varied considerably (Fig. 1A and Table 4). Average body mass at initiation of remigial molt increased with later emergence date, but with considerable variation in both intercepts and slopes across lakes, years, and age classes (Fig. 2A). Also, the effect of emergence date was relatively weak compared with other parameters, as indicated by 85% confidence intervals that marginally overlapped zero. Both male age classes, on both lakes, in both years, exhibited increased average mass during remigial growth (Fig. 1A). Taken together, these findings indicate a general, progressive increase in male goldeneyes' body mass during remigial molt.

Average body mass was consistently higher at Leddy Lake than at Cardinal Lake, after accounting for molt stage, emergence dates, and structural size (Figs. 1A and 2A; Table 4). Average mass varied to a smaller degree across years and tended to be higher in 2010 than in 2009 after accounting for other effects (Figs. 1A and 2A; Table 4).

TABLE 3. Generalized least-squares model-selection results to explain variation in nocturnal foraging effort of radiomarked after-second-year male Barrow's Goldeneyes molting on Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. LKYR is a four-level categorical variable (CL2009, CL2010, LL2009, LL2010). "Molt" refers to stage of molt (days since emergence of ninth primary). "Time" refers to time since sunrise. Models with Akaike weights <0.03 were not included in the table.

| Response variable | Model | *k* | $\Delta\text{AIC}_c$ | $w_i$ |
|---|---|---|---|---|
| Foraging effort (min $h^{-1}$) | LKYR + time + $\text{time}^2$ + molt + $\text{molt}^2$ + LKYR * time + LKYR * $\text{time}^2$ | 18 | 0.00 | 0.50 |
| | LKYR + time + $\text{time}^2$ + LKYR * time + LKYR * $\text{time}^2$ | 16 | 2.02 | 0.18 |
| | LKYR + time + $\text{time}^2$ + molt + $\text{molt}^2$ | 12 | 2.24 | 0.10 |
| | LKYR + time + $\text{time}^2$ | 10 | 4.14 | 0.06 |
| | LKYR + time + $\text{time}^2$ + emergence + $\text{emergence}^2$ + LKYR * time + LKYR * $\text{time}^2$ | 18 | 5.41 | 0.03 |

TABLE 4. Parameter estimates (± SE) for the best-supported model (global model) explaining variation in body mass of male Barrow's Goldeneyes during remigial molt at Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. "Intercept" refers to average mass (g) of after-second-year (ASY) males on CL in 2009 on the earliest remigial emergence date. Remaining parameter estimates denote the effect of each parameter on the change in body mass. Molt and emergence estimates are in g $day^{-1}$. "Molt" refers to stage of molt (days since emergence of ninth primary). "Emergence" refers to emergence date (earliest day in study; 26 July = 0). "Age" is a categorical variable with two levels, second-year (SY) or ASY, with ASY as the reference level. "Lake" is a categorical variable with two levels (CL or LL), with CL as the reference level. "Year" is a categorical variable with two levels (2009 or 2010), with 2009 as the reference level. Size estimate denotes the rate at which body mass changes with increasing structural size (increasingly positive PC1 scores). All parameter likelihoods = 0.99.

| Parameter | Parameter estimate |
|---|---|
| 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 |
| Size (PC1) | 17.40 ± 1.36 |

*Female mass dynamics during remigial molt.*—The model containing molt stage, emergence date, age, lake, year, and size main effects best explained variation in body mass of female goldeneyes ($AIC_c$ weight = 0.38, $r^2 = 0.29$; Table 1). Several other models containing all main effects also received moderate support ($AIC_c$ weights = 0.08–0.16, $r^2 = 0.26$–$0.29$; Table 1). Despite model uncertainty, there was consistent support for all main effects, with high parameter likelihoods for emergence date, lake, year, age, structural size, and molt stage (Table 5).

As with males, average mass of females was greater on Leddy Lake than on Cardinal Lake, and greater in 2010 than in 2009 (Figs. 1B and 2B; Table 5), although trajectories did not differ. Also similar to males, average body mass of female goldeneyes increased during remigial molt (Fig. 1B), as well as with later emergence dates (Fig. 2B), indicating persistent seasonal mass increases. Differences related to age class were minor (Table 5).

*Remigial molt mass in the annual cycle.*—Increasing mass observed during remigial molt appeared to be part of an increasing trend that extended into early winter (Fig. 3). Mass decreased over winter, reaching levels similar to those during remigial molt by early spring.

*Foraging effort during remigial molt.*—Average foraging effort of radiomarked ASY male goldeneyes was approximately 120–140 min $day^{-1}$ during remigial molt (Fig. 4). Although birds on both lakes, in both years, foraged similar average amounts per day (approximately 8–10%), timing of foraging differed dramatically, in that Cardinal Lake birds foraged mostly diurnally and Leddy Lake birds foraged mostly nocturnally (Fig. 4).

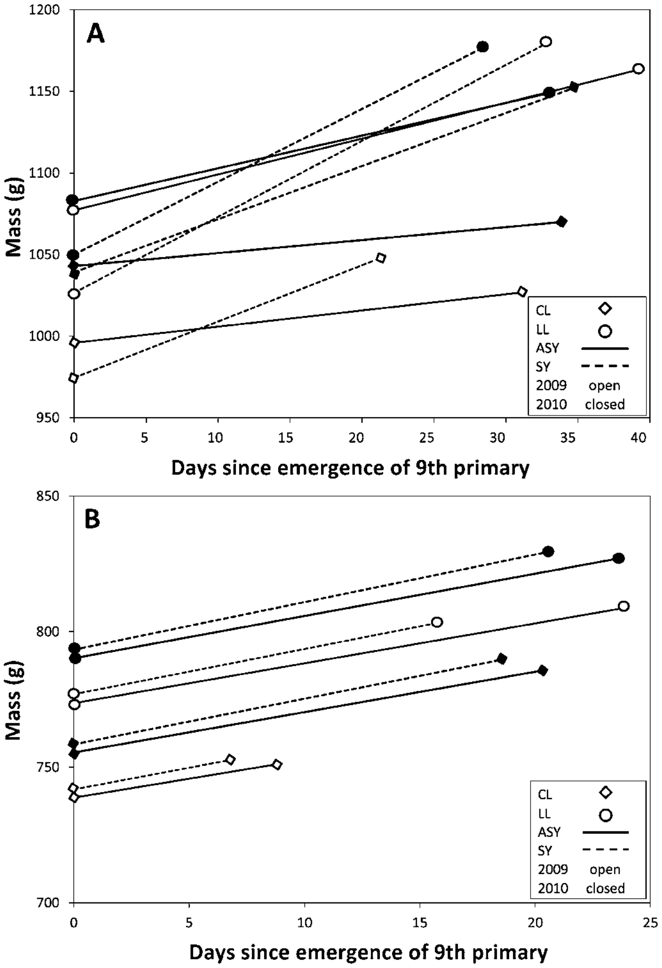

FIG. 1. Relationship between predicted body mass and stage of molt (days since emergence of ninth primary) for after-second-year (ASY) and second-year (SY) (A) male and (B) female Barrow's Goldeneyes molting on Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. Predicted mass was calculated using the model-averaged parameter estimates and data from captured individuals, holding emergence date and PC1 constant at the average values.

The best-supported model explaining variation in diurnal foraging effort included LKYR, time since sunrise, and molt stage variables and the LKYR and molt stage interaction ($AIC_c$ weight = 0.94; Table 2). All other models were weakly supported ($AIC_c$ weight ≤ 0.03; Table 2).

The best-supported model explaining nocturnal foraging effort included LKYR, time since sunset, and molt stage variables as well as the LKYR and time since sunset interaction ($AIC_c$ weight = 0.50; Table 3). Two models received moderate support ($AIC_c$ weight = 0.18 and 0.16; Table 3), both of which included LKYR and time since sunset. All other models received little support ($AIC_c$ weight ≤ 0.06). The LKYR (parameter likelihood = 1), time since sunset (parameter

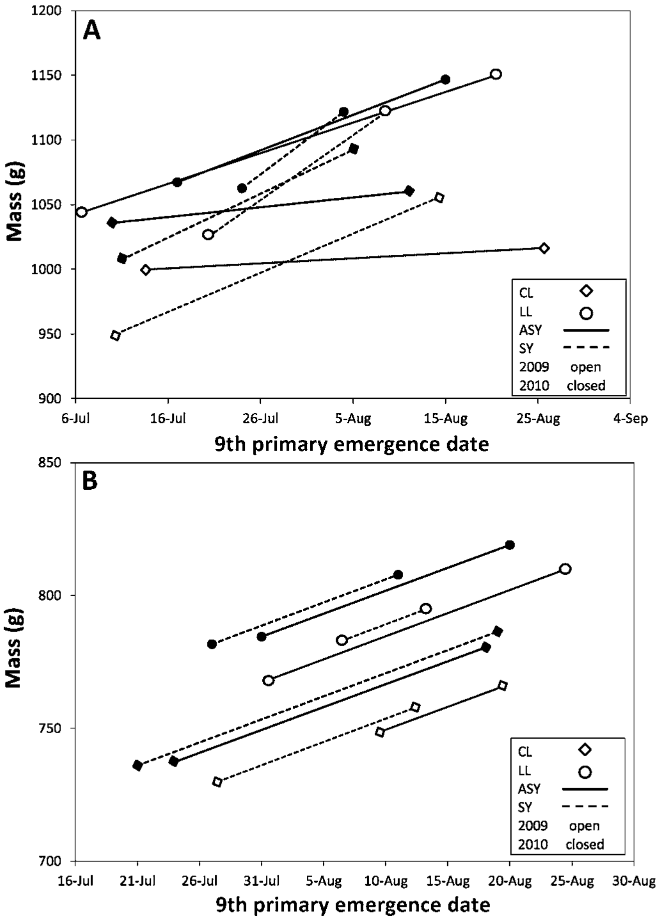

FIG. 2. Relationship between predicted body mass and emergence date for after-second-year (ASY) and second-year (SY) (A) male and (B) female Barrow's Goldeneyes molting on Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. Predicted mass was calculated using model-averaged parameter estimates and data from captured individuals, holding molt stage and PC1 constant at the average values.

likelihood = 0.99), molt stage (parameter likelihood = 0.68), and LKYR and time since sunset interaction (parameter likelihood = 0.74) variables received the most support in the model set. These results, along with those for the diurnal foraging models, suggest strong environmental influences (e.g., perceived predation risk, food availability, time of day) on foraging effort during remigial molt.

TABLE 5. Model-averaged parameter estimates (± unconditional SE) for variables explaining variation in body mass of female Barrow s Goldeneyes during remigial molt at Cardinal and Leddy lakes, Alberta, 2009 and 2010. Parameters and reference values are the same as those described in Table 1.

| Parameter | Model-averaged estimate | 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 |
| Size (PC1) | 11.26 ± 3.71 | 1.00 |

## DISCUSSION

We found a high degree of intraspecific variation in body mass and foraging effort of goldeneyes during remigial molt driven by effects of cohort, year, and lake. Adult males were heavier than subadults, Leddy Lake birds were heavier than Cardinal Lake birds, and birds on both lakes were heavier in 2010 than in 2009. In all age and sex cohorts, average body-mass trajectories were positive, consistent with a general strategy of increasing body mass during the postbreeding period. However, despite separation by only 25 km, average mass of all age and sex cohorts in all years was consistently higher on Leddy Lake than on Cardinal Lake, which suggests that body-mass dynamics varied in relation to environmental conditions. This conclusion is further supported by comparison with body-mass dynamics of male goldeneyes undergoing remigial molt ~1,700 km farther northwest at Old Crow Flats, Yukon, where average body mass declined during remigial molt (van de Wetering and Cooke 2000).

Adult male goldeneyes molting at Cardinal and Leddy lakes foraged approximately 8–10% of the day, which is similar to, or less than, foraging rates of other molting ducks of similar size (Adams et al. 2000, Döpfner et al. 2009, Craik et al. 2011, Dickson 2011). They also foraged at rates similar to those observed for goldeneyes during fall staging (D. Hogan unpubl. data), and rates similar to, or less than, those of 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, Schummer et al. 2012). However, Leddy Lake birds foraged primarily at night, whereas Cardinal Lake birds foraged primarily diurnally, which once again suggests environmental influences on energy management strategies. Given this, and our data regarding site-specific differences in body mass, we conclude that goldeneyes' energetic strategies are plastic during remigial molt and likely influenced by site-specific environmental conditions, such as food availability, predation risk, and weather. Also, observed increases in average body mass and low foraging effort during remigial molt strongly suggest that birds at our study sites primarily relied on exogenous energy and nutrient sources during this stage of the annual cycle.

Site-specific plasticity of body-mass and foraging strategies also has been observed in other waterfowl species during remigial molt and other stages in the annual cycle. For example, Panek and Majewski (1990) found that Mallards (*Anas platyrhynchos)* lost mass during remigial molt in Poland, whereas Young and Boag (1982) observed no significant mass loss for this species at a molting location in central Canada. Dubowy (1985) found that male Blue-winged Teal (*A. discors)* gained mass during molt in central Manitoba, whereas Brown and Saunders (1998) observed decreases in mass in Kansas. Barnacle Geese (*Branta leucopsis)* in Svalbard maintained mass and increased foraging effort in a molt study by Owen and Ogilvie (1979), whereas

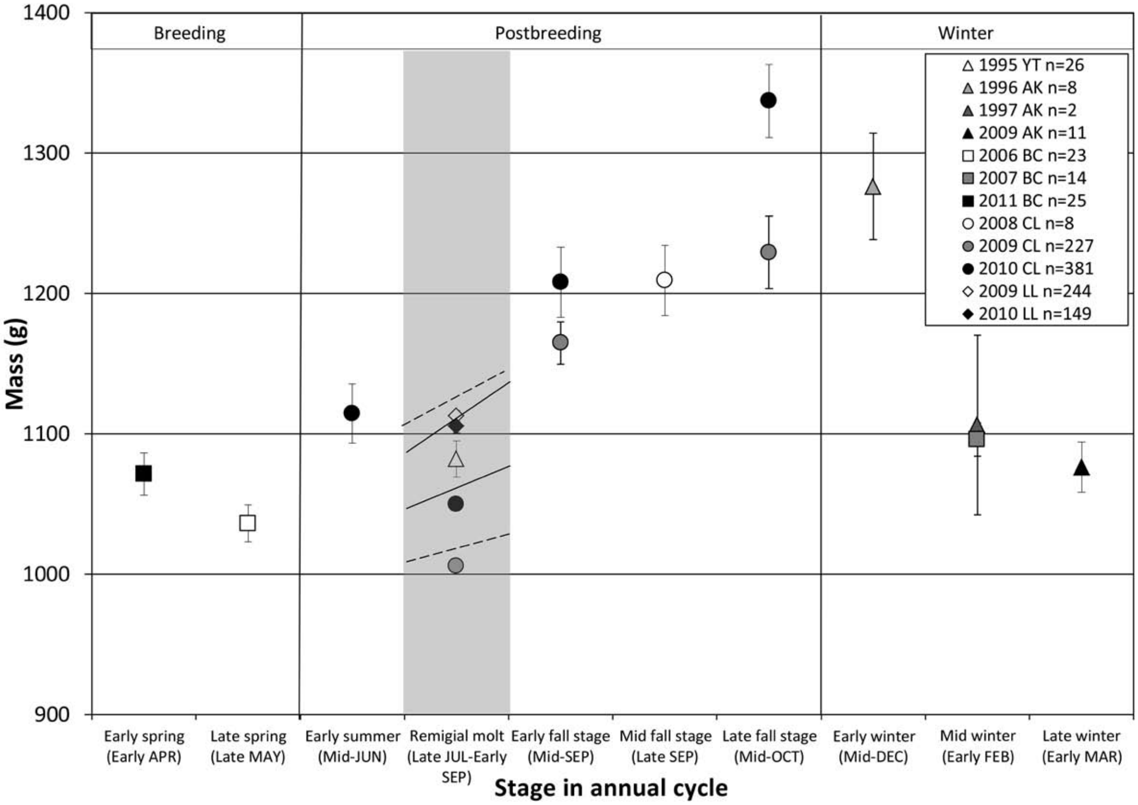

FIG. 3. Average body mass (± SE) of after-second-year male Barrow's Goldeneyes captured in Alaska (AK), Yukon Territory (YT), British Columbia (BC), and Alberta (CL and LL), 1995–2011, at various stages of the annual cycle. Mass for Yukon Territory birds was taken from van de Wetering (1997). Trend lines during remigial molt represent body-mass gain of birds from Cardinal Lake (CL, solid lines) and Leddy Lake (LL, hashed lines), Alberta. Sample size for 2009 CL birds is divided into molt ($n = 205$), early fall ($n = 13$), and late fall ($n = 9$). Sample size for 2010 CL birds is divided into early summer ($n = 15$), molt ($n = 347$), early fall ($n = 9$), and late fall ($n = 10$).

birds from the United Kingdom lost mass and decreased foraging effort in another study by Portugal et al. (2007). In addition, wintering American Black Ducks (*A. rubripes*) exhibited different protein-mass dynamics in Maine and Virginia (Morton et al. 1990); spring-staging male Lesser Scaup maintained constant lipid reserves in the lower Great Lakes, but increased lipid reserves at more northern staging sites (Badzinski and Petrie 2006); and wintering Blue-winged Teal and Northern Pintails weighed less in Yucatan, Mexico, than at more northern wintering sites in the southern United States (Thompson and Baldassarre 1990). Intraspecific variation in mass and foraging strategies thus appear to be common among waterfowl taxa throughout their annual cycle.

*Cohort variation in mass.*—Accounting for size differences, male goldeneyes showed a large difference in mass between age classes (~83 g), with SY males being ~12% lighter than ASY males. Age-class difference in mass is common in many species and presumably results from subadult birds having yet to achieve their full adult mass (Morton et al. 1990, Rhodes et al. 2006). This may also help to explain why SY males gained slightly more mass per day during molt than ASY males; they were still growing.

Female goldeneyes exhibited a small, biologically insignificant difference in mass between age classes (~3 g [<1%]). The similarity between SY and ASY female mass might be attributed to differences

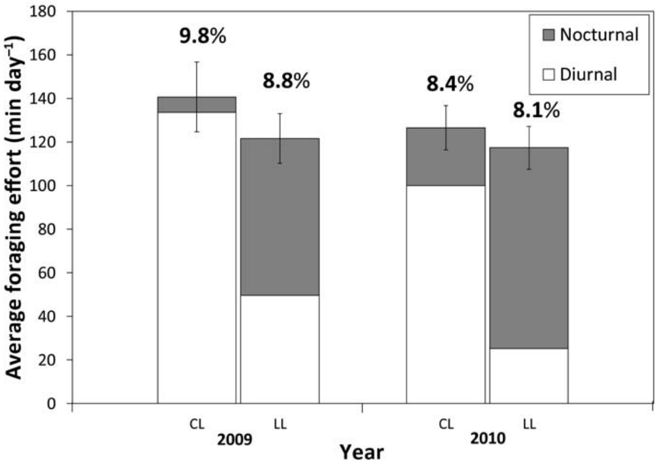

FIG. 4. Average foraging effort (± SE) of radiomarked after-second-year male Barrow's Goldeneyes molting on Cardinal Lake (CL) and Leddy Lake (LL), Alberta, 2009 and 2010. Averages were estimated by multiplying nocturnal and diurnal hourly foraging rates by the number of nocturnal and diurnal hours in a day. Percentages above each bar indicate the proportion of total time spent foraging per day.

in breeding status. Although SY birds might be expected to be lighter than ASY birds because they are not fully grown, subadult birds have not expended energy breeding (Eadie et al. 2000), a costly stage in the annual cycle during which adult females often rely on somatic stores 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 (i.e., during molt) because of the high energetic costs and subsequent reductions in mass experienced by adult females during the breeding period. This hypothesis could be tested by comparing average body masses of female age cohorts prior to the breeding season.

Birds that started molt later were heavier than birds that started molt earlier in all age and sex cohorts. The postbreeding period, in general, is a period of mass gain for goldeneyes (Fig. 3); thus, it is likely that these trends are related to the increase in mass with molt stage, in that they represent separate portions of the same daily accumulation of mass over the postbreeding period.

Female goldeneyes at our study sites began remigial molt 1–2 weeks after males, presumably because of differences in brood-rearing obligations (Hogan 2012). Trapping became inefficient when male cohorts regained flight capabilities, because these cohorts comprised >85% of molting individuals on the lakes (Hogan et al. 2011). As such, trapping efforts stopped when most females were 2–3 weeks into remigial molt, and the patterns in female mass dynamics described above are based on individuals that, on average, were in the first half of remigial molt. Similarities in patterns of male and female body mass in the present study suggest that observed female patterns likely continued during the latter half of remigial molt, as was observed for males.

*Site and year variation in mass.*—Male and female goldeneyes were heavier, on average, in 2010 than in 2009; however, this annual variation may not be biologically significant (38 g [4%] and 17 g [2%] for males and females, respectively). Male and female goldeneyes also were heavier on Leddy Lake than on Cardinal Lake (35 g [4%] and 35 g [5%], respectively). It is unlikely that the differences observed result from differences in energy expended during molt migration, because satellite telemetry (S. Boyd unpubl. data) suggests that birds are coming from similar breeding areas, and Leddy and Cardinal lakes are close to one another geographically (~25 km). Perhaps, as a smaller lake, Leddy provides a less reliable food source and birds molting there accumulate greater somatic nutrient stores prior to molt than birds on Cardinal Lake as insurance against stochasticity or deteriorating food conditions, as has been suggested for some wintering waterfowl (Peterson and Ellarson 1979, Reinecke et al. 1982, Robb et al. 2001). This notion is supported by birds radio-marked on Leddy Lake during remigial molt that moved to Cardinal Lake soon after they regained flight (Hogan 2012); however, an in-depth study of invertebrate communities at Cardinal and Leddy lakes is needed to further evaluate this hypothesis. Alternatively, Leddy Lake may provide a more abundant and/or nutritious food supply than Cardinal Lake, which allows birds to gain more mass prior to and during molt (birds arrive at molt sites ≤1.5 months before the start of molt; Hogan 2012). Future work might focus on investigating average masses of pre-molting individuals on each lake, as well as the invertebrate community of each lake, which may help shed light on the proximate causes of the differences in remigial-molt mass dynamics between birds using Cardinal and Leddy lakes.

*Site variation in foraging strategy.*—Foraging effort was similar between lakes and years (<2% difference), but Cardinal Lake birds foraged primarily diurnally, whereas Leddy Lake birds foraged primarily at night. Possible explanations for this difference in foraging behavior are that (1) the perceived risk from diurnal predators was higher on Leddy, causing birds to be more vigilant on Leddy Lake during the day and leaving less time for foraging (Evans and Day 2001); and/or (2) daily activity patterns of prey organisms differed between lakes, with Leddy Lake prey being more available at night. Survival of molting birds on both Cardinal and Leddy lakes was high (0.95; Hogan et al. 2013) and avian predators were rarely observed on either lake during remigial molt (D. Hogan pers. obs.). However, the small size and almost continuous forest cover of Leddy Lake compared with Cardinal Lake (4 $km^2$ vs. 50 $km^2$) may have caused birds to perceive a higher risk of predation on Leddy as a result of being closer to shore (Merkel and Mosbech 2008). Biweekly benthic invertebrate sampling of the lakes during the molting period (early August to early September, D-net sweep) suggested that invertebrate communities were similar, consisting of mainly amphipods, chironomids, and corixids (D. Hogan unpubl. data). However, although dense aggregations of gammarid amphipods were observed along the shoreline of Leddy Lake during one nocturnal sampling event, the same phenomenon was never observed on Cardinal Lake. This suggests that amphipods may be more active at night on Leddy Lake than on Cardinal Lake, which may have instigated the nocturnal foraging behavior of birds on Leddy Lake. More intensive invertebrate sampling of the lakes would be required to confirm this observation.

*Remigial-molt mass in the annual cycle of Barrow's Goldeneye.*—Average masses of ASY male goldeneyes at the beginning of remigial molt were low in relation to masses of ASY males at other stages in the annual cycle (Fig. 3). Birds gained body mass during remigial molt with relatively low foraging effort, and continued to do so during the fall staging period, which suggests that low mass at the start of remigial molt was adaptive. Increasing or constant mass during remigial molt also has been found for some other waterfowl species (Hohman et al. 1988, 1992; Thompson and Drobney 1996; Fox et al. 2008; Dickson 2011). Postbreeding mass gain may not only ensure adequate energy for fall migration (Salomonsen 1968) but is possibly relied upon to sustain individuals throughout the wintering period when resources are limited (Peterson and Ellarson 1979, Reinecke et al. 1982, Robb et al. 2001). This suggests that postbreeding habitat quality could have cross-seasonal effects on goldeneyes. Cardinal and Leddy lakes are two of only five sites in North America known to sustain large aggregations of postbreeding Barrow's Goldeneyes and are the only sites at which postbreeding increases in mass are known to occur; thus, conservation efforts should strive to protect these valuable postbreeding habitats.

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