

Is mass loss in Brünnich's guillemots *Uria lomvia* an adaptation for improved flight performance or improved dive performance?

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Breeding Brünnich's guillemots *Uria lomvia* show stepwise mass loss at the time of hatch. This mass loss has usually been explained as an adaptation to reduce the cost of flight during the chick-rearing period because flight time increases during that period. It is possible, however, that mass loss also increases dive performance during the chick-rearing period because time spent diving also increases during that period. Reduced mass could reduce basal metabolic rate or costs associated with buoyancy and therefore increase aerobic dive limit. To examine the role of mass loss in dive behavior, we attached time-depth-temperature recorders for 24–48 h to chick-rearing and incubating Brünnich's guillemots at Coats Island, Nunavut (2005: $n = 45$, 2006: $n = 40$), and recorded body mass before and after each deployment. There was no relationship between mass and dive duration during either incubation or chick-rearing. Seventeen of the birds we sampled during incubation were resampled during chick-rearing. For this group, dive duration increased with mass loss between incubation and chick-rearing ($r^2 = 0.67\text{--}0.75$). Mass loss occurred through reductions in metabolically-active tissues (liver, bladder) and buoyant tissues (lipids) although muscle and gut mass did not change. Despite the large change in lipids, buoyancy only changed by 0.1%, and mass loss therefore did not have much effect on costs associated with buoyancy. Nonetheless, surface pause duration for a given dive depth decreased during chick-rearing, supporting the idea that reduced mass led to increased aerobic dive limit through reduced metabolic rate and inertial costs; oxygen stores did not increase. We also attached neutrally ($n = 9$) and negatively ($n = 11$) buoyant handicaps to the legs of adults to assess the effect of artificial mass increases on time budgets. Artificially increasing mass decreased total time spent diving but did not change time spent flying. There was no change in shift length between incubation and chick-rearing, and therefore no support for the idea that mass loss reflected a change in fasting endurance requirements. An energetic model suggested that the observed mass reduction reduced dive costs by 5–8% and flight costs by 3%. We concluded that mass loss may be as important for increasing dive performance as increasing flight performance.

Reduced mass in birds increases flight maneuverability and takeoff performance but decreases fuel storage capability (Witter and Swaddle 1997, Rands and Cuthill 2001, Macleod et al. 2005). Despite reduced fuel storage capabilities, some waterfowl reduce mass during periods of food shortage (e.g. winter or moulting periods), even when provided with food *ad lib*, as this reduces metabolic rate and, therefore, energy demands (Loesch et al. 1992, Barboza and Jorde 2002, Portugal et al. 2007). Similarly, migrating shorebirds reduce the mass of organs not required for flight, which increases flight efficiency and, thus, migration distance (Piersma and Gill 1998, Dekinga et al. 2001, Landys-Cianelli et al. 2003). Adult mass of some seabirds decreases over the breeding season in response to increased energy demands (Wendeln and Becker 1996, Kitaysky et al. 1999, Golet and Irons 1999, Moe et al. 2002). Thus, mass is carefully modulated, for many different reasons, across a wide variety of avian taxa.

Because the energy costs associated with flight increase with body mass (Rayner 1999), it has been hypothesized that mass loss during the chick-rearing period, when adult birds must increase their flight time to provision nestlings, may reduce adult energy requirements and lead to more food delivered to nestlings (Freed 1981, Norberg 1981, Niizuma et al. 2001). As predicted, adults of many species show a stepwise decrease in mass at the time of hatch (Moreno 1989, Wendeln and Becker 1996, Holt et al. 2002, Cichon 2001). In some cases, this reduction is likely a stress response to reduced food availability (Moreno 1989, Holt et al. 2002, Suárez et al. 2005). Nonetheless, some species show rapid mass loss at the time of hatch even when the time of hatch has been artificially delayed (Gaston and Perin 1993, Cichon 2001), or when environmental conditions are good (Quillfeldt et al. 2006), suggesting that mass loss is programmed. Furthermore, in house wrens *Troglodytes aedon* this decline occurs as markedly in individuals

that have been provided food *ad lib* as those that have not (Cavitt and Thompson 1997). A similar programmed mass loss has also been observed in moulting waterfowl (Brown and Saunders 1997, Fox and Kahlert 2005, Kahlert 2006), including those fed *ad lib* (Portugal et al. 2007).

As alcids increase flight time during breeding, especially post-hatch (Benvenuti et al. 2002), they might be expected to show a pronounced programmed mass loss. Indeed, several species of alcids undergo mass loss that is thought to be programmed (Gaston and Jones 1989, Croll et al. 1991, Jones 1994, Niizuma et al. 2002). In Brünnich's guillemots *Uria lomvia*, mass loss within each individual is stepwise and coincides precisely with time of hatch (Croll et al. 1991, Gaston and Perin 1993).

An alternative explanation for programmed mass loss in auks is that it is an adaptation for improved dive performance. For example, Brünnich's guillemots increase time spent underwater during the chick-rearing phase (Benvenuti et al. 2002), likely owing to increased time needed to provision chicks. Reducing all organs except those required for locomotion (wing and leg muscles) and blood storage (blood hemoglobin volume, myoglobin volume) would reduce diving metabolic rate (e.g. Schreer and Kovacs 1997, Green et al. 2005); heavier animals usually dive deeper and for longer than smaller ones (Watanuki and Burger 1999, Walker and Boersma 2003, Cornick and Horning 2003, *contra* Beck et al. 2000, MacArthur et al. 2001). Alternatively, loss of buoyant tissues (i.e. lipids) could reduce energy costs associated with buoyancy and lead to reduced diving metabolic rate (Lovvorn et al. 1999, 2004, Beck et al. 2000, Sato et al. 2003). Reducing diving metabolic rate allows for increased dive duration without penalty of increased surface pause duration, thereby increasing bottom time, and, presumably, prey encounter rate (Ydenberg and Clark 1989, Houston and Carbone 1992).

Some animals reduce diving metabolic rate during periods of the year when dive duration increases by reducing body core temperature (Handrich et al. 1997, Green et al. 2005). As guillemots do not reduce body core temperature (Niizuma et al. 2007), possibly because the high cost of transport for a low body mass coupled with the needs for aerial flight result in heat generated by the muscles during diving being greater than that lost to water, this is not an option for guillemots. Instead, this may be why they reduce total body mass. The effect of reduced mass on metabolic rate depends heavily on what body components actually decrease (Scott and Evans 1992, Scott et al. 1996, Niizuma and Watanuki 1997). For example, reduced body mass through reduced metabolically-active tissues reduces resting metabolic rate (Bech et al. 2002), whereas reduced body mass through reduced lipids may increase resting metabolic rate (Niizuma and Watanuki 1997), but reduce buoyancy (Niizuma et al. 2002). Consequently, the hypothesis that reduced mass may improve dive performance depends heavily on what organs change.

Brünnich's guillemots are ideal models for studying connections between mass loss and dive behaviour as they were among the first-recognized examples of programmed mass loss (Croll et al. 1991) and there is a large body of information on dive behaviour obtained through bird-borne recorders (e.g. Falk et al. 2000, 2002, Jones et al.

2002, Paredes et al. 2004, 2006). The mass loss likely has both "programmed" and "responsive" components; individuals lose mass stepwise at the time of hatch (Croll et al. 1991, Gaston and Perin 1993), yet mass is lower for inexperienced birds or during poor years (Gaston and Hipfner 2006a,b). Both parents share incubation (~30 d) and chick-rearing (~20 d) duties for their single chick approximately equally until fledging, when the male parent accompanies the chick to sea. Mass trajectories are similar for males and females (Gaston and Hipfner 2006a,b).

In this paper, we correlate mass and dive duration among Brünnich's guillemots equipped with time-depth-temperature recorders (TDRs) and we examine the effect of experimentally increasing mass on dive and flight activity. We also examine changes in the size of body components, especially lipid stores, between chick-rearing and incubation. Because reduced fasting endurance during chick-rearing has been cited as an explanation for reduced mass during chick-rearing (e.g. Groscolas 1986, Croll et al. 1991, Hohtola et al. 2004), we also examined fasting endurance between incubation and chick-rearing. It is worth noting that during the breeding season risk of predation or kleptoparasitism for guillemots while at-sea is virtually non-existent (survival $\approx 100\%$ and we do not observe either predation or kleptoparasitism while at-sea). Thus, risk of predation is unlikely to explain any of the patterns we observe (cf. Rogers and Smith 1993, Gosler et al. 2002).

Methods

Our dive behaviour observations were made at the Coats Island west colony (62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005a,b) during 2005 (n=45) and 2006 (n=40). Parental guillemots at their nests were caught with a noose pole. Handling time was always less than ten minutes and usually less than five minutes. Adults used for comparison between chick-rearing and incubation were captured 5–10 d prior to chick hatch and again ~5 d after hatch to reduce variation due to egg or chick age (Gaston and Hipfner 2006a,b). All handling and deployment methodology was approved under the guidelines of the Canadian Committee for Animal Care (Protocol Number F04-030).

TDR observations

We attached LOTEK 1100LTD (Lotek Marine Technology, St. John's, Newfoundland, Canada) time-depth-temperature recorders (TDRs) to plastic bands that were attached to the legs of guillemots (2005: n=36 chick-rearing, 9 incubating; 2006: n=31 chick-rearing, 9 incubating). The TDRs were cylindrical (mass=4.5g; diameter=1 cm; length=3.3 cm; sampling rate=3 s; precision = ± 0.1 m; accuracy $\approx \pm 2$ m). Whereas larger, back-mounted TDRs are known to impact guillemot provisioning rates (Watanuki et al. 2001, Hamel et al. 2004, Paredes et al. 2004), number of foraging trips (Tremblay et al. 2003, Hamel et al. 2004, Paredes et al. 2004), adult attendance (Paredes et al. 2004), mass loss (Croll et al. 1992, Falk et al. 2000, 2002, Watanuki et al.

2001) and dive depth and duration (Elliott et al. 2007), our leg-mounted TDRs had no impact on provisioning rates, trip duration or mass loss (Elliott et al. 2008c). We used the temperature log from the TDR to determine flight time and incubation/brooding shift length (Tremblay et al. 2003, Elliott et al. 2008c). Water temperature was $<6^{\circ}\text{C}$, air temperature was $8\text{--}15^{\circ}\text{C}$ and colony temperature was $>20^{\circ}\text{C}$ (guillemots sit on their legs, so the TDR approaches body surface temperature), allowing us to distinguish between time on the water, time in the air and time at the colony. Mass of adults restrained in a cloth bag was measured using a 1.5 kg pesola to the closest 10 g before and after each TDR deployment. The average value of the deployment and retrieval mass per adult was used for analysis. To address the issue of fasting endurance (e.g. Groscolas 1986, Hohtola et al. 2004), we compared the duration of the first incubating shift post-attachment for 20 incubating birds to the duration of the first brooding shift post-attachment for the same 20 birds during chick-rearing.

Measurements of body components

We analyzed data from 28 breeding adult guillemots previously collected for contaminants analysis at the south colony on Prince Leopold Island ($74^{\circ}13'\text{N}$, $90^{\circ}00'\text{W}$), Nunavut, Canada (Gaston et al. 2005a,b) during breeding season 2002, a particularly poor season for guillemots at this location (Gaston et al. 2005b). All required permits were obtained for these collections: Canadian Wildlife Service Migratory Birds Collection Permit NUN-SCI-01-03; Wildlife Research Permit WL000174 from Government of Nunavut; National Wildlife Research Centre Animal Care Committee Permit 02M00G02; University of Ottawa Animal Care Committee Permit BL-172, ACVS. We obtained 19 incubating adult guillemots between 27 July and 10 August and 9 chick-rearing adult guillemots

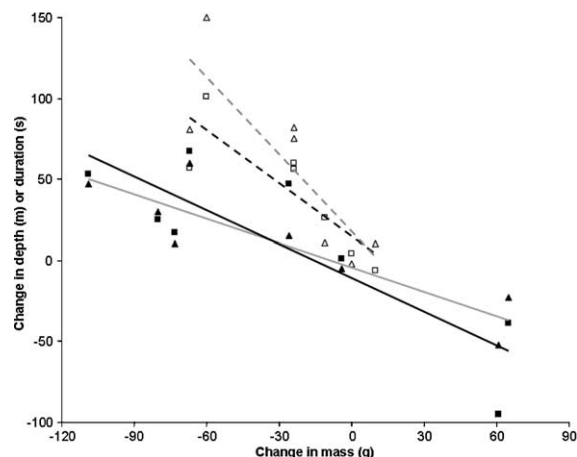


Figure 1. Change in average depth (squares, black lines) and duration (triangles, grey lines) between chick-rearing and incubating periods for individual Brünnich's guillemots at Coats Island, Nunavut in 2005 ($n=8$, closed symbols, filled lines) and 2006 ($n=7$, open symbols, dashed lines). Regression equations for 2005 are Duration = $0.45 \text{ Mass} - 4.25$ ($r^2=0.75$; $P=0.008$) and Depth = $0.71 \text{ Mass} - 7.88$ ($r^2=0.74$; $P=0.005$) and for 2006 are Duration = $1.01 \text{ Mass} + 17$ ($r^2=0.67$; $P=0.03$) and Depth = $1.47 \text{ Mass} + 22$ ($r^2=0.64$; $P=0.03$).

between 9 and 10 August. We collected the birds near the start of their shift. At the time of collection, 5–10 ml of blood was collected as part of another project. As the ice left in early July (Gaston et al. 2005b), these birds are likely to have recovered from a period of low foraging during extreme ice conditions in June. The incubating birds had eggs likely within 10 d of hatch and the chick-rearing birds had chicks <10 d old. The carcasses were immediately frozen and shipped to a laboratory, where they were dissected and the following components were weighed: bladder, gizzard, gonads, heart, intestine, kidneys, liver, lungs, right breast muscle, stomach, and total body lipids. Because wing length was allometrically related to mass ($R^2=0.16$, $P=0.02$), during both breeding periods, we corrected each body component weight by wing length allometrically (natural logarithm), to account for individual variation in size. Hematocrit was measured on 9 chick-rearing (9 August; chicks >10 d old) and 11 incubating guillemots (18 July; eggs ~ 20 d old) at Coats Island in 2008. We use Bonferroni-corrected two-tailed t-tests to determine differences in body component mass, corrected for size, and hematocrit between incubation and chick-rearing.

Energetic model

To estimate the impact of mass changes on flight and dive energetic costs, we used mathematical models obtained from the literature. The flight model assumes that basal metabolic rate is almost negligible during flight and, thus, the affects of mass change will influence flight energy costs primarily through a change in the cost of lift (Pennycuick et al. 1996, Kvist et al. 2001, Rayner 2001). For flight costs, we used the Pennycuick model (Pennycuick 1997):

$$P = R \left(\frac{P_{\text{aer}}}{\eta} + \text{RMR} \cdot M \right);$$

$$P_{\text{aer}} = \frac{2kM^2g^2}{\pi b^2 \rho U} + \frac{1}{2} \rho S_b C_{D\text{par}} U^3 + 4^{5/4} 3^{-3/4} k^{3/4} C_2 \frac{S}{b^2} \times \frac{(Mg)^{3/2} S_b C_{D\text{par}}}{\pi^{3/4} \rho^{1/4} b^{3/2}}$$

with the parameters listed in the Appendix. The effect of mass on the Pennycuick model is unreliable for birds flying at or near their maximum range speed (Pennycuick 1995, Rayner 1999, 2001), which likely applies to guillemots (Elliott and Gaston 2005). Consequently, we used the Pennycuick model to estimate energy costs during chick-rearing, and then assumed that metabolic rate during flight increased as $M^{0.35}$, from an empirical study on another fast-flying charadriiform bird (Kvist et al. 2001).

For dive costs, we used three models. The first model was based on guillemot dive costs measured in a shallow dive tank (Croll et al. 1992; Croll and McLaren 1993) and assumed a constant diving metabolic rate:

$$P_{\text{dive}} = 3 \cdot \text{RMR} \cdot M$$

Model 2 assumed that diving metabolic rate was three times RMR, as in Model 1. Changes in RMR were estimated from the changes in body components, rather than total body mass. We used the following values for RMR from

Scott and Evans (1992) for another charadriiform bird, knot *Calidris alpina*: adipose tissue ($0.06 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$), liver ($0.84 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$) and muscle ($0.65 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$). We assumed that bladder, gonads, kidney and liver had the same value as liver and that the remaining tissues did not change in size and had same value as muscle (Scott and Evans 1992). Models 1 and 2 ignore buoyancy costs because buoyancy costs are expected to be low except for very shallow dives (Lovvorn et al. 1999, 2004) and because changes in buoyancy associated with changes in mass may be mitigated by changes in respiratory or plumage air storage (Sato et al. 2002, Elliott et al. 2007).

Model 3 accounted for costs associated with buoyancy. We considered the change in buoyancy between incubation and chick-rearing to be only associated with a decrease in lipids, and that the buoyancy of lipids is equal to 0.729 N kg^{-1} (Lovvorn et al. 1999). We assumed dive depth was 56 m (mean value, see Results). We subdivided the dive into descent, bottom and ascent phases and used the mean value for each period (see Results). We calculated descent and bottom costs using the model provided by Lovvorn et al. (1991) and ascent costs assuming that ascent was completely passive and thus equal to RMR:

$$E_{\text{dive}} = (\eta P_d + \text{RMR} \cdot M) T_d + (\eta P_b + \text{RMR} \cdot M) T_b + \text{RMR} \cdot M \cdot T_a$$

where P_d was calculated by assuming work per stroke is equal to the product of displacement and drag + buoyancy (Lovvorn et al. 1991). We assumed that the cumulative drag component was equal to 200 J at 56 m (Lovvorn et al. 2004; Fig. 8). Work per stroke was then integrated over the power phase of each stroke in 0.1 s increments and added inertial work. P_b was similarly calculated following Lovvorn et al. (1991):

$$P_b = \frac{B_b^2 T_b}{2(M + 0.2\rho_w V)} + D_b U_b$$

We assumed that during the bottom phase the birds traveled at 1.0 m s^{-1} and that volume was given by the formula $V = 0.0137 + 1.43M$ (Lovvorn et al. 1991).

Handicap experiment

We designed a handicap experiment to examine additional mechanical costs potentially associated with diving. During the incubation and chick-rearing periods (July 15–August 13; all chicks < 5 d old), we attached negatively ($n = 11$; mass = $22.5 \pm 0.9 \text{ g}$ —2.3% of adult mass or about 10% of intra-annual variation in adult mass and decreased buoyancy by $0.075 \pm 0.001 \text{ N}$) and neutrally buoyant ($n = 9$; mass = $15.0 \pm 0.1 \text{ g}$ when filled with water, $5.0 \pm 0.1 \text{ g}$ when empty—0.5% of adult mass or about 2% of intra-annual variation in adult mass) handicaps to the legs of adults at five different locations (Jb, Q, S, T and Z plots; Elliott et al. 2007). The neutrally buoyant handicaps filled with water when submerged and emptied when out of the water, but were otherwise identical to the negatively-buoyant handicaps. Attachment of handicaps to the tibiotarsus minimized the confounding effects of drag and mimicked natural mass loss, which occurs primarily in the posterior portion of the body. Each handicap was attached

for 24–48 h (one or two feeding cycles). To control for individual variation, sex and breeding status, we monitored (with a TDR) each individual for an additional 24–48 h prior to attachment of handicaps or after removal of handicaps, so that all comparisons were made pairwise within individuals (e.g. comparisons were made within the same individual with and without handicaps).

Statistical analyses

All statistical analyses were completed in R 3.2.1. Prior to using parametric statistics, we tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levine's test). All percentages were arcsine-transformed prior to analysis. We only analysed dives with maximum depth > 3 m. To minimize any bias associated with the diel light cycle, all dives between 22:00 and 04:00 were excluded (Croll et al. 1992). As gender affects dive behavior in Brünnich's guillemots (Jones et al. 2002, Paredes et al. 2006) we examined separately a subsample of birds where gender was determined by PCR on blood samples from the tarsus taken after TDR removal and preserved on filter paper (2005: 10 males, 13 females; 2006: 14 males, 12 females). Gender does not affect mass or mass loss trajectories (Gaston and Hipfner 2006a,b). To evaluate whether mass caused changes in dive parameters, we calculated separate linear regressions with (1) dive duration and (2) depth as dependent variables, and (1) mass and (2) mass loss as independent variables. There is a stronger relationship between surface pause duration and depth than duration (Elliott et al. 2007, 2008a,b). Thus, to examine the effect of breeding status (incubation vs. chick-rearing) on surface pause duration, we completed an ANCOVA between ln-transformed surface pause duration and depth for individuals monitored during both chick-rearing and incubation ($n = 17$). We included breeding status as a covariate. For analyses of the handicap experiment, we completed all analyses comparing similar 24 h periods to avoid the impact of diel activity cycles on time budgets (Jones et al. 2002). Because we had strong *a priori* expectations, we used one-tailed paired t-tests to compare the number of seconds spent flying and diving within the first comparable 24 hr period sampled for each individual during periods with and without handicaps. We used one-tailed heteroscedastic t-tests to compare between individuals handicapped with neutrally and negatively buoyant handicaps. All values reported are means \pm SE.

Results

TDR observations

Dive depth and duration increased during the chick-rearing period (Table 1). Mean and maximum dive depth and mean and maximum dive duration did not vary with mass (Table 1). This remained true for subsamples within fixed breeding status or gender (Table 1). Nonetheless, there was a significant positive relationship between change in mass and decrease in average dive depth and duration (Fig. 1). Furthermore, surface pause duration was greater, for a given dive depth ($F_{3624,1} = 805.24$, $P < 0.001$) and dive duration

Table 1. Regression parameters for dive variables relative to mass for Brünnich's guillemots at Coats Island in 2005 and 2006.

Parameter	Status	Gender	n	Mean	SE	t	P	r ²
Mean depth	Chick	Pooled	77	79	4	-0.06	0.95	0.03
		Male	24	64	6	0.60	0.56	0.08
		Female	25	79	8	0.08	0.94	0.09
Mean duration	Incubation	Pooled	20	36	2	0.62	0.55	0.09
		Chick	77	122	4	0.24	0.81	0.03
		Male	24	89	8	0.77	0.46	0.05
Max depth	Chick	Female	25	125	10	0.68	0.51	0.05
		Pooled	20	71	7	0.73	0.49	0.06
		Male	24	88	6	0.07	0.94	0.04
Max duration	Incubation	Female	25	108	13	0.95	0.36	0.01
		Pooled	20	76	4	0.42	0.69	0.01
		Male	24	165	9	0.55	0.60	0.06
Max duration	Chick	Female	25	195	12	0.67	0.52	0.07
		Pooled	20	147	4	0.21	0.84	0.07
		Female	25	195	12	0.67	0.52	0.07

($F_{3624,1} = 578.62$, $P < 0.001$) during incubation as compared to chick-rearing (Fig. 2). There was no relationship between change in mass and change in flight time per day between the two periods (2005: $t_7 = 0.35$, $P = 0.73$, $r^2 = -0.11$; 2006: $t_6 = 0.54$, $P = 0.51$, $r^2 = 0.09$). There was also no difference in at-colony shift length between incubation (11.9 ± 0.6 h) and chick-rearing (12.6 ± 0.6 h; $t_{37} = 0.77$, $P = 0.44$). Thus, we found no evidence that mass loss was related to lower fasting endurance.

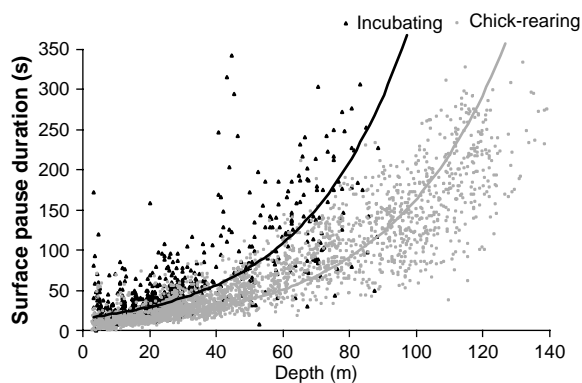
Changes in body components

Guillemots collected at Prince Leopold Island lost about 60 g between incubation and chick-rearing (Table 2). Thawed mass was 92% of actual mass ($R^2 = 0.55$), suggesting that some water loss occurred during death (e.g. blood loss during decapitation) or refrigeration. Thus, the wet weights listed in Table 2 are likely somewhat underestimated. Lipids accounted for most of the change, with 21 g lost between incubation and chick-rearing. Lipids as a percent of body

mass changed from $7.51 \pm 0.66\%$ during incubation to $5.55 \pm 0.38\%$ during chick-rearing ($t = 2.65$, $df = 11$, $P = 0.02$). Skin, including lipids, also showed a significant decrease (28 g) although this is unsurprising as skin lipids accounted for 53% of total lipids by mass. There was no change in lean skin mass between periods (incubation: 71.9 ± 3.0 ; chick-rearing 60.4 ± 10.4 ; $t = 0.76$, $df = 11$, $P = 0.76$). Significant reductions also occurred in the liver (4.9 g), bladder (0.86 g) and gonads (0.78 g). The change in liver mass occurred after removing lipids from the liver (incubation: 35.9 ± 1.1 g; chick-rearing 31.8 ± 1.4 g; $t = 2.39$, $df = 11$, $P = 0.03$) showing that the change in liver mass was not due to a reduction in lipids associated with the liver; we did not measure lipids associated with bladder or gonads. There was no difference in gut mass (stomach, intestines, gizzard) between the two periods (Table 2). Thus, even after correcting for potential desiccation, we were only able to account for about $27.6 \text{ g} \div 0.92 = 30.0$ g or about half the total mass loss. The remaining mass loss must occur through changes in body water content or minor, undetected, changes in other body components. Hematocrit did not change between incubation and chick-rearing (Table 2).

Table 2. Mass \pm SE (in g) of various body components for incubating ($n = 19$) and chick-rearing ($n = 9$) Brünnich's guillemots at Prince Leopold Island in 2002. Also shown is blood hematocrit value for incubating ($n = 12$) and chick-rearing ($n = 10$) guillemots at Coats Island in 2008. Significant results are shown in bold.

Body component	Incubation	Chick-rearing	t (df)
Body (total)	895 ± 15	836 ± 29	1.62 (11)
Breast muscle	93.3 ± 1.8	92.7 ± 3.2	0.03 (11)
Carcass	407 ± 7	406 ± 10	0.07 (11)
Lipids	67.7 ± 6.5	46.9 ± 4.3	2.89 (11)
Skin	112 ± 5	84 ± 11	2.28 (11)
Organs (total)	77.2 ± 1.8	76.8 ± 3.5	0.04 (10)
Bladder	2.19 ± 0.25	1.33 ± 0.10	3.21 (10)
Gizzard	11.8 ± 0.6	12.6 ± 1.1	0.67 (11)
Gonads	1.16 ± 0.35	0.38 ± 0.05	2.29 (11)
Heart	9.98 ± 0.27	9.98 ± 0.48	0.11 (11)
Intestines	24.7 ± 0.9	24.2 ± 1.7	0.23 (11)
Kidneys	11.0 ± 0.2	10.4 ± 0.6	0.75 (11)
Liver	38.4 ± 1.3	33.5 ± 1.6	2.36 (11)
Lungs	9.61 ± 0.34	8.74 ± 0.60	1.17 (11)
Stomach	8.2 ± 0.8	9.3 ± 1.2	0.86 (11)
Hematocrit	47.6 ± 1.2	46.2 ± 1.4	0.77 (11)

Figure 2. Surface pause duration as a function of dive depth for the same individual Brünnich's guillemots ($n = 17$) during incubation and chick-rearing.

Energetic model

Mass for chick-rearing birds averaged 937 ± 9 g ($n = 46$), and for incubating birds mean was 1032 ± 11 g ($n = 18$). Average daily time spent submerged was $13,340 \pm 1509$ s and time spent flying was 5693 ± 678 s during chick-rearing and 8067 ± 640 s and 5322 ± 837 s, respectively, during incubation. During chick-rearing, average dive depth was 56 ± 5 m, average descent phase 37 ± 3 s, average ascent phase was 32 ± 3 s, average bottom phase was 20 ± 4 s and average number of dives per day was 151 ± 10 . Surface buoyancy during incubation was 4.90 N (based on average mass of 1032 g and using the formula -0.659 N kg^{-1} given by Lovvorn et al. (2004) and including their values for respiratory and plumage air volumes) and 4.86 N during chick-rearing (based on average mass of 937 g with 50 g fewer lipids and 50 g fewer neutrally buoyant tissue). The energetic model calculated that a mass loss of 95 g reduced flight costs by 1.9 W, or 10.8 $\text{kJ} \cdot \text{d}^{-1}$ (3.2%). Model 1 calculated that dive costs were reduced by 2.2 W, or 29.7 $\text{kJ} \cdot \text{d}^{-1}$ (9.2%), Model 2 calculated that dive costs were reduced by 1.3 W or 18.1 $\text{kJ} \cdot \text{d}^{-1}$ (5.5%) and Model 3 calculated that dive costs were reduced by 1.4 W, or 16.7 $\text{kJ} \cdot \text{d}^{-1}$ (5.2%).

Handicap experiment

Guillemots with negatively buoyant handicaps spent significantly less time diving (handicapped: 117 ± 69 $\text{mins} \cdot \text{d}^{-1}$, unhandicapped: 201 ± 78 $\text{mins} \cdot \text{d}^{-1}$; one-tailed paired $t_{10} = 3.25$, $P = 0.004$), but showed no difference in time spent flying (handicapped: 80 ± 47 $\text{mins} \cdot \text{d}^{-1}$, unhandicapped: 94 ± 30 $\text{mins} \cdot \text{d}^{-1}$; $t_{10} = 0.78$, $P = 0.23$), whereas guillemots with neutrally buoyant handicaps showed no difference in time spent diving (handicapped: 191 ± 255 $\text{mins} \cdot \text{d}^{-1}$, unhandicapped: 139 ± 54 $\text{mins} \cdot \text{d}^{-1}$; $t_8 = 0.69$, $P = 0.25$) or flying (handicapped: 84 ± 122 $\text{mins} \cdot \text{d}^{-1}$, unhandicapped: 69 ± 54 $\text{mins} \cdot \text{d}^{-1}$; $t_8 = 0.38$, $P = 0.32$). There was no difference in time spent diving ($t_9 = 1.73$, $P = 0.05$) or flying ($t_9 = 0.59$, $P = 0.28$) when comparing paired differences between individuals handicapped with neutrally or negatively buoyant handicaps. The energetic model suggested that the handicaps increased the cost of flight by about 1.0%, and the cost of the bottom phase during diving by 3.5%.

Discussion

Birds that lost more mass between incubation and chick-rearing showed a greater increase in dive depth and duration (Fig. 1). This was associated with a decrease in metabolically-expensive organs, such as the liver and bladder, and a decrease in buoyant body components, such as lipids (Table 2). We interpret these results to mean that mass loss may partially be an adaptation to reduce the effect of increased dive costs during chick-rearing. During incubation, stable isotopes indicate that adult guillemots at Coats Island feed primarily on pelagic invertebrates, but switch to fish for both their chicks and themselves during the chick-rearing period (Woo et al. 2008). This change is coupled

with a decrease in surface pause duration for a given dive depth (Fig. 2). As the relationship between surface pauses and dive depth in guillemots varies with energy expenditure, but not prey type (Elliott et al. 2008a,b), we conclude that this change reflects a reduction in energy expenditure during diving rather than because of a change in prey type.

Other animals also alter their dive physiology in response to seasonal changes in energy requirements. Penguins likely alter their internal physiology (e.g. body temperature, heart rate, fat stores) seasonally in response to the need for increased dive duration during winter, leading to reduced post-dive intervals for a given dive duration (Green et al. 2001, 2005, Charrassin et al. 2002). Oxygen stores and metabolic rate in muskrats vary seasonally, resulting in no net change in their calculated aerobic dive limit (MacArthur 1990, MacArthur et al. 2001, 2003). Great cormorants *Phalacrocorax carbo* wintering in Greenland reduce heart rate and body temperature during periods of late winter food shortage, when dive depth and foraging effort increases (Grémillet et al. 2005). A reduction in metabolic rate through a reduction in mass also occurs in waterfowl during the wing moult, although which organs cause the reduction in overall body mass can be variable (Kahlert 2006, Portugal et al. 2007, Fox et al. 2008).

It is important that whereas the impact of reduced flight energy costs would be a reduction in daily energy expenditure, reduced dive energy costs could both reduce daily energy expenditure and increase aerobic dive limit. Thus, whereas reduced flight costs acts at the scale of days (reduced daily energy expenditure), reduced dive costs acts both at the scale of days (reduced daily energy expenditure) and at the scale of seconds (extended dive duration). A 5% change in daily energy expenditure would require a 5% change in energy intake to maintain a balanced energy budget, which may involve a much lower change in effort than that required by interannual changes in prey abundance. On the other hand, a 5% increase in dive duration, for a fixed depth, would increase bottom time and, therefore, prey encounter rates (see Mori et al. 2002) by 30% given that bottom time was 20% of dive duration (see Results). This would explain why auks that regularly exceed their ADL (e.g. Brünnich's guillemots Croll et al. 1992, rhinoceros auklets *Cerorhinca monocerata* Kuroki et al. 2003) show stepwise mass loss, whereas auks that do not regularly exceed their ADL (e.g. marbled murrelets *Brachyramphus marmoratus* Jodice and Collopy 1999) show no within-season variation in mass despite having similar or greater flight costs (Hull et al. 2001, 2002, Elliott et al. 2004).

Most of the observed mass loss occurs through a reduction in skin lipids, with significant declines also observed in the liver and bladder. Organ mass decreased by 39% (bladder), 30% (lipid) and 13% (liver) between incubation and chick-rearing, while the body as a whole decreased by only 6%. It is not surprising that guillemots do not reduce gut or muscle size, because energy consumption and therefore food intake increases during chick-rearing and large guts and muscles are necessary to capture and assimilate large volumes of prey. Waterfowl moulting in an exceptionally rich environment reduce wing muscles, but show no change in lipids, liver or guts (Fox et al. 2008), while waterfowl moulting in a nutritionally-challenging

environment reduce wing muscles, liver, guts and lipids (Fox and Kahlert 2005). Kittiwakes *Rissa tridactyla* also reduce expensive organs (kidney, liver) disproportionately to mass during chick-rearing, resulting in a decrease in basal metabolic rate (Bech et al. 2002) while mass loss in rhinoceros auklets occurs primarily through a decline in skin lipids (Niizuma et al. 2002).

Despite most of the mass loss in guillemots occurring through reductions in lipid content, buoyancy only changed by 0.1%. Thus, energy savings during diving due to mass loss are likely associated with reduced basal metabolic rate rather than buoyancy (cf. Beck et al. 2000, Sato et al. 2003). The decrease in surface pause duration relative to dive depth between incubation and chick-rearing provides strong support for the idea that ADL increased between the two periods. It is unlikely that the change in ADL between incubation and chick-rearing could reflect an increase in oxygen storage capacity as the lungs did not change in size and water volume—and presumably blood volume—appeared to decline between incubation and chick-rearing. Blood parameters (e.g. hematocrit, Table 2) also apparently do not change. Rather, it appears that diving metabolic rate decreased, presumably through reduced organ metabolic demands.

Our handicap experiments provided more evidence that mass impacts dive behavior. Specifically, mass-handicapped individuals did not alter time spent flying but did reduce time spent diving. The reduction in time spent diving was accompanied by a reduction in average dive depth, duration, descent rate and adult mass (Elliott et al. 2007), which presumably reflected short-term adjustments to increased dive costs (cf. Paredes et al. 2004). Interestingly, this suggests that increased mass increases underwater locomotory costs, aside from physiological costs associated with increased metabolic rate, presumably because more mass must now be pulled through the water during each wingstroke reducing maximum instantaneous accelerations (Lovvorn et al. 1999, 2004). There also may have been adjustments in flight speed and, therefore, flight distance, resulting from increased load that were not reflected by our measurements (Nudds and Bryant 2000, 2002), as guillemots are known to be able to use a wide range of speeds (Elliott and Gaston 2005).

Our models suggest that programmed mass loss may reduce dive costs as much as it reduces flight costs. However, our flight and dive costs are particularly sensitive to variations in muscle efficiency and drag coefficient, which are both poorly known and likely variable (Ellington 1991, Pennycuik 1995, Pennycuik et al. 1996, 2000, Rayner 1999, 2001, Ward et al. 2001, 2004, Elliott et al. 2004). Assuming an efficiency of 0.10 (Nudds and Bryant 2000) would roughly double flight and dive costs and, therefore, energy savings due to mass loss. We ignored the cost of thermoregulation although reduced lipid stores may increase metabolic rate by increasing heat loss or decrease metabolic rate by increasing the potential for birds to enter torpor during diving (e.g. Handrich et al. 1997) or by preventing overheating (Niizuma et al. 2007). These caveats notwithstanding, our models support our contention that, based on the relationship between mass loss and dive duration and the influence of experimental manipulations on total time diving, programmed mass loss in guillemots

may improve dive performance as much as flight performance.

In conclusion, mass loss between incubation and chick-rearing in breeding Brünnich's guillemots was associated with an increase in time spent flying and diving. Energetic models suggested that the mass loss would reduce flight costs by about 8% and dive costs by 5–9%. Among individuals, mass loss correlated better with dive time than flight time. Furthermore, experimental animals showed greater changes in dive behaviour than flight behaviour in response to increased mass. There was no change in shift length between incubation and chick-rearing, and therefore no support for the idea that mass loss reflected a change in fasting endurance requirements. Mass loss occurred through reductions in metabolically-active tissues (liver, bladder) and lipids although muscle and gut mass did not change. Thus, mass loss likely reduced dive costs by reducing metabolic rate (liver, bladder) and inertial costs (lipids) while also reducing flight costs (lipids). A similar reduction in metabolic rate through a reduction in mass occurs for moulting waterfowl (Kahlert 2006, Portugal et al. 2007).

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Appendix 1.

Symbol	Name	Value	Source
b	Wingspan	0.72 m	Croll et al. 1991, 1992
B _b	Buoyancy of bird during bottom phase		
C _{Dpar}	Parasite Drag Coefficient	0.1	Elliott et al. 2004
C ₂	Profile Drag Factor	8.4.	Pennycuick 1995, 1997
D _b	Drag during bottom phase	2.526 N	Lovvorn et al. 2004
E _{diver}	Energy expended during dive		
g	Acceleration due to gravity	9.81 m·s ⁻²	Pennycuick 1995, 1997
k	Induced Power Factor	1.2	Pennycuick 1995, 1997
M	Mass		
P	Power		
P _a	Mean power during ascent		
P _{aer}	Aerodynamic Power		
P _b	Mean power during bottom		
P _d	Mean power during decent		
R	Ventilation Factor	1.1	Pennycuick 1995, 1997
RMR	Resting Metabolic Rate	7.8 W·kg ⁻¹	Croll and McLaren 1993
S _b	Body cross-sectional area	0.009 m ²	Croll et al. 1991, 1992
S	Wing area	0.055 m ²	Croll et al. 1991, 1992
T _a	Ascent time	32 s	See Results
T _b	Bottom time	20 s	See Results
T _d	Descent time	37 s	See Results
U	Forward flight speed	21 m·s ⁻¹	Elliott and Gaston 2005
U _b	Dive speed at bottom phase	1 m·s ⁻¹	
V	Bird volume		
η	Metabolic efficiency	0.23	Pennycuick 1995
ρ _w	Density of water	1026.9 kg m ⁻³	
ρ	Density of air	1.23 kg·m ⁻³	Pennycuick, 1995, 1997