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Composition of the eggs of the great tit (Parus major) and the pied flycatcher (Ficedula hypoleuca)

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The dimensions, composition and energy contents of 41 great tit and 48 pied flycatcher eggs, collected as freshly laid from nestboxes in the Oulu area, are presented.

Egg volume as well as egg weight correlated with calculated energy contents in both species studied. The proportion of yolk correlated well with egg size in the great tit but to a lesser extent in the pied flycatcher. The eggs of the pied flycatcher contained more lipids and energy than those of the great tit. The positive correlation between egg size and its energy contents was due to a higher proportion of albumen in the pied flycatcher but due to higher proportions of both yolk and albumen in the great tit.

In the great tit the egg size affected chick survival in two out of five years, but no such relation was noted in the pied flycatcher. This effect may result in situations where food supplies are unpredictable at the time of hatching, although generally the between-female differences in egg size must be considered as parts of the reproductive strategy in each species.

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1. Introduction

The composition of eggs from species of commercial importance is well known (e.g. the domestic hen, Romanoff & Romanoff 1949), as are those of the Larids, which are ecologically interesting as they invest energy unequally into the eggs of one clutch (e.g. Parsons 1976, Nisbet 1978).

Variability in the egg size and the changing egg quality could conceivably form a part of the reproductive strategy of birds (cf. Lack 1968, O'Connor 1978).

Only a few publications deal with the composition of the eggs of altricial birds. Papers by Ricklefs (1974, 1976, 1977a) on the starling (*Sturnus vulgaris*) and by Jones (1979) on the great white pelican (*Pelecanus onocrotalus*) were among the first on the topic. The variation in the proportions of yolk and albumen and also the variation in energy contents in eggs of species from various orders of birds have been discussed by several authors (e.g. Heinroth 1922, Asmundson et al. 1943, Romanoff & Romanoff 1949, Ricklefs 1977b, Ar & Yom-Tov 1978 and Carey et al. 1980). These variations are thought to have evolved through natural selection, ultimately for producing maximum numbers of young.

The aims of this paper are firstly to present data on weights, proportions and contents (lipid, water, fat-free dry matter) of egg yolk, albumen and shell and to test the relation of egg size to its energy content in two passerine species, the great tit (*Parus major*) and the fied flycatcher (*Ficedula hypoleuca*). Secondly, the relative amounts of yolk and albumen, in particular, and their energy contents are studied in context to compare the investment strategy of these two birds, which breed in unpredictable environments (e.g. Järvinen 1979) and have different wintering strategies. Preliminary results of the effect of egg size on chick survival are also presented. This paper is a continuation of those of Ojanen et al. (1978, 1979 and 1981) dealing with egg size and factors affecting them.

2. Material and methods

In a nest-box area near Oulu, northern Finland (c. 65°N, 25°30′ E) the egg-laying of great tits and pied flycatchers was followed daily from May 20 to June 9 1978. New eggs were marked and when the clutch was complete (or the female had begun to incubate) all eggs were transported to the laboratory. Their lengths and breadths were measured with sliding calipers to the nearest 0.05 mm and they were weighed to an accuracy of 0.1 mg. Eggs were prepared immediately, or were kept in a refrigerator (+4°C, maximum two weeks) until preparation. In all, 41 great tit and 48 pied flycatcher eggs from four and nine females, respectively, were collected (one pied flycatcher egg was lost after weighing and measuring).

To prepare the eggs, their shells were broken and the albumen and yolk poured into small pre-weighed cups. Egg components (albumen, yolk, shell) were dried at 80°C for 24 h, and after reweighing the lipids were extracted in a mixture of petroleum ether and chloroform (5:1) (Ricklefs 1977a). After extraction the samples were dried at 80°C for 24 h, and were weighed again, the difference between these two weighings being stated as the lipid weight. The fat-free dry material was then put into a small pre-weighed crucible and ashed in a muffle furnace at 600°C for 24 h to obtain the proportions of fat-free organic matter and ash. The usual combustion temperature of 550°C (see e.g. Ricklefs 1974) was not effective enough with our furnace.

A further 14 great tit and 24 pied flycatcher eggs were collected as freshly laid or from the recently abandoned nests of one and nine females, respectively. These eggs were treated whole according to the procedures described above. Egg volumes were calculated from their linear measurements according to formulae given in Ojanen et al. (1978). Albumen contents were calculated as total weight minus yolk and shell weight for eliminating the loss in processing, which amounted to 3.7 % and 3.1 % for the eggs of great tit and pied flycatcher, respectively.

Paine (1972) pointed out that the calculation of caloric equivalents from egg contents contains little error. Thus the energy contents of the eggs were calculated using energy equivalents of 9.5 kcal/g lipid and 5.65 kcal/g non-lipid dry matter (Ricklefs 1974). These constants exceed the energy contents of egg components to the extent that inorganic material and carbohydrate (4.1 kcal/g dry matter) are included in the non-lipid dry weight component. However, they form only a small proportion (1.2 % and 1.1 % ash in fresh yolk in eggs of great tit and pied flycatcher and 0.6 % in egg albumen in both species, and usually below 1 % carbohydrates, see also Ricklefs 1974). Using this method my results are comparable with those published.

The notation a±b refers to a mean value plus or minus its standard deviation. The significance of statistical tests is usually shown with the aid of asterisks. In this paper calories are used as the unit of energy, as in many other papers on this topic.

3. Results

3.1 Egg weights and dimensions

The eggs weigh about the same in both species (Table 1), although great tit females are much heavier than pied flycatcher females just prior to the laying season (18 g and 14 g, respectively). The length, breadth, shape index (100 x length/breadth) and calculated volumes of eggs of both species are presented in Table 1. In the eggs of the great tit analysed for the egg components (N=41) the coefficients of variation (CV) of egg breadth and volume were smaller (F=4.58*** and 5.16***, respectively) than in the 5007 eggs Ojanen et al. 1978) collected in 1969–1973 from the Oulu area. Thus the correlations between variables may perhaps be weaker than in a sample with a normal range of egg sizes for this species.

The correlation coefficients between the egg weight and volume were self-evidently significant for both species. The proportion of common variance ($100\times r^2$) was 86 % for the great tit and 95 % for the pied flycatcher. One can estimate egg weights rather accurately from the linear measurements of the egg by calculating the volume using methods presented in Ojanen et al. (1978) and multiplying this by a factor of 1.08 in the case of the great tit and by 1.10 in the pied flycatcher. This may be an advantage since linear measurements are easily obtained in the field.

Table 1. Dimensions of eggs of the great tit and pied flycatcher.

Dimension	Great tit				Pied flycatcher			
	Mean	SD	CV	N	Mean	SD	CV	N
All eggs								
Egg weight (g)	1.58	0.09	5.48	55	1.67	0.13	7.46	72
Egg length (mm)	17.74	0.72	4.04	55	17.58	0.80	4.56	72
Egg breadth (mm)	13.06	0.23	1.78	55	13.38	0.35	2.63	72
Egg shape index	135.90	5.81	4.28	55	131.14	5.28	4.03	72
Egg volume (cm³)	1.46	0.08	5.19	55	1.52	0.12	7.65	72
Eggs of component analysis								
Egg weight (g)	1.61	0.05	3.25	41	1.65	0.13	7.70	48
Egg volume (cm³)	1.48	0.05	3.34	41	1.50	0.11	7.59	48

Table 2. Weights (g) and proportions of components of eggs of the great tit and pied flycatcher.

	Great tit (N=41)			Pied flycatcher (N=47)		
	Mean	SD	CV	Mean	SD	CV
Albumen [1]	1.11	0.08	7.2	1.10	0.11	10.0
% of total	69.1	1.7	2.5	66.8	2.3	3.4
Shell	0.18	0.02	11.1	0.18	0.02	11.1
% of total	11.1	1.5	13.5	11.2	1.4	12.5
Dry shell	0.10	0.004	3.7	0.095	0.01	8.7
% of total	6.3	0.3	4.0	5.7	0.4	6.3
Yolk	0.32	0.02	6.3	0.37	0.05	13.5
% of total	19.9	1.2	6.0	22.1	1.8	8.1

[1] The weight of albumen was calculated as Total weight of egg – weight of shell – weight of yolk.

3.2. The egg components

The pied flycatcher eggs contained significantly more yolk than those of the great tit (Table 2, p<0.001). The variation in yolk weights was significantly greater for the pied flycatcher than for the great tit (CV 13.2 versus 6.2; F-test, p<0.01). The average amounts of albumen and shell as well as their CV values were almost equal for both species (Table 2). The proportions of albumen and dry shell were, however, significantly smaller in pied flycatcher eggs than in those of the great tit (p<0.001 in both cases;

t-test using arcsine values of percentages).

The amounts and proportions of lipid were significantly greater in eggs of the pied flycatcher than in those of the great tit (Table 3, $p<0.001$ in both comparisons; *t*-test using arcsine values of percentages). Moreover, the dry yolks of the pied flycatcher contained 5.4 percentage units more lipid than those of the great tit. The amount of yolk increased as egg weight increased for the great tit, but not for the pied flycatcher (slope $b=0.30$, $r=0.67$** and $b=-0.02$ NS, $r=-0.07$ NS, respectively). The percentage of yolk remained constant as egg weight increased for the great tit, but decreased significantly for the pied flycatcher ($r=0.14$ NS, and -0.67***, Table 3).

As there were similar proportions of lipid in the whole eggs (see methods) and in the component eggs, data from both groups was combined for calculating regressions for lipid weight and lipid as a percentage of egg weight. The amount of lipids increased with increasing egg size in both species (Fig. 1), but the lipid percentage remained constant with increasing egg size in the great tit ($r=-0.06$, NS), and decreased significantly in the pied flycatcher ($r=-0.43$***)

The proportion of water and non-lipid dry matter was about the same in the albumen of both species (Table 3). Large eggs contained proportionately more albumen than small eggs in the pied flycatcher ($r=0.66$**), but no such trend was seen in the great tit ($r=0.12$, NS).

Table 3. Composition of yolk, albumen and shell and the correlation between some egg components and egg weight in the great tit and pied flycatcher.

	Great tit ($N=41$)		Pied flycatcher ($N=47$)	
	Mean	*SD*	Mean	*SD*
Yolk				
% water	59.1	5.1	56.5	3.0
mg lipid	79.1	4.9	103.4	7.5
% lipid	24.5	3.7	28.3	2.4
% non-lipid dry matter	16.5	2.3	15.2	1.1
lipid (% dry)	59.6	3.7	65.0	2.0
Albumen				
% water	90.2	0.4	89.5	0.5
% extractable material	0.1	0.1	0.3	0.1
% non-lipid dry matter	9.7	0.3	10.3	0.6
Shell				
% water	41.8	6.8	48.2	5.1
% extractable material	0.4	0.4	0.7	0.4
% non-lipid dry matter	57.7	6.8	51.2	5.1
Correlation coefficients (*r*) for				
egg yolk weight and egg weight	0.67***		-0.07 NS	
egg lipid weight and egg weight[1]	0.62***		0.43***	
% lipid and egg weight[1]	-0.06 NS		-0.43***	
albumen weight and egg weight	0.66***		0.91***	
% albumen and egg weight	0.12 NS		0.66***	
egg shell weight and egg weight	-0.29 NS		0.43*	
% wet shell and egg weight	-0.34*		-0.20 NS	
dry shell weight and egg weight	0.33**		0.73***	
% dry shell and egg weight	-0.48**		-0.27 NS	

[1]) note: includes results from whole eggs (see methods); for great tit eggs $N=55$, for pied flycatcher eggs $N=71$.

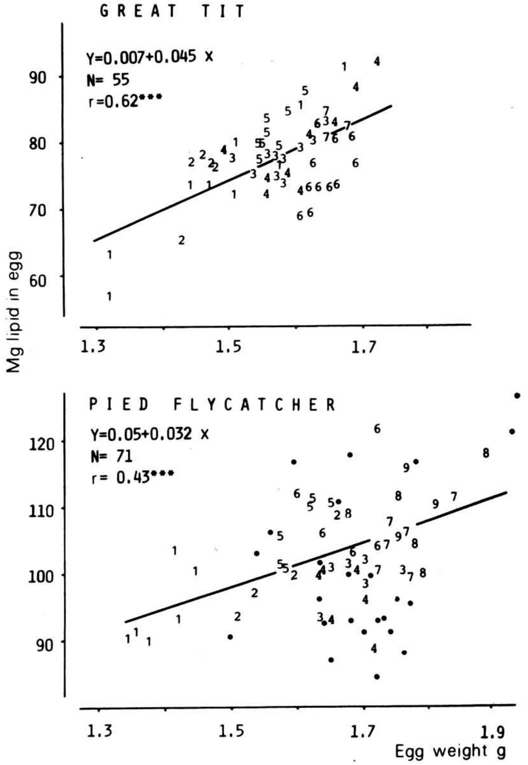

Fig. 1. Relation between the amount of lipid in egg yolk and the egg weight in great tit and pied flycatcher. The same numbers denote eggs from the same females in the great tit and also 9 pied flycatcher females for component eggs. The additional 1 to 7 eggs from 9 other females of the latter species (see methods) are represented by dots.

The fraction of shell was about the same in the great tit and pied flycatcher eggs (11 %). The egg shell contained about 6 percentage units more water in the great tit than in the pied flycatcher (Table 3). The *CV* values of the percentages of water in the shell were large, amounting to 16.3 and 10.6 % for the great tit and pied flycatcher, respectively. The correlation between shell weight and egg weight was slightly negative (not significantly) for the great tit but significantly positive for the pied flycatcher (r=0.43*, Table 3). There were greater amounts of moisture in smaller shells in both species, as the correlation between dry shell and egg weight was positive for both species (Table 3), and also better for the pied flycatcher than the correlation between wet shell and egg weight.

3.3. The energy contents of eggs

The energy of egg components, total egg energy and energy density of the eggs are presented for both species in Table 4. Heavier eggs contained more energy (excluding shell energy) than light ones in both species. The proportion of common variance was 70 % for the great tit and 59 % for the flycatcher; thus egg weight (and volume) corresponds closely to its energy content.

Pied flycatcher eggs had greater caloric density (kcal/g fresh egg including shell) than those of the great tit (Table 4). The caloric density was not influenced by egg size in the great tit, (b=0.05, r=0.11 NS), but small eggs of the pied flycatcher contained proportionately more energy than large ones (b=-0.27, r=-0.57**).,

The correlation coefficients between the energy of yolk or albumen and egg weight were usually high for both species (Table 4). Partial correlations revealed that in the great tit albumen and yolk contributed equally to the energy content of the egg, but in the field flycatcher egg albumen was the main contributor to the correlation between egg weight and energy content.

Egg shells of the great tit (mean dry weight 0.102 g) contained 0.33 kcal energy and those of the pied flycatcher (0.095 g) 0.27 kcal. Hence the energy of the egg contents must be multiplied by 1.198 in great tit and by 1.138 in pied flycatcher to find the gross energy contents of the eggs (including shell energy).

Table 4. Energy content (kcal) of albumen, yolk lipids, yolk, egg contents, energy density of eggs and correlations between energy of egg components and egg weight in the eggs of the great tit and pied flycatcher.

	Great tit (N=41)		Pied flycatcher (N=47)	
	Mean	*SD*	Mean	*SD*
Energy in albumen	0.62	0.03	0.66	0.07
Energy in yolk lipids	0.72	0.09	0.96	0.11
Total energy in yolk	1.06	0.05	1.30	0.09
Yolk albumen energy ratio	1.73		1.94	
Energy of egg contents	1.67	0.07	1.95	0.13
Energy density (kcal/g egg fresh weight including shell)	1.04	0.02	1.19	0.06
Correlation coefficients (r) for				
energy of egg contents and egg weight	0.84***		0.77***	
energy density and egg weight	0.11 NS		-0.57**	
albumen energy and egg weight	0.70***		0.86***	
yolk energy and egg weight	0.69***		0.49***	
albumen energy and yolk energy	0.34*		0.44**	
Partial correlations				
$r_{wt\ alb\ .\ yolk}$	0.69***		0.67***	
$r_{wt\ yolk\ .\ alb}$	0.82***		0.24 NS	

4. Discussion

4.1. The composition of eggs of altricial species

A short comparison of the components of eggs of altricial species (with brief notes on precocial species) is given first as only a few papers have been published describing these properties in the altricial group. In the great tit the yolk weight correlated with egg weight and the percentage of yolk remained constant as egg weight increased (r=0.14 NS). The relationship between the percentage of yolk and egg weight was negative in the pied flycatcher (r=-0.67***), as in the starling (r=-0.52*, Ricklefs 1977a) and great white pelican (r=-0.47***, Jones 1979). A similar situation, in which the percentage of yolk (or lipid) decreases with increasing egg size is also found in a few species with precocial development; the domestic hen (Romanoff & Romanoff 1949), Japanese quail, *Coturnix coturnix japonica* (Ricklefs et al. 1978) and common and roseate terns, *Sterna hirundo* and *S. dougallii* (Nisbet 1978).

The percentage of water in the albumen was almost the same, about 90 %, in these species, and varied at the same level as recorded for many species, between 85 and 90 % (e.g. Ricklefs 1977a). Low water levels reported for the brown pelican (*Pelecanus occidentalis*) (81 %, Lawrence &

Schreiber 1974) and for the laughing gull (*Larus atricilla*) (79 %, Schreiber & Lawrence 1976) were due to some water loss during handling and processing (see Ricklefs 1977b). The *CV* for water contents was generally small, varying from 0.3 to 1.5 % with the five species presented by Ricklefs (1977b) and being 0.4 % in the great tit and 0.6 % in the pied flycatcher.

The proportion of shell in the eggs of great tit and pied flycatcher (11 %) was slightly less than the respective value in the starling (12.5 %, Ricklefs 1977a). From values in Ricklefs (1977b) I calculated water percentages as varying between 49.6 and 54.4 % for shells of starling, Japanese quail and mourning dove (*Zenaida macroura*). The respective values in the great tit (41.8 %) and in the pied flycatcher (48,2 %) were of the same magnitude. For the mallard (*Anas platyrhynchos*) the water content of the shell was only 12 %, but this was perhaps erroneous because the percentages of egg components did not make up 100 %.

Yolk lipids contributed most of the total energy contents of eggs in pied flycatchers, but least in the great tit (Table 5). This comparison includes only four species with altricial development for which data were available. The fat-free dry yolk contributed relatively little to total energy in the starling and great white pelican because these species produce small yolks. The fraction of energy in albumen varied between 33 and 43 %.

4.2. The ecological importance of egg energetics

There is a considerable variation in the proportions of yolk and hence in the energy contents in the eggs of birds with atricial development. The proportion of yolk varied from 12 to 38 % of the egg weight in 52 altricial species ($\bar{x}$=21.3±4.79, *CV*=22.5, Ar & Yom-Tov 1978), and also the energy density of the egg mass (kcal/g egg mass, excluding shell) of this group varied in 23 species between 0.89 and 1.56 kcal/g (averaging 1.13±0.16, *CV*=14.1 %, Carey et al. 1980). The yolk percentages were 19.9 and 22.1 %,

Table 5. Proportion (%) of energy in egg components in four species with altricial development.

	Yolk lipids	Yolk fat-free	Albumen dry
Great white pelican[1]	44.8	14.0	41.1
Great tit	43.1	20.4	36.5
Pied flycatcher	49.2	17.4	33.3
Starling[2]	47.6	9.4	43.0

[1] Jones 1979, values partly recalculated.
[2] Ricklefs 1974.

and the caloric contents of egg mass 1.11 and 1.25, respectively, for the great tit and pied flycatcher, these values being near the averages of the altricial species.

Lack (1968) stated that "In consider all the breeding habits and other features discussed in this book have been evolved through natural selection so that, in the natural habitats where they were evolved, the birds concerned produce, on average, the greatest possible number of surviving young".

Why is the energy content of the eggs of the pied flycatcher greater than in great tit eggs? Does this allow the chicks of the former species to develop more rapidly at the early part of the growth period, thus being an insurance against environmental unpredictability (growth rate for pied flycatcher young, see e.g. Askenmo 1973, for great tit young, e.g. Gibb 1950)? As the production of the more energy-rich egg suggests a higher risk for the female, the problem of how much energy to invest in eggs is complicated. At the individual level low investment into eggs causes lower risk to the female, but may increase mortality of the young during times of decreased food availability. With high investment in the reproductive efforts (energy-rich eggs) the mortality of females perhaps increases, but at the same time the probability of survival of the young increases due to the initial advantage of hatching from better-quality eggs. Thus the energy content of eggs is involved in the reproductive strategy of a species and it contains a complex of intercting factors combining to maximize the species' and invidual's fitness.

Howe (1978) was able to show that there was a direct correlation between egg content dry weights (excluding shell) and fresh weights in 10 clutches of eggs of the common grackle *Quiscalus quiscula* (*r*=0.89***). Thus the direct correlation between hatchling weight and fresh egg weight (Howe 1976) is due to provisioning with nutrients, not only water. Larger eggs of swifts *Apus apus* produced heavier chicks than smaller ones (*r*=0.37***) and chick wing length was positively correlated with egg size (*r*=0.35***, O'Connor 1979). Thus there is an initial advantage in hatching from a large egg. However, the positive correlation between egg size and chick size decreased as the young matured (for passerines, e.g. Schifferli 1973, and O'Connor 1975).

Does then the egg size affect the production of young in some species? To my knowledge, no studies on this question have been published about passerine species, although the correlation between egg size and chick survival in *Laridae* is well known (e.g. Parsons 1970, Nisbet 1973, Lundberg & Väisänen 1979). A preliminary analysis on great tits from the Oulu area showed that in certain years the mean egg size of the clutch may really affect the productivity of the females. In 1969 and 1973 more young fledged from clutches containing large eggs than from those containing small (r=0.59*, N=19 for all clutches in 1969 and r=0.36**, N=81 for first clutches, containing at least 8 hatchlings; correlation calculated between percentage of young fledged from those hatched and normalized egg size: the mean of the egg size in each clutch was subtracted from the grand mean for the year and the rest divided by the standard deviation). However, the 1970-1972 results show no correlation between these variables. Preliminary testing of the data of pied flycatcher from 1970-1973 showed no correlation between egg size and production of young. However, these relations are more thoroughly discussed in a later paper.

Perhaps the advantage of hatching from a large egg is only of short duration and soon disappears (O'Connor 1975). In years when the weather is poor during the hatching time and it is difficult to gather food for the young, the laying of large eggs is advantageous, as seen in the example of the great tit. The cost of forming such energy-rich eggs may be the disadvantage which explains why not all individuals lay large eggs. In terms of reproductive strategy, any investment in present offspring involves a decrease in the future investment of the individual. Therefore, in fluctuating environments both low and high investors (those laying small or large eggs) have basically similar long-term advantages in producing offspring (for further details of the concept of reproductive strategy, see e.g. Pianka 1976 and 1978 and references therein).

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