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DURATION AND PHENOLOGY OF REMIGIAL MOLT OF BARROW'S GOLDENEYE

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Abstract. We quantified the duration and phenology of remigial molt of Barrow's Goldeneyes (*Bucephala islandica*) in northwestern Alberta, Canada. We estimated that the remiges' average (± SE) growth rate was 3.94 ± 0.13 mm day^{-1}, slightly slower than that of most waterfowl. Barrow's Goldeneyes regained flight with the ninth primary 77% grown, a percentage similar to or greater than that of most waterfowl. By several metrics, remigial molt of Barrow's Goldeneye was longer than that of most waterfowl. We estimated that it took 6.5 ± 1.2 days for a new ninth primary to become visible once the old primary was dropped (pre-emergence interval). The periods in which males and females were flightless were 30 ± 0.4 and 28 ± 0.5 days, respectively, and 36.5 ± 0.5 and 34.5 ± 0.8 days, respectively, including the pre-emergence interval. Complete maturation of primaries after emergence took 39 ± 0.5 and 36 ± 0.7 days for males and females, respectively, and 45.5 ± 0.6 and 42.5 ± 0.9 days, respectively, including the pre-emergence interval. These results suggest a lack of strong selective pressure to reduce the duration of remigial molt in this species. Initiated over a range of nearly 2 months, remigial molt was asynchronous both between and within age and sex cohorts, suggesting a lack of strong temporal optima for remigial molt of Barrow's Goldeneyes at our study sites.

Key words: Alberta, Barrow's Goldeneye, Bucephala islandica, *molt phenology, remigial molt, remigial growth rate.*

Duración y Fenología de la Muda de las Remeras en *Bucephala islandica*

Resumen. Cuantificamos la duración y la fenología de la muda de las remeras en *Bucephala islandica* en el noroeste de Alberta, Canadá. Estimamos que la tasa promedio (± EE) de crecimiento de las remeras fue 3.94 ± 0.13 mm día^{-1}, ligeramente más baja que la de la mayoría de las aves acuáticas. *B. islandica* recuperó la capacidad de vuelo con el crecimiento del 77% de la novena primaria, un porcentaje similar a o mayor que el de la mayoría de las aves acuáticas. Considerando varias medidas, la muda de las remeras en *B. islandica* fue más larga que la de la mayoría de las aves acuáticas. Estimamos que llevó 6.5 ± 1.2 días para que una novena primaria se vuelva visible luego de la caída de la vieja primaria (intervalo de pre-emergencia). Los períodos en los cuales los machos y las hembras no pudieron volar fueron de 30 ± 0.4 y 28 ± 0.5 días, respectivamente; 36.5 ± 0.5 y 34.5 ± 0.8, respectivamente, incluyendo el intervalo de pre-emergencia. La maduración completa de las primarias luego de la emergencia llevó 39 ± 0.5 días y 36 ± 0.7 días para los machos y las hembras, respectivamente; 45.5 ± 0.6 y 42.5 ± 0.9 días, respectivamente, incluyendo el intervalo de pre-emergencia. Estos resultados sugieren una falta de presión selectiva fuerte para reducir la duración de la muda de las remeras en esta especie. Iniciada en un rango de cerca de 2 meses, la muda de las remeras fue asincrónica tanto entre como dentro de las cohortes de edad y sexo, sugiriendo la falta de un óptimo temporal fuerte para la muda de las remeras en *B. islandica* en nuestros sitios de estudio.

INTRODUCTION

Molt is essential to the maintenance and function of the flight feathers. The duration and timing of remigial molt varies by species, lasting from a few weeks to multiple years (Howell 2010). Waterfowl (family Anatidae) are one of 11 bird families that undergo simultaneous remigial molt, shedding and replacing all flight feathers at once (Hohman et al. 1992). As a result, each year, waterfowl are rendered flightless during remigial molt. Among waterfowl, the duration of remigial molt varies widely, from 20 to 40 days (Hohman et al. 1992), suggesting that it is a trait that could be responsive to costs and benefits. For example, feathers can be heavier and more durable when grown more slowly (Dawson et al. 2000), but this

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could leave the bird flightless longer. However, some evidence suggests that some molting waterfowl adaptively lose mass to reduce wing-loading, allowing attainment of flight earlier in molt, in response to the cost of flightlessness (e.g., Brown and Saunders 1998).

For waterfowl, the timing of remigial molt often varies by age, sex, and reproductive status. Immature and nonbreeding individuals tend to initiate remigial molt earlier than breeding individuals (Salomonsen 1968, Gates et al. 1993). Furthermore, breeding females tend to initiate remigial molt later than males of the same species as a result of rearing a brood. For example, Savard et al. (2007) found that female Surf Scoters (*Melanitta perspicillata*) whose nests failed migrated to molt sites 6 weeks later, on average, than male scoters but still arrived earlier than females that bred successfully.

Timing of remigial molt also may be influenced by temporal optima, i.e., timing of the annual cycle to maximize fitness benefits relative to costs. In many waterfowl, other stages of the annual cycle are temporally optimized; for example, migration of the Pink-footed Goose (*Anser brachyrhynchus*) is timed to track availability of food resources along migration pathways (Duriez et al. 2009); time of initiation of Wood Duck (*Aix sponsa*) nests is influenced by the cost of incubation at cooler temperatures early in the breeding season (Hepp and Kennamer 2011); initiation of Common Eider (*Somateria mollissima*) nests is timed to ensure ice-free foraging for ducklings (Love et al. 2010). Temporal optima can lead to a high degree of synchrony in the timing of individuals' life cycles. Synchronous remigial molt of waterfowl at northern latitudes suggests the possibility of an temporal optimum associated with this stage in the annual cycle as well (Owen and Ogilvie 1979, Taylor 1995, Craik et al. 2009). For example, Craik et al. (2009) found that ~75% of adult male Red-breasted Mergansers (*Mergus serrator*) in the upper Gulf of St. Lawrence initiated remigial molt within the same two-week period. The benefits of this synchrony may have been related to maximizing foraging efficiency and evasion of predators during remigial molt (Craik et al. 2009).

In many waterfowl, particularly those of the sea duck tribe (Mergini), the ecology of remigial molt remains poorly studied. Barrow's Goldeneye (*Bucephala islandica*), a mid-sized sea duck found mainly west of the Rocky Mountains from Alaska to Oregon, is no exception. Although the number of Barrow's Goldeneyes in western North America is estimated between 125 000 and 200 000 (Bellrose 1980, Eadie et al. 2000), only five locations have been identified as major sites for molt, and these account for <20% of that population during the postbreeding period (King 1963, van de Wetering 1997, Hogan et al. 2011). The only previous study of the ecology of Barrow's Goldeneye molt took place at Old Crow Flats, Yukon Territory, in the late 1990s (van de Wetering and Cooke 2000). All reported recoveries of birds banded at Old Crow Flats were from Alaska, suggesting that most of these birds molt at the northern end of the species' range (van de Wetering 1997). Recently, aerial surveys and satellite telemetry revealed two locations of molt in northwestern Alberta for Barrow's Goldeneyes breeding farther south in western Canada (Hogan et al. 2011), though the ecology of these birds' molt has never been studied. We quantified the duration and timing of remigial molt of Barrow's Goldeneyes at Cardinal and Leddy Lakes, Alberta, to better understand the ecology of remigial molt and to evaluate temporal constraints or optima at this stage of the species' annual cycle. We predicted that the duration of the goldeneye's remigial molt relative to that of other waterfowl should reflect the specific costs and benefits of rates of feather growth. We also predicted that the birds' remigial molt should be synchronous if a strong temporal optimum influenced initiation of molt. Also, we expected subadults to initiate remigial molt before adults and males to initiate remigial molt earlier than immature and adult females, which generally stay at breeding sites longer to prospect for future breeding sites or care for broods (Eadie and Gauthier 1985, Eadie et al. 2000).

METHODS

STUDY AREA

Cardinal Lake (56° 14′ N, 117° 44′ W) is a large lake (~50 km^2) located in the boreal transition zone of northwestern Alberta. The lake rarely exceeds a depth of 2 m, has a bottom primarily of sand, mud, and gravel, has abundant submerged vegetation, and is hypereutrophic. Leddy Lake (56° 23′N, 117° 27′ W) is small (~4 km^2), slightly eutrophic, and located ~25 km northeast of Cardinal Lake. It is shallow (<2 m), has a primarily muddy bottom, and has a mat of very dense submerged vegetation in its middle. Combined, these lakes support 5000–7000 molting Barrow's Goldeneyes annually, the majority of which are adult males (Hogan et al. 2011).

CAPTURES AND COLLECTIONS

We captured Barrow's Goldeneyes by drive trapping (van de Wetering 1997) on Cardinal and Leddy lakes in 2009 and 2010. Captures started as soon as we observed flightless birds in late July and ended when nearly all birds had regained flight in early September. Upon capture, each bird was fitted with a uniquely numbered U.S. Fish and Wildlife Service stainless steel band on the tarsus. We recorded morphological measurements, including the length of the ninth primary measured to the nearest 1 mm from the point where it emerged from the skin to its tip. We used the ninth primary as an indicator of molt stage because it is the longest remex in waterfowl and thus less subject to measurement error. Previous studies of molting waterfowl have also used the ninth primary to indicate molt stage, recognizing that growth of all primaries and secondaries is highly synchronous. We sexed the birds by the cloaca and plumage (Hochbaum 1942, Carney 1992) and aged them by the depth of the bursa of Fabricius (Mather and Esler 1999, Iverson et al. 2003). We categorized birds with a bursa ≥10 mm deep as second year (SY; hatched just over one year earlier) and those with a bursa <10 mm deep as after second year (ASY; more than 2 years since hatching). In addition, ASY male Barrow's Goldeneyes were collected on Cardinal Lake by shooting in the falls of 2008, 2009, and 2010 and in late spring of 2010 as part of a study of the dynamics of postbreeding birds' mass. Collected birds were also measured as described above.

STATISTICAL ANALYSIS

Remigial growth rate. We calculated the remigial growth rate (RGR) for individuals captured twice in the same year by dividing the difference between the length of the ninth primary at first and second captures by the number of days between captures. Calculation of average RGR excluded individuals that were first captured with no visible new ninth primary because these birds were either functionally flightless but had not yet shed their old ninth primaries or their stage in the pre-emergence interval was unknown and their inclusion may have biased the average RGR estimates low. We used Akaike's information criterion corrected for small sample size (AIC_c) to contrast two models to determine a priori if RGR differed by sex. A model with sexes grouped was slightly better supported (AIC_c weight = 0.51) than one with estimates generated separately for each sex (AIC_c weight= 0.49), and the effect of sex was weak (85% confidence intervals overlapped zero), indicating that the sexes' RGR was similar, which also has been observed in other sea ducks (Dickson et al. 2012). Therefore, we estimated a single RGR for all individuals, regardless of sex.

Emergence date. We refer to "emergence date" as the date that a new remex becomes visible as it emerges from the skin. This date has traditionally defined the start of remigial molt, and the total length of molt has been estimated as the time it takes a newly erupted primary to reach maturity (Sjöberg 1988, van de Wetering and Cooke 2000, Iverson and Esler 2007). However, very few studies have considered the time it takes for a new primary to erupt from the skin once an old primary has been dropped (Owen and Ogilvie 1979, Panek and Majewski 1990, Miller et al. 1992, Dickson et al. 2012), which we refer to as the "pre-emergence interval." In this study we define the start of remigial molt and the period of flightlessness by the time at which an old primary is dropped. Thus the entire period of remigial molt encompasses both the pre-emergence interval and the time it takes a newly erupted primary to reach maturity.

We calculated the emergence date for all captured individuals by dividing the length of the ninth primary at first capture by the average RGR for all individuals and subtracting this number of days from the date of first capture. Birds first captured with a ninth primary length of zero were assigned an emergence date the same as their capture date.

We used multiple linear regression models to examine variation in emergence date as a function of explanatory parameters including cohort (a four-level categorization based on 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), comprising various combinations of main effects and interaction terms and representing a set of a priori, biologically plausible hypotheses. 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 we assumed this variable to have an effect from the phenology of Barrow's Goldeneye breeding (i.e., males and females spend different amounts of time in the breeding stage of the annual cycle) and the phenology of molt in other waterfowl. However, we categorized cohorts in two ways to determine if differences among them were driven primarily by the difference between adult females and all other cohorts or if the timing of each cohort was unique. One cohort categorization included all four cohorts as different categories, whereas another lumped males of all ages with SY females and contrasted those with a category for adult females (Table 1). We used Akaike's information criterion, corrected for small sample size (AIC_c; Burnham and Anderson 2002), to indicate the most parsimonious models and the difference between each model and the most

TABLE 1. Selection of general linear models explaining variation in dates of emergence of the ninth primary among Barrow's Goldeneyes molting on Cardinal and Leddy Lakes, Alberta, 2009–2010. Cohort is a four-level combination of age and sex. FASY (female, after-second-year) is a two-level variable grouping adult females separately from all other cohorts.

Model	*K*	ΔAIC_c	w_i
Cohort + lake + year	7	0.00[a]	0.72
Cohort + lake + year + lake × year	8	1.99	0.27
Cohort + lake + year + cohort × lake × year	17	8.61	0.01
Cohort + year	6	21.50	0.00
Cohort + year + cohort × year	9	26.25	0.00
Cohort + lake	6	86.68	0.00
Cohort + lake + cohort × lake	9	86.92	0.00
FASY + lake + year	5	122.79	0.00
FASY + lake + year + lake × year	6	124.75	0.00
FASY + lake + year + FASY × lake × year	9	128.59	0.00
Cohort	5	137.94	0.00
FASY + year	4	143.73	0.00
FASY + year + FASY × year	5	145.09	0.00
FASY + lake	4	199.70	0.00
FASY + lake + FASY × lake	5	200.86	0.00
FASY	3	248.89	0.00
Null	2	425.77	0.00

[a] AIC = 7282.28

parsimonious model ($\Delta\mathrm{AIC}_c$) and AIC_c weights (w_i) to evaluate the relative support for each model. To evaluate the level of support for the variable within the candidate model set, we calculated likelihood values (Σw_i) for each variable, as well as weighted parameter estimates ± unconditional 95% CIs (Burnham and Anderson 2002). For these analyses we used R 2.12.1 (R Core Development Team 2010).

Pre-emergence interval. Lacking a strong precedent for calculating the pre-emergence interval, we estimated it by three methods, then averaged their results. As the variance surrounding the average of each of the three methods was independent, we used propagation of variance to calculate the error surrounding the average across methods.

Method 1: We marked the shaft of the right ninth primary of birds with fully grown remiges collected from Cardinal Lake where it emerged from the skin. We then plucked the feather and measured the distance between the proximal umbilicus to the mark. Using the estimated average RGR, we calculated the number of days required to grow this amount of feather. Provided that RGR was constant over the entire molt, the average of all individuals represented an average value of the pre-emergence interval.

Method 2: With birds first captured with ninth primary equal to zero, then captured later in the same year, we estimated the pre-emergence interval by the methods of Panek and Majewski (1990). We calculated the date of emergence of each bird's ninth primary as above from the second capture date. We doubled the number of days between the calculated emergence date and the first capture date to estimate the length of the pre-emergence interval, assuming that, on average, birds were first captured in the middle of the pre-emergence period. Then we averaged the values of all individuals.

Method 3: We assumed the ratio of birds captured with ninth primary equal to zero to total birds captured to be equal to the ratio of days that birds have a ninth primary length of zero to days that birds are flightless and thus available for capture. This method makes the following assumptions: (1) capture effort was consistent over time, (2) captures took place over the entire period of flightlessness, and (3) all flightless individuals were equally trappable, which were met in our case. Given these assumptions, we calculated the length of the pre-emergence period in days by solving for x in the following equation:

$$\frac{\text{No. birds with zero ninth primary}}{\text{Total no. birds captured}} = \frac{x}{\text{Flightless period} + x}$$

Duration of flightlessness and molt. 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. Therefore, we used the 97.5th percentile of the length of the ninth primary of birds captured during remigial molt as a conservative estimate of the minimum length of the ninth primary required for the bird to regain flight. We calculated the duration of flightlessness as the number of days required for the ninth primary to grow from zero to the minimum length required for flight, plus the number of days in the pre-emergence interval. The total duration of the molt, including the period in which the ninth primary was not fully grown but the bird was flight capable, was calculated similarly with the estimated length of the mature ninth primary in place of the minimum length required for flight. We calculated the average length of a mature ninth primary for male and female Barrow's Goldeneyes from birds captured from February to May in Alaska and British Columbia from 2005 to 2011, as well as birds with fully grown primaries collected at Cardinal Lake 2008–2010. Average values reported under Results are means ± SE.

RESULTS

REMIGIAL GROWTH RATES AND PRE-EMERGENCE INTERVAL

The average RGR of males and females was similar, estimated at 3.94 ± 0.13 mm day^{-1} over all individuals ($n = 38$). The average length of the pre-emergence interval varied somewhat by method of calculation (method 1: 6.0 ± 0.6 days, method 2: 4.5 ± 0.9 days, method 3: 9.1 ± 3.0 days) but averaged over all three methods was 6.5 ± 1.2 days, which corresponds to that estimated for other sea ducks (Dickson et al. 2012).

DURATION OF FLIGHTLESSNESS AND MOLT

Average lengths of mature ninth primaries of nonmolting Barrow's Goldeneyes caught in British Columbia, Alaska, and Alberta were 155 ± 0 mm ($n = 247$) for males and 141 ± 1 mm ($n = 65$) for females. On the basis of the 97.5th percentile of lengths of ninth primaries of males captured during remigial molt, 77% (120 mm) of the total length was required for males to regain flight. We did not catch enough females late in remigial molt to have confidence in estimates of primary length required for females to fly, so we assumed that the value was similar to that for males, as in other sea ducks (Dickson et al. 2012). The number of days necessary for males and females to regrow enough of the ninth primary to regain flight was 30 ± 0.4 and 28 ± 0.5 days from emergence, respectively. The total duration of flightlessness, including the pre-emergence interval, was 36.5 ± 0.5 and 34.5 ± 0.8 days for males and females, respectively.

On the basis of the average RGR, the number of days required to grow the mature ninth primary from the time of emergence was 39 ± 0.5 days for males and 36 ± 0.7 days for females. The overall duration of remigial molt, including the pre-emergence interval, was 45.5 ± 0.6 and 42.5 ± 0.9 days for males and females, respectively.

EMERGENCE DATE

The average date of emergence of the ninth primary differed by age and sex cohort (Fig.1). The model containing cohort (a four-level combination of age and sex), lake, and year as main effects received most support for explaining variation in emergence dates (AIC$_c$ weight = 0.72, $r^2 = 0.31$, Table 1). The model containing cohort, lake, and year as main effects and an interaction of lake and year was the next best supported model (AIC$_c$ weight = 0.27, $r^2 = 0.31$, Table 1). All other models received far less support from the data (AIC$_c$ weight ≤0.01, Table 1).

Parameter likelihoods also supported cohort, lake, and year as the variables best explaining variation in emergence dates (likelihood values = 1). Model-averaged parameter estimates for cohort indicate that the ninth primaries of ASY females emerged an average of 5.1 ± 1.2 days later than those of SY females, 12.3 ± 0.8 days later than those of ASY males, and 16.8 ± 1.0 days later than those of SY males. Emergence dates for each cohort were 1.8 ± 0.5 days earlier on Cardinal Lake than on Leddy Lake and 3.3 ± 0.4 days earlier in 2010 than 2009. The lake and 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% CIs for this parameter estimate overlapped zero, indicating that the effect of this parameter was weak.

Emergence dates also were highly variable within each age and sex cohort (Fig. 1). The ranges within each cohort were 31 days for ASY females, 29 days for SY females, 46 days for ASY males, and 34 days for SY males. Given that it takes 39 days for a new ninth primary to reach maturity, Barrow's Goldeneyes were molting at our study sites for 85 days (range within a cohort: 65–85 days). This asynchrony within each cohort suggests a lack of temporal optima at this stage in the annual cycle.

DISCUSSION

Relative to other waterfowl, Barrow's Goldeneyes grew feathers slowly and were flightless longer. We also found that the initiation of remigial molt was asynchronous within each age and sex cohort, although it varied by cohort as described for other waterfowl. The long duration of remigial molt and the lack of synchrony among individuals (initiation of remigial molt extended over nearly 2 months and molting individuals were at our study sites for more than 3 months) suggests that there were no strong selective or proximate pressures to accomplish remigial molt either quickly or during a specific period.

REMIGIAL GROWTH RATE

The RGR estimated for Barrow's Goldeneyes at our study sites (3.94 ± 0.13 mm day^{-1}) was slower than that estimated for many ducks: Mallard (*Anas platyrhynchos*), 5.5 ± 0.06 mm day^{-1} (Panek and Majewski 1990); Northern Pintail (*A. acuta*), 4.2 ± 0.2 mm day^{-1} (Miller et al. 1992); Green-winged Teal (*A. crecca*), 4.8 mm day^{-1} ± 0.14 (Sjöberg 1988).

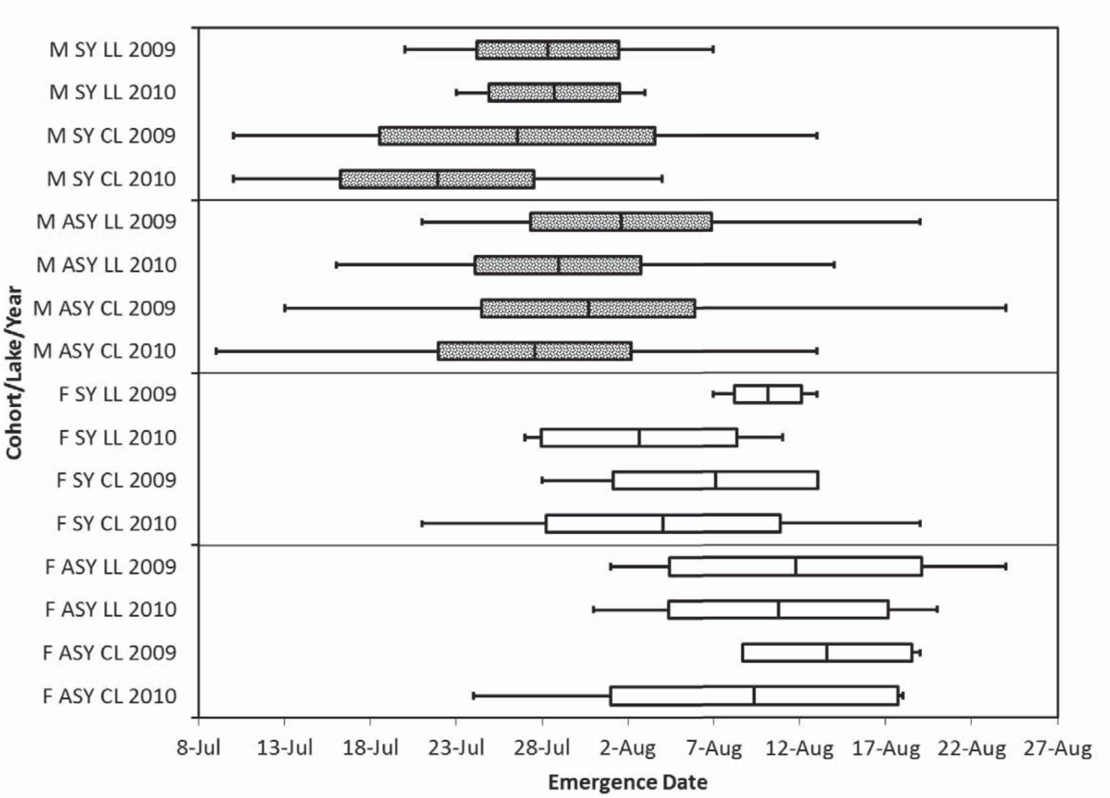

FIGURE 1. Dates of emergence of ninth primaries of Barrow's Goldeneye by age and sex cohort on Cardinal and Leddy Lakes, Alberta, 2009–2010. Bars show average emergence date ± SD. Whiskers represent earliest and latest dates for each cohort. Filled bars represent male cohorts, empty bars represent female cohorts. Abbreviations along *y* axis: 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).

But it was similar to the 4.04 ± 0.05 mm day^{-1} van de Wetering and Cooke (2000) reported for Barrow's Goldeneyes molting at higher latitudes, as well as that of other sea ducks, such as the Harlequin Duck (*Histronicus histronicus*), 3.5 ± 0.06 mm day^{-1} (Iverson and Esler 2007); Surf Scoter, 3.93 ± 0.2 mm day^{-1} and White-winged Scoter (*Melanitta fusca*), 4.3 ± 0.2 mm day^{-1} (Dickson et al. 2012). The rate at which feathers are grown can have a significant effect on their quality, with feathers grown faster being lighter and less durable than feathers grown more slowly (Dawson 2000, de la Hera et al. 2009). Barrow's Goldeneyes, and other sea ducks, may grow their primaries at a rate slightly slower than that of similarly sized dabbling ducks to ensure growth of high-quality feathers. High-quality feathers may be more important for sea ducks because of their high wing loading, which may increase wear on feathers. Alternatively, the relatively slow growth of the primaries of Barrow's Goldeneye could reduce daily nutritional demands by spreading the cost of feather growth over a longer period. This might be expected if remigial molt was nutritionally challenging for Barrow's Goldeneye. At our study sites, however, this is not the case, as the birds gained mass and foraged little during remigial molt (Hogan et al. 2013a).

DURATION OF FLIGHTLESSNESS

The pre-emergence interval excluded, male and female Barrow's Goldeneyes were flightless for an estimated 30 ± 0.4 and 28 ± 0.5 days, respectively, a period long for a duck: Mallard, 20–27 days (Panek and Majewski 1990); Northern Pintail, 25 days (Miller et al. 1992); Green-winged Teal, 19 days (Sjöberg 1988); 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, Yukon Territory, were also flightless for a relatively long period, 31 days (van de Wetering and Cooke 2000). Although the longer flightlessness of Barrow's Goldeneye could be interpreted to reflect nutritional constraints on feather growth, as described above, it could also be an artifact of wing loading in this species being greater than in many other ducks. If this were the case, Barrow's Goldeneyes should require a greater percentage of the ninth primary to be grown before they regain flight capability. We estimated that Barrow's Goldeneyes achieved flight with 77% of the ninth primary grown, which falls within the upper range for waterfowl reported by Hohman et al. (1992) (55%–85%). The White-winged and Surf Scoters require an even higher percentage (83–99%; Dickson et al. 2012). In any case, at our study sites Barrow's Goldeneyes did not appear to be under pressure to complete remigial molt quickly, despite having food sufficient to do so, indicating that they are probably not under intense risk of predation, which has been hypothesized to shorten the period of flightlessness of some waterfowl (Sjöberg 1988, Panek and Majewski 1990). A lack of intense predation pressure during this period also is supported by the high rate of survival of Barrow's Goldeneyes during remigial molt at these sites (Hogan et al. 2013b).

VARIATION IN EMERGENCE DATE

We found that in Barrow's Goldeneye the date of emergence of the ninth primary differed in each age and sex cohort (Fig. 1). Timing of molt differing by age and sex cohort 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 between the sexes in parental duties. The estimated difference in average emergence date between the cohort of Barrow's Goldeneye molting earliest, SY males, and that molting latest, ASY females, was about 2.5 weeks. Males generally molted earlier than females, and subadults generally molted earlier than adults, as found in other waterfowl. Adult females may molt later than other cohorts because they stay on breeding grounds longer to attend to broods (Eadie et al. 2000). Subadult females may molt later than either subadult 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 each age and sex cohort was high (Fig. 1). Variation was greatest in adult males, with some individuals initiating remigial molt over 46 days earlier than others. This asynchrony suggests that timing of remigial molt of Barrow's Goldeneyes at Cardinal and Leddy Lakes was not strongly influenced by temporal optima.

PRE-EMERGENCE INTERVAL

The average length of the pre-emergence interval estimated by three methods was 6.5 ± 1.2 days, similar to estimates of the pre-emergence interval for the Surf and White-winged Scoters (Dickson et al. 2012). This interval is considerably longer than that assumed or calculated for other waterfowl in the few studies that have considered it (2 days; Owen and Ogilvie 1979, Sjöberg 1988, Panek and Majewski 1990). Thus the pre-emergence interval may vary from species to species. Also, the total duration of flightlessness and remigial molt for many waterfowl may be underestimated by almost a week through failure to account for this stage. Perhaps the most reliable method of calculation of the pre-emergence interval is based on measuring the length of feather shaft that is sheathed in the skin of the wing, as this requires only the single assumption that the rate of feather growth remain constant throughout molt. Future studies of the phenology and duration of molt in other species should incorporate the pre-emergence interval into estimates of the length of remigial molt.

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