



Changes in body composition during breeding: Reproductive strategies of three species of seabirds under poor environmental conditions

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ABSTRACT

Seabirds differ dramatically in life history traits and breeding strategies. For example, gulls have short incubation shifts (several hours) and high metabolic rates, auks have medium-length incubation shifts (12–24 h) and high metabolic rates, and petrels have long incubation shifts (days) and low metabolic rates. How these different strategies affect the dynamics of body components is poorly known. We compared body, organ and lipid mass changes among three different seabirds (gull: black-legged kittiwake *Rissa tridactyla*; auk: thick-billed murre *Uria lomvia*; petrel: northern fulmar *Fulmarus glacialis*) at Prince Leopold Island, Nunavut, Canada during 2002 (a year with low reproductive success and poor chick growth across all three species). This study is among the first to compare mass and lipid dynamics among different species foraging in the same food web and at similar trophic levels during the same breeding season (same environmental conditions). In fulmars and murre, most of decreases in body mass reflected decreases in lipid mass while in kittiwakes the increase in body mass reflected an increase in lean mass, especially the muscle. The species with the longest fasting endurance (incubation shift length) had the highest percent body lipids during incubation (fulmars: 13.3%, murre: 7.3%, kittiwakes: 6.9%), the highest variability in body lipids, tended to regulate body mass primarily through lipid stores and tended to regulate exercise and digestive organs separately. In contrast, in the species with the highest metabolic rate, all organ systems were adjusted similarly and in relation to body mass, and in a similar manner between incubation (stress due to heavy ice conditions) and chick-rearing (lower stress due to ice-free conditions). In high metabolic rate species, we suggest that organ size varies in response to environmental stress. We conclude that the organ dynamics of seabirds are set by a combination of key life history traits (like incubation shift and metabolic rate) and environmental conditions.

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1. Introduction

Phenotypic flexibility of organ size occurs in response to environmental factors or physiological states in birds, mammals and reptiles (molt: Fox and Kahlert, 2005; Bauchinger and Biebach, 2006; diet: Secor and Diamond, 1995; Starck, 1999; Dekinga et al., 2001; altitude: Hammond et al., 2001). Changes in organ size and lipid reserves allow identification of flexibility in organ mass, suggesting they are strategies for dealing with annual life history events (Piersma and Lindström, 1997). For example, large energy stores (lipids) are expected prior to extended fasting (e.g. incubating penguins) or energy utilization (e.g. migration) and smaller energy stores are expected when food is readily available, and when predation risk or

energy costs associated with extra lipids outweigh the benefit of additional energy stores (Loesch et al., 1992; Barboza and Jorde, 2002; Portugal et al., 2007). Nonetheless, while it was once assumed that only lipid reserves varied in migratory birds (Odum et al., 1964), it is now known that the non-lipid body components are also flexible; the digestive organs of some migrating birds hypertrophy while flight muscles for some migrating birds atrophy to facilitate fuelling, then the reverse occurs prior to departure to improve flight performance (Gaunt et al., 1990; Hume and Biebach, 1996; Jehl, 1997; Piersma, 1998; Piersma and Gill, 1998; Landys-Ciannelli et al., 2003).

Programmed organ changes in breeding birds are less often studied than changes in response to migration and molt (but see Jehl, 1997; Christians and Williams, 1999; Vézina and Williams, 2003), despite mass loss during reproduction being a common phenomenon (Moreno, 1989; Gaston and Perin, 1993). Seabirds are of particular interest because many have exceptionally long breeding seasons and foraging ranges, and so have high energy costs and extended periods for

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adjustment of organ size (Gaston, 2004). The breeding season is characterized by periods of fasting during incubation and high energy demand during chick-rearing. As such, energy stores are likely to be important during incubation to increase fasting endurance, exercise and digestive organs may be important during chick-rearing, and the relative importance of each likely varies with the length of the fasting period and energy demands during provisioning. For example, because some procellariiform seabirds (long fasting period, low flight metabolic rate) show a dramatic decline in body mass through a loss of lipids at the most energetically-costly time, it is often considered “responsive” to the environment (Weimerskirch and Lys, 2000; Weimerskirch et al., 2001). In contrast, mass loss in several charadriiform seabirds (short fasting period, high flight metabolic rate) is often classified as “programmed” because it occurs stepwise at the time of hatching (Gaston and Jones, 1989; Gaston and Perin, 1993; Jones, 1994; Niizuma et al., 2002; but see Hull et al., 2002; Elliott et al., 2004), can occur through a change in lean mass (Bech et al., 2002) and can lead to reduced basal, flight and dive costs during the chick-rearing period (Croll et al., 1991; Bech et al., 2002; Elliott et al., 2008). The “responsive” and “programmed” paradigms are not exclusive and programmed trajectories are modulated in response to environmental cues (e.g. Gaston and Hipfner, 2006a,b). Thus, although seabirds from different taxonomic groups show mass loss during reproduction, the body components responsible for such mass loss may differ, presumably reflecting variation in life histories.

Because past studies of organ dynamics in seabirds were conducted at different locations, variation in organ dynamics among seabirds may represent variation in the environmental conditions experienced during particular research projects rather than species-specific life histories. Thus, we investigated changes in body composition of three coexisting seabirds with very different life histories (Table 1) in a year when heavy ice cover meant that all breeding biology indicators suggested that all three species were at the limits of their ability to reproduce (see Gaston et al., 2005b for details). For the purposes of this study, the challenging environmental conditions were fortuitous. Birds presumably had little surplus energy for allocation, were investing heavily in reproduction, and breeding was largely synchronous. Thus, confounding variations due to time of breeding and parental quality were presumably reduced. We asked: 1) What is the relative contribution of fat and organs to changes in body mass? 2) Do organ masses change in a predictable manner according to life history or are they conserved across species? Birds rely on stored energy during long incubation shifts (rather than high energy intake and turnover during chick-rearing), and we hypothesize that lipids should decrease during chick-rearing while liver and kidney increase due to increased energy intake and higher metabolic demand (Hammond and Janes, 1998). The fasting endurance hypothesis states that variation in body size among animals is determined by the predictability of food resources; large animals evolve in habitats where large prey items are encountered infrequently (long fasts) while small animals occur in predictable environments where food is always available but in small quantities (short fasts; Millar and Hickling, 1990). Based on the fasting endurance hypothesis, we predict that those seabirds with the longest incubation fasts (fulmars) would

have the highest variability in lipids during incubation while those seabirds with the highest field metabolic rates (murre/murres/kittiwakes) would have the highest variability in lean mass and exercise organs.

2. Materials and methods

During June–August 2002, we collected 41 thick-billed murre (*Uria lomvia*; TBMU; 18 males, 23 females), 31 northern fulmars (*Fulmarus glacialis*; NOFU; 24 males, 7 females), and 30 black-legged kittiwakes (*Rissa tridactyla*; BLKI; 16 males, 14 females) from a breeding colony at Prince Leopold Island, Nunavut, Canada (74°02'N, 90°00'W). The species studied feed within the same Arctic food web, taking similar prey (Bradstreet, 1982; Hobson and Welch, 1993; Hobson, 1993). Based upon studies of mass dynamics, samples were taken at times when the variation in body condition between sampling periods was expected to be greatest (see Gaston and Hipfner, 2006a, b; Elliott et al., 2010): (1) early incubation (0–10 d post-lay for TBMU and BLKI, 10–20 d post-lay for NOFU); (2) late incubation (TBMU only, 20–30 d post-lay); and (3) chick-rearing (0–10 d post-hatch). Immediately after capture, each bird was weighed, killed using a guillotine, and placed in a sealed plastic bag. Morphometric measures (wing, leg, and culmen lengths) were taken from all birds after death. Carcasses were placed in frozen storage (approx. –20 °C) until they were shipped to the laboratory on ice in a well sealed cooler. Ethical concerns associated with the killing of wild birds were carefully considered and all birds were used in conjunction with two other research projects with specimen material shared after the completion of the current project.

2.1. Laboratory procedures

Bird carcasses were allowed to thaw partially and all but the head and wing feathers were removed. The abdomen and breast feathers of murre were shaved because they were very difficult to pluck without extracting fat and muscle from beneath the skin. After plucking and weighing the feathers, the birds were refrozen until they were thawed completely for dissection. Total fat was measured by adding the contributions from breast muscle, liver, skin (including subcutaneous fat), combined visceral organs (except liver), and combined carcass (including bones). The skin, organs, and carcass were homogenised prior to the collection of the sub-samples. Breast muscle and liver samples were collected from the whole, unground organ. Each tissue was homogenised in Folch reagent (chloroform: methanol, 2:1 v/v). After filtration (Whatman 1) to remove solid material, 0.25% KCl was added to help remove any remaining aqueous components. The samples were placed in a water bath at 70 °C for 5 min to separate aqueous and organic phases. After removal of the aqueous phase, the organic phase was evaporated and total lipids were weighed (± 0.001 g). Based upon the fat mass in each subsample, total fat mass was determined for each whole tissue. Total fat mass for the individual bird (minus the legs, wings and head) was the sum of these five values. Protein mass of tissues was calculated by subtracting the lipid mass from the total mass.

Table 1
Changes in lipids and coefficients of variation (CV) relative to life history for black-legged kittiwakes, thick-billed murre and northern fulmars. Incubation period (IP), shift length (ISL), clutch size (Clutch) and field metabolic rate as a multiple of BMR (FMR) from the literature (Baird, 1994; Hatch and Nettleship, 1998; Gaston and Hipfner, 2000; Gaston et al., 2005a,b; Mallory et al., 2008); other data from this study.

Species	Mass	IP	ISL	Clutch	% lipids ^a	FMR	Metabolic rate (kJ/d/g)	% change ^b	Organs involved	CV (body mass)	CV (lipids)
Kittiwake	359 g	26 d	~4 h	2–3 ^c	6.9%	5×	2.3 ^d	+10%	Muscle	0.099	0.31
Murre	722 g	33 d	~12–24 h	1 ^c	7.3%	10×	2.4 ^d	–5.4%	Lipid	0.081	0.34
Fulmar	875 g	50 d	~168 h	1	13.3%	2–4×	1.8 ^e	–7.2%	Lipid	0.100	0.35

^a Percent of body mass.

^b Difference between incubation (late incubation for murre) and chick-rearing body mass as a percent of average body mass.

^c Can relay if first egg is lost.

^d Kitaysky et al. (2000), KHE, unpubl. data.

^e Furness and Bryant (1996).

Further details for murres are available elsewhere (Elliott et al., 2008; their “bladder” should be “gall bladder”).

2.2. Statistical analysis

We used Principal Components Analysis (PCA) to develop an index of body size using bill depth, culmen, tarsus, wing chord and tube length (fulmar only). We calculated the residual values of the logarithm of organ mass on the logarithm of scaled PC1 for body size to account for body size, and used those values in all further analyses. We used PCA to group our organs/tissues into related groups and to allow us to determine the direction and strength of the inter-relationships among organs. We considered the heart, lungs and breast muscle to be exercise tissues and the stomach, gizzard, intestine, kidneys and liver to be digestive tissues. To account for desiccation, we included percent difference between fresh and frozen weight (mean = $92 \pm 2\%$) in all PCAs. Because the stomach, gizzard and gonads were not normally distributed, they were excluded from PCAs. We determined the significance of PC's using *P* values generated by randomizations of eigenvalues performed by PC-ORD. We used ANCOVA to test for differences between breeding stages while correcting for body mass. Because the large number of tissues involved would mean many multiple comparisons, and power analyses showed that we would be unlikely to find significance at the Bonferroni-corrected values, thus making Type II errors, we only compared the principal components among periods. PCA were carried out using PC-ORD 5.0 (McCune and Mefford, 1999) and SYSTAT version 8.0 for ANCOVAs and other tests. Comparisons were considered significant at $\alpha = 0.05$ level.

3. Results

Fulmar body mass was lower during chick-rearing than during incubation (period: $F_{1,27} = 4.43$, $P = 0.045$, sex: $F_{1,27} = 9.04$, $P = 0.006$, interaction: $F_{1,27} = 2.47$, $P = 0.13$). Fulmar PC1 for body size increased with mass ($t_{30} = 3.00$, $R^2 = 0.24$, $P = 0.005$) and was significantly higher for males than for females (i.e. males were larger than females; $t_8 = 4.35$, $P = 0.002$). Murre body mass was lower during chick-rearing than late incubation (period: $F_{2,30} = 8.56$, $P = 0.006$, sex: $F_{1,30} = 0.04$, $P = 0.85$, interaction: $F_{2,30} = 0.21$, $P = 0.65$), with no difference between early and late incubation (period: $F_{2,35} = 1.73$, $P = 0.192$, sex: $F_{1,35} = 0.09$, $P = 0.78$, interaction: $F_{2,35} = 0.37$, $P = 0.70$). Murre PC1 for body size was independent of mass ($t_{41} = 0.27$, $R^2 = 0.00$, $P = 0.79$) and with no difference between males and females ($t_{18} = 0.18$, $P = 0.90$). Kittiwake body mass was higher during chick-rearing than during incubation (period: $F_{1,27} = 11.59$, $P = 0.002$, sex: $F_{1,27} = 7.2$, $P = 0.012$, interaction: $F_{1,27} = 0.46$, $P = 0.50$). Kittiwake PC1 for body size decreased with mass ($t_{31} = -2.85$, $R^2 = 0.22$, $P = 0.008$) and was significantly lower for males than for females (i.e. males were larger than females; $t_{15} = 5.06$, $P = 0.0001$). Thus, fulmars and murres were heavier in incubation while kittiwakes were heavier in chick-rearing. Bigger fulmars and kittiwakes, but not murres, tended to be male.

All three species showed significant differences in body composition among the sampling periods (fulmars: PC1, $t_{17} = 3.09$, $P = 0.003$, PC2, $t_{17} = 2.67$, $P = 0.01$; murres: PC1, $F_{2,39} = 23.6$, $P < 0.0001$, PC2, $F = 10.2$, $P = 0.003$; kittiwakes: PC1, $t_{24} = 2.32$, $P = 0.01$, PC2, $t_{24} = 1.19$, $P = 0.12$). For fulmars, digestive organs were intercorrelated (highly loaded on PC2), heavier during chick-rearing and largely unrelated to body mass (Table 4, Fig. 1). Skin, lipids and heart were heavier during incubation and largely related to

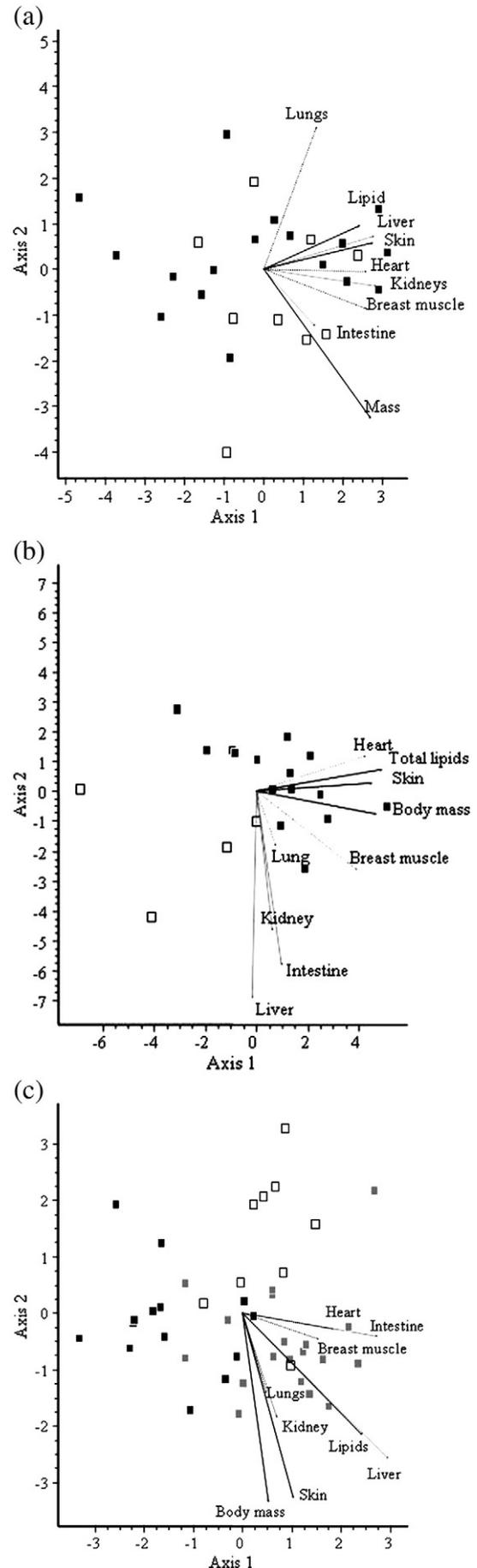


Fig. 1. Principal Components Analysis of the residual of organ size on overall body size during early incubation (closed symbols), late incubation (grey symbols) and chick-rearing (open symbols) for (a) black-legged kittiwakes, (b) northern fulmar and (c) thick-billed murre.

Table 2
Mean mass of body tissues in northern fulmars and black-legged kittiwakes during incubation and chick-rearing.

Tissue	Fulmar			Kittiwake		
	Mass \pm SD (g)		Change ^a	Mass \pm SD (g)		Change
	Incubation	Chick-rearing		Incubation	Chick-rearing	
Body	741 \pm 63	688 \pm 78	0.93	337 \pm 31	373 \pm 32	1.11
Body lipid	114 \pm 34	58 \pm 19	0.51	26 \pm 11	24 \pm 7	0.92
Skin	108 \pm 31	64 \pm 15	0.59	27 \pm 7	30 \pm 8	1.11
Skin lipid	60 \pm 25	25 \pm 10	0.42	9 \pm 5	9 \pm 4	1.00
Lean	562 \pm 39	548 \pm 67	0.98	288 \pm 32	305 \pm 28	1.06
Gonads	0.28 \pm 0.07	0.19 \pm 0.01	0.68	0.25 \pm 0.19	0.13 \pm 0.09	0.52
Liver	13.6 \pm 2.0	15.9 \pm 2.7	1.17	12.6 \pm 2.1	13.1 \pm 2.0	1.04
Intestine	11.7 \pm 2.1	12.8 \pm 1.9	1.09	5.2 \pm 1.3	5.3 \pm 0.7	1.02
Gizzard	7.4 \pm 0.9	5.3 \pm 2.4	0.72	4.6 \pm 0.8	4.7 \pm 1.5	1.02
Stomach	8.7 \pm 4.8	6.7 \pm 3.4	0.77	3.0 \pm 0.9	3.2 \pm 1.2	1.07
Kidneys	5.3 \pm 0.7	5.6 \pm 0.7	1.06	3.4 \pm 0.5	3.4 \pm 0.4	1.00
Lungs	7.3 \pm 1.7	6.6 \pm 1.6	0.90	5.0 \pm 1.0	4.5 \pm 0.6	0.90
Heart	6.9 \pm 0.9	6.1 \pm 0.9	0.88	4.7 \pm 0.5	4.9 \pm 0.7	1.04
Breast muscle	70 \pm 8	68 \pm 10	0.97	48 \pm 6	52 \pm 6	1.08

^a Change = value during chick-rearing – value during incubation.

body mass (Tables 2 and 4). Exercise organs (except heart) were intercorrelated and higher during chick-rearing and highly loaded on PC3 (Fig. 1). For murres, digestive organs were intercorrelated and highly loaded on PC2, and heavier during late incubation than other times (Fig. 1). Exercise organs were intercorrelated on PC1, heaviest during late incubation and relatively unrelated to body mass (Fig. 1). Skin, lipids and liver were all also heavier during late incubation and correlated with body mass (Tables 3 and 4). For kittiwakes, both exercise (except lungs) and digestive organs were intercorrelated on PC1, heaviest during chick-rearing and relatively unrelated to body mass (although breast muscle and intestine mass were correlated with body mass, Fig. 1, Table 2). Stomach mass had a bimodal distribution for fulmars and murres. Thus, digestive and exercise organs made natural groupings for murres and fulmars, but less so for kittiwakes. Furthermore, digestive organs tended to be heavier for murres during late incubation and for kittiwakes and fulmars during chick-rearing.

4. Discussion

The species with longest incubation shifts and lowest locomotory costs (the procellariiform life history strategy) showed strong demarcation between exercise and digestive organs (Fig. 1), the highest percent lipids (Tables 3 and 4) and the highest variability in lipid stores (Table 1). Thus, the organ dynamics of fulmars appeared to reflect its strategy of exceptionally long fasts during incubation

(Table 1), when digestive organs are reduced, possibly to reduce metabolic costs when they are not needed, and lipid stores are augmented to increase fasting endurance in the case of the mate delaying return. The importance of lipids during fasting was demonstrated by a pair caught during their changeover. The male, which was about to leave, weighed 630 g and had 66 g of total body lipid while the returning female weighed 720 g and had 120 g of total body lipid. In contrast, the species with the shortest incubation shifts and higher locomotory costs (the charadriiform life history strategy) showed simultaneous, similar changes in exercise and digestive organs (Fig. 1), the lowest percent lipids (Tables 3 and 4) and the lowest variability in lipid stores. The organ dynamics of kittiwakes therefore appeared to reflect little adaptation for fasting but strong adaptation for high metabolic rate and energy turnover during chick-rearing (larger exercise and digestive organs). Both kittiwakes and fulmars showed higher variation in body mass than murres (Table 1), presumably because their lower wing-loading provides them with higher flexibility with respect to flight demands (Elliott and Gaston, 2005). Murres, intermediate in incubation shift and with also high locomotory costs showed relationships intermediate between kittiwakes and murres. Exercise and digestive organ changes were decoupled, but not to the extent of fulmars, while percent lipid and variability in lipid stores were intermediate.

The effect of the very poor ice conditions in 2002, leading to among the poorest reproductive success and chick growth rate on record for murres and kittiwakes (Gaston et al., 2005b), could be seen in the organ dynamics. While kittiwakes elsewhere decline in body mass between incubation and chick-rearing (Golet and Irons, 1999; Moe et al., 2002), kittiwakes increased in body mass during our study. We suggest that during the incubation period, when ice dominated virtually the entire foraging range of kittiwakes in the vicinity of the colony (Gaston et al., 2005b), lipid and muscle mass were both low. By chick-rearing, when open water was present close to the colony and feeding conditions were back to “normal”, kittiwakes replenished their own muscle stores. Thus, in accordance with previous studies, lean and body mass reflected “body condition” (Golet and Irons, 1999; Moe et al., 2002), and this improved during the breeding season due to reduced stress (increased food availability, see Kitaysky et al., 2006; Schultz and Kitaysky, 2008). The strong effect of ice conditions in 2002 may also be evident in the murre data set; presumably, some of the increase in organ size (especially digestive organs) between early and late incubation represents replenishing of material lost when feeding was poor because ice covered the foraging range of murres during early incubation. The advantage of the procellariiform life history strategy (long incubation shifts, low metabolic rate) was also clearly evident. Fulmars were less impacted by ice conditions because they

Table 3
Mean mass of body tissues in thick-billed murres during early incubation (EI), late incubation (LI), and chick-rearing (CR).

Tissue	Mass (g \pm SD)			Change (EI vs. LI)	Change (LI vs. CR)
	EI	LI	CR		
Body	871 \pm 46	888 \pm 61	836 \pm 88	1.02	0.94
Body lipid	45 \pm 17	65 \pm 26	48 \pm 13	1.44	0.74
Skin	93 \pm 18	109 \pm 18	84 \pm 32	1.17	0.77
Skin lipid	24 \pm 12	38 \pm 20	24 \pm 5	1.58	0.63
Lean	745 \pm 34	760 \pm 71	739 \pm 52	1.02	0.97
Gonads	3.2 \pm 1.7	1.3 \pm 1.7	0.3 \pm 0.1	0.41	0.23
Liver	31 \pm 5	39 \pm 3	32 \pm 5	1.26	0.82
Intestine	20 \pm 4	24 \pm 3	19 \pm 1	1.20	0.79
Gizzard	10 \pm 2	11 \pm 1	10 \pm 3	1.10	0.91
Stomach	8.4 \pm 3.4	7.5 \pm 2.5	6.6 \pm 2.9	0.89	0.88
Kidneys	10.2 \pm 1.0	10.9 \pm 0.8	10.2 \pm 1.6	1.07	0.94
Lungs	9.1 \pm 1.5	9.4 \pm 1.8	8.8 \pm 1.2	1.03	0.94
Heart	8.9 \pm 1.2	9.8 \pm 1.1	9.2 \pm 1.5	1.10	0.94
Breast Muscle	180 \pm 12	184 \pm 14	186 \pm 20	1.02	1.01

Table 4

Loadings for first three principal components for each species. Significant loadings (randomization test) are shown in bold.

	Murre			Fulmar			Kittiwake		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Variation explained	35%	16%	11%	41%	16%	12%	36%	17%	10%
Mass	0.41	−0.24	0.05	0.33	−0.05	0.08	0.36	− 0.43	0.05
Skin	0.31	−0.22	− 0.33	0.31	−0.01	0.07	0.36	0.08	0.25
Lipids	0.35	−0.05	−0.29	0.35	0.06	0.06	0.32	0.13	0.27
Breast muscle	0.25	−0.22	0.57	0.28	−0.19	0.21	0.34	−0.11	0.11
Heart	0.41	0.10	−0.10	0.30	0.09	0.10	0.34	−0.01	− 0.32
Lungs	0.35	−0.08	−0.02	0.05	−0.13	0.58	0.18	0.41	0.17
Liver	0.30	0.37	0.03	−0.01	− 0.50	−0.01	0.37	0.10	−0.14
Intestine	0.21	0.46	0.00	0.07	− 0.42	−0.11	0.17	−0.16	− 0.54
Kidneys	0.23	0.08	−0.18	0.04	− 0.33	0.04	0.38	−0.05	0.13

forage much further away (Gaston et al., 2005b), which may explain why they were capable of adjusting exercise and digestive organs in different directions whereas kittiwakes adjusted all organs downwards during the time of greatest stress (incubation).

Reproductive success for murre was particularly low in 2002 (Gaston et al., 2005b), which supports our prediction that parents were working at a maximum physiological threshold (Magrath, 1991; Gaston et al., 2005a,b). Those individuals collected during chick-rearing may have included a higher proportion of older birds than in an average year due to environmental conditions. We consider this sampling bias as an advantage for the identification of thresholds since it would be likely that younger birds would have a heavier threshold than older birds. The finding suggests that these birds maintained an energy buffer and that there was a threshold below which effects on the current reproductive effort were observed. Many seabirds show a decrease in mass during reproduction until reaching a common mass and, therefore, a lower coefficient of variation, late in the breeding season (Gaston and Jones, 1989; Velando and Alonzo-Alvarez, 2003; Gaston and Hipfner, 2006a). In murre, the decline in coefficient of variation in total lipids may suggest an optimal level or, given the challenging environmental conditions, a minimum threshold for the size of lipid stores below which reproductive effort may cease. This idea is further supported by the observation that when two birds abandoned following attachment of handicaps during another experiment (Elliott et al., 2007), their partners maintained brooding of the small chicks for ~48 h before eventually abandoning. One bird went from 980 g to 860 g, whereas another went from 930 g to 850 g. The final measurements were made within 5 h of abandonment. This suggests that below a minimum threshold of about 850 g (just above the average mass of chick-rearing birds in this study) murre decide to abandon in favour of replenishing their reserves. Gaston and Hipfner (2006a) also suggested an average mass at abandonment of about 850 g, although breeding murre as light as 800 g have been observed.

The bimodal distribution for stomach size in fulmars and murre may reflect dietary specialization, as individual murre are known to specialize on certain prey items, such as invertebrates (quick digestion) or large fish (longer digestion; Hilton et al., 2000; Woo et al., 2008).

With few exceptions, lipid mass variation is the main source of body mass variation for most birds, and this was the case in our study for both fulmars and murre. Changes in lipid mass can occur either to optimize competing demands of locomotion and fasting endurance (programmed) or in response to change in energy demands or intake (responsive) (Monaghan et al., 1989; Robin et al., 2001). Changes in lean mass, including muscle mass, are often associated with stress-related mass reduction although they may also be part of a strategy to reduce energy costs through removal of metabolically-expensive tissues (Blem, 1990; Gaunt et al., 1990; Robin et al., 2001; Kullberg et al., 2002).

In our case, mass variation from incubation to chick-rearing was accompanied by variation in organ size, the extent of which correlated

with the amount of overall mass change. As organs were often adjusted in opposite directions during our study, and in the manner predicted by their life history, we suggest that changes were at least partly programmed. Nonetheless, the strong stress induced by ice conditions in 2002 was also evident. Thus, organ dynamics in seabirds are a combination of their life histories and specific environmental conditions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.cbpb.2010.09.011.

References

- Baird, P.H., 1994. Black-legged kittiwake. In: Poole, A., Gill, F. (Eds.), *The Birds of North America* no. 92. The Birds of North America, Inc, Philadelphia.
- Barboza, P.S., Jorde, D.G., 2002. Intermittent fasting during winter and spring affects body composition and reproduction of a migratory duck. *J. Comp. Physiol. B* 172, 419–434.
- Bauchinger, U., Biebach, H., 2006. Transition between moult and migration in a long-distance migratory passerine: organ flexibility in the African wintering area. *J. Ornithol.* 147, 266–273.
- Bech, C., Langseth, I., Moe, B., Fyhn, M., Gabrielsen, G.W., 2002. The energy economy of the arctic-breeding kittiwake (*Rissa tridactyla*): a review. *Comp. Biochem. Physiol.* A 133, 765–770.
- Blem, C.R., 1990. Avian energy storage. In: Power, D.M. (Ed.), *Current Ornithology*. Plenum Press, New York, pp. 59–113.
- Bradstreet, M.S.W., 1982. Occurrence, habitat use and behaviour of seabirds, marine mammals and arctic cod at the Pond Inlet ice edge. *Arctic* 35, 28–40.
- Chistians, J.K., Williams, T.D., 1999. Organ mass dynamics in relation to yolk precursor production and egg formation in European starlings *Sturnus vulgaris*. *Physiol. Biochem. Zool.* 72, 455–461.
- Croll, D.A., Gaston, A.J., Noble, D.G., 1991. Adaptive mass loss in thick-billed murre. *Condor* 93, 496–502.

- Dekinga, A., Dietz, M.W., Koolhaas, A., Piersma, T., 2001. Time course and reversibility of changes in the gizzards of red knots alternatively eating hard and soft food. *J. Exp. Biol.* 204, 2167–2173.
- Elliott, K.H., Gaston, A.J., 2005. Flight speeds of seabirds: a test of Norberg's hypothesis. *Ibis* 147, 783–789.
- Elliott, K.H., Hewett, M., Kaiser, G.W., Blake, R.W., 2004. Flight energetics of the marbled murrelet *Brachyramphus marmoratus*. *Can. J. Zool.* 82, 644–652.
- Elliott, K.H., Davoren, G.K., Gaston, A.J., 2007. The influence of buoyancy and drag on the dive behaviour of an arctic seabird, the thick-billed murre. *Can. J. Zool.* 85, 352–361.
- Elliott, K.H., Jacobs, S.R., Ringrose, J., Gaston, A.J., Davoren, G.K., 2008. Is mass loss in Brünnich's guillemots *Uria lomvia* an adaptation for improved flight performance or improved dive performance? *J. Avian Biol.* 39, 619–628.
- Elliott, K.H., Crump, D., Gaston, A.J., 2010. Sex-specific behaviour in a monomorphic seabird represents risk partitioning. *Behav. Ecol.* 21, 1024–1032.
- Fox, A.D., Kahlert, J., 2005. Changes in body mass and organ size during wing moult in non-breeding greylag geese *Anser anser*. *J. Avian Biol.* 36, 538–548.
- Furness, R.W., Bryant, D.M., 1996. Effect of wind on field metabolic rates of breeding northern fulmars. *Ecology* 77, 1181–1188.
- Gaston, A.J., 2004. Seabirds: a natural history. *AJ Poyser*. London UK.
- Gaston, A.J., Hipfner, J.M., 2006a. Body mass changes in Brünnich's guillemots *Uria lomvia* with age and breeding stage. *J. Avian Biol.* 37, 101–109.
- Gaston, A.J., Hipfner, J.M., 2006b. Breeding Brünnich's guillemots balance maintenance of body condition against investment in chick growth. *Ibis* 148, 106–113.
- Gaston, A.J., Jones, I.L., 1989. The relative importance of stress and programmed anorexia in determining mass loss by incubating ancient murrelets. *Auk* 106, 653–658.
- Gaston, A.J., Perin, S., 1993. Loss of mass in breeding Brünnich's guillemots *Uria lomvia* is triggered by hatching. *Ibis* 135, 472–474.
- Gaston, A.J., Gilchrist, H.G., Hipfner, J.M., 2005a. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brünnich's guillemot (*Uria lomvia* L.). *J. Anim. Ecol.* 74, 832–841.
- Gaston, A.J., Gilchrist, H.G., Mallory, M.L., 2005b. Variation in ice conditions has strong effects on the breeding of marine birds at Prince Leopold Island, Nunavut. *Ecography* 28, 331–344.
- Gaunt, A.S., Hikida, R.S., Jehl, J.R., Fenbert, L., 1990. Rapid atrophy and hypertrophy of an avian flight muscle. *Auk* 107, 649–659.
- Golet, G.H., Irons, D.B., 1999. Raising young reduces body condition and fat stores in black-legged kittiwake. *Oecologia* 120, 530–538.
- Hammond, K.A., Janes, D.N., 1998. The effects of increased protein intake on kidney size and function. *J. Exp. Biol.* 201, 2081–2090.
- Hammond, K.A., Szewczak, J., Krol, E., 2001. Effects of altitude and temperature on organ phenotypic plasticity along an altitudinal gradient. *J. Exp. Biol.* 204, 1991–2000.
- Hilton, G.M., Furness, R.W., Houston, D.C., 2000. A comparative study of digestion in North Atlantic seabirds. *J. Avian Biol.* 31, 36–46.
- Hobson, K.A., 1993. Trophic relationships among high Arctic seabirds – insights from tissue-dependent stable-isotope models. *Mar. Ecol. Prog. Ser.* 95, 7–18.
- Hobson, K.A., Welch, H.E., 1993. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* 84, 9–18.
- Hull, C.L., Vanderkist, B., Loughheed, L., Kaiser, G.W., Cooke, F.J., 2002. Body mass variation in marbled murrelets in British Columbia. *Ibis* 144, E88–E96.
- Hume, J.D., Biebach, H., 1996. Digestive tract function in the long-distance migratory garden warbler, *Sylvia borin*. *J. Comp. Physiol.* 166, 388–395.
- Jehl, J.R., 1997. Cyclical changes in body composition in the annual cycle and migration of the eared grebe *Podiceps nigricollis*. *J. Avian Biol.* 28, 132–142.
- Jones, I.L., 1994. Mass changes of least auklets *Aethia pusilla* during the breeding season: evidence for programmed loss of mass. *J. Anim. Ecol.* 63, 71–78.
- Kitaysky, A.S., Hunt, G.L., Flint, E.N., Rubega, M.A., Decker, M.B., 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar. Ecol. Prog. Ser.* 206, 283–296.
- Kitaysky, A.S., Kitaiskaia, E.V., Piatt, J.F., Wingfield, J.C., 2006. A mechanistic link between chick diet and decline in seabirds? *Proc. R. Soc. Lond. B* 273, 445–450.
- Kullberg, C., Metcalfe, N.B., Houston, D.C., 2002. Impaired flight ability during incubation in the pied flycatcher. *J. Avian Biol.* 33, 179–183.
- Landys-Ciannelli, M.M., Piersma, T., Jukema, J., 2003. Strategic size changes of internal organs and muscle tissue in the bar-tailed godwit during fat storage on a spring stopover site. *Funct. Ecol.* 17, 151–159.
- Loesch, C.R., Kaminski, R.M., Richardson, D.M., 1992. Endogenous loss of body mass by mallards in winter. *J. Wildl. Manage.* 56, 735–739.
- Magrath, R.D., 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.* 60, 335–351.
- Mallory, M.L., Gaston, A.J., Forbes, M.R., Gilchrist, H.G., Cheney, B., Lewis, S., Thompson, P.M., 2008. Flexible incubation rhythm in northern fulmars: a comparison between oceanographic zones. *Mar. Biol.* 154, 1031–1040.
- McCune, B., Mefford, M.J., 1999. PC-ORD: multivariate analysis of ecological data, version 5.0. MjM Software Design, Gleneden Beach, Oregon.
- Millar, J.S., Hicking, G.J., 1990. Fasting endurance and the evolution of mammalian body size. *Funct. Ecol.* 4, 5–12.
- Moe, B., Langseth, I., Fyhn, M., Gabrielsen, G.W., Bech, C., 2002. Changes in body condition in breeding kittiwakes *Rissa tridactyla*. *J. Avian Biol.* 33, 225–234.
- Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C., Blackwood, J., 1989. The relationship between food supply, reproductive effort and breeding success in Arctic terns (*Sterna paradisaea*). *J. Anim. Ecol.* 58, 261–274.
- Moreno, J., 1989. Strategies of mass change in breeding birds. *Biol. J. Linn. Soc.* 37, 297–310.
- Niizuma, Y., Araki, Y., Mori, H., Takahashi, A., Watanuki, Y., 2002. Responses of body components to changes in the energetic demand throughout the breeding status of rhinoceros auklets. *Can. J. Zool.* 80, 1549–1555.
- Odum, E.P., Rogers, D.T., Hicks, D.L., 1964. Homeostasis of the nonfat components of migrating birds. *Science* 143, 1037–1039.
- Piersma, T., 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of refuelling and flight? *J. Avian Biol.* 29, 511–520.
- Piersma, T., Gill, R.E., 1998. Guts don't fly: small digestive organs in obese bar-tailed godwits. *Auk* 115, 196–203.
- Piersma, T., Lindström, Å., 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol. Evol.* 12, 134–138.
- Portugal, S.J., Green, J.A., Butler, P.J., 2007. Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): the importance of wing moult. *J. Exp. Biol.* 210, 1391–1397.
- Robin, J.-P., Fayolle, C., Decrock, F., Thil, M.A., Cote, S.D., Bernard, S., Groscolas, R., 2001. Restoration of body mass in king penguins after egg abandonment at a critical energy depletion stage: early vs. late breeders. *J. Avian Biol.* 32, 303–310.
- Schultz, M.T., Kitaysky, A.S., 2008. Spatial and temporal dynamics of corticosterone and corticosterone-binding globulin are driven by environmental heterogeneity. *Gen. Comp. Endocrinol.* 155, 717–728.
- Secor, S.M., Diamond, J., 1995. Adaptive responses to feeding in Burmese pythons: pay before pumping. *J. Exp. Biol.* 198, 1313–1325.
- Starck, J.M., 1999. Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Zool.* 202, 3171–3179.
- Velando, A., Alonso-Alvarez, C., 2003. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental efforts in the blue-footed booby. *J. Anim. Ecol.* 72, 846–856.
- Vézina, F., Williams, T.D., 2003. Plasticity in body composition in breeding birds: what drives the metabolic costs of egg productions? *Physiol. Biochem. Zool.* 76, 716–730.
- Weimerskirch, H., Lys, P., 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biol.* 23, 733–744.
- Weimerskirch, H., Chastel, O., Cherel, Y., Henden, J.-A., Tveraa, T., 2001. Nest attendance and foraging movements of northern fulmars rearing chicks in Bjornoya Barents Sea. *Polar Biol.* 24, 83–88.
- Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J., Davoren, G.K., 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.* 77, 1082–1091.