

EGG COMPOSITION IN RELATION TO FEMALE AGE AND RELAYING: CONSTRAINTS ON EGG PRODUCTION IN THICK-BILLED MURRES (*URIA LOMVIA*)

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ABSTRACT.—There is growing awareness that costs associated with egg production play a significant role in shaping avian life histories. The life-history strategy of the Thick-billed Murre (*Uria lomvia*), a colonial, cliff-breeding seabird of Arctic waters, is characterized by a high annual adult survival rate, deferred breeding, and laying of a single-egg clutch. The single-egg clutch is a widespread phenomenon among seabirds and is generally thought to reflect demands of chick provisioning, rather than egg production. We compared composition of eggs laid by Thick-billed Murres most likely to be physiologically constrained in their capacity to produce eggs (young females with no prior experience, and females forming replacement eggs) to that of first eggs laid by early laying females (typically older, more experienced members of the population). Young, inexperienced females laid 4–18 days past the population-wide median laying date, and their eggs averaged 13% lighter in mass than those laid by early layers. Compared to early laid eggs, shell mass on young females' eggs was similar to that predicted from egg mass, but their eggs had a lower yolk-to-albumen ratio. There was little difference between the two groups in relative protein content of albumen, relative protein or lipid content of yolk, or amino acid makeup of protein in yolk or albumen. Replacement eggs averaged 6% lighter in mass than first eggs laid by the same females earlier that season. As with young females' eggs, replacement eggs had shells similar in mass to that predicted from egg mass, but lower yolk-to-albumen ratios, when compared to early laid eggs. Both protein and lipid concentrations in yolk were similar in first and replacement eggs, but replacements were deficient in albumen protein. Amino acid makeup of protein in yolk and albumen was similar in the two groups. Those results suggest that any limitations on egg production acting on young, inexperienced females are manifested in delayed laying and reductions in overall egg mass and proportional yolk content, but not in variation in biochemical composition of their eggs. Limitations on females forming replacement eggs are manifested not only in reduced egg mass and yolk content (as with young females), but also in changes in the biochemical composition of eggs; in particular, evidence suggests that relaying females may face a deficit of endogenous protein. The existence of such limitations suggests that demands of egg production can be significant even in a species that lays a single-egg clutch. *Received 3 January 2002, accepted 3 February 2003.*

RÉSUMÉ.—Il y a une prise de conscience grandissante concernant les coûts associés à la production d'œufs qui jouent un rôle significatif en façonnant les traits d'histoire de vie chez les oiseaux. Chez le Guillemot de Brünnich (*Uria lomvia*), un oiseau des mers Arctiques, colonial et nichant sur les falaises, la stratégie en matière de traits d'histoire de vie se caractérise par un taux de survie annuel très élevé chez l'adulte, une reproduction pouvant être différée, et la ponte d'un seul œuf. Ce type de couvée est un phénomène répandu chez les oiseaux de mer. Ce

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phénomène est généralement considéré comme le reflet de la demande en approvisionnement par les jeunes, plutôt que la demande pour la production d'œufs. Nous avons comparé la composition d'œufs pondus par des Guillemots de Brünnich caractérisés par une plus grande tendance à être contraints physiologiquement quant à leur capacité à produire des œufs (i.e. les jeunes femelles sans expérience, et les femelles produisant des œufs de remplacement) à des œufs pondus par des femelles pondant plus tôt (typiquement plus âgées et possédant une plus grande expérience). Les jeunes femelles inexpérimentées, ayant pondu de 4 à 18 jours après la date médiane de ponte de la population, présentaient des œufs 13% plus légers en moyenne que ceux pondus par les femelles ayant pondu plus tôt. Comparativement aux œufs pondus plus tôt, la masse de la coquille des œufs des jeunes femelles était similaire à ce qui pouvait être prédit à partir de la masse des œufs, mais leurs œufs présentaient un rapport vitellus/albumen plus bas. Il y avait peu de différences entre les deux groupes dans la teneur relative en protéines de l'albumen, la teneur relative en protéines et en lipides du vitellus, et la constitution en acides aminés des protéines du vitellus ou de l'albumen. Les œufs de remplacement étaient 6% plus légers en moyenne que les premiers œufs pondus par les mêmes femelles mais plus tôt en saison. Comme pour les œufs pondus par les jeunes femelles, les œufs de remplacement avaient des masses de coquille similaires à ce qui pouvait être prédit à partir de la masse des œufs, mais un rapport vitellus/albumen plus faible par rapport aux œufs pondus plus tôt. Les concentrations en protéines et en lipides dans le vitellus étaient similaires dans les œufs initialement pondus et les œufs de remplacement, mais ces derniers étaient déficients quant à la quantité de protéines contenue dans l'albumen. La composition en acides aminés des protéines contenues dans le vitellus et l'albumen était similaire dans les deux groupes. Ces résultats suggèrent que toute limitation agissant sur la production d'œufs par des jeunes femelles inexpérimentées se manifeste par une ponte retardée, une réduction de la masse des œufs et de la teneur relative en vitellus, mais pas dans la composition biochimique de leurs œufs. Les limitations agissant sur les femelles produisant des œufs de remplacement se manifestent non seulement par une réduction de la masse des œufs et de la teneur en vitellus (comme dans le cas des jeunes femelles) mais aussi dans des changements de leur composition biochimique. En particulier, les résultats suggèrent que ces femelles pourraient faire face à un déficit en protéines endogènes. L'existence de telles limitations suggère que la demande nécessaire à la production d'œufs peut être significative et ce même au sein d'une espèce qui ne pond qu'un seul œuf par couvée.

AVIAN EGG PRODUCTION was an important topic in the development of life-history theory, mainly as a consequence of Lack's (1947) research on clutch size. Lack argued that egg production was not a particularly demanding process for birds, at least compared to chick-rearing, a conclusion he reached based largely on the apparent ease with which many species replace lost eggs and clutches. Inspired by Lack's thinking, research on avian life-history evolution for a long time focused on the chick-rearing period, while largely ignoring costs incurred during earlier phases of breeding (Monaghan et al. 1995, Monaghan and Nager 1997). However, recent research has shown that females that produce more than the usual number of eggs may be more susceptible to disease (Oppliger et al. 1996), and that they may subsequently provision their offspring less well (Heaney and Monaghan 1995). In addition, offspring that hatch from extra eggs may suffer higher-than-normal mortality, because they are of low

intrinsic quality (Monaghan et al. 1998, Nager et al. 2000). In some species, the female's capacity to produce eggs may be proximately constrained by food supply (Eldridge and Krapu 1988, Hochachka 1988, Oro et al. 1999), being limited by availability of energy (Nager and van Noordwijk 1992), calcium (Beintema et al. 1997), or protein (Robbins 1981), and in the latter case, by specific amino acids (Murphy 1994). In addition, relaying may be more common among females in better condition (Houston et al. 1983, Hegyi and Sasvári 1998), and among those that are older and more experienced (Wheelwright and Schultz 1994, Wiebe and Martin 1998). Egg and clutch size also increase with female age in many species (Coulson and White 1958, Robertson et al. 1993), a pattern that would not be expected if it was easy to produce large numbers of large eggs. Taken together, those observations suggest that demands of egg production can be significant, because of factors either internal or external to the female, and that

those demands may be important factors shaping avian life histories.

Thick-billed Murres (*Uria lomvia*) are highly colonial, cliff-breeding seabirds of Arctic waters. They employ a life-history strategy that is typical for a marine bird, with several years deferred breeding, a high annual adult survival rate, and a single-egg clutch (Gaston and Hipfner 2000). The single-egg clutch is generally thought to have evolved mainly in response to the extreme demands of raising offspring on patchy, unpredictable prey gathered at long distances from the colony, rather than to costs of egg production (Lack 1968). However, there is evidence that egg-production costs may be significant for murres within the framework of their life history. First, egg size increases with female age, and laying date advances over her first few breeding attempts (Hipfner et al. 1997). Second, usually only about 20–30% of females relay after they lose their egg (Gaston and Nettleship 1981, Birkhead and Nettleship 1987a), mainly because those females that lose eggs tend to be young and inexperienced (de Forest and Gaston 1996, Hipfner et al. 1999). In addition, there is a remarkably consistent 5–6% average reduction in the size of a female's replacement egg compared to her first egg (Birkhead and Nettleship 1982, Hipfner et al. 1997). Birkhead and Nettleship (1982, 1984) suggested that late-laying murres, including those forming replacement eggs, might facultatively reduce egg size to advance laying, ahead of a seasonal deterioration in feeding conditions. However, several lines of evidence suggest that it is unlikely that seasonal reductions in egg size reflect time-saving, evolutionary strategies for murres: (1) experienced females that lay late, and concurrently with young females, lay full-sized first eggs (Hipfner et al. 1997); (2) a large egg confers a time-saving advantage during posthatching chick development (Hipfner and Gaston 1999, Hipfner et al. 2001a); and (3) at low-Arctic colonies, feeding conditions do not deteriorate late in the season to an extent that the ability of capable parents to raise chicks is affected (de Forest and Gaston 1996, Hipfner 1997, Hipfner 2001). In fact, capable Thick-billed Murres show a clear willingness to continue to relay even until very late in the laying period, which suggests that relaying is an important component of their overall life-history strategy (Hipfner et al. 1999, 2001b). Although effects of

female age and laying date on egg size, and the ecology of relaying, have now been well studied in Thick-billed Murres, there has been no study of egg composition in relation to female age or relaying. That information could potentially shed light on whether physiological constraints, rather than strategic adjustments, are most important in limiting egg production in murres and other long-lived seabirds.

Here we examine the crude and biochemical composition of Thick-billed Murre eggs in an attempt to try to identify factors that might limit egg production. Our specific goals are to (1) describe characteristics of eggs laid prior to median laying date in two years at a low-Arctic colony, to examine how egg composition varies among years and in relation to egg size (i.e. allometry). Those data on the composition of eggs laid by early laying females (generally older, more experienced members of the population) provide a benchmark against which to make subsequent comparisons; (2) compare the composition of eggs laid by young females with no prior experience to that of early laid eggs; and (3) compare the composition of replacement eggs to that of first eggs laid previously by the same early laying females.

STUDY AREA AND METHODS

The study was conducted at the Thick-billed Murre colony of 30,000 pairs at Coats Island, Nunavut, Canada (62°57'N, 82°00'W), during 1998 and 1999. That colony is situated in the low-Arctic oceanographic zone (Nettleship and Evans 1985). A banding program to study demography of Thick-billed Murres has been ongoing there since 1984 (Gaston et al. 1994).

Egg collections.—To collect eggs from females that laid prior to median laying date, plots that held known numbers of breeding pairs were observed daily from viewing blinds beginning during the pre-laying period in both years. We measured timing of laying using Type I methods (Birkhead and Nettleship 1980). First eggs were collected within 24 h of laying in areas away from those plots on 20–21 June in 1998 ($n = 23$) and on 20–22 June in 1999 ($n = 17$). Median laying dates fell on 23 June in 1998, and 24 June in 1999. Locations of the 40 sites from which we removed eggs were recorded on sketch maps, and eggs were photographed with a Polaroid camera. In both years, we rechecked the 40 breeding sites from which we had taken eggs daily beginning 10 days after egg removal and continuing for an additional 15 days. When a new egg was found, it was compared

to the Polaroid photograph of the egg previously collected at the site to ensure that it was the appropriate replacement (the background color and pattern of markings are repeated on eggs laid by the same female). At accessible sites, replacement eggs were collected within 24 h of laying in both years for analysis of their composition ($n = 24$).

In 1999, we collected eggs laid by four and five year old females that had not been recorded breeding on plots observed daily in previous years ($n = 9$). Those eggs were laid 4–18 days after the median laying date for the population and were collected within 24 h of laying. To the best of our knowledge, none of those nine young females laid a replacement egg. All eggs were collected under permit from the Canadian Wildlife Service.

Analysis of crude composition.—All collected eggs were measured (length and maximum breadth to within 0.1 mm using vernier calipers; and mass to within 0.1 g on an electronic balance). They were boiled for 12 min, allowed to cool, reweighed, and then separated into shell and membranes, albumen, and yolk. Shell and membrane and yolk were both weighed to within 0.1 g on an electronic balance; because water is lost from albumen through boiling, albumen mass was taken to be the mass of the fresh, preboiled egg minus the mass of the shell and membranes and yolk. For each egg, shell thickness was measured to within 0.01 mm using a micrometer gauge at 10 points close to the egg's equator, and the average of those 10 measurements was calculated. The components of each egg were then packed into plastic bags and frozen for biochemical analysis.

Analysis of biochemical composition.—From among the eggs collected in the field in 1998, we selected seven early laid first eggs and seven replacement eggs laid by the same females for biochemical analysis. Those seven pairs of eggs were selected on the basis of visual inspection of their general condition upon arrival in the laboratory (i.e. we selected those that appeared to be in the best condition after the trip out of the field). Similarly, we selected the six eggs laid by young females in 1999 that appeared to be in the best condition for analysis of their biochemical composition.

For those 20 eggs, total lipids in yolk were determined gravimetrically following extraction with chloroform:methanol (2:1 v:v) as described by Folch et al. (1957). To determine protein content of albumen, a portion of each albumen was powdered in liquid nitrogen and dissolved in 0.1 N NaOH, and its protein content determined using the Biuret method (Layne 1957). To determine protein content of yolk, lipid was removed from a portion of yolk (Brocherhoff and Yurkowski 1965), and remaining protein dissolved in 0.1 N NaOH. Amino acid composition of both albumen and yolk was determined by hydrolyzing 0.5–2 mg samples in 1 mL of 6 N HCl with 0.05% phenol using 16 × 100 mm tubes with teflon-lined

screw caps. Tubes were purged for 5 min with nitrogen before capping. The HCl was removed under vacuum and the dried sample reconstituted with pH 2.2 lithium citrate buffer 0.2 M NaLi⁺ prior to analysis (Blackburn 1978, Gehrke et al. 1985). Methionine and cystine were determined after conversion to methionine sulfone and cysteic acid, respectively, via performic acid oxidation of samples, prior to hydrolysis in 6N HCl (Schram et al. 1954, Blackburn 1978, Ozols 1990). Briefly, 2 mL of performic acid solution (9 parts formic acid and 1 part 30% hydrogen peroxide) was added to 100–300 mg of powdered egg white or yolk, and oxidation was carried out overnight at room temperature. Performic acid was removed in a vacuum oven and hydrolysis in HCl and amino acid analysis was carried out as described above.

Field conditions necessitated that eggs be boiled and then frozen, and they experienced several periods of thawing and refreezing on the trip from field to laboratory. As a result, absolute measures of protein and lipid concentrations may be inaccurate. In particular, loss of water from albumen through boiling, and from albumen and yolk through freezing, will cause protein and lipid to be concentrated in the sample that remains. Therefore, we focus on relative measures, which we assume will be reliable because all eggs were processed in the same way. In those comparisons we use values in eggs laid by early laying females as benchmarks, then measure deviations from those values in the young females' eggs and in replacement eggs. Throughout, means are reported ± 1 SD.

RESULTS

Interyear variation in egg composition.—Information on mass and crude composition of early laid Thick-billed Murre eggs is presented in Table 1. Mean egg mass differed little between 1998 and 1999 ($t = 0.83$, $df = 38$, $P = 0.41$). Analyses of covariance (ANCOVA, on log-transformed data) showed that each of shell mass, albumen mass, and yolk mass increased strongly with egg mass, and that for all components, neither the elevations (year term) nor the slopes (interaction term) of the relationships differed significantly between samples (Table 2). With the two samples combined, the 40 eggs averaged 111.7 ± 8.5 g in mass, and by mass consisted of $12.6 \pm 0.8\%$ shell, $54.6 \pm 2.4\%$ albumen, and $32.8 \pm 2.2\%$ yolk; yolk-to-albumen ratios averaged 0.60 ± 0.07 , and the fraction of yolk in egg contents averaged 0.37 ± 0.03 . The 95% confidence bounds on the slopes of the regression lines relating log component masses to log egg mass showed that shell mass scaled with

TABLE 1. Variation in composition (mean \pm SD) of Thick-billed Murre eggs in relation to year, female age, and relaying.

Parameter	Early laid eggs			Eggs laid by the same female	
	Coats 1998	Coats 1999	Young 1999	First ^a	Replacement
<i>n</i>	23	17	9	24	24
Laying dates (range)	20–21 June	20–22 June	28 June–11 July	20–22 June	1–5 July
Whole egg (g)	110.7 \pm 9.1	113.0 \pm 7.6	98.8 \pm 6.4	110.3 \pm 7.6	103.8 \pm 7.5
Shell (g)	14.1 \pm 1.3	14.1 \pm 1.1	12.3 \pm 1.2	13.8 \pm 1.2	12.6 \pm 1.0
Percent whole egg	12.7 \pm 0.7	12.5 \pm 0.9	12.5 \pm 1.1	12.6 \pm 0.8	12.1 \pm 0.9
Thickness	—	0.54 \pm 0.04	0.54 \pm 0.05	0.53 \pm 0.04	0.51 \pm 0.04
Albumen (g)	59.8 \pm 6.8	62.9 \pm 6.0	53.6 \pm 5.1	60.2 \pm 5.5	57.9 \pm 5.3
Percent whole egg	53.9 \pm 2.5	55.6 \pm 2.0	54.2 \pm 1.9	54.5 \pm 1.8	55.7 \pm 2.5
Yolk (g)	36.9 \pm 2.6	35.9 \pm 1.9	32.8 \pm 1.7	36.2 \pm 2.1	33.4 \pm 3.3
Percent whole egg	33.4 \pm 2.4	31.9 \pm 1.7	33.3 \pm 1.7	32.9 \pm 1.7	32.1 \pm 2.4
Yolk:albumen	0.62 \pm 0.07	0.58 \pm 0.05	0.62 \pm 0.05	0.60 \pm 0.05	0.58 \pm 0.07
Fraction of yolk in contents	0.38 \pm 0.03	0.36 \pm 0.02	0.38 \pm 0.02	0.38 \pm 0.02	0.37 \pm 0.03

^aThe 24 first eggs are from the Coats Island samples of early laid eggs in 1998 and 1999

egg mass at very nearly the predicted value of 0.75, that albumen mass scaled with egg mass at $>1:1$ (positive allometry), and that yolk mass scaled at $<1:1$ (negative allometry; Table 3, Fig. 1). Because relative albumen mass increased with egg mass whereas relative yolk mass decreased, yolk-to-albumen ratios decreased as egg mass increased (Fig. 2).

The amino acid composition of the protein of the albumen and yolk from seven first early laid eggs from Coats Island in 1998 is presented in Table 4.

Composition of eggs laid by young females.—Information on the mass and crude composition of nine eggs laid by young females with no prior breeding experience is presented in Table 1. Eggs laid by young females averaged 12.6% lighter in mass than those laid by early laying females in the same year ($t = 4.76$, $df = 24$, $P < 0.001$). Because of small sample sizes, we compared composition of young females' eggs to that of early laying females' eggs by comparing observed values to values predicted from total egg mass using the regression lines in

Figures 1 and 2 (rather than using ANCOVA). Those comparisons showed that the mean shell mass on young females' eggs was similar to that predicted from egg mass when compared to early laid eggs ($t = 0.36$, $df = 16$, $P = 0.72$; Fig. 1). Conversely, although eggs laid by young females had in absolute terms a higher yolk-to-albumen ratio than early laid eggs (Table 1), the ratio was actually significantly lower than that predicted from egg mass (observed mean = 0.62 ± 0.05 , predicted mean = 0.66 ± 0.03 ; $t = 2.35$, $df = 16$, $P = 0.03$; Fig. 2).

Biochemical analyses show that none of the relative protein content of the albumen, nor the relative protein or lipid content of the yolk, differed significantly between eggs laid by young females and early layers (Table 5). In addition, the amino acid composition of protein in the yolk and albumen of six young females' eggs was similar to that in early laid eggs (Table 4).

Composition of replacement eggs.—The interval between removal of the first egg and the laying of a replacement varied from 12 to 16 days, with a mean of 13.7 ± 1.0 days ($n = 24$). Information

TABLE 2. Analyses of covariance (ANCOVA) relating log component mass to log egg mass for early laid Thick-billed Murres at Coats Island in 1998 and 1999 ($n = 40$)

Component	Model R^2	Egg mass		Year		Interaction	
		F^a	P	F^a	P	F^a	P
Shell	0.52	27.20	<0.001	2.41	0.13	2.44	0.13
Albumen	0.91	324.06	<0.001	0.37	0.55	0.42	0.52
Yolk	0.39	18.79	<0.001	0.00	0.98	0.00	0.99

^a $df = 1$ and 36

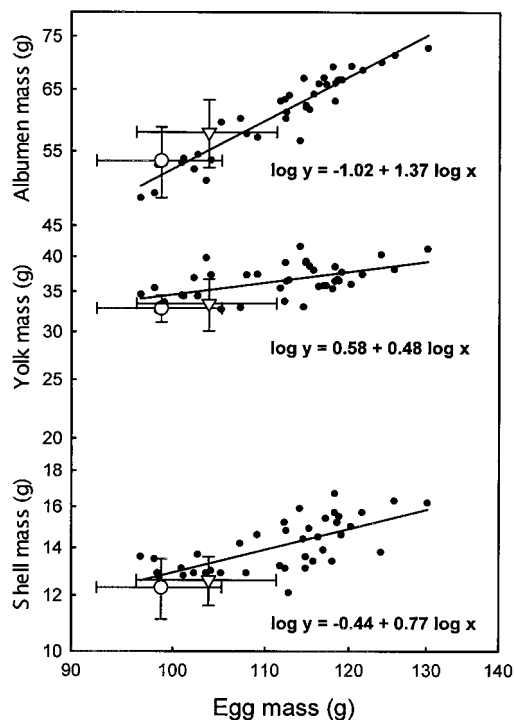


FIG. 1. Regressions relating log component masses to log egg mass for Thick-billed Murre eggs laid at Coats Island in 1998 and 1999 ($n = 40$). All regressions are significant at $P < 0.001$. Mean \pm SD values for eggs laid by young females (open circle; $n = 9$) and for replacement eggs (open triangle; $n = 24$) are superimposed.

on mass and composition of first and replacement eggs laid by the same females at Coats Island in 1998 and 1999 is provided in Table 1. Replacement eggs averaged 5.9% lighter in mass than first eggs laid by the same females (paired $t = 6.21$, $df = 23$, $P < 0.001$). Masses of first and replacement eggs were positively correlated, as were masses of all components (Fig. 3). As with young females' eggs, the mean shell mass on the replacement eggs did not differ significantly from that predicted for their mass ($t = 1.58$, $df = 46$, $P = 0.12$; Fig. 1), although the replacement eggs had slightly, but significantly, thinner shells (by 0.02 mm or 3.8%; paired $t = 3.48$, $df = 23$, $P = 0.002$; Table 1). As with young females' eggs, yolk-to-albumen ratios in replacement eggs were significantly lower than predicted from their mass (observed mean = 0.58 ± 0.05 , predicted mean = 0.64 ± 0.04 ; $t = 3.50$, $df = 46$, $P < 0.001$; Fig. 2). That difference was apparent when compared

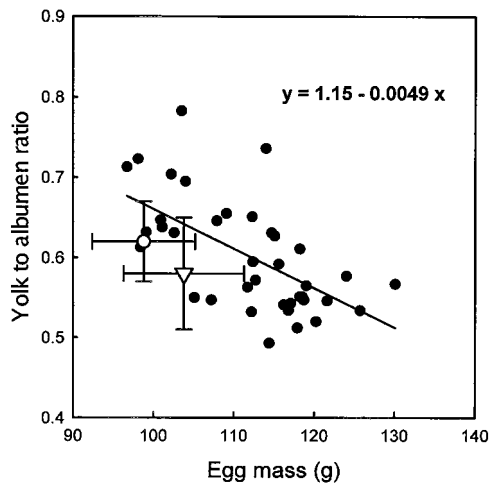


FIG. 2. Yolk-to-albumen ratios in relation to egg mass for Thick-billed Murre eggs laid at Coats Island in 1998 and 1999 ($n = 40$). Regression line is significant ($r^2 = 0.37$, $P < 0.001$). Mean \pm SD values for eggs laid by young females (open circle; $n = 9$) and for replacement eggs (open triangle; $n = 24$) are superimposed.

directly to first eggs laid by the same females earlier that season (paired $t = 1.96$, $df = 23$, $P = 0.06$; but paired $t = 3.49$, $df = 22$, $P = 0.002$ with the one clear outlier removed; Fig. 4).

Biochemical analyses showed that albumen in replacement eggs had a significantly lower protein concentration (the difference presumably made up by water), but that protein and lipid concentrations of yolk did not differ significantly in first and replacement eggs (Table 5). The amino acid content of albumen and yolk in replacement eggs was very similar to that in first eggs (and in young females' eggs): as a fraction of the combined total of all amino acids (i.e. total moles per gram of protein), the means dif-

TABLE 3. Regressions relating log component mass to log egg mass for Thick-billed Murre eggs at Coats Island in 1998 and 1999 ($n = 40$). All regressions are significant at $P < 0.001$. Slopes of the regression lines are given with the lower and upper 95% confidence bounds.

Component	r^2	95% confidence bounds on slopes			Allometry
		Lower	Slope	Upper	
Shell	0.48	0.51	0.77	1.04	
Albumen	0.90	1.22	1.37	1.52	Positive
Yolk	0.32	0.25	0.48	0.71	Negative

TABLE 4. Amino acid content (mean \pm SD; in micromoles per gram of protein) of first eggs laid by early laying ($n = 7$), and young ($n = 6$) Thick-billed Murres.

Amino acid ^a	Albumen ($\mu\text{mol g}^{-1}$)		Yolk ($\mu\text{mol g}^{-1}$)	
	Early laid	Young	Early laid	Young
Essential amino acids				
Histidine	178 \pm 31	152 \pm 13	199 \pm 26	204 \pm 12
Lysine	410 \pm 64	379 \pm 11	495 \pm 47	410 \pm 22
Isoleucine	420 \pm 55	407 \pm 15	410 \pm 45	371 \pm 17
Leucine	770 \pm 119	814 \pm 37	682 \pm 85	705 \pm 32
Valine	587 \pm 94	557 \pm 24	528 \pm 66	497 \pm 19
Methionine	324 \pm 27	316 \pm 10	242 \pm 21	263 \pm 14
Phenylalanine	369 \pm 68	442 \pm 22	290 \pm 37	314 \pm 14
Threonine	541 \pm 103	584 \pm 24	455 \pm 55	348 \pm 13
Nonessential amino acids				
Arginine	147 \pm 42	188 \pm 10	404 \pm 50	324 \pm 14
Alanine	582 \pm 89	580 \pm 23	659 \pm 87	632 \pm 27
Aspartic acid ^b	739 \pm 107	726 \pm 41	671 \pm 129	738 \pm 19
Cystine	124 \pm 12	130 \pm 8	123 \pm 10	117 \pm 19
Glutamic acid ^c	943 \pm 137	1012 \pm 51	860 \pm 111	872 \pm 45
Glycine	506 \pm 79	563 \pm 49	465 \pm 68	561 \pm 31
Proline	409 \pm 63	422 \pm 26	396 \pm 54	410 \pm 21
Serine	641 \pm 101	648 \pm 30	610 \pm 70	430 \pm 18
Tyrosine	288 \pm 39	319 \pm 21	278 \pm 33	312 \pm 15

^aData for tryptophan not provided because that amino acid is destroyed by acid hydrolysis.

^bAsparagine and aspartic acid combined because asparagine is converted to aspartic acid during hydrolysis.

^cGlutamine and glutamic acid combined because glutamine is converted to glutamic acid during hydrolysis.

ferred by <1% in both yolk and albumen for all paired first and replacement egg comparisons.

DISCUSSION

Egg composition in Thick-billed Murres.—There was little between-year variation in egg mass among early laying Thick-billed Murres at Coats Island in 1998 and 1999. In addition, the manner in which each of shell mass, albumen mass, and yolk mass scaled with egg mass was

similar in the two years. The strong relationships observed between each of the component masses and egg mass indicate that, as in other birds (e.g. Hochachka 1986), the among-female variation in crude composition of Thick-billed Murre eggs is largely a function of variation in egg size. Nonetheless, small but statistically significant annual variation in egg composition has been reported in Common Murres (*Uria aalge*), mainly because of variation in absolute albumen content. That was thought to reflect variation in environmental conditions during the prelaying period in two years, although the biological significance of the difference was not investigated (Hatchwell and Pellatt 1990).

Thick-billed Murre eggs show some characteristics of precocial species (e.g. relatively large yolks), consistent with independent measures that place murres well towards the precocial end of the altricial-precocial continuum of avian posthatching development (Starck and Ricklefs 1998). Not surprisingly, the composition of Thick-billed Murre eggs is generally similar to that of Common Murre and Razorbill (*Alca torda*) eggs (Birkhead and Nettleship 1984, Hipfner et al. 2001b), two of the three other extant members of the tribe Alcini (along with the Dovekie [*Alle alle*]), and the only other species that employ the same posthatching developmental strategy as Thick-billed Murres (what Sealy [1973] called the "intermediate" strategy). However, compared to Razorbills, both species of murres lay eggs with thick, heavy shells (Birkhead and Nettleship 1984, Hipfner et al. 2001b), probably because they lay their eggs on bare rock, and incubate with the weight of the body directly on the egg. Whereas murres have a single ventral brood patch, Razorbills have two lateral brood patches and incubate with the egg to one side of the midline and tucked under a wing (Hipfner and Chapdelaine 2002).

TABLE 5. Variation in protein and lipid concentrations of Thick-billed Murre eggs in relation to female age and egg number, measured in standard deviations from the mean concentrations in first eggs of early-laying females ($n = 7$). There were no significant differences between concentrations in eggs laid by young females ($n = 6$) and early laid first eggs (independent samples *t*-tests, $df = 11$, all $P > 0.1$). Conversely, replacement eggs had lower albumen protein concentrations than did first eggs (paired $t_6 = 4.35$, $P = 0.005$; in bold); no other differences were statistically significant.

Component	Parameter	Replacement eggs	Young females' eggs
Albumen	Relative protein concentration	-1.35 \pm 0.82	-0.59 \pm 1.04
Yolk	Relative protein concentration	1.06 \pm 1.93	-0.07 \pm 1.25
	Relative lipid concentration	0.32 \pm 0.88	-1.20 \pm 1.67

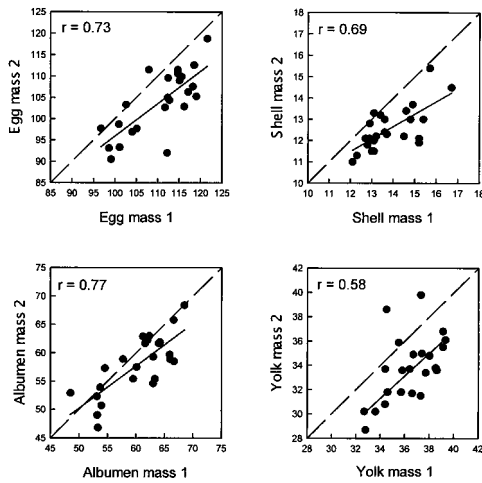


FIG. 3. Relative egg masses, and masses of egg components, for first and replacement Thick-billed Murre eggs laid by the same females ($n = 24$). Dashed lines indicate 1:1 relationships. Correlation coefficients relate masses of replacement egg components to first egg components.

However, it should be noted that the slope of the line relating log yolk mass to log egg mass among Thick-billed Murres at Coats Island was low for a relatively precocial species (0.48, with 95% confidence bounds 0.25–0.71); eggs of precocial species typically show isometry or positive allometry for yolk content (Williams 1994, Hill 1995). The slope for yolk also was substantially lower than has been recorded previously in Common Murre and Razorbill eggs from the Gannet Islands, Labrador, Canada (Birkhead and Nettleship 1984, J. M. Hipfner unpubl. data), and was considerably lower than the slope recorded in 30 eggs laid by early laying Thick-billed Murres there (0.95, with 95% confidence bounds 0.40–1.50; J. M. Hipfner unpubl. data). That latter observation suggests that that putatively important egg characteristic can show considerable intraspecific variation, although we have no basis on which to speculate on the causes and consequences of that variation. At the same time, the slope for albumen was very large in our sample (1.37, with 95% confidence bounds 1.22–1.52); albumen is composed mainly of water (85–90% by mass, the remainder being largely protein), and experiments with chicken eggs have shown that that water may have an important role in determining the structural size of the chick (Finkler et al. 1998).

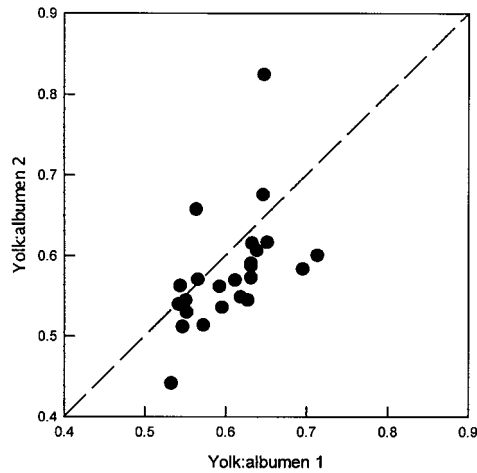


FIG. 4. Yolk-to-albumen ratios in first and replacement Thick-billed Murre eggs laid by the same females ($n = 24$). Dashed line indicates a 1:1 relationship.

Analysis of the amino-acid makeup of protein in yolk and albumen in Thick-billed Murre eggs shows that they are similar to those of other avian species in that feature, further supporting the notion that that characteristic is relatively invariant in birds (Murphy 1994). For that reason, it is perhaps not surprising that amino-acid makeup showed relatively little variation with female age or relaying. Our data also indicate that, as in other birds (Murphy 1994), the amino acid composition of protein in the yolk and albumen of Thick-billed Murre eggs is generally similar. Moreover, the high nutritional quality of egg protein is evident from our data in that fully 45% of the amino acids are essential amino acids.

Variation in egg composition in relation to female age and experience.—Variation in egg size in relation to female age and experience is well documented in seabirds (e.g. Coulson and White 1958, Croxall et al. 1992). In contrast, there is very little information on how egg composition varies with female age in long-lived species. Our results show that eggs laid by four and five year old Thick-billed Murres with no prior breeding experience were substantially smaller than those laid by early laying females (by 13%), and that they were laid well past the population-wide median laying date (by 4–18 days). Those patterns have been reported previously in that species (Hipfner et al. 1997), and in others including Razorbills (Lloyd 1979). Although

they were small and laid late, the mean shell mass on eggs laid by young females was similar to that predicted from egg mass compared to eggs laid by early layers. Therefore, young, inexperienced females did not exhibit any demonstrable limitations on their capacity to produce shells for their small eggs. Conversely, eggs laid by young females had a lower yolk-to-albumen ratio than predicted from their mass compared to early laid eggs; there were no significant differences in concentrations of yolk lipid, yolk protein, or albumen protein. In addition, amino-acid makeup of protein in albumen and yolk of young females' eggs was similar to that in early laid eggs. Those observations suggest that age- or experience-related constraints on egg production are manifested as delayed laying of small eggs with less yolk and more albumen than expected, and not through adjustments in biochemical composition. Moreover, the constraints operate during yolk production, which in a previous study was found to take somewhat longer (14 vs. 13 days on average, although the difference was not statistically significant), and to occur at a slower rate, in inexperienced than in experienced Thick-billed Murres (Hipfner et al. 1997). In precocial species, including Common Murres and Razorbills (Birkhead and Nettleship 1984), yolk contains most of the total protein in the egg and virtually all of the lipid (Carey et al. 1980, Sotherland and Rahn 1987, Williams 1994). Thus, our results indicate that eggs laid by young female Thick-billed Murres have less lipid and protein, but presumably more water, than do eggs of similar size laid by early laying females.

Factors affecting recruitment age are not well understood in murres (Noble 1990), but studies of demography of Thick-billed Murres at Coats Island have shown that few young females recruit in years in which the population lays late (3- and 4-year-olds are especially affected, A. J. Gaston unpubl. data). Because environmental conditions, such as spring and early summer ice conditions, are known to affect timing of laying by Thick-billed Murres (Birkhead and Nettleship 1987b, Gaston and Hipfner 1998), that observation suggests that more recruitment occurs in years in which environmental conditions are favorable early in the season. That tendency is also observed in other seabirds (e.g. Brandt's Cormorant [*Phalacrocorax pencillatus*]; Boeckelheide and Ainley 1989), and as in other

seabirds (e.g. Wandering Albatross [*Diomedea exulans*]; Weimerskirch 1992); the decision on whether or not to recruit is likely to be mediated through the physiological condition of individual females. The nature and extent of lipid and protein constraints on egg production in young, inexperienced birds, and how they relate to female condition and her probability of recruitment, might be a fruitful area for future investigations. In particular, it might be interesting to relate the savings in terms of protein and energy associated with producing the small eggs laid by young females to background rates of protein and energy turnover in the female while she forms the egg.

Differences in the composition of first and replacement eggs.—As in previous studies of Thick-billed Murres (Birkhead and Nettleship 1982, Hipfner et al. 1999), replacement eggs averaged ~6% smaller than first eggs laid by the same females earlier that same season. The overall reduction in egg size was associated with reductions of generally similar magnitude (4–9%) in the masses of shell, albumen, and yolk. For whole eggs and all components, there were strong correlations between masses in first and replacement eggs, indicating that there is a strong, female-specific component to egg size and egg composition in Thick-billed Murres (Hipfner et al. 1997). Measures of egg production capacity show strong female-specific variation in other species as well (Christians and Williams 2001).

The mass of the shell on the replacement eggs, like that on young females' eggs, was similar to that predicted by egg mass compared to eggs laid by early laying females. There was however, a small (4%) but statistically significant reduction in thickness of the shell, and thus presumably in its strength. If a reduction in shell strength allows the chick to break out of the egg more quickly, then it may at least partly explain why the incubation period of replacement eggs averages about one day less than that of first eggs (Hipfner et al. 2001c). However, although the mean shell mass was similar to that predicted from egg mass compared to early laid eggs, the yolk-to-albumen ratio in replacement eggs was lower than predicted from egg mass. Moreover, although relative concentrations of lipid and protein did not differ significantly in the yolks of first and replacement eggs, the albumen in replacement eggs had a lower protein

concentration than that in first eggs. That observation suggests that, unlike in young females, constraints on egg production operating on females forming replacement eggs are manifested not only in differences in size and crude composition of their eggs (reduced absolute amounts of yolk and albumen, and a decrease in relative yolk content), but also in their biochemical composition (reduced protein content of albumen).

In other species, replacement clutches typically contain fewer eggs (Brown and Morris 1996, Grand and Flint 1996), which is usually considered to be a strategic adjustment to a smaller optimal clutch size later in the season (e.g. Arnold 1993). The situation with egg size in replacement clutches is less clear, those eggs being smaller than those in first clutches in some species (Feare 1976, Brown and Morris 1996), the same size in some others (Rohwer 1986, Arnold 1993), and larger in others (Duncan 1987a, Sandercock and Pederson 1994). Production of large replacement eggs could be a strategic response if large hatchlings with large reserves have an advantage late in the season, when environmental conditions are likely to be unfavorable (Sandercock and Pederson 1994). Alternatively, egg size could increase because food is more available during the time when females are forming replacement eggs (Duncan 1987b). At the same time, production of small replacement eggs also could be a strategic response if small eggs can be formed more quickly (as suggested for Thick-billed Murres by Birkhead and Nettleship 1982), but egg size also may decrease if, having produced one clutch already, females have fewer endogenous reserves with which to produce a replacement (Houston et al. 1983, Monaghan et al. 1998).

In some species, egg production appears to be limited by quality and quantity of protein available to the female as she forms eggs (e.g. Robbins 1981, Bolton et al. 1992); some of the amino acids used to produce egg proteins are drawn from endogenous reserves laid down before egg production begins (Houston et al. 1995). For example, in Lesser Black-backed Gulls (*Larus fuscus*), a female's ability to replace eggs lost within a single clutch appears to be limited by size of her protein reserves, but not her lipid reserves (Houston et al. 1983). Dietary protein also may be important for reneesting females: protein-supplemented Northern Pintails (*Anas acuta*) laid larger eggs in replacement clutches

than in first clutches, whereas nonsupplemented birds laid smaller eggs in replacement clutches (Duncan 1987b). Avian species vary in the extent to which they rely on endogenous and exogenous sources during egg production (Drent and Daan 1980, Meijer and Drent 1999), and we do not know where Thick-billed Murres lie along that capital-income continuum. However, food is likely to be more available when females at Coats Island are forming replacement eggs than when they form first eggs, because sea ice is retreating in northern Hudson Bay in the interim (Gaston and Hipfner 1998). Moreover, birds at that colony generally gain mass over the course of incubation, which suggests that food availability increases through the early part of the season (Gaston and Hipfner 1998). Therefore, it seems unlikely that any protein deficit for relaying females would be due to a shortage of dietary protein, which implicates a limit on endogenous sources. Endogenous reserves may supply specific amino acids that could limit egg production if birds were relying solely on dietary protein (Murphy 1994, Houston et al. 1995). Because their breeding habits leave them vulnerable to egg loss, retaining sufficient endogenous protein to be able to produce a replacement egg of adequate size in a timely fashion may be an important evolutionary determinant of the investment that Thick-billed Murres make in first eggs (Hipfner et al. 2001b). Again, a comprehensive analysis of the biological significance of the savings to the laying female in terms of protein and energy associated with producing small, protein deficient replacement eggs, might be enlightening.

Finally, if replacement eggs laid by Thick-billed Murres are of slightly lower quality because of a low albumen protein content, a low yolk-to-albumen ratio, or thin eggshells, we might expect that to translate into low fitness of young that hatch from those eggs. For example, thinner eggshells have been linked to reduced hatching success in Black Terns (*Chlidonias niger*) (Beintema et al. 1997); in Lesser Black-backed Gulls, which lay a three-egg clutch, nestlings from experimentally induced fourth eggs suffered from inflated mortality rates, apparently because they were lighter in mass (Monaghan et al. 1998). Thick-billed Murre hatchlings from replacement eggs are also lighter in mass than those from first eggs (J. M. Hipfner unpubl. data), but there is no evidence

that hatching or fledging success (de Forest and Gaston 1996, Hipfner et al. 1999), chick growth rates (de Forest and Gaston 1996, Hipfner 1997), or survival to recruitment age (Hipfner 2001) are adversely affected. However, the colonies where that research has been conducted (Coats Island and the Gannet Islands) both are colonies where feeding conditions during chick-rearing appear to be particularly favorable (Gaston et al. 1983, Bryant et al. 1999). Consequences of hatching from replacement eggs may be more significant where feeding conditions are less favorable.

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