



# Do Seaducks Minimise the Flightless Period?: Inter- and Intra-Specific Comparisons of Remigial Moul

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## Abstract

Remigial moult is one of the crucial events in the annual life cycle of waterfowl as it is energetically costly, lasts several weeks, and is a period of high vulnerability due to flightlessness. In waterfowl, remigial moult can be considered as an energy-predation trade-off, meaning that heavier individuals would minimise the flightless period by increasing feather growth rate and energy expenditure. Alternatively, they could reduce body mass at the end of this period, thereby reducing wing-loading to increase flight capability. We studied timing of remigial moult, primary growth rates, flightlessness duration, and the pattern of body mass variation in 5 species of captive seaducks (*Melanitta fusca*, *M. perspicillata*, *Clangula hyemalis*, *Histrionicus histrionicus*, and *Somateria mollissima*) ranging in size from 0.5 to 2.0 kg. Their feather growth rates weakly increased with body mass ( $M^{0.059}$ ) and no correlation was found at the intra-specific level. Consequently, heavier seaduck species and especially heavier individuals had a longer flightless period. Although birds had access to food *ad libitum*, body mass first increased then decreased, the latter coinciding with maximum feather growth rate. Level of body mass when birds regained flight ability was similar to level observed at the beginning of remigial moult, suggesting they were not using a strategic reduction of body mass to reduce the flightlessness duration. We suggest that the moulting strategy of seaducks may be the result of a compromise between using an intense moult strategy (simultaneous moult) and a low feather growth rate without prejudice to feather quality. Despite the controlled captive status of the studied seaducks, all five species as well as both sexes within each species showed timing of moult reflecting that of wild birds, suggesting there is a genetic component acting to shape moult timing within wild birds.

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**Data Availability:** The authors confirm that all data underlying the findings are fully available without restriction. Data for the present study are available from the Dryad Digital Repository under the DOI doi:10.5061/dryad.p2kfo.

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## Introduction

During the annual cycle, numerous factors lead to the wear of feathers: mechanical abrasion induced by flight, reproduction and foraging activities [1], and degradation by ultraviolet light or by parasitic and bacterial infections [2], [3], [4]. As a result of flight feather degradation, flight performance is reduced [5], [6], [7]. Because feathers are somatic dead structures it is crucial for birds to replace periodically worn feathers during a process known as moult, which represents the major event of somatic production in the annual cycle of birds [8], [9].

Anatidae are among relatively few bird families that shed their flight feathers simultaneously once a year, rendering them flightless up to several weeks, with variations between species, age, and sex [10], [11]. Birds exhibiting simultaneous wing feather replacement are mainly aquatic, and function without flight, in contrast to sequential moulters, which replace a few flight feathers at a time. Simultaneous remigial moult in diving ducks is energetically costly [12], [13] comparatively to birds replacing flight feathers sequentially.

The length of the flightless period depends on the number of simultaneously growing feathers (moult intensity), the proportional length feathers when birds regain their flight ability, and the feather growth rate. Former investigations have shown that little variance exists in feather growth rate among birds ranging in size [14], [15]. Feather growth rate could be limited by an architectural constraint at the follicle level [16]. Recently, Rohwer *et al.* [16] demonstrated by allometric relationships that body mass increases much faster than feather growth rate, indicating that heavier species require more time to moult. A major implication of a low feather growth rate is that it could increase flightlessness duration for large simultaneous moulters. Thus, this would expose for example heavier diving birds to a higher predation risk and so it may be advantageous to minimise the flightless period [17], [18], [19], [20]. Here we replicate Rohwer *et al.* [16] work for a specific group of simultaneous moulters among the *Mergini*.

Flightless birds are subjected to different pressures leading to variation in flightlessness duration which is associated at benefits as well as at costs. First, flightless birds may be more vulnerable to predation [21], [22], [23], [24], [25] since the potential to escape

predator attack is reduced. Some recent studies have shown that this stage could not be more unsafe than other stages of the annual cycle of birds [26], [27] nevertheless there are still few studies on this subject. Secondly, birds moulting at high latitude face to environmental constraints as onset of winter and freezing conditions, and so may have lower time to allocate to moult [28], [29]. Furthermore, it was recently shown that birds with less time to moult and with higher feather growth rate had poorer feather quality [30], [31], [32]. Finally, the capacity that birds have to meet nutritional and energy demands through exogenous and/or endogenous resources can also influence moult in terms of feather quality, timing and duration [33], [34], [35], [36]. Some authors have reported reduction of body mass during the flightless period of Anseriformes and have suggested that it was an adaptive strategy to reduce the duration of the flightless period [18], [19], [37]. Other authors have not reported any body weight loss during remigial moult [10], [38], [39], which contradicts that hypothesis [20], [37], [40], [41]. Therefore, we also tested the prediction that seaducks, especially heavier species, use strategic reduction of body mass to reduce the flightless period.

Using measurements of feather growth and body mass of 5 species of captive seaducks, the objectives of this study were to: 1) model and compare flight feather (9<sup>th</sup> primary) growth rate between species and sexes, 2) compare the estimated timing and duration of flightlessness between species and between males and females, 3) test the hypothesis stipulating that heavier seaducks should have faster growth rate to minimise their flightless period, and 4) test the prediction that body mass reduction during remigial moult is associated with the regain of flight ability.

## Materials and Methods

### Ethics statement

All bird manipulations were approved by the Animal Care and Use Committee (ACUC, SOP No 007), for seaducks kept at the Patuxent Wildlife Research Center (Patuxent), and by the animal care committee of the Université du Québec à Rimouski (CPA-44-11-96), for Common Eiders kept at Rimouski. Eider eggs were collected under permit from Environment Canada - Canadian Wildlife Service (Permit Number: SC-24).

### Care of captive seaducks

All individuals of 4 species, 16 White-winged Scoters (*Melanitta fusca*, 9 males and 7 females, WWSC), 8 Surf Scoters (*M. perspicillata*, 5 males and 3 females, SUSC), 9 Long-tailed Ducks, (*Clangula hyemalis*, 3 males and 6 females, LTDU) and 19 Harlequin Ducks (*Histrionicus histrionicus*, 13 males and 6 females, HADU) were kept in captivity in monospecific groups. Eggs were collected with appropriate permits from the wild in Canada respectively from Redberry Lake (Saskatchewan), Lac Malbaie (Quebec), and Churchill (Manitoba), whereas HADU were obtained from a private propagator (Mr. A. Shouten) and were collected from the Olympic Peninsula (Washington). All eggs were hatched at the Patuxent Wildlife Research Center, Laurel, MD in USA, ducklings raised the same way, and were well acclimated to captivity. Birds were housed outside at Patuxent, and each pen, 4.3×8.6 m, contained a pool of fresh water with a diameter of 3.7 m and average depth of 0.5 m. Nine Common Eiders (*Somateria mollissima dresseri*, 4 males and 5 females COEI) were reared from eggs collected at Pointe-Métis, Quebec, with appropriate permits, in 2010. They were housed at Rimouski, Quebec in an indoor enclosure, 6.7×3.7 m with natural photoperiod and containing a pool, 6.0×1.7 m with continuously flowing fresh water of 0.4 m deep. Under these conditions eiders

maintained their seasonal cycles of moult in synchrony with those of free-living individuals (AV, pers. obs.). All 5 species of seaducks were fed with Mazuri Sea duck Diet (#5681; 21.5% protein) *ad libitum* on a daily basis.

### Measurements from seaducks

All 4 species of captive seaducks kept at Patuxent were adults from 3 to 6 years old during this study. At a weekly interval from 8<sup>th</sup> July to 8<sup>th</sup> October 2008, all birds were caught with a landing net and held in a cat carrying case until being measured. The 9<sup>th</sup> primary length (P9) was measured with a vernier caliper to the nearest millimetre, from the rim of the follicle to the distal tip of the feather. At 2-week intervals, birds were weighed ( $\pm 1$  g) with a digital scale. Measurements were made in a similar way on 2-year old Common Eiders between 27 July and 27 October 2012. Handling times were approximately 2–4 min per bird.

### Modelling feather growth

We tested 2 models commonly used for modelling biological growth: the logistic and Gompertz models. For our analyses, we retained the Gompertz, because it had the lower AIC<sub>C</sub> score (Akaike's Information Criterion, corrected for small sample size [42]) and it was 5.76 times more support than the logistic model. For each bird of each species we estimated  $A$ ,  $\mu$  and  $\lambda$  as defined by the following function:

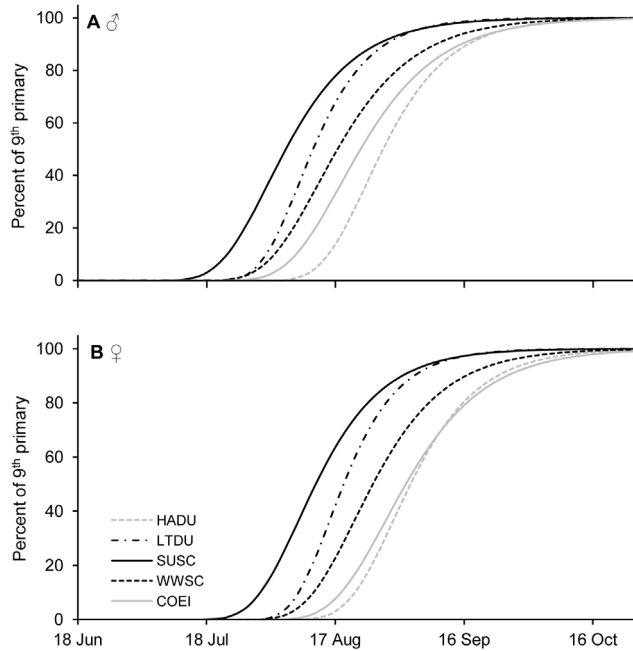
$$y(t) = A \cdot \exp \left[ - \exp \left( \frac{\mu \cdot \exp(1)}{A} (\lambda - t) + 1 \right) \right]$$

where  $A$  represents the asymptotic value which is an estimate of the maximum length of the feather,  $\mu$  the maximum growth rate of P9, and  $\lambda$  the lag-phase. For each bird, we determined the delta growth rate between 5% and 90% of the final length of 9<sup>th</sup> primary feather by calculated the change in P9 length divided by change in time. From each growth curve, the day of shedding of old P9 was estimated when feather reached artificially 1 mm long with Gompertz model (this value of 1 mm has been determined from shedding dates of old P9 noted in some of our captive individuals). Finally, the time between the day of shedding of old P9 and the day at which seaducks can fly again, estimated around 90% of P9 final length [43], was calculated for each bird to determine the flightlessness duration during moult.

### Modelling moult allometry

For simultaneous moulters, the delta growth rate of the longest flight feather (9<sup>th</sup> primary) and its length, represent the best indicators of moult duration. Thus, to explore the time required to replace flight feathers in seaducks, we used the same scaling method as Rohwer *et al.* [16]. First, at the inter-specific level, we modeled the relationship between the length of the 9<sup>th</sup> primary (mm) and the initial body mass (M in g). We also modeled the relationship between the delta growth rate of the 9<sup>th</sup> primary (mm.day<sup>-1</sup>) and initial body mass. We used the allometric function  $Y = aM^b$ , where “ $a$ ” is a scaling constant and “ $b$ ” the power of the relationship of  $Y$  to mass. Our sample consisted of 5 species, but only 4 genera (*Clangula*, *Histrionicus*, *Melanitta*, and *Somateria*). The SUSC and WWSC are congener species and so could be a source of phylogeny mediated bias. We performed analysis of covariance on log-transformed values based on type III sums of squares with taxonomic genus entered as a main effect and we tested the interaction between genus and the independent variable. For all models the interactions were not significant, so the slopes of each genus could be modelled as one by the regression



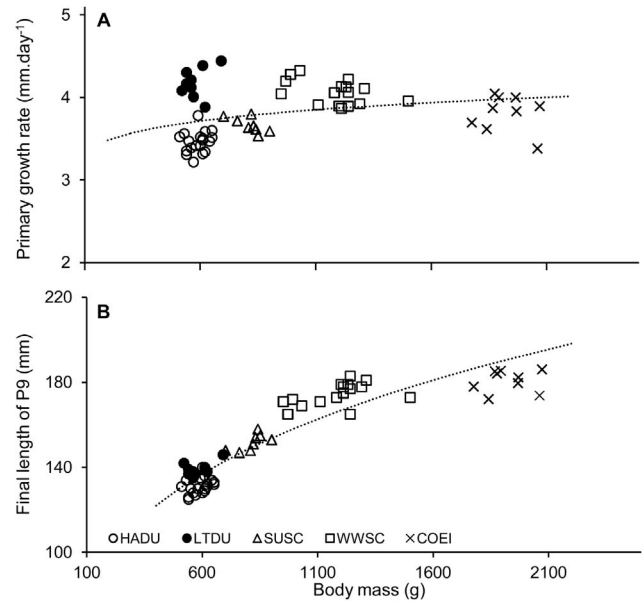


**Figure 1. Feather growth rates of the 5 seaduck species.** Gompertz 9<sup>th</sup> primary growth models for 5 seaduck species; Harlequin Ducks (*Histrionicus histrionicus*, HADU), Long-tailed Ducks (*Clangula hyemalis*, LTDU), Surf Scoters (*Melanitta perspicillata*, SUSC), White-winged Scoters (*Melanitta fusca*, WWSC) and Common Eiders (*Somateria mollissima dresseri*, COEI) with (A) representing males and (B) females. doi:10.1371/journal.pone.0107929.g001

LTDU, while the delta growth rate ranged between  $3.43 \pm 0.10$  and  $4.20 \pm 0.13$  mm.day<sup>-1</sup> (Table 1). The daily percent change in feather length over the period of 5% to 90% of feather development for the 5 species varied between 2.1% and 3.1%. The maximal feather growth rate of LTDU was faster than the maximal feather growth rate of the 4 other species, while HADU had the slowest (see statistical details in the legend of Table 1). COEI had a similar maximal feather growth rate as the 2 scoter species, while WWSC and SUSC had different maximal growth rates (Table 1). HADU had a slower delta growth rate than the 4 other species (see statistical details in legend of Table 1). The feather delta growth rates of LTDU and WWSC were the fastest and similar (Table 1). It was similar for COEI and SUSC and slower than delta growth rates of LTDU and WWSC (Table 1). For each species, maximal and delta growth rates of P9 did not differ between females and males ( $U = 48.00$ ,  $p = 0.430$ ;  $U = 7.00$ ,  $p = 0.606$ ;  $U = 4.00$ ,  $p = 0.297$ ;  $U = 26.00$ ,  $p = 0.560$  and  $U = 11.00$ ,  $p = 0.806$ , respectively for HADU, LTDU, SUSC, WWSC, and COEI).

### Moult allometries

Among the 5 species, average daily delta growth rate of P9 scaled to body mass as  $M^{0.059}$  (Fig. 2A;  $r = 0.305$ ,  $p = 0.017$ , 59 d.f. and 95% CI 0.011–0.107) and the terminal length of the 9<sup>th</sup> primary scaled to body mass as  $M^{0.285}$  (Fig. 2B,  $r = 0.931$ ,  $p < 0.0001$  and 95% CI 0.256–0.314). As these species undergo a simultaneous replacement of the primaries, the time required to replace all flight feathers increases as 0.226 the power of the body mass ( $M^{0.285}/M^{0.059} = M^{0.226}$ ). At the intra-specific level, no correlations were found between feather delta growth rate and body mass ( $r = 0.200$ ,  $p = 0.415$  for HADU,  $r = 0.321$ ,  $p = 0.399$  for LTDU,  $r = 0.683$ ,  $p = 0.062$  for SUSC,  $r = 0.459$ ,  $p = 0.074$  for



**Figure 2. Relationships between body mass and primary growth rate, and P9 length in 5 seaduck species.** Allometric relationships among 5 seaduck species between: (A) body mass (g) and delta 9<sup>th</sup> primary growth rate (mm.day<sup>-1</sup>), (B) body mass (g) and final length of 9<sup>th</sup> primary (mm). Dotted line represents the allometric relation for the 5 species (HADU, LTDU, SUSC, WWSC and COEI) (A) allometric relation:  $M^{0.059}$ , (B) allometric relation:  $M^{0.285}$ . doi:10.1371/journal.pone.0107929.g002

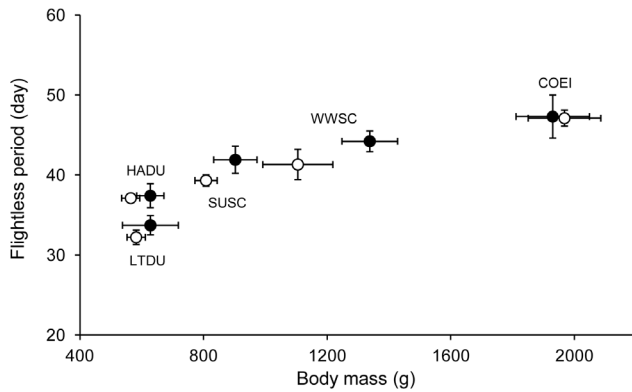
WWSC and  $r = 0.141$ ,  $p = 0.717$  for COEI). However, there was a hint of a possible relationship in SUSC and WWSC if we used the  $\alpha = 0.10$  level.

### Duration of estimated flightless period

The estimated flightlessness duration varied among the 5 seaduck species (Anova,  $F_{4,56} = 104.584$ ,  $p < 0.0001$ ). However, flightlessness duration did not differ between sexes except for the WWSC ( $U = 56$ ,  $p = 0.010$ ), which was also the species showing the greatest sexual dimorphism at the level of 9<sup>th</sup> primary length and body mass. The shortest flightless period was recorded for LTDU with  $32.2 \pm 0.9$  and  $33.7 \pm 1.3$  days respectively for females and males (Fig. 3). COEI had the longest estimated flightless period with  $47.1 \pm 1.0$  and  $47.3 \pm 2.7$  days respectively, for females and males. HADU had an estimated flightlessness duration around 37 days ( $37.1 \pm 0.4$  and  $37.4 \pm 1.5$ , respectively for females and males). Scoters had similar estimated flightless periods (Tukey's Post Hoc,  $p = 0.067$ ). SUSC were flightless for  $39.3 \pm 0.7$  and  $41.9 \pm 1.7$  days, respectively, for females and males. Females of WWSC were flightless for  $41.3 \pm 1.9$  days, while males were flightless for  $44.2 \pm 1.3$  days.

### Variation of body mass during flight feather moult

During remigial moult, body mass of both sexes tended to increase at the beginning of moult after which it declined until it stabilized around initial body mass at the end of the moult. This pattern was more pronounced in females than males (Fig. 4.). The increase of body mass at the beginning of moult was significant for both sexes in HADU ( $F_{5,20} = 12.075$ ,  $p < 0.001$ , Dunnett's test  $p = 0.013$  and  $F_{5,44} = 2.823$ ,  $p = 0.027$ , Dunnett's test  $p < 0.001$ , respectively for females and males) and for female scoters ( $F_{5,7} = 11.816$ ,  $p = 0.003$ ,  $p < 0.001$  and  $p = 0.021$ , Dunnett's test  $p = 0.038$  and  $F_{5,21} < 0.001$ , Dunnett's test  $p < 0.001$ , respectively



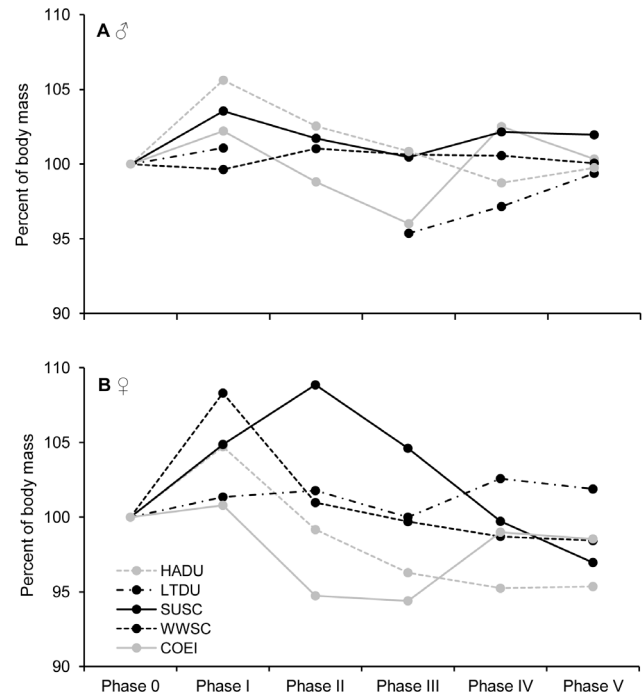
**Figure 3. Relationship between body mass of 5 seaduck species and flightless period.** Representation of the flightless period (days) according to the body mass for the 5 seaduck species (HADU, LTDU, SUSC, WWSC and COEI). Females are represented by white circles and males by black circles. doi:10.1371/journal.pone.0107929.g003

for SUSC and WWSC). During remigial moult, female COEIs and HADUs were the only species/sex cohorts that reached a lighter body mass than the initial value ( $F_{5,38} = 4.61$ ,  $p = 0.002$ , Dunnett's test  $p = 0.025$  and  $F_{5,20} = 12.075$ ,  $p < 0.001$ , Dunnett's test  $p = 0.031$ , respectively). Female HADUs were the only cohort that was significantly lighter at the end of the moult ( $p = 0.002$  at the maximal 9<sup>th</sup> primary feather length, phase V). Finally, to test the hypothesis that birds lose body mass during remigial moult to shorten flightlessness, we also compared the initial body mass with body mass reached at phase IV, when birds are able to fly again. The mean body mass reached at the phase IV was not lighter than the mean initial body mass except for females of HADU (Fig. 5).

## Discussion

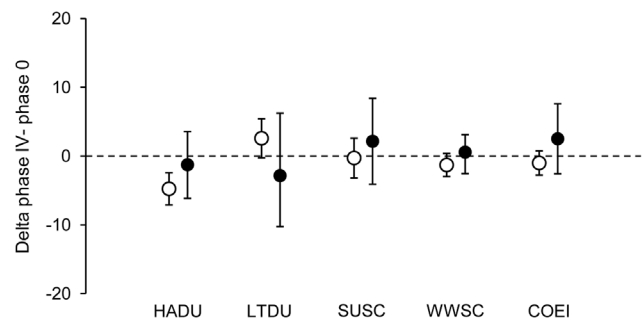
### Applicability to wild seaducks

In this study, the results obtained for the timing, flightlessness duration, and growth rates of remigial moult were comparable to those obtained on wild birds. Indeed, our data that the timing of remigial moult differ among species and sexes, with an initiation of remigial moult earlier in males than females, has been observed in most wild waterfowl species [10], [43], [49], [50], [51], [52]. The initiation dates of remigial moult for males of the 5 studied species are similar to dates reported in the wild [43], [50], [53], [54], [55], [56], [57]. In contrast, for captive females the mean shedding dates were earlier than their wild counterparts. As a consequence, differences between sexes are in average only of 6 to 11 days in our study while, depending on species, it is about 3 weeks in the wild [49], [51], [54], [58], [59], [60]. We thus suggest that the differences in the start of moult, observed between captive and wild females, are related to their status of non-breeders in our study as none were in a breeding state before they started moulting. For instance, there is evidence that moult starts later in breeding birds in the wild [5], [10], the mechanism here being that elevated level of prolactin associated with parental care inhibits the onset of moult [61]. Indeed, it is well known that sex hormones but also environmental conditions (light levels, temperature, food availability, etc.) are factors acting in moult timing [62], [63], [5]. Interestingly, among the 5 studied species of seaducks, and despite the non-breeding status of birds, and controlled environment due to captivity, females still moulted later than males. These results underline a potential involvement of genetic/sex-specific factor in the launching of moult mechanisms. Such a result would not be



**Figure 4. Inter-specific body mass variation during remigial moult.** Changes in mean body mass of birds (as percentage of initial weight) based on the percentage growth of the 9<sup>th</sup> primary for 5 seaduck species; Harlequin Ducks (HADU), Long-tailed Ducks (LTDU), Surf Scoters (SUSC), White-winged Scoters (WWSC) and Common Eiders (COEI) with (A) representing males and (B) females. Phase 0 corresponds to the value of initial weight before the shedding of flight feathers, Phase I represents feather emergence and the start of feather growth, Phase II corresponds to the period of fast feather growth rate and where maximal growth rate is reached, Phase III is the period of the first slowing down of growth rate, Phase IV corresponds to the second slowing down of growth rate and the period during which birds are able to fly again, Phase V is the end of the remigial moult when final length of P9 is reached. doi:10.1371/journal.pone.0107929.g004

possible to obtain in natural wild settings, and we are unaware of other studies clearly showing a sex-specific genetic component shaping moult timing after environmental factors have been



**Figure 5. Intra-specific body mass variation for the studied species.** Average deltas, representing the difference between body mass recorded at the phase IV of the moult in which seaducks are able to re-fly and initial body mass, and their respective confidence intervals. When the confidence intervals exclude the zero line, the delta is declared significant at 5% level (see Materials and methods). doi:10.1371/journal.pone.0107929.g005

controlled. The interaction between genetic and environmental effects on moult strategies in birds deserves further investigation.

The estimates of flightlessness duration, based on the Gompertz growth model and the 90% of P9 final length generate results comparable to values from the literature. However, differences are observed for HADU [50] and COEI [12]. Indeed, Robertson *et al.* [50] used the value of 70% of P9 final length reported by Hohman *et al.* [10] to estimate HADU flightless period, while it has been estimated to be higher for most seaduck species [43], [51], [64] (around 80% for male SUSC, SG, pers. obs.). For COEI, Guillemette *et al.* [12] used a behavioural technic to estimate flightlessness duration, which may have caused the discrepancy. Again, the difference may also stem from a general value (90%) applied to all species, while it was observed to be lower for COEI (AV, pers. obs.).

The delta primary growth rates for each studied species were consistent with previous results on wild birds [43], [50], [26]. Similarly, the absence of difference in feather growth rates found between sexes conforms to former investigations [10]. However, no data relating to primary growth rates of COEI and LTDU were available. For COEI, our estimates of delta and maximal primary growth rates represent respectively, 2.1% and 3.0% daily change in length, which fall within the range of daily change values found for most waterfowl species (2–3%, [10]). LTDU presented higher values (respectively 3.1% and 4.3% for females and 2.9% and 4.1% for males). Among all five species, LTDU breeds at the furthest north [65] while HADU, the slowest moult in this study, is the southern-most species [52]. Thus, the timing constraint and weather factors at this latitude might be important factors for a rapid moult as it is the case for others birds such the White-crowned sparrow (*Zonotrichia leucophrys nuttalli* and *Z. l. Pugetensis*) [29], shorebirds [66], [52], and the least Auklets (*Aethia Pusilla*) [28]. As with our sex-specific results, the finding that moult timing of our non-breeding captive birds reflected that of each species in the wild suggests a genetic component interacting with environmental factors (such as light-level regimes at different latitudes, food resources, and climatic conditions found under natural conditions) to shape moult timing.

### Allometry of feathers growth

Our study is based on the assumption that a flightless state is under numerous constraints (predation risk, temporal constraints, food availability etc). Thus, it would be advantageous for birds to minimise the flightless period by increasing feather growth rate. In the present study, we showed that heavier seaduck species required more time to grow their flight remiges, which qualitatively supports the findings of Rohwer *et al.* [16]. More specifically, primary growth rate scales as  $M^{0.059}$ , which is 3 times lower than the allometric exponent derived by Rohwer *et al.* [16] for birds in general ( $M^{0.171}$ ). Indeed, doubling the body mass in our allometric relationship only results in an increase of 4.0% growth rate against 12.6% for Rohwer's *et al.* [16] study. Now, using the length of the longest primary, these authors reported 2 power estimates for their allometric relationship relating feather length and body mass (one in result section and a different one in the methods section). Using the raw data of Rohwer *et al.* [16], we validated the result found in their methods section where the longest primary feather increases as the power of 0.325 of body mass (95% CI 0.302–0.346), which is close but higher to our result ( $M^{0.285}$  with 95% CI, 0.256–0.314). Thus, the time required to complete moult increases as the power 0.154 of body mass [16] while it is higher for *Mergimi* with  $M^{0.226}$ . As a result, flightlessness duration increases with body mass in seaducks (Fig. 3).

At the intra-specific level and for each of the 5 species studied, no significant correlation between feather growth rate and body mass was found at the  $\alpha=0.05$  level but there were marginally significant correlations for SUSC and WWSC. Clearly larger sample sizes are needed to determine whether scoters differ from other species on that point. The absence of relationship at the intra-specific level and the disproportionate (slow) increase of feather growth rate in relation to body mass at the inter-specific level may reflect the physiological and structural limits at which feathers can be produced [14], [15], [16]. Thus, our results support the original hypothesis of Prevost [14] stating that it is mainly Anseriformes that may have reached the limit of feather growth rates. Based on allometric principles, Rohwer *et al.* [16] deduced that structural constraints at the level of the cylindrical growing region of primary feathers might lead to a physiological bottleneck. More specifically, the diameter of the follicle and the number of rows of dividing cells could limit feather growth rate of large birds and could increase the flightlessness duration for simultaneous moulters (Fig. 3). This may also be the result of a trade-off between the use of a fast moult strategy (simultaneous moulters vs. sequential moulters) and feather quality. Indeed, some recent studies have shown that fast moulters had lower feather quality compared to slow moulters, in terms of mass, coloration, and physical proprieties of the feather [30], [31], [32], [67], [68], [69].

### Variations in body mass during remigial moult

Wing-loading of an individual is an important parameter that influences takeoff and ability to escape successfully from a predator attack [70], [71], [34], [72]. Captive seaducks of the 5 species studied showed variations in their body mass during remigial moult despite that they had access to food *ad libitum*. The range and pattern of body variations differ between species, sex, and size. We interpret the marked increase of body mass 15 days after the primaries were shed (Phase I), followed by a decrease of body mass (Phase II), as a strategy to allocate body reserves to a period coinciding with the highest rate of feather growth (Phase II, Fig 4). In other words, the decrease of body mass of phase II corresponds to the steep slope of feather growth models, hence a period of high energy demand. Similar observations of body mass loss during remigial moult were recorded for different species of waterfowl in both captive and wild situations [10], [17], [64], [73], [74]. However, the SUSC and WWSC male scoters did not show any significant variation of body mass in our study, as observed for Common Scoters (*Melanitta nigra*) [39].

One pervasive idea in the literature is that body mass loss observed during the remigial moult may be an adaptive strategy to reduce flightlessness duration in a way, that lighter birds will accelerate the regain of flight ability [17], [75]. Comparing body mass at regain of flight ability (phase IV) with initial body mass (phase 0), we observed a trend for lower body mass of females at phase IV. In contrast, we observed an opposite trend for males. Nevertheless, most studied species, excepted females of HADU, did not have a lighter body mass at regain of flight ability (between 80% to 100% of final 9<sup>th</sup> primary length, Fig. 5). Thus, our results under controlled environment (constant food supply, no predation risks, etc.) do not support the idea of a strategic body mass management that would reduce flightlessness duration in these species. Variations in body mass observed in wild birds, such the reduction in mass of moulting male LTDU in the Beaufort Sea [76] could simply result from a depletion of their food since birds congregate and exploit a smaller foraging habitat. Ouellet *et al.* [77] reviewed the various mechanisms that could increase lift during takeoff of birds and, apart wing-loading reduction, they

pin-point to (1) the enhancement of mechanical power with larger pectoral muscles and (2) improvement of muscle metabolic output with increased enzyme activity. Several studies have documented changes in the mass of legs and flight muscle mass in waterfowl with muscle mass decreasing at the beginning of remigial moult and increasing towards the end [20], [39], [76]. Such a level of organ flexibility might enhance flight capability despite the fact that body mass remains constant. Further studies should investigate these potential strategies in moulting birds.

In conclusion, our results concerning timing and flightlessness duration are similar to various published studies although we did not find any support for the idea that body mass reduction at the end of remigial moult is used to minimise the flightless period. In addition, our power estimate of the allometric relationship relating body mass and feather growth rate is lower than birds in general, indicating that seaducks do not use a high feather growth rate to minimise flightlessness duration. Further investigations should seek potential explanations for that observation in terms of physiological or structural constraint, although we contend that the relationship between feather quality and feather growth rate seems to be the most potential avenue to explain such a difference.

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