

## Effects of laying sequence and ambient temperature on the composition of eggs of the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*

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Ojanen, Mikko 1983: Effects of laying sequence and ambient temperature on the composition of eggs of the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*. — Ann. Zool. Fennici 20: 65-71.

The effects of laying sequence and ambient temperature were tested on 41 great tit and 47 pied flycatcher eggs and the egg components (yolk, albumen and shell).

In pied flycatchers, clutches (females) contributed about 40-70 % of the variation in egg components, the values being apparently smaller in great tits. Laying sequence contributed 17 % and 8 % to the variation in wet weight of yolk and albumen, respectively, but not to dry weights or energy contents of yolk or to total egg weight in the pied flycatcher. Thus the increase in size caused by the laying sequence in large clutches reported earlier for the pied flycatcher is due to inclusion of water, not of nutrients. Only the fresh weight of the yolk tended to decrease with sequence in the great tit, large interactions indicating that females invested the components differentially with the sequence.

With regard to the relation between the egg sequence variation and growth strategies, both species apparently follow the clutch adjustment strategy.

Changes in ambient temperature caused up to 10-15 % of the total variation in the egg components in the great tit, but only 2-3 % of that in the pied flycatcher.

Birds have the potential to use considerable amounts of energy for maintenance if adverse weather occurs during the laying period, this exceeding the energy needed to produce an egg each day by a factor of about two. The main factor affecting egg size and components (egg quality) is the large, phenotypic female component, which perhaps reaches values close to the heritability of these characters. The influence of other factors, such as the ambient temperature, is small.

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### 1. Introduction

The important position of eggs in the reproduction of birds (Parsons 1970, Howe 1976) motivates interest in the relationship between egg properties and reproductive strategies.

The importance of the within-clutch variation in passerine eggs was stressed by Howe (1976), who proved that in clutches of the common grackle *Quiscalus quiscula* the size of eggs increases with advancing sequence. This increase in size was thought to ensure the survival of young hatched from the egg laid last during periods when food is scarce just after hatching, but increases rapidly later on.

Howe (1978) was further able to show that larger common grackle eggs contained greater amounts of dry matter than smaller ones. A large egg size appeared to be a good predictor of a high energy content of the egg in the great tit and pied flycatcher, too (Ojanen 1983). However, conflicting

results have been published about the correlation between the egg size and its presumed contents; Bryant (1978) suggested that the eggs of the house martin *Delichon urbica* were perhaps of unequal quality within the sequence, although about the same size within a clutch (Bryant 1975).

This study deals with the relation between ambient temperature, position in laying sequence, and the egg components. Answers were sought to the following questions:

- 1) How is the within-clutch variation related to between-clutch variation in egg components? This relationship gives us the female component (repeatability, see Falconer 1960) of the character.
- 2) Does the female invest equally into the components of eggs within the laying sequence?
- 3) How strong is the effect of ambient temperature during egg formation on the egg components?
- 4) What are the biological effects of differential investment into the egg components in a clutch?

This paper comprises the second part of the study of egg composition in relation to the reproductive strategies in the great tit and pied flycatcher (see Ojanen 1983).

## 2. Material and methods

The study area is situated near Oulu (c. 65°N, 25°30'E), where the laying of great tits and pied flycatchers was followed daily. New eggs were marked and the eggs collected as soon as the clutch was completed or the female began to incubate. In the laboratory, egg length and breadth were measured to the nearest 0.05 mm and eggs were weighed to an accuracy of 0.1 mg. Their shells were broken and albumen, yolk, and shell were deposited into small preweighed cups. The contents were dried at 80°C for 24 h. After reweighing, the lipids were extracted in a mixture of petroleum ether and chloroform (Ricklefs 1977). After again drying at 80°C for 24 h and reweighing, the difference between these two values was stated as the lipid weight. The fat-free dry matter was then ashed in a muffle furnace at 600°C 24 h to find the proportions of ash and ash-free organic matter (for methods, see also Ojanen 1983).

For this analysis, 41 eggs from four great tit females (11, 10 and 8 eggs from the first three, and from a fourth 3 eggs from the first clutch and 9 from a repeat clutch) and 50 eggs from nine pied flycatcher females (3, 2 x 5, 5 x 6 and 7 eggs) were collected, the laying order of the eggs being known exactly. Three of the pied flycatcher eggs were lost during collection or processing. Some clutches were perhaps not complete when they were collected, because the eggs were taken as soon as the female had started incubation.

A nested model of two way analysis of variance (anova) was used for dividing the total variance into components in order to produce estimates of interactions (see Sokal & Rohlf 1969: 298–320 for details). Treatment was similar to that used in Ojanen et al. 1981; e.g. for great tits, "four-egg" clutches were designed in which the first "egg" consisted of the original first and second eggs, the second "egg" consisted of the third and fourth original eggs, and the last two "eggs" consisted of the original last four eggs. For the pied flycatcher, two "egg" clutches were designed for the analysis. Thus all the median eggs were rejected.

In consequence the cells of the analysis matrix contained four "eggs", each with one replicate, for the great tit, and two "eggs" for the pied flycatcher. Using anova models with full matrices we can obtain estimates for interaction components (between-female – within-sequence).

The temperature parameters taken for analysis were the daily minimum, mean and maximum from one to nine days before laying. The minimum, mean and maximum temperatures (abbreviated as  $T_{\min}$ ,  $T_{\text{mean}}$ ,  $T_{\max}$ ), calculated for different periods of days before laying, were also used. In order to eliminate the effect of the female from the egg parameters, the percentage differences from clutch means were used for temperature analysis.

The temperature data was taken from Oulu Airport (monthly reports from the Finnish Meteorological Institute).

## 3. Results

### 3.1. Laying sequence and the components of eggs

In the great tit eggs, the fresh weight of yolk tended to be lower the later they were laid in the sequence and to vary significantly, but sequence had no effect on the other parameters studied (Table 1). Generally, the clutch component

Table 1. Variation in the great tit and pied flycatcher egg components and their energy contents in relation to sequence in the clutch. Two successive eggs are used as replicates (see text). Two-way analysis of variance (mixed model): percentage estimates given for components of variation and the significance of *F*-tests shown by asterisks.

Variable	Clutches	Replicates	Variation components (%)			
			Clutches	Sequence	Interaction	Residual
Great tit						
Egg weight	4	4x2	14***	-0	70***	16
Water weight <sup>1</sup>	4	4x2	11***	-0	71***	18
Egg energy	4	4x2	14***	-0	53***	33
Albumen weight	4	4x2	38***	-0	43**	19
Albumen dry	4	4x2	51***	-0	20	29
Yolk weight	4	4x2	49.0***	8.5*	26.1**	16.5
Yolk dry	4	4x2	35***	-0	41***	23
Yolk lipid weight	4	4x2	-0	-0	60**	40
Yolk energy	4	4x2	6*	-0	59*	35
Shell dry	4	4x2	30***	-0	44**	27
Pied flycatcher						
Egg weight	6	2x2	85.9***	8.9**	1.2	3.9
Water weight <sup>1</sup>	6	2x2	82.7***	11.0***	0.6	5.7
Egg energy	6	2x2	16**	-0	-0	84
Albumen weight	6	2x2	66***	8*	-0	25
Albumen dry	6	2x2	73***	1	-0	26
Yolk weight	6	2x2	40.7***	17.3*	7.1	34.9
Yolk dry	6	2x2	45*	6	-0	49
Yolk lipid weight	6	2x2	38*	-0	-0	62
Yolk energy	6	2x2	43.6*	7.5	2.9	46.1
Shell dry	6	2x2	50.4**	3.7	7.4	38.5

<sup>1</sup>Egg weight minus weights of dry yolk, albumen and shell

(females) accounted for about 10–50 % of the total variation, but the percentage estimates were not particularly large. The interactions were significant and had large numerical values (Table 1). These were caused by the fact that the last eggs and their components in the clutches of three females were slightly (not significantly) smaller than the first ones, but in one clutch the sequence was reversed (again, not significantly).

In the pied flycatcher, fresh egg, water and albumen weights increased and fresh egg yolk weight decreased significantly with the laying sequence (Table 1). The values of sequence components were usually small. The total energy was not affected by the sequence, and the female component was especially low due to proportionately energy rich first eggs in two five-egg clutches. If the four remaining six-egg clutches were treated separately (as 3 x 2 replicates, see methods) the female component comprised 69 %, but the sequence component remained at the zero level.

Interactions were small and insignificant between laying sequence and females in all egg components. The clutch (female) components were especially large (Table 1).

Table 2. The correlation between energy contents of different components of great tit and pied flycatcher eggs (percentage of clutch mean) and ambient temperatures on single days prior to laying.

Day prior to laying	Great tit ( $N=41$ )				Pied flycatcher ( $N=47$ )				
	7	5	3	1	9	7	5	3	1
$T_{\min}$									
Yolk energy	-0.17	0.12	0.33*	0.22	-0.10	-0.10	-0.13	0.22	-0.06
Shell + albumen energy	0.09	0.21	0.06	0.07	0.18	0.22	-0.19	-0.14	0.36*
Total energy of egg <sup>1</sup>	-0.07	0.17	0.25	0.20	0.27	-0.01	-0.13	0.11	0.10
$T_{\text{mean}}$									
Yolk energy	-0.01	0.35*	0.39*	0.23	0.31*	0.31*	0.00	0.08	-0.05
Shell+albumen energy	0.04	0.40**	0.47**	0.39*	-0.20	0.21	0.18	0.10	0.17
Total energy of egg <sup>1</sup>	-0.01	0.39*	0.51***	0.34*	0.13	0.34*	0.09	0.12	0.03
$T_{\max}$									
Yolk energy	0.08	0.31*	0.37*	0.20	0.21	0.36*	0.01	-0.02	-0.02
Shell+albumen energy	0.12	0.37*	0.51***	0.44**	-0.28	0.07	0.00	0.17	0.08
Total energy of egg	0.10	0.41*	0.51***	0.34*	0.05	0.31*	0.18	0.10	0.02

<sup>1</sup>Including shell

### 3.2. Effect of ambient temperature on the investment into eggs

As the egg yolk is formed over a couple of days, followed by c. 24 h period when albumen is secreted and the shell formed (Romanoff & Romanoff 1949), I divided the total energy contents of the eggs (including the energy in the shell) into two components; energy of the yolk (lipids and non-lipid matter) and energy contents of albumen and shell (energy of albumen and energy of organic material of the shell).

In the great tit, temperature significantly affected the total energy in the yolk and also the energy in the albumen and shell (Tables 2 and 3). In particular the mean and maximum temperatures of days three and five preceding laying had effects on the energy contents of egg components (yolk, albumen and shell, Table 2). The minimum temperature of day three affected only yolk energy significantly (Table 2). The correlations

between yolk and total energy of egg and temperatures of periods of varying lengths had their maximum value at five days (Table 3). The effects of temperature on egg energetics was thus clearly better seen when using periods longer than one day in the great tit.

In the pied flycatcher, temperatures had less effect than in the great tit on egg energetics. Yolk energy correlated with mean and maximum temperatures of nine and seven days before laying, while albumen and shell energy correlated only with the minimum temperature of one day prior to laying (Table 2). When tested over periods of varying lengths the maximum temperature correlated with the yolk energy only for the period of nine days (Table 3). Yolk energy was also correlated at same strength with  $T_{\max}$  for three day means of days 6-8 and 7-9 prior to laying. The total egg energy was also correlated with the temperatures of  $T_{\text{mean}}$  and  $T_{\max}$  of the nine day

Table 3. The correlation between energy contents of different components of great tit and pied flycatcher eggs (percentage of clutch mean) and mean temperatures of periods of different lengths prior to laying.

Period length prior to laying <sup>1</sup>	Great tit ( $N=41$ )				Pied flycatcher ( $N=47$ )				
	7	5	3	1	9	7	5	3	1
$T_{\min}$									
Yolk energy	0.38*	0.61***	0.51***	0.22	0.07	-0.11	0.16	-0.11	-0.06
Shell + albumen energy	0.37*	0.37*	0.10	0.07	0.29*	0.32*	0.04	0.20	0.36*
Total energy of egg <sup>2</sup>	0.44**	0.60***	0.44**	0.20	0.20	0.06	0.10	0.29*	0.13
$T_{\text{mean}}$									
Yolk energy	0.35*	0.41**	0.39*	0.23	0.23	-0.02	-0.06	-0.11	-0.05
Shell + albumen energy	0.48**	0.55***	0.48**	0.39*	0.35*	0.36*	0.31*	0.36*	0.17
Total energy of egg <sup>2</sup>	0.47**	0.55***	0.50***	0.34*	0.34*	0.16	0.10	0.13	0.03
$T_{\max}$									
Yolk energy	0.33*	0.37*	0.33*	0.20	0.39**	0.08	-0.06	-0.16	-0.02
Shell + albumen energy	0.48**	0.52***	0.50***	0.44**	0.26	0.38**	0.32*	0.34*	0.08
Total energy of egg <sup>2</sup>	0.45**	0.50***	0.47**	0.34*	0.43**	0.23	0.11	0.07	0.02

<sup>1</sup>7 = days 1 to 7 prior to laying, etc.<sup>2</sup>Including shell

period, and also the  $T_{\min}$  of the three final days prior to laying was significant (Table 3). Shell plus albumen energy correlated interestingly with temperatures: strong correlations were observed for both a period of about seven days and a period of about three (to one) days (Table 3).

## 4. Discussion

### 4.1. The heritability of egg components

The heritability of the egg components of the domestic hen has been thoroughly studied because of the bird's commercial importance. Several reviews cover this topic (e.g. Scheinberg et al. 1953, Tijen & Kuit 1970 and Washburn 1979). Yolk weight heritability is reported to vary within the range 0–1.12, and albumen heritability within the range 0.68–1.12 (Scheinberg et al. 1953, and Tijen & Kuit 1970). Albumen and yolk solids also have high heritabilities;  $h^2$  values of 0.5–0.6 for albumen solids (Sørensen & Ambrosen 1978) and an  $h^2$  value of 0.5 for yolk solids (Rodda et al. 1977). Egg shell also has a relatively high heritability, reported  $h^2$  values varying between 0.18 and 0.56 (Farnsworth & Nordskog 1955, Tijen & Kuit 1970, Rodda 1972, Tijen 1977a–c). Although diet accounts for a great deal of variance between various egg components in commercial species (e.g., the review of Naber 1979), heritable effects have a strong effect on many chemical components of eggs such as albumen quality, total protein content of egg, amount of cholesterol, and amount of fatty acids and vitamins (e.g. review of Washburn 1979).

The heritability estimates of egg quality obtained by different authors show a wide range of variation, which, according to Tijen & Kuit (1970), can be caused by factors such as:

1. Kind of distribution of genes
2. Kind of environment
3. Method of estimation
4. Precision of the estimate, for instance in connection with a number of families and number of animals as well as the variation of these numbers.

With regard to point (1) the different stocks may have different heritabilities on measured traits because of the variation in the gene pools of the founder stocks and because of the intensity of selection of the traits in question.

The average coefficients of variation ( $CV$ ) in yolk, albumen and shell weight of great tit and pied flycatcher eggs were 9.3 and 10.4 % (Ojanen 1983). These figures are about the same as the  $CV$  of egg size in four passerine bird species (Ojanen et al. 1978). Thus there is moderate variation in the

egg weights and the components studied. Further, as the effect of laying sequence in the pied flycatcher was generally smaller than the female components in the traits studied (see the results section), individual females differ from each other in their ability to invest material into the eggs.

In the domestic hen, phenotypic and genotypic correlations tended to be similar for total egg weights and weights and percentages of egg components, including the shell (Hill et al. 1966). As it is very difficult to obtain eggs from a number of females and their daughters in order to measure mother-daughter phenotypic correlation, one must compromise by measuring only the female component (or the repeatability of the measurement). According to Falconer (1960) the repeatability separates out the special environmental component, but leaves the other component of environmental variation — that due to the general environment — confounded with the genotypic variance. The female component is an approximation of the upper limit of heritability (broad sense, see Falconer 1960) if the general environmental component approaches zero and no interaction exists between the genotype and the environment. The female components ranged from approximately 0.2 to 0.8 for various egg components in the pied flycatcher in the present study. In the great tit the values were about 0.1–0.5, the large interactions indicating differential sequential effects in these four females. Generally, the female components were smaller than the average heritability of the egg weight or size ( $h^2 = 0.6–0.86$ , Jones 1973, Ojanen et al. 1979, van Noordwijk et al. 1980) for the great tit.

Thus, part of the variation observed within egg components has a heritable nature. In the following I shall discuss the relative strengths of this and environmental factors as part of the investment strategy of female passerines.

### 4.2. Variation in contents due to sequence and breeding strategies

A number of species lay their eggs unequally within the sequence. This is thought to be connected with their breeding strategy (e.g. Ojanen et al. 1981 for further discussion). As the egg size is a good predictor of its energy contents (Ojanen 1983), the within-clutch variation in size corresponds almost exactly to the within-clutch variation in energy contents. Some species may differ in this respect; Bryant (1978) showed that in the house martin *Delichon urbica* the relative dry weight of embryos was correlated with the laying sequence, not with egg size. In this species, the eggs laid last contained small yolks, giving rise to

small hatchling, which were more likely to die even if there was sufficient food (Bryant 1978). However, this aerial insectivore has a breeding strategy such that the female enhances weight differences between siblings by an unequal investment into the eggs and also by starting incubation before the clutch is completed. By inducing brood reduction with these methods, this species is able to cope with periods of low food availability coinciding with high demands by the growing siblings. The young hatching last probably survives only if food is abundant. Species having similar strategies may, however, be few.

In the great tit, only the fresh weight of the yolk tended to correlate with the laying order, other egg parameters not being affected. These results were thus consistent with earlier results, in which no sequential variation in egg dimensions were usually found (Ojanen et al. 1981).

In the pied flycatcher, the fresh weight of the eggs or their components were affected by the sequence, but dry weights or caloric contents were not. The egg breadth and volume in clutches of six to eight eggs increased according to the sequence (Ojanen et al. 1981), this being consistent with an increase in fresh weight and albumen with laying order. Thus the increase in egg weight within a clutch is only due to inclusion of water, and not of dry matter, in this species. These results are also confirmed by the facts that in the pied flycatcher the caloric content correlated negatively with the egg size (Ojanen 1983), and the percentage water content increased with increasing egg size ( $b=4.0$ ,  $r=0.6^{***}$ ,  $N=47$ ). As the female component was very large in this species (about 60–80 % in egg volume, Ojanen et al. 1981 and about 85 % in egg weight, Table 2) the observed, large between-female variation in egg weights clearly involves differential investments into different clutches, but the relatively small-scale within-clutch variation means approximately equal investments for all eggs in a clutch.

O'Connor's theory (1978) on the growth strategies of passerines involved within-clutch variation in egg sizes, which should be large in species with brood reduction strategy, intermediate in species with resource storage strategy and small in species with clutch adjustment strategy. If the egg size largely matches its energy contents in the species involved, this theory seems true. This is true in the great tit, for which even the present meagre data show equal investments, irrespective of the position in laying. However, this is not the case in the pied flycatcher. The within-clutch variation in egg quality is far smaller than between-female variation in the latter species, and as nestling mortality is low (e.g. Haartman 1951), the clutch adjustment strategy

seems adequate for this species, too, as we have earlier assumed (Ojanen et al. 1981).

#### 4.3. The effect of ambient temperature on the egg components

In the spring of 1978 great tit females laid their eggs within wider temperature ranges than the pied flycatchers: during the laying period (from 5 days before the first egg and until the last was laid) of the great tit, the mean temperature varied between 17.9 and 9.4°C (*CV* 44.6 %), while the corresponding range for the field flycatcher was 15.1–9.4°C (*CV* 11.7 %), the difference between *CV* values being significant ( $P<0.05$ ).

The weaker variation in egg sizes due to temperature in the pied flycatcher was presumably due to the fact that great tits had to use more energy for temperature regulation so that less was available for the developing eggs. To test this the variation in the existence metabolism (*EM*, the energy used by caged birds for maintaining constant body weight including the heat increment of feeding and a limited amount of locomotor activity) was calculated within the temperature ranges measured during the laying period of the eggs collected for this study. This was to help discover the magnitude of the variation in the caloric demands for body temperature regulation. The estimated difference in *EM* between birds laying during the time of observed high or low temperature was 3.03 kcal/bird/day in the great tit (range 8.5°C, see above). The corresponding figure for the pied flycatcher was 1.92 (range 5.7°C). These amounts of energy are equivalent to the formation of 1.06 great tit eggs and 0.61 pied flycatcher eggs (energy of whole egg from Ojanen (1983) and the partial efficiency of energy utilization taken as 70 % (King 1973)).

The maximum ranges of mean temperature within which these species have laid eggs in the Oulu area during the main laying season (covering over 95 % of the first clutches laid and being May 4–31 for the first clutches in the great tit and May 25–June 15 for the pied flycatcher, between 1969 and 1980: unpubl.) were 20.1°C for both species (see Fig. 1).

The corresponding difference in the caloric demands for body temperature regulation were 7.17 kcal/bird/day for the great tit and 6.79 kcal/bird/day for the pied flycatcher (Fig. 1). These values represent 115 and 131 % of the respective basal metabolic rates (BMR, the rate of energy utilization at rest, unstimulated by the digestion and assimilation of food or by low temperature; the values of BMR being calculated by the formulae for the rest-time according to Aschoff & Pohl 1970). Thus a bird laying in very



low temperatures must use about twice the energy needed for egg formation simply for temperature regulation (see also Fig. 1).

The recorded variation in egg components due to temperature fluctuation must thus be considered normal, especially as birds laying during average temperatures tend to have a large fraction of uncommitted time in their energy budgets, and have the potential to lay eggs even during harsh times (Ettinger & King 1980).

The habit of slightly moderating egg size and egg components according to the ambient temperature is adaptive. It allows females to lay eggs under a wider range of environmental conditions than would otherwise be possible. An alternative to this is to lay eggs strictly according to heritable factors, and delay laying during adverse weather. Actually, delays in very cold weather have been reported for many species (e.g. for great tit, Winkel 1970, for pied flycatcher, Winkel & Winkel 1974, for swift *Apus apus*, O'Connor 1979).

The correlations between egg size or its components and ambient temperature averaged about 0.3–0.4 for the great tit and about 0.0–0.2 for the pied flycatcher, these values being perhaps slightly greater than those reported earlier (about 0.1–0.2, Ojanen et al. 1981). The proportion of common variance was generally of the magnitude of 10–15 % and 2–3 %, respectively, for these species.

The egg size is thus held within certain limits, below which the hatchability and survival of the hatchlings may rapidly decrease (e.g. Murton et al. 1974). The main factor affecting the size and quality of the eggs is most probably the genome and other factors have only a minor, though adaptive role in this process.

*Acknowledgements.* Thanks are due to Raija Järvinen and Liisa Ojanen for their help in analyzing the eggs. Esa Hohtola, Samuel Panelius, Seppo Pasanen, Risto A. Väisänen and two unknown referees made useful improvements to the manuscript.

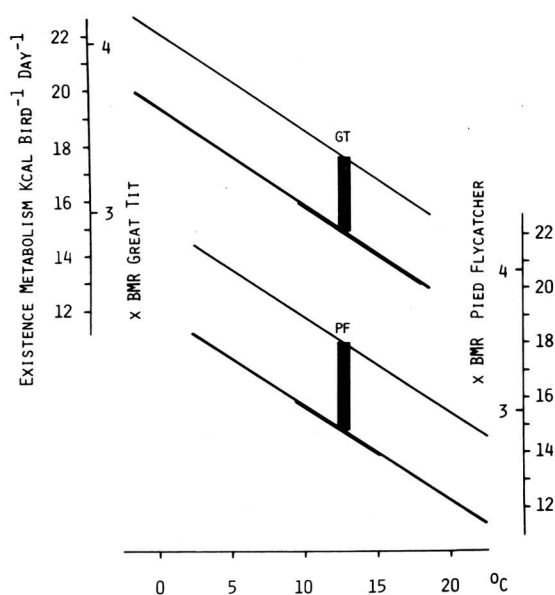


Fig. 1. A model showing the change in the existence metabolism ( $EM$ , see text) due to the change in the ambient mean temperature in the great tit and pied flycatcher. The thick part of the lower line shows the change in  $EM$  within the observed temperature ranges during laying period in Oulu in spring 1978 when the sample was collected. The thin part shows the observed maximum temperature variation during 1969–1980, within which both species laid their eggs during the main breeding season (see text). In building the model the following equations were used; for an 18 g great tit female,  $M = 21.7 - 0.3566 T$  and for a 14 g pied flycatcher female  $M = 19.1 - 0.3378 T$ , where  $M = \text{kcal/bird/day}$  and  $T = ^\circ\text{C}$  (equations calculated according to formulae 5.34 and 5.20 in Kendeigh et al. 1977, and accepting the equations for long (15-h) photoperiods; the weight of birds was taken to represent the value of pre-laying season; for the great tit female the estimate was taken from Orell 1976 and for the pied flycatcher female the weight of arriving birds measured at Tauvo bird station (13.7 g,  $N=154$ ) was chosen). The upper line represents the  $EM$  plus the amount of energy needed for egg formation each day (=the height of the bars; for further details, see text).  $BMR$ =basal rate of metabolism,  $GT$ =great tit,  $PF$ =pied flycatcher.

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Received 26.IV.1982

Printed 6.V.1983