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THE SIZE AND SHAPE OF EGGS FROM A WELSH POPULATION OF PIED FLYCATCHERS—TESTING HOYT'S USE OF EGG DIMENSIONS TO ASCERTAIN EGG VOLUME

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Abstract.—A miniaturized version of the volumeter described by Székely et al. (1994) was used to measure the volume of several hundred eggs from Welsh populations of the Pied Flycatcher (*Ficedula hypoleuca*) and to compare volumes so measured with those calculated from the eggs' dimensions using Hoyt's equation. As Székely et al. (1994) discovered on a small sample of plover eggs, Hoyt's formula consistently overestimates egg volume, in the case of Pied Flycatcher eggs by about 2%. The eggs of flycatchers that nest in central Wales are similar in size and shape to those reported for European and English populations of this species. Egg length (L), breadth (B), and volume (V) averaged 17.74 mm, 13.32 mm, and 1.58 cm^3, respectively. The egg's elongation or shape index (L/B) was most often between 1.30 and 1.35. Volume can be measured directly (and easily) using a volumeter, but it can also be estimated, if necessary, at least in so far as Welsh birds are concerned, from the dimensions of the egg using the formula $V = 0.1178 + 0.4637LB^2$ or from the egg's volume coefficient of 0.500, in which case $V = 0.500LB^2$.

TAMAÑO Y FORMA DE LOS HUEVOS DE UNA POBLACIÓN DE *FICEDULA HYPOLEUCA*: PONIENDO A PRUEBAS LA FÓRMULA DE HOYT PARA DETERMINAR EL VOLUMEN DE LOS HUEVOS

Sinopsis.—Se utilizó una versión en miniatura del volúmetro descrito por Székely et al. (1994) para medir el volumen de varios cientos de huevos de individuos de *Ficedula hypoleuca* de la población de Welsh, y comparar estos volúmenes con los calculados por la fórmula de Hoyt (utilizando la dimensión de los huevos). Székely et al. (1994) utilizando una pequeña muestra de ocho huevos de playero, descubrieron que la fórmula de Hoyt sobreestimaba consistentemente el volumen de los huevos. No obstante, en huevos de *Ficedula* el sobreestimado es de aproximadamente 2%. Los huevos de papamoscas que anidan en la parte central de Gales son similares en tamaño y forma que los informados para poblaciones de Inglaterra y Europa. El largo de los huevos (L), ancho (B) y volumen (V) promedió 17.74 mm, 13.32 mm y 1.58 cm^3, respectivamente. El índice de alargamiento y forma de los huevos (L/B) fue por lo general entre 1.30 y 1.35. El volumen de los huevos puede ser medido directamente utilizando un volúmetro o puede ser estimado, al menos en la población de papamoscas de Welsh, de las dimensiones del huevo, utilizando la formula $V = 0.1178 + 0.4637LB^2$ o del coeficiente de volumen del huevo de 0.500 en cuyo caso $V = 0.500LB^2$.

Many investigators have shown that volume is an important biological characteristic of an egg. It determines the size of a chick at hatch and/or fledging (Järvinen and Ylimaunu 1984, Ricklefs et al. 1978. Schifferli 1973), the nutrient reserves on which chicks must rely before and immediately after they hatch (Ojanen 1983a, Ricklefs 1977, Ylimaunu and

Järvinen 1987), and in some cases fledgling survival (Bolton 1991, Galbraith 1988, Howe 1976, Lundberg and Väisänen 1979). As a result of surface-to-volume relationships, egg size also influences gas exchange between the egg and its environment (i.e., embryonic metabolism), as well as heat and water loss from an egg (Rahn and Paganelli 1990). In some cases, egg size indicates the position of the egg in the laying sequence (Bollinger 1994, Ojanen et al. 1981, Slagsvold and Lifjeld 1989); the age, size and genotype of the female that laid the egg (Ojanen 1979, 1983b); and ambient conditions under which the egg was produced (i.e., the nutritional status of the laying female) (Ojanen 1983b, Ylimaunu and Järvinen 1987).

Measuring egg volume especially in the field has, however, been difficult because of the highly variable shape of bird eggs, and investigators have developed a series of mathematical expressions that enable them to use an egg's dimensions to ascertain its volume (literature summarized in Hoyt 1979, Smart 1991). Perhaps the most widely used equation is that of Hoyt (1979), in which the volume of an egg (V, in cm^3) can be obtained from its length (L, in cm) and breadth (B, in cm) using the formula $V = 0.51LB^2$.

Székely et al. (1994) have recently developed a "volumeter" with which one can easily measure egg volume in the field. With this device, they found that Hoyt's formula overestimates the volume of Snowy Plover (*Charadrius alexandrinus alexandrinus*) eggs by about 5%. Their sample size, however, was only eight eggs.

Using a miniaturized version of their device, we measured the volume of several hundred eggs of the Pied Flycatcher (*Ficedula hypoleuca*) to determine how accurately Hoyt's formula predicts the volume of eggs much smaller than those of Charadriiformes. Pied Flycatcher eggs turned out to be particularly useful for such a study because of the large range of sizes and shapes that they exhibited at our study sites: some were nearly round or at the other extreme strongly pointed, in contrast to most which were ellipsoidal or biconical. Ojanen et al. (1981) reported similar variation in egg shape within Scandinavian populations of *F. hypoleuca*. In addition, our study permitted us to compare the eggs of Pied Flycatchers that nest in central Wales with those from populations in northern and central Europe (Ojanen et al. 1978).

MATERIALS AND METHODS

Origin of eggs.—The eggs used in our study came from nestboxes in three deciduous woods within 1.5 km of Newbridge-on-Wye, Powys, Wales (52°N, 3°W): Llethr Woods, Caegarw Woods, and Llanwrthwl Woods. A total of 347 eggs from 67 clutches were included in the study. Most of them were examined during egg-laying or early incubation.

Measurements.—The length and breadth of each egg was measured to the nearest 0.01 mm with a Max-Cal electronic digital caliper (Model 54-200-000, Cole-Parmer). We used the elongation (also called the "shape index") of the egg (= L/B; Preston 1968) as an indicator of egg shape.

The volume of the eggs was determined by water displacement using a volumeter similar to that of Székely et al. (1994), but smaller. This consisted of a 5-ml pipet, graduated in 0.1-ml increments, sealed at one end and welded at the other to a glass reservoir which could be closed by a ground glass stopper. The hollow center of the glass stopper was filled with a rubber plug. Székely et al. (1994) put eggs in a wire container, which they lowered into the reservoir of their volumeter in order to measure the egg's volume. We simply suspended eggs in the water-filled reservoir and used three pointed glass "stops," which were built into the neck of the volumeter and angled toward the pipet (and away from the reservoir), to prevent eggs with large air cells from blocking the end of the pipet, while allowing water to move freely back and forth between reservoir and pipet during measurements.

For a typical measurement, the volumeter was filled with 10-11 ml of water, carefully stoppered, inverted, and the water level noted. It was turned upright again and the stopper removed, care being taken to prevent water loss. The reservoir was then tilted slightly so that the egg would roll into the water without splashing. The unit was restoppered, inverted, and the new water level determined.

Several things affect the accuracy and repeatability of measurements made with volumeters such as ours (Loftin and Bowman 1978). It is essential that the device be clean. If an egg is cracked or pipped, albumen gets into the water and causes bubbles to form. Time must also be allowed for the water on the sides of the pipet to drain completely into the water reservoir before one attempts to make a reading. It is particularly important that the volumeter be held vertically when the glass stopper is inserted or removed to prevent water loss.

We assumed that the volumeter accurately measured egg volume based on the work of Székely et al. (1994). We checked the repeatability of measurements made with the device, however, by having two individuals measure the volume of 18 eggs, 5-6 times each. The coefficient of variation (CV) for measurements on these 18 eggs as a group averaged 1.57%. For individual eggs, the CV ranged between 0.59 and 3.31%. There was no statistically significant difference between the measurements made by the two investigators (mean volumes of the same 18 eggs: 1.51 ± 0.12 cm^3 vs. 1.54 ± 0.13 cm^3, $t = 0.7471$, $P > 0.20$). We did not test the repeatability of measurements of the eggs' dimensions because we have several years of experience measuring egg size. On several occasions, however, eggs were inadvertently measured twice. The average difference in measurements was 0.01 mm ($n = 16$).

Eggs were taken from a nest, measured, and then immersed briefly (no more than 30 s) in water to determine their volumes. (All measurements of egg dimensions and volume were made by Kern.) Each was dried with paper toweling and then returned to the nestbox. Hatching success was 89%, somewhat higher than the 68–85% (78% on average) at our study sites between 1990 and 1993.

In addition to describing the relationship between an egg's volume and its dimensions, Hoyt (1979) developed an allometric equation that describes the relationship between an egg's *mass when freshly laid* and its dimensions. We assessed the validity of this equation as well in a sample of 60 flycatcher eggs. We periodically weighed these eggs to the nearest 0.1 mg (Mettler microbalance) during the incubation period to determine their rate of water loss, and then by least squares analysis (of egg mass vs. day of incubation on which the egg was weighed) obtained the mass that the egg would have had on the first day (day 0) of incubation by extrapolation. Flycatcher eggs may, however, be laid as many as 8 d before incubation begins and during this time they lose an average of 5 mg of water per day (Kern et al. 1993). We knew the day on which all of these eggs had been laid and were consequently able to correct for this loss as well.

Values that appear in this paper, unless indicated otherwise, are means $\pm$ 1 SD.

RESULTS AND DISCUSSION

Egg dimensions, shape and volume.—Egg length averaged 17.74 mm (Table 1) with lengths between 17.00 and 18.50 mm being most common (Fig. 1A). Egg breadth averaged 13.32 mm (Table 1) with values between 13.00 and 13.50 mm being most common (Fig. 1B). Values for elongation, most often between 1.30 and 1.35, were clearly skewed in the direction of pointedness (Fig. 1C). The most nearly round eggs had elongation values as low as 1.21; the most pointed eggs values as high as 1.52. For comparison, the nearly round eggs of owls have elongation values of 1.10 (Hoyt 1976) and the extremely pointed eggs of megapodes values of 1.87 (Preston 1969). In short, Pied Flycatcher eggs were usually ellipsoidal or more strongly pointed, less often nearly round.

Egg volume averaged 1.58 cm^3 (Table 1) and was most commonly 1.50–1.55 cm^3 (Fig. 1D). It was not affected by egg shape ($r^2 = 0.01$).

As illustrated in Table 1, eggs of Welsh flycatchers are similar in dimensions, shape and volume to those of European and English populations. Our data support the finding of Ojanen et al. (1978) that there is little geographical variation (except perhaps in the egg's L) in Pied Flycatcher eggs throughout central and northern Europe.

In general, Hoyt's (1979) equation, $V = 0.51LB^2$, overestimates the volume of Pied Flycatcher eggs, but only by about 2% (Fig. 2). The difference is highly significant, however ($t = 11.14$, $P \ll 0.001$, paired *t*-test, 2-tailed, df = 345). The relationship between the two measures of volume is best described ($r^2 = 0.85$; $n = 346$), by the equation

$$V_{est} = 0.2137 + 0.8842V_{act}$$

in which V_{est} = the volume based on the egg's dimensions, and V_{act} = the volume measured by water displacement.

Allometric relationships between egg dimensions, mass and volume.—Hoyt (1979) developed mass (K_w) and volume (K_v) coefficients that describe the relationship between the dimensions (in cm) of an egg and its mass

TABLE 1. Mean dimensions, volume and shape reported for eggs of Pied Flycatchers nesting in the United Kingdom and Europe. Studies other than ours have used the egg's dimensions to estimate egg volume.

Location	Length (mm)	Breadth (mm)	Volume (cm^3)	Shape Index (L/B)	Source
Finland	17.58–17.80	13.37–13.44	1.52–1.56	1.31–1.32	Ojanen et al. (1978)
					Järvinen and Väisänen (1983)
					Ojanen (1983a)
Norway	—	—	1.60–1.74	—	Slagsvold and Lifjeld (1989)
Sweden	17.14	13.50	1.51	1.27	Rosenius (1926–29)[a]
Germany	17.84	13.45	1.56	1.33	Sternberg and Wlnkel (1970)[a]
England	17.93	13.42	1.56	1.34	Makatsch (1976)[a]
Wales[b]	17.74 ± 0.75 (15.64–20.47)	13.32 ± 0.38 (11.98–14.45)	1.58 ± 0.14 (1.00–2.04)	1.33 ± 0.06 (1.21–1.52)	This study
Central Europe	17.16–17.80	13.39–13.47	1.51–1.55	1.27–1.33	Rey (1912)[a]
					Makatsch (1976)[a]

[a] As reported by Ojanen et al. (1978: Table 3).
[b] Values in this row are means ± 1 SD (range); n = 346–347 eggs.

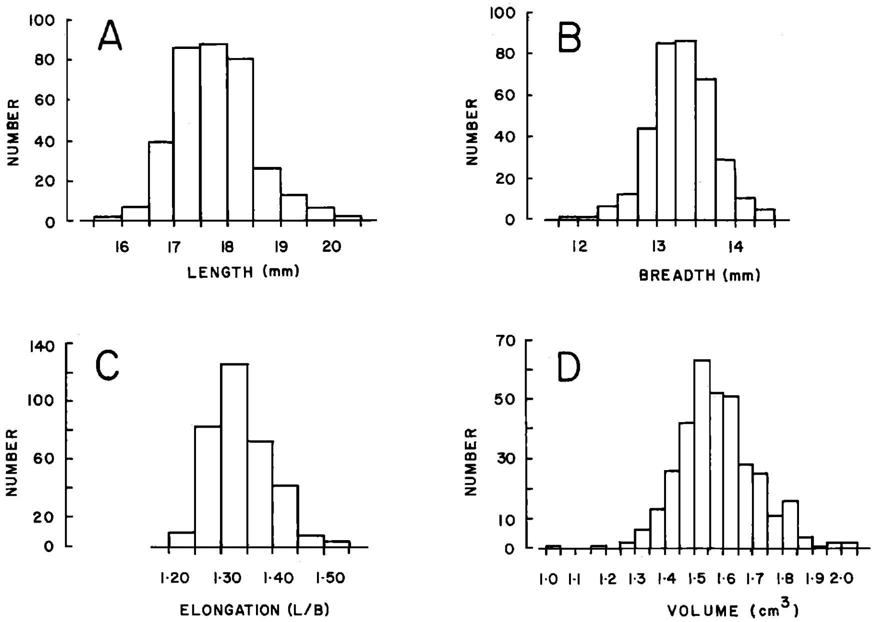

FIGURE 1. Distributions of eggs of Pied Flycatchers on the basis of their dimensions and volume. Values on the ordinates in A–D are numbers of eggs.

(W, in g) when freshly laid and volume (in cm^3), respectively: $W = K_wLB^2$ and $V = K_vLB^2$. Using our dimensions and actual measured volumes, $K_w = 0.549 \pm 0.012$ ($n = 60$; range = 0.532–0.586) and $K_v = 0.500 \pm 0.017$ ($n = 345$; range = 0.341–0.542) for flycatcher eggs (Fig. 2).

These coefficients conform well with the averages of 0.548 and 0.507, respectively, reported by Hoyt (1979) for 26 other avian species of which the smallest was the American Robin (*Turdus migratorius*). The *intra*specific variation among flycatchers in values of K_v (0.201) is, however, almost an order of magnitude larger than the *inter*specific variation (0.025) found by Hoyt.

The volume (in cm^3) of the egg can also be expressed mathematically as a function of its mass (in g) at the time it is laid, as done elsewhere for other characteristics of the eggs of a large number of avian species (Paganelli et al. 1974). The equation

$$V = 0.9825W^{0.8748}$$

provides a reasonable description ($r^2 = 0.87$; $n = 60$) for Pied Flycatchers, but the (non-logarithmic) linear equation

$$V = 0.1833 + 0.8116W$$

is slightly better ($r^2 = 0.87$; $n = 60$).

Paganelli et al. (1974) present (in their Table 1) egg volume and mass

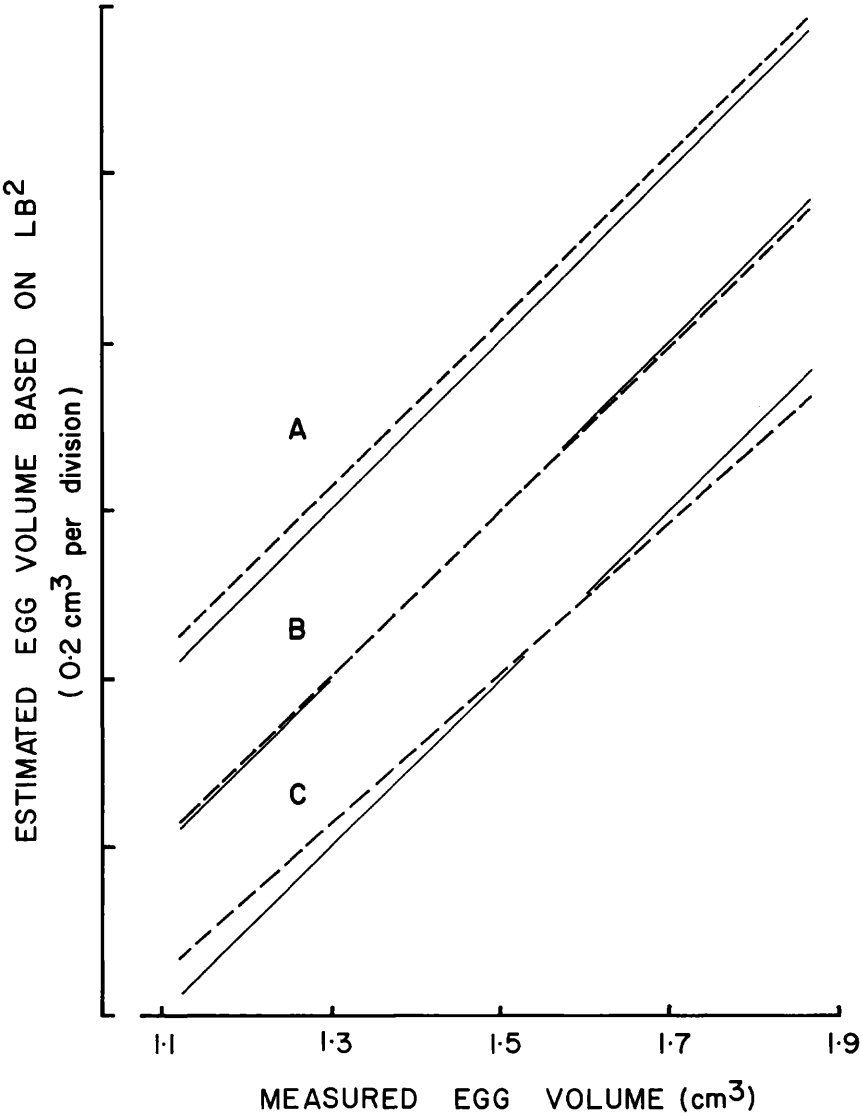

FIGURE 2. Concordance of allometric equations used to estimate the volume of Pied Flycatcher eggs and the eggs' actual measured volume. The solid, fine lines in A, B, and C indicate the case where estimated volume = measured volume. The hatched lines illustrate the deviation from such a perfect fit when estimates based on the egg's dimensions are used to estimate the egg's volume. Here, the estimates are (A) $V = 0.51 LB^2$ (Hoyt 1979), (B) $V = 0.50 LB^2$ (this paper), and (C) $V = 0.1178 + 0.4637 LB^2$ (this paper).

data for 29 species of birds ranging in size from the wren to the ostrich. Using their data, egg volume can be best (r^2 = 0.99) described in terms of egg mass by the linear equation

$$V = 1.7106 + 0.9110W$$

an equation considerably different from that for the Pied Flycatcher. Indeed, if we substitute the average mass of freshly laid flycatcher eggs (1.74 g) into this equation, the predicted volume of the flycatcher egg would be 3.30 cm^3 or about 109% larger than it actually is. On the other hand, if the mass and volume data in Paganelli et al. (1974) are compared logarithmically, in which case $V = 0.9540W^{0.9973}$, the predicted volume is only about 5% different from the actual volume of the egg. This illustrates, we believe, the danger of applying allometric relationships based on many species with a wide range of sizes to individual species of very small (or for that matter very large) size.

Finally, a general expression for the egg's volume can also be obtained by regressing the *dimensions* of individual eggs against their volumes. In our study, the equation which best describes this volume-dimension relationship (r^2 = 0.80; n = 346; Fig. 2) is

$$V = 0.1178 + 0.4637LB^2$$

This relationship is somewhat different from that reported earlier (Ojanen et al. 1978) for Pied Flycatcher eggs: $V = -0.042 + 0.4976LB^2$. The latter expression underestimates the size of eggs produced by Welsh flycatchers by about 3.5% and was obtained by weighing museum eggs that had been filled with water, rather than by water displacement. The shell is about 5% of the mass of a flycatcher's egg when it is freshly laid or 90 mg (Kern et al. 1993, Paganelli et al. 1974). On the basis of its density (= 1960 mg/ml), which we calculated using allometric equations in Paganelli et al. (1974), the shell therefore represents 3% of the total egg volume. Hence, the underestimate of egg volume using the formula of the Ojanen group may be due to shell volume because the technique of Székely et al. (1994) includes the thickness of the shell, whereas the injection technique of the Ojanen group does not.

Given the ease with which egg volume can now be measured in the field, we agree with Székely et al. (1994:63) that ". . . it is more accurate to measure volume than to estimate it from linear measurements." Figure 2 illustrates why.

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