

Causes and consequences of egg size variation in Swallows *Hirundo rustica*

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Abstract - Relationships between egg mass, egg composition, hatchling mass, female characteristics and environmental conditions during egg formation were investigated for Swallows *Hirundo rustica* in Central Scotland. Egg dimensions were highly correlated with egg mass. 60% of variation in egg mass originated from differences between females. Egg mass was repeatable (repeatability=0.54) for individual birds but was not related to other female characteristics such as measures of structural size. Egg mass was not related to clutch size, hatchability or position in the clutch. Eggs contained more lipid if favourable environmental conditions prevailed during egg formation. Heavier eggs contained more lipid and lean dry component. A sample of eggs was hatched in a incubator so that hatchlings could be matched with the eggs from which they emerged. Egg mass explained 60% of variation in hatchling mass. 79% of variation in hatchling mass was explained by the first component in a principal component analysis which used egg mass, length and breadth to describe egg size. Heavier eggs produce larger hatchlings which generally grow faster and have greater survival across 34 studies of non-passerine birds. Although larger passerine eggs produce hatchlings which are initially larger and grow faster (n=7 studies) this does not lead to increased survival. Hirundines lay relatively small eggs for their body size although production of larger eggs was predicted to have little extra cost for a Swallow and should be advantageous as larger hatchlings would be more likely to survive periods of food shortage.

Introduction

Causes and consequences of egg mass variation are of significance for two complimentary reasons. Firstly, egg size is a readily quantifiable component of reproductive investment by female birds. Secondly, there is substantial variation in egg mass in most species, much of which occurs between birds. This variation is potentially related to variation in reproductive output.

Consequences of egg mass variation potentially include reduced hatchability of small eggs, an influence on the extent of any nestling hierarchy, and affects on hatchling mass, growth or survival. Previous studies have shown that hatchability is not related to egg mass, except in the case of rare dwarf eggs which do not hatch (Schifferli 1973, O'Connor 1979, Bancroft 1984, Reid and Boersma 1990, Magrath 1992a, Williams *et al.* 1993). Hatching asynchrony is generally more important than egg mass variation in establishment of nestling hierarchies (Slagsvold *et al.* 1984). Egg mass does influence hatchling mass, growth rate and survival in both precocial and altricial birds (Williams 1994).

Relationships between the mass of individual eggs and hatchlings have been studied in relatively few passerines because it is difficult to match hatchlings with eggs in large clutches which hatch synchronously. I investigated causes of egg mass variation in an aerial insectivorous passerine, the Swallow, and examined the consequences of egg mass for hatchability, nutrient content and hatchling size. Hirundines have small eggs relative to their body size (Rahn *et al.* 1975), suggesting that effects of small egg size might be particularly pronounced in this species.

Methods

The study was carried out between 1989 and 1991 in Central Scotland (56°8'N 3°59'W) within 10 km of Stirling University. Swallows nested inside open barns at farms which were evenly spaced in mixed arable and grazing land. Farms had 1-12 pairs of nesting Swallows, each of which generally occupied a separate shed. Nests were visited at 1-3 day intervals between mid May and the end of July to record laying dates,

clutch sizes and hatching dates. Incubation began on the day upon which the final egg of a clutch was laid (eggs found warm) and the eggs hatched after 16.0 days (sd = 1.2, n = 93 clutches). Each egg was marked with a non-toxic waterproof marker pen. Egg length, breadth and mass were recorded before the onset of incubation (to 0.01 cm, vernier callipers or to 0.01 g, 5 g Pesola balance). Eggs do not change in mass before the start of incubation (O'Connor 1979, Nilsson and Svensson 1993) but lose mass during incubation. The fresh mass of eggs which were found after incubation had started was calculated from the formula: fresh egg mass (g) = $c.L.B^2$, where $c = 0.531$ (sd = 0.02, n = 440 eggs weighed before the start of incubation) and L and B are egg length and breadth. No more than 1 egg per day appeared in 80 nests which were visited daily during laying. Egg dumping was therefore assumed to be infrequent in this population of Swallows although it occurs in other areas (Møller 1987). Eggs which failed to hatch were candled to determine whether they were infertile or whether the embryo had failed during development.

Female Swallows were captured on or near the nest at night (between 2230 and 0400 h) using a hand net or in mist nets suspended within barns during the day. Each was marked with an individually numbered ring. Wing, keel, head+bill and tarsus lengths were measured (Svensson 1992). Swallows rarely moved between farms within the study area (Thompson 1992) so unmarked females were assumed to be one year old when they were caught at farms at which all breeding females had been ringed in the previous year.

A sample of eggs (n = 57 from 27 clutches) was moved to an incubator 1-2 days before they were due to hatch in 1989. Eggs hatched after 1-3 days and hatchlings were returned to their nests. Female Swallows did not desert if at least 3 eggs were left in the nest. The incubator was kept at 35-40°C with a tray of water to provide a moist atmosphere. Eggs were placed in a cardboard (chicken) egg tray and turned through 45° 4-6 times a day. The incubator was checked for the emergence of new chicks every 2-8 h. Hatchlings were weighed (to 0.01 g, 5 g Pesola balance). Wing length and tarsus length were measured (to 0.1 mm, vernier callipers). Nests were also visited on the day that the eggs were due to hatch, but as clutches tended to hatch synchronously and parents soon fed the young only 9 unfed chicks could be matched with their eggs. Chicks which had been fed were heavier than the egg from which they had hatched and a dark insect bolus could be seen through the thin skin of the abdomen.

Egg composition was determined for 20 eggs (1 randomly selected egg per clutch). Eggs were boiled for 2 minutes to allow separation of shell, albumen and

yolk. All components were freeze dried and weighed prior to extraction of the lipid component with 5:1 ether: chloroform in a Soxhlet apparatus, followed by freeze drying and weighing to determine lean dry mass. Maximum and minimum temperature and precipitation were recorded daily at the Parkhead weather station on the Stirling University campus. Insect supply was assessed at Parkhead with a 12.2 m high suction trap which was emptied daily (Taylor and Palmer 1972, Bryant 1978b). Large nocturnal insects were removed and the log transformed catch volume (log V+1) used as an index of food availability for Swallows.

Statistical tests were performed with SPSSX or Minitab. Probability levels given refer to 2 tailed tests of statistical significance.

Results

Causes of egg mass variation

Mean egg dimensions, calculated from mean measurements from 231 clutches, were: mass 1.97 g (sd = 0.14, range 1.67-2.30), length 1.96 cm (sd = 0.08, range 1.76-2.18), breadth 1.37 cm (sd = 0.04, range 1.28-1.49). Comparison of the mean egg mass of all birds that laid each year revealed no systematic variation in egg mass between years (ANOVA, $F_{2,160} = 0.57$, $p = 0.57$) or between first and second clutches (paired t-test, $t = 0.89$, $p = 0.38$, n = 68 double brooded females). Mean egg mass was the same as that determined by Turner (1980) in the same area 10 years previously. Mean egg mass was not related to clutch size (Pearson correlation, $r = -0.08$, $p = 0.3$, n = 231 clutches), keel length ($r = 0.03$, $p = 0.5$, n = 140 birds), head+bill length ($r = -0.03$, $p = 0.5$, n = 142 birds), tarsus length ($r = 0.02$, $p = 0.5$, n = 105 birds), wing length ($r = 0.04$, $p = 0.5$, n = 142 birds) or female age (t-test, 114 first year vs 49 older females, $t = 0.59$, $p = 0.56$; paired t-test, 18 females which nested in consecutive years, $t = 0.78$, $p = 0.44$). 59.6% of variation in egg mass occurred between females (Table 1). Repeatability of egg mass by individual

Table 1. Analysis of variance of Swallow egg mass. Each egg laid by each female was treated as the sampling unit.

Source of variation	df	SS	MS	F	P
Between females	125	15.31	0.12	10.05	<0.001
Within females	851	10.37	0.01		
Total	976	25.68			

Table 2. Pearson correlations between fresh mass and dimensions of Swallow eggs and the mass, wing length and tarsus length of hatchlings (n = 30). ns indicates $p > 0.05$, * indicates $0.05 \leq p < 0.01$, ** indicates $0.01 \leq p < 0.001$.

Egg length	0.67 **				
Egg breadth	0.88 **	0.23 ns			
Hatchling mass	0.78 **	0.51 **	0.69 **		
Wing length	0.53 *	0.39 ns	0.43 *	0.52 *	
Tarsus length	0.71 **	0.62 **	0.50 *	0.48 *	0.68 **
	Fresh egg mass	Egg length	Egg breadth	Hatchling mass	Wing length

females was 0.54 (calculated after Lessells and Boag (1987) from Table 1). Egg mass did not vary consistently with position in the clutch (ANOVA: $F_{3,290} = 0.26$, $p = 0.86$; $F_{4,602} = 1.72$, $p = 0.14$ and $F_{5,120} = 1.02$, $p = 0.41$ for clutches of 4, 5 and 6 eggs respectively).

Experiments with lipophilic dyes showed that each yolk was deposited over 6 days, although most was formed in the 3 days prior to ovulation (Ward 1992). Albumen and shell were deposited in 24 hours between ovulation and laying. The mean egg mass (of each clutch) was related to maximum temperature during the period when most egg material was deposited, i.e., from the day before the first egg of a clutch was laid until the day before the final egg was laid (mean egg mass = $1.85 (0.005) + 0.005 (0.002)$ max T; $r^2 = 0.02$, $p = 0.03$, $n = 222$ clutches; numbers in brackets represent standard errors). Mean egg mass also increased with mean temperature during this period, but the relationship was not significant ($p = 0.06$). Mean egg mass was not related to maximum, minimum or mean temperature, precipitation or insect suction trap catch during other periods prior to or during egg deposition (regressions, all $p > 0.14$).

Consequences of egg mass variation

Egg mass was not related to hatchability as the fresh mass of eggs which were infertile or in which the embryo died ($n = 99$) did not differ from that of eggs which hatched ($n = 766$) (t-test, $t = 0.41$, $p = 0.6$). Egg mass varied less within than between clutches (Table 1) so data from more than one egg per clutch in which egg and hatchling mass were measured were not independent. One egg was therefore selected randomly from each clutch which reduced the sample size of matched hatchlings and eggs to 30. Fresh egg mass and hatchling mass did not differ between eggs which hatched in their nests ($n = 7$) and those which

hatched in the incubator ($n = 23$) (t-tests, $t < 1.94$, $p > 0.07$). Fresh egg mass and hatchling mass did not differ between first and second clutches (t-test, $t < 1.82$, $p = 0.08$, $n = 18$ eggs from first clutches and 12 eggs from second clutches). The mass of hatchlings from the incubator was not correlated with the number of days since the start of incubation or with the number of hours since the incubator was last checked (Pearson correlations, $r > -0.17$, $p > 0.39$, $n = 23$). Larger, heavier eggs produced heavier hatchlings which had correspondingly longer wings and tarsi (Fig. 1, Table 2). In a regression analysis fresh egg mass explained 60.3% of variation in hatchling mass (Fig. 1). Hatchling mass was also correlated with egg

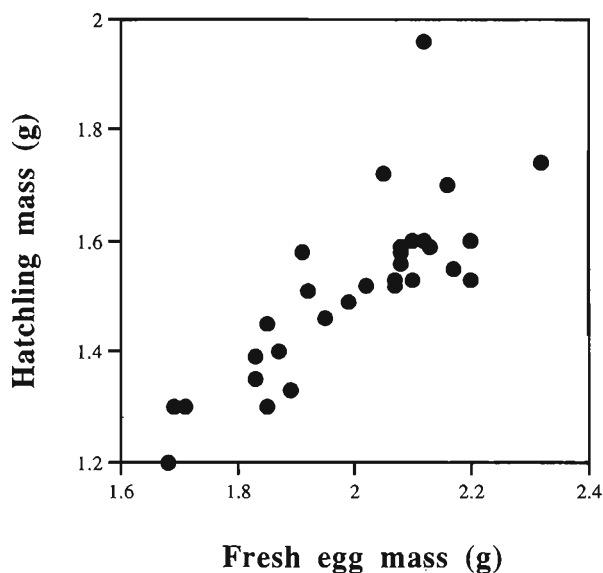


Figure 1 - Relationship between fresh egg mass and the mass of unfed hatchling Swallows aged 0.5-8 hours ($y = 0.775 (0.119) x - 0.041 (0.239)$, $r^2 = 0.603$, $p < 0.0001$, $n = 30$, numbers in brackets are standard errors).

dimensions, but as egg mass, length and breadth were themselves intercorrelated (Table 2), a principal components analysis was used to produce a single measure of egg size from egg mass, length and breadth (Table 3). PC1 explained 79.0% of variation in hatchling mass, almost 20% more than egg mass alone. In a multiple regression analysis, PC2 and PC3 did not add significantly to the percentage variation in hatchling mass explained by PC1 ($p > 0.09$).

Lean dry and lipid components of yolk, albumen and whole egg increased with egg mass except in the case of yolk lipid which increased disproportionately with egg mass (Table 4). The lipid content of whole egg and of egg yolk increased with insect suction trap catch during the 6 days before the egg was laid (Table 5). Whole egg, yolk and albumen composition were not related to temperature or rainfall during this period, or to any of the environmental factors measured during 3 other periods prior to or during egg

deposition (3 days prior to start of yolk deposition, last 3 days of yolk deposition, day of albumen deposition, all $p > 0.06$).

Discussion

Most variation in egg mass is accounted for by consistent differences between eggs laid by individual females (Ankney and Bisset 1976, Galbraith 1988, LeBlanc 1989, Wiggins 1990, Nilsson and Svensson 1993, Potti 1993, this study). Larger eggs are laid by structurally larger females in some species (Nol *et al.* 1984, Naylor and Bendell 1989, Potti 1993), but egg size is not related to morphological characteristics in Swallows or the majority of other studies (De Steven 1980, Murphy 1986, LeBlanc 1989, Wiggins 1990, Grant 1991, Nilsson and Svensson 1993). Egg mass is also heritable (van Noordwijk *et al.* 1981). Other affects upon egg mass must be quite substantial if they are to be detected, as variation will be superimposed upon differences between birds that are determined genetically. It is therefore not surprising that mean egg mass is usually not correlated with factors such as female age, date, clutch size, food availability during egg formation or territory quality (no trends: Pinowski 1979, LeBlanc 1989, Naylor and Bendell 1989, Rohwer and Eisenhauer 1989, Ekman and Johansson-Allende 1990, Nager 1990, Arnold *et al.* 1991; trends recorded: Horsfall 1984, Magrath 1992b). Mean Swallow egg mass increased significantly with maximum temperature during the period that the majority of egg material was deposited, but as temperature explained only 2% of variation in egg mass, environmental conditions were not important in the determination of Swallow egg size. Exceptionally poor weather can reduce food availability so much that egg formation stops or small eggs are produced (Bryant 1978a, O'Connor 1979, Ojanen *et al.* 1981, Ojanen 1983, Magrath 1992b, Ward 1992) but these very poor conditions do not affect the majority of laying birds. In 3 years, only 3 Swallows in this study area suffered interrupted laying due to bad weather (Ward 1992). Swallow egg composition was related to environmental conditions during egg deposition. Insect suction trap catch explained 23-24% of variation in yolk and whole egg lipid content (Table 5). This variation in egg composition might account

Table 3. Principal components analysis of Swallow egg size.

	PC1	PC2	PC3
Eigenvalue	2.14	0.79	0.07
Proportion of variance explained	0.71	0.26	0.03
Fresh egg mass	-0.66	0.12	0.74
Egg length	-0.44	-0.86	-0.26
Egg breadth	-0.60	0.51	-0.62

Table 4. Allometric (log-log) regressions of egg components on fresh egg mass ($n = 20$). a and b are the intercept and slope in the equation $\log Y = a + b \log X$, S_b is the standard error of b , R^2 is the coefficient of determination.

	a	b	S_b	R^2
Lean dry yolk	3.52	1.12	0.23	0.61
Lean dry albumen	4.39	0.71	0.42	0.15
Lean dry egg	4.74	0.85	0.27	0.39
Yolk lipid	3.80	1.67 ¹	0.30	0.67
Albumen lipid	2.17	0.80	0.60	0.10
Egg lipid	3.96	1.58	0.28	0.67

¹ Slope significantly greater than 1.

Table 5. Regressions of egg composition upon insect suction trap catch during the 6 days before the egg was laid ($n = 20$).

Egg component	a	S_a	b	S_b	R^2	P
Whole egg lipid	23.8	9.8	83.7	26.6	0.24	0.02
Yolk lipid	21.9	9.3	73.6	25.4	0.23	0.03

for some of the 20% of variation in hatchling mass that was not explained by egg size.

Larger eggs produced young which were heavier when they hatched in 39 of the 41 studies of which I am aware (Table 6). Relationships between individual egg and hatchling mass have been investigated less frequently in passerine birds ($n = 7$) than in non-passerines ($n = 34$), due to difficulty in determining from which egg each hatchling emerged in the large clutches typical of passerine birds. This difficulty was avoided in the present study by hatching eggs in an incubator. Mean egg mass has been correlated with mean hatchling mass in passerines, although relationships are less tight than those between individual egg and hatchling mass due to affects of hatching asynchrony and feeds by the parents (Bryant 1978a, Nilsson and Svensson 1993). Larger eggs contain more nutrients across a wide range of species (this study and reviewed by Williams 1994), which is consistent with emergence of larger, heavier hatchlings. The majority of studies of both passerine and non-passerine birds show that heavier eggs produce chicks which are structurally larger, have greater energy reserves and grow more quickly (Table 7), although increased growth rates were often only observed during the first few days of nestling growth. Non-passerine chicks from larger eggs showed greater rates of survival, whilst egg size had either no affect or an ambiguous affect upon survival of passerine chicks. In the majority of studies (Table 6), parental or territory quality could affect both egg mass and chick growth or survival, so the relationship between egg mass and hatchling fitness has strictly only been assessed in three studies in which eggs of different sizes were swapped between nests. Egg mass and parental (or territory) quality had independent effects upon chick survival in Lesser black-backed gulls *Larus fuscus* (Bolton 1991), parental quality alone was important for Magellanic penguins *Spheniscus magellanicus* (Reid and Boersma 1990) and growth but not survival was affected by egg size in Blackbirds *Turdus merula* (Magrath 1992a). Larger eggs were therefore intrinsically advantageous for Lesser black-backed gulls, but not for Magellanic penguins or Blackbirds. Differing importance of large egg size could be related to the degree of exposure of the young to bad weather and the probability of food shortage for species with varied foraging modes. Chicks of passerine birds are protected within a more benign thermal environment than are those of the majority of non-passerines such as gulls and penguins. The penguin study was carried out in a particularly favourable breeding season, when the potentially greater resistance of larger chicks to food shortage was not needed in order to survive until fledging.

Hirundines have small eggs for their body size relative to other passerines (Rahn *et al.* 1975), possibly to lower costs of egg formation or to reduce the affect of the additional mass of oviduct and developing eggs upon flight costs or performance. Swallow eggs contained a mean of 10 kJ ($sd = 0.9$, $n = 20$), so if egg was deposited with an efficiency of 70% (King 1973) each egg would require an investment of 14.3 kJ. Each Swallow egg takes 7 days to form (3 days of minimal deposition of yolk, 3 days of substantial yolk deposition and 1 day for albumen formation, Ward 1992). The greatest daily allocation of energy for egg formation would be upon the day before the first egg of a clutch was laid when the equivalent of an almost entire egg would be deposited. Daily energy expenditure of a laying Swallow averages 105-113 kJd^{-1} (Ward, in press) so if mean egg mass were increased by 10%, investment on the day before the first egg was laid would change by only 1.4 kJ, or 1.3% of daily energy expenditure. Potential changes in egg formation costs would be lower on all other days. A Swallow laying a clutch of 5 eggs carries an additional 0.2 to 2.8 g of reproductive material for 7 days prior to and during laying (Ward 1992). A 10% increase in egg mass would lead to a 0.3 g rise in the peak mass of egg material carried which seems of minor importance in relation to routine daily fluctuations in Swallow mass and represents less than the mass of a Swallow dropping (Jones 1987, Ward 1992). An increase in egg size would apparently represent only a small change in egg formation and flight costs for a female Swallow.

There is more evidence for a fitness benefit to laying large eggs by non-passerine than passerine birds. Although large hatchling size would theoretically always be advantageous, within the relatively protected environment of a nest or when food is plentiful, initial size may be a relatively unimportant contributor to passerine nestling fitness when differences are between rather than within broods. Aerial foraging birds such as Swifts and Swallows might be expected to experience greater benefits of large egg size than other altricial birds, for although the chicks are protected within a nest, large and unpredictable fluctuations in the food supply can require chicks to survive periods when little food is brought into the nest (O'Connor 1978, Bryant and Gardiner 1979). If a period of food shortage occurred shortly after hatching, larger hatchlings would be more likely to survive. This hypothesis is supported by the correlation between egg size and chick survival in Swifts *Apus apus* (O'Connor 1979), although the relationship between hatchling size and survival is still to be investigated in Swallows.

Table 6. Studies of relationships between individual egg mass and hatchling mass, structural size, energy reserve, growth rate or survival for a) non-passerine and b) passerine birds. √ indicates a positive relationship ($p < 0.05$) between egg mass and that hatchling characteristic, x indicates that no significant relationship was found and - that the relationship between egg size and this characteristic was not examined in that study. No significant negative relationships were found between egg mass and hatchling characteristics.

Species	Hatchling characteristic			Growth	Survival	Reference
	Mass	Structural size	Energy reserve			
a) Non-passerines						
Canada goose <i>Branta canadensis maxima</i>	√	-	√	x	-	Thomas & Peach Brown 1988
Snow goose <i>Chen caerulescens</i>	√	-	√	-	√	Ankney 1980
Wood duck <i>Aix sponsa</i>	√	-	-	-	-	Hepp <i>et al.</i> 1987
Mallard <i>Anas platyrhynchos</i>	√	-	-	-	-	Batt & Prince 1979
Mallard <i>Anas platyrhynchos</i>	√	-	-	-	-	Eldridge & Krapu 1988
Coot <i>Fulica atra</i>	√	x	-	-	-	Horsfall 1984
American coot <i>Fulica americana</i>	√	√	x	-	-	Hill 1988
Lesser golden plover <i>Pluvialis dominica</i>	√	-	-	-	-	Ricklefs 1984
Semipalmated plover <i>Charadrius semipalmatus</i>	√	-	-	-	-	Ricklefs 1984
Whimbrel <i>Numenius phaeopus</i>	√	-	-	-	-	Ricklefs 1984
Whimbrel <i>Numenius phaeopus</i>	√	√	-	-	√	Grant 1991
Hudsonian godwit <i>Limosa haemastica</i>	√	-	-	-	-	Ricklefs 1984
Lesser yellowlegs <i>Tringa flavipes</i>	x	-	-	-	-	Ricklefs 1984
Stilt sandpiper <i>Calidris himantopus</i>	√	-	-	-	-	Ricklefs 1984
Dunlin <i>Calidris alpina</i>	√	-	-	-	-	Ricklefs 1984
Least sandpiper <i>Calidris minutilla</i>	x	-	-	-	-	Ricklefs 1984
Northern phalarope <i>Lobipes lobipes</i>	√	-	-	-	-	Ricklefs 1984
Lapwing <i>Vanellus vanellus</i>	√	√	√	-	√	Galbraith 1988
Great skua <i>Catharacta skua</i>	√	√	-	x	√	Furness 1983
Laughing gull <i>Larus atricilla</i>	√	√	√	-	-	Ricklefs <i>et al.</i> 1978
Herring gull <i>Larus argentatus</i>	√	x	√	-	√	Parsons 1970
Herring gull <i>Larus argentatus</i>	√	-	-	√	√	Davies 1975
Lesser black-backed gull <i>Larus fuscus</i>	√	√	x	-	√	Bolton 1991
Black-headed gull <i>Larus ridibundus</i>	√	-	-	-	√	Lundberg & Väisänen 1979
Roseate tern <i>Sterna dougallii</i>	-	-	-	√	√	Nisbet 1978
Common tern <i>Sterna hirundo</i>	-	-	-	√	√	Nisbet 1978
Common guillemot <i>Uria aalge</i>	√	x	√	-	-	Birkhead & Nettleship 1984
Thick-billed murre <i>Uria lomvia</i>	√	x	√	√	-	Birkhead & Nettleship 1982
Brünnich's guillemot <i>Uria lomvia</i>	√	x	√	-	-	Birkhead & Nettleship 1984
Razorbill <i>Alca torda</i>	√	x	√	-	-	Birkhead & Nettleship 1984
Puffin <i>Fratercula arctica</i>	√	x	√	-	-	Birkhead & Nettleship 1984
Magellanic penguin <i>Spheniscus magellanicus</i>	√	√	-	√	x	Reid & Boersma 1990
Shag <i>Phalacrocorax aristotelis</i>	√	√	-	-	√	Amundsen & Stokland 1990
Fork-tailed storm-petrel <i>Oceanodroma furcata</i>	-	-	-	-	√	Boersma <i>et al.</i> 1980
Red grouse <i>Lagopus lagopus scoticus</i>	√	-	-	-	√	Moss <i>et al.</i> 1981
Japanese quail <i>Coturnix coturnix japonica</i>	√	√	√	-	-	Ricklefs <i>et al.</i> 1978
Swift <i>Apus apus</i>	√	√	x	-	√	O'Connor 1979
b) Passerines						
Magpie <i>Pica pica</i>	√	√	x	-	-	Birkhead 1991
Hooded crow <i>Corvus corvus cornix</i>	√	√	√	-	-	Rofstad & Sandvik 1987
Blackbird <i>Turdus merula</i>	√	√	√	√	x	Magrath 1992a
Yellow headed blackbird <i>Xanthocephalus xanthocephalus</i>	√	√	-	-	-	Richter 1984
Great tit <i>Parus major</i>	√	-	-	√	x	Schifferli 1973
Great tit <i>Parus major</i>	-	-	-	√	√	Perrins in press
Tree swallow <i>Tachycineta bicolor</i>	√	-	-	-	x	De Steven 1978
Swallow <i>Hirundo rustica</i>	√	√	√	-	-	This study

Table 7. Studies of non-passerine and passerine birds which investigated relationships between individual egg mass and hatchling characteristics. n = number of studies which investigated that relationship. % corr. indicates the percentage of studies which found a positive relationship ($p < 0.05$) between egg mass and that hatchling characteristic. The remaining studies found no significant relationship between egg mass and that hatchling characteristic. Studies included are those listed in Table 6.

Hatchling characteristic	Non-passerine birds		Passerine birds	
	n	% corr.	n	% corr.
Mass	34	94	7	100
Structural size	17	59	5	100
Energy reserve	14	79	4	75
Growth	7	71	3	100
Survival	15	93	4	25 ¹

¹ Survival was lower for young hatched from the heaviest eggs as well as for those hatched from lighter eggs.

Acknowledgments - I would like to thank David Bryant for advice during the study and comments upon this manuscript, Maimie Thompson for help with fieldwork, two anonymous referees who suggested improvements to the manuscript, John Speakman for advice upon statistics and my husband Robin for typing the references. I am very grateful to the farmers in the Stirling area who allowed me to work on their land and the staff in the animal house at the University of Stirling who turned the eggs in the incubator. Funding was provided by NERC studentship GT4/88/TLS/54.

Riassunto - In una popolazione di Rondine *Hirundo rustica* della Scozia centrale si sono studiate le relazioni tra massa e composizione delle uova, massa dei pulcini alla schiusa, caratteristiche somatiche delle madri e condizioni ambientali. Dimensioni e peso delle uova sono strettamente correlate. Il 60% di questa variabilità è spiegata dalle differenze tra le femmine. La massa delle uova deposte da ciascuna femmina presenta ripetibilità (ripetibilità = 0.54) ma non è correlata con le dimensioni del genitore. Inoltre il peso delle uova non è correlato alla dimensione della covata, al loro tasso di schiusa, né al rango di deposizione. Le uova contengono più lipidi se le condizioni ambientali sono favorevoli nei giorni precedenti la schiusa. Le uova più pesanti contengono più lipidi e più componente secca non lipidica. Inoltre le uova schiuse in incubatore sono state paragonate ad un campione naturale; la massa delle uova spiega il 60% della variabilità nella massa del pullo alla schiusa. Con l'analisi delle componenti principali si evidenzia che il 79% della variabilità nella massa alla schiusa è spiegato da fattori relativi alla dimensione delle uova. Come riportato in letteratura per molti non-passeriformi le uova più pesanti originano pulli più grossi, a crescita più veloce e con migliore sopravvivenza. In conclusione si ipotizza che gli irundinidi depongano uova piccole rispetto alle proprie dimensioni corporee, sebbene la produzione di uova più grandi avrebbe costi di poco superiori e dovrebbe essere vantaggiosa, considerando che nidiacei appena schiusi di dimensioni maggiori dovrebbero avere più probabilità di sopravvivere a periodi di mancanza di cibo.

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