

Oomorphology: A New Method

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The morphology of avian eggs has been studied extensively, especially in poultry breeding where the measurements and shape of eggs serve as indicators of productivity. Problems of shape connected with egg transportation and storage have great economic significance. The individual variability of the eggs of wildfowl is also of interest to ecomorphologists (Yablokov 1966, Paaver 1976, Bock 1977, James 1982). Because field studies are often of limited duration, a simple, quick, and exact method of evaluating the size and shape of eggs is desirable.

Until now, three main methods were used to estimate egg volume in the field: (1) Direct measurement in a device based on the principle of volume displacement (Hanson 1954, Tarassov 1977, Loftin and Bowman 1978, Thomas and Lumsden 1981). These devices are clumsy and are limited in the case of very small eggs because of the surface tension of water. (2) Indirect evaluation of the volume by weight and density (Barth 1953). For example, egg volume can be determined from the difference between the weight of the egg in air and when suspended in water (Hoyt 1979). Unfortunately, these methods do not yield data on other morphological parameters (linear measurements, shape, eggshell surface). (3) Indirect evaluation derived from the length and the maximum diameter of the egg (Asmundson 1931, Schönwetter 1925, Bergtold 1929, Grossfeld 1933, Worth 1940, Romanoff and Romanoff 1949, Westerskov 1950, Hoyt 1979). The virtues of this method are quickness and simplicity. It has relatively low accuracy because the influence of intraspecific differences of the egg shape on volume (Hoyt 1979) is not taken into account. The eggshell surface area is derived arithmetically from volume (Tatum 1977). The shape of an egg is described mainly by means of two dimensions, i.e. the length and the maximum diameter. A sliding caliper or a special indexometer (Sergeyeva 1984) is used for this purpose. Unfortunately, only one aspect of an egg's shape, its "elongation," can be described using these two measures. Other aspects of egg shape (e.g. roundness of the ends of eggs, asymmetry, etc.) are also of interest. Indeed, Preston (1953, 1968) worked out the basis for describing the shape of avian eggs geometrically. Unfortunately, Preston's methods have not been used widely because his method of measuring the image of eggs by hand is time-consuming and not adequate for studying intraspecific variability. In addition, the profile-transfer step is not suitable for very small eggs.

We present a new method to estimate the size and shape of avian eggs. The method has several advantages. First, it reduces considerably the time spent

handling eggs in the nest. One photograph accommodates an entire clutch, an advantage in the case of species that lay many eggs. Any disturbance is reduced, which is particularly important when dealing with easily frightened species. Second, the image of the egg can be magnified considerably, an indisputable advantage when handling small eggs. Third, several parameters can be measured directly from the photograph with no time restrictions. Finally, all information about the egg contour can be stored on diskettes. Therefore, it is not necessary to handle the image repeatedly for subsequent computations.

The method was used successfully during two years in morphological studies of the eggs of the Great Tit (*Parus major*) and other species.

To take photographs, a special stand, camera, and support were used (Figs. 1 and 2). The stand was made of polystyrene foam and had an elevated rim to prevent the eggs from rolling off. In the middle of the stand there were 14 cavities for eggs. The arrangement of the cavities accommodated an entire clutch (usually no more than 14 eggs) in as small an area as possible. The effect was to minimize the distortion of scale resulting from the fact that the eggs lie at different angles with respect to the focal axis of the lens. A scale for calibrating was placed 5 mm above the surface, so the axial plane of the eggs was on approximately the same level as the scale. The surface surrounding the cavities was painted black to increase contrast. A white cardboard screen was fixed to the stand to protect the eggs from direct sun and to reflect dispersed light onto them. The use of the screen depended on light conditions. The screen prevented contrasting shades on the photographs, which would have made it more difficult to analyze the image. The lens extension tubes were surrounded by a tight rubber ring with four holes drilled in it. Steel support rods 400 mm long were pressed into these holes, with the opposite ends resting on corresponding metal sockets in the stand. Pictures were taken with the lens 330 mm from the axial plane of the clutch.

The apparatus is light, easily disassembled, and fits into a small waterproof bag. These characteristics were essential for fieldwork. Working in pairs, it took 5–8 min to photograph one clutch. A 35-mm film was used. The device is especially well suited for photographing small eggs. If necessary, other devices or Preston's "profile-copying machine" may be used without interfering with the subsequent analysis of image.

Image analysis.—To analyze the photographic image, an Apple II+ microcomputer and the Apple

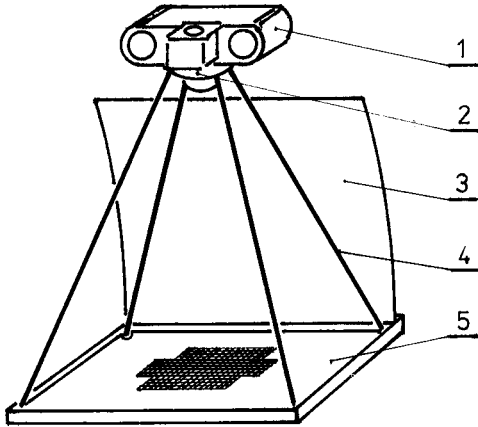


Fig. 1. Photographing device in working position. 1 = camera, 2 = rubber ring, 3 = screen, 4 = steel rods, 5 = stand.

Graphics Tablet were used. A special menu-driven program, OMELETTE, was composed of two main segments. The first segment stored the data, and the second computed the main parameters. The program OMELETTE is written mainly in FORTRAN (only a few 8080 Assembly language subroutines are included) and runs under a CP/M Operating System (version 2.2 and higher). Operations for analyzing a separate clutch were simple. The photograph was fixed on the Graphics Tablet with adhesive tape. The image was calibrated from the scale on the photograph and egg contour was traced using a special moving cursor. Input accuracy was quite important, and we assumed that input error did not exceed 1% of the egg's contour dimensions. The first segment of the program selects approximately 130-150 points per contour and displays them on the screen, thus enabling verification of the inserted contour. Descriptive data for each clutch were written into a disk file for independent processing. The second segment of the program contains no machine-dependent subroutines and therefore runs in any CP/M environment. To compute an egg's parameters, the principal axis of the egg was first found. Then parameters L , B , l_1 , l_2 , b_1 , and b_2 (Fig. 3) were found by approximating appropriate areas of contour points with second-order curves using the least-squares method. The volume and the surface of the egg were computed using trapezoidal integration. The axes used to calculate the linear and shape parameters are given in Fig. 3. The parameters are volume (V); linear measurements of length (L) and maximum diameter (B); area (A); and the shape parameters [sphericity (Sph) = $100B/L$, ovoidness (Ov) = $(L - l_1)/l_1$, pear-shapedness (Psh) = $100(b_1 - b_2)/b_1$, conicity (Con) = $100(b_1 - b_2)/B$, blunt-end convexity (Bec) = $(2b_1/B) - 1$, sharp-end convexity (Sec) = $(2b_2/B) - 1$, and plumpness

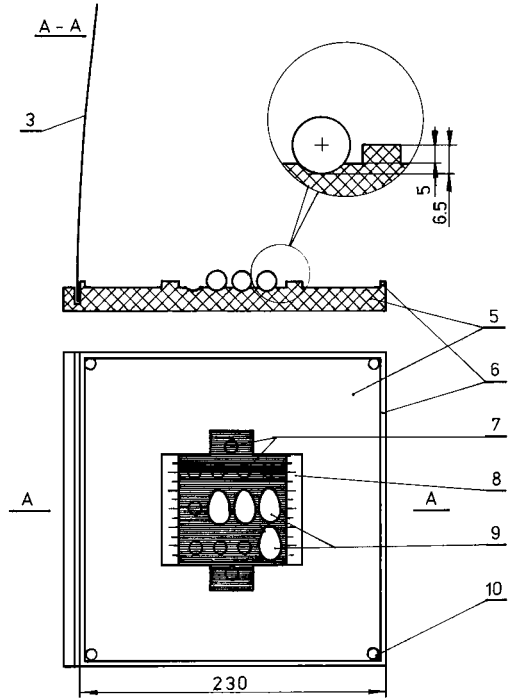


Fig. 2. Stand for photographing eggs. 3 = screen, 5 = stand, 6 = elevated rim, 7 = cavities for eggs, 8 = scale for calibrating, 9 = eggs, 10 = metal socket.

(Pmp) = $400V/\pi LB^2$]. The analysis of a 10-egg clutch takes approximately 10 min.

Sph , Ov , Psh , and Con were derived from the indices proposed by Kostin (1977); Bec , Sec , and Pmp are our creation. It is not difficult to adjust the program OMELETTE to calculate Preston's (1953, 1968) shape parameters. Our use of the index system does not mean that we prefer it to Preston's method.

The data are stored in the text file, which can be processed further. Moreover, the resultant text file is fully compatible with Database Management System dBASE II (Ashton-Tate Inc.). Hence, it is possible to combine the egg-shape parameters under dBASE II with other data on nesting biology, morphological characteristics of parents, etc. for subsequent statistical analysis.

Copies of the program with all necessary comments are available from the authors.

Hardware requirements.—(1) An Apple II+ with 16K RAM card or Apple IIe, (2) a Z80 card to run CP/M (we have a Microsoft SoftCard), (3) at least one disk drive, and (4) an Apple Graphics Tablet (when using another digitizing pad, only the coordinate-reading subroutine must be modified). An 80-column card and printer are optional.

Measurement error.—To characterize the accuracy of the method, eggs of the Great Tit, Common Black-

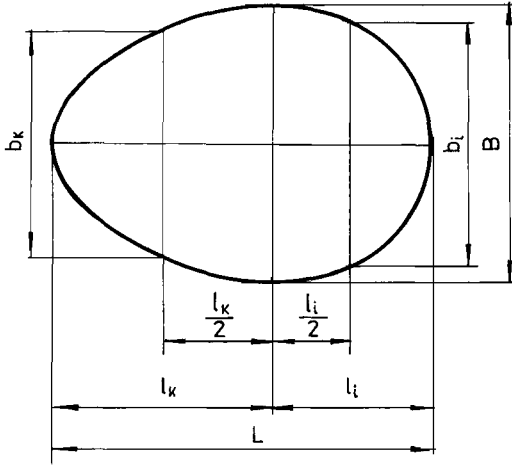


Fig. 3. Axes used to calculate an egg's morphological parameters. See text for details.

headed Gull (*Larus ridibundus*), and Common Eider (*Somateria mollissima*) were studied. These varied widely in size and shape. The following procedures were performed on each species. First, a randomly chosen egg was measured 10 times, and the standard deviation of each morphological parameter was estimated. In this case, total variation was due to measurement error only. Second, all eggs were measured in clutches chosen at random, and for each clutch the standard deviation of all parameters was estimated separately. After this, an average intraclutch standard deviation was evaluated for each parameter. In this case, total variation was caused both by intraclutch differences between eggs and by measurement error. Third, randomly chosen eggs from several clutches (1 egg/clutch) were measured, and the standard deviation of each parameter was estimated. In this case, total variation was caused by interclutch and intraclutch differences between eggs and by measurement error. Finally, randomly chosen eggs of 8 bird species (1 egg/species) were measured, and the standard deviation of all parameters was estimated. The total variation was caused by interspecific, interclutch, and intraclutch differences between eggs and by measurement error.

Average coefficients of variation (CV) caused by measurement error only were as follows: $L = 0.1$, $B = 0.1$, $V = 0.2$, $A = 0.1$, $Sph = 0.2$, $Ov = 0.8$, $Psh = 5.2$, $Con = 5.3$, $Bec = 0.4$, $Sec = 0.6$, and $Pmp = 0.2$ ($CV = 100SD/\bar{x}$, where SD is the standard deviation and \bar{x} is the arithmetical mean). The 95% upper bounds for the relative importance of measurement error in the total variation of egg parameters was influenced by several sources (Table 1). In all but one case, error was significantly ($P < 0.05$ by F -test) smaller than the observed intraclutch, interclutch, or interspecific variation of studied parameters. With egg volume,

TABLE 1. Relative importance of measurement error in the observed variation of morphological parameters in some bird eggs.^a

Sources of variation	Species ^b	df	Parameter										
			L	B	V	A	Sph	Ov	Psh	Con	Bec	Sec	Pmp
Intraclutch differences (IC) + measurement error (ME)	PM	95	0.10	0.09	0.12	0.08	0.22	0.39	0.28	0.29	0.50	0.22	0.34
	LR	16	0.11	0.13	0.12	0.08	0.16	0.42	0.60	0.62	1.00	0.51	0.49
	SM	22	0.08	0.09	0.07	0.11	0.13	0.44	0.26	0.25	0.37	0.57	0.57
Interclutch differences (EC) + IC + ME	PM	140	0.04	0.05	0.06	0.04	0.09	0.26	0.25	0.26	0.35	0.19	0.25
	LR	7	0.05	0.07	0.05	0.03	0.18	0.29	0.53	0.57	0.61	0.34	0.30
	SM	8	0.05	0.09	0.07	0.10	0.08	0.51	0.26	0.25	0.42	0.60	0.73
Interspecific differences + EC + IC + ME	SPP	7	0.01	0.01	0.01	0.01	0.13	0.11	0.17	0.16	0.39	0.29	0.35

^a Data were calculated by the formula $SD_E / (SD_T / \sqrt{F_{0.05}})$, where SD_E is the standard deviation of the variation caused by measurement error only, SD_T is the standard deviation of total variation caused by sources listed in the first column of the table, and $F_{0.05}$ is the critical value of F -distribution (by the significance level $P < 0.05$ and the corresponding pairs of df).

^b PM = *Parus major*, LR = *Larus ridibundus*, SM = *Somateria mollissima*, SPP = 8 species listed in Table 2.

^c See text for definitions of abbreviations.

TABLE 2. Means and standard errors of egg morphological parameters for 8 bird species.

Parameter*	Somateria		Anas		Larus		Larus		Larus		Sterna		Parus	
	<i>anser</i> (n = 4)	<i>mollissima</i> (n = 31)	<i>platyrhynchos</i> (n = 11)	<i>argentatus</i> (n = 12)	<i>canus</i> (n = 9)	<i>ridibundus</i> (n = 24)	<i>hirundo</i> (n = 6)	<i>major</i> (n = 207)						
L (mm)	85.50 ± 1.20	79.31 ± 0.44	57.75 ± 0.50	70.57 ± 0.74	60.74 ± 0.83	53.25 ± 0.37	41.85 ± 0.23	17.72 ± 0.05						
B (mm)	57.20 ± 0.54	51.44 ± 0.27	41.05 ± 0.31	49.83 ± 0.48	42.71 ± 0.40	36.98 ± 0.22	30.70 ± 0.22	13.48 ± 0.02						
V (cm ³)	140.83 ± 3.80	107.57 ± 1.49	49.80 ± 1.07	87.78 ± 2.45	55.03 ± 0.71	36.37 ± 0.62	19.46 ± 0.28	1.62 ± 0.01						
A (cm ²)	134.61 ± 2.42	112.99 ± 1.02	66.83 ± 0.95	97.36 ± 2.06	71.70 ± 0.59	54.41 ± 0.62	35.68 ± 0.33	6.80 ± 0.02						
Sph	66.90 ± 1.04	64.90 ± 1.01	71.06 ± 0.53	70.09 ± 0.45	70.76 ± 1.05	69.48 ± 0.47	73.33 ± 0.74	76.16 ± 0.18						
Ov	1.14 ± 0.03	1.22 ± 0.01	1.15 ± 0.02	1.31 ± 0.02	1.32 ± 0.03	1.29 ± 0.01	1.25 ± 0.02	1.25 ± 0.004						
Psh	3.00 ± 0.53	3.33 ± 0.27	3.41 ± 0.24	7.00 ± 0.34	6.18 ± 0.44	6.56 ± 0.30	7.63 ± 0.68	5.03 ± 0.10						
Con	2.50 ± 0.45	2.88 ± 0.24	2.94 ± 0.21	6.08 ± 0.29	5.36 ± 0.38	5.67 ± 0.26	6.63 ± 0.65	4.34 ± 0.08						
Bec	0.70 ± 0.004	0.73 ± 0.003	0.72 ± 0.003	0.73 ± 0.004	0.72 ± 0.004	0.73 ± 0.002	0.73 ± 0.008	0.72 ± 0.001						
Sec	0.65 ± 0.008	0.67 ± 0.003	0.66 ± 0.003	0.61 ± 0.007	0.62 ± 0.008	0.62 ± 0.004	0.59 ± 0.01	0.64 ± 0.001						
Pmp	64.00 ± 0.22	65.19 ± 0.13	65.01 ± 0.16	63.57 ± 0.30	63.49 ± 0.33	63.50 ± 0.15	62.77 ± 0.38	64.00 ± 0.006						

* See text for definitions of abbreviations.

area, and two linear measurements, error usually constitutes no more than 10% of total intraclutch or interclutch variation, and 1% of observed interspecific variation. Consequently, the method is precise for describing the biological variation of these four parameters. For most shape parameters (except Sph), measurement error is relatively high and can constitute up to 60-70% of total variation. Nevertheless, with sufficiently large numbers of measurements, the method is precise enough for describing the biological variation of shape parameters.

We examined the possible sources of measurement error. To diminish the error, four preconditions must be considered. The longitudinal axis of an egg should be almost parallel to the surface of the stand; the photographs should have as high contrast as possible; the egg's image should be magnified as much as possible to diminish measurement error; and maximum care should be taken when entering the egg's contour and the scale. The location of separate eggs on the stand does not influence accuracy.

By this method eggs of Anatidae had on the average lower ovoidness, pear-shapedness, and conidity and greater plumpness and sharp-end convexity than did those of Laridae (Table 2). Additional data are necessary for further conclusions.

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Differential Digestion Rates of Prey by White-chinned Petrels (*Procellaria aequinoctialis*)

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We investigated the gastric digestion rates in the White-chinned Petrel (*Procellaria aequinoctialis*), which is a generalist feeder (Croxall and Prince 1980, Croxall et al. 1984, A. Berruti pers. comm., S. Jackson unpubl. data). The natural diet of White-chinned Petrels includes the three prey types used in the experiments: light-fish (*Mauroliscus muelleri*), squid (*Loligo reynaudi*), and antarctic krill (*Euphausia superba*) (A. Berruti pers. comm., S. Jackson unpubl. data).

Seven fledgling White-chinned Petrels were removed from their burrows on subantarctic Marion Island (46°52'S, 37°51'E) and kept in separate wire-mesh cages (40 × 40 × 60 cm) for 12 days before the start of the experiment. We maintained the birds at approximately constant mass on diets of equal proportions of light-fish, squid mantle flesh and heads, and antarctic krill. We noted the total numbers of squid beaks fed to the birds throughout their period of captivity.

For the experiment, we fed each bird a mixed meal comprising 40 g each of light-fish (approximately 40 individuals), squid (1 head and several pieces of mantle), and krill (approximately 60 individuals). All the food had been frozen, but was thawed slowly and handled with care during feeding to avoid tissue damage that could have affected the rate at which food was digested.

We stomach-pumped individual birds 15 min and

1, 2, 4, 7, 12, and 24 h after feeding, using a water-offloading technique (Wilson 1984). We then killed the birds and dissected their oesophagi, stomachs, and gizzards. The samples were drained and weighed. We counted identifiable food objects separately, noting the apparent state of digestion. We counted all cephalopod beaks recovered and noted their state of wear. We also counted otoliths and krill eye lenses.

The mass of all food types recovered after 15 min increased by less than 5%, presumably due to the water added during stomach pumping, or to initial water absorption by the prey. We compensated with a correction factor (C) such that $C = I/F'$, where I = initial mass of a food type and F' = mass of that food type recovered after 15 min. We assumed that the mass gain of each food type was proportionally the same for the birds stomach-pumped after different time intervals. We expressed the mass of food recovered as a percentage of the mass initially fed to the bird after each time interval.

White-chinned Petrels digested light-fish more rapidly than they digested either squid or krill: no traces of fish remained in the stomach after 12 h (Fig. 1). The results of similar experiments on Jackass Penguins (*Spheniscus demersus*; Wilson et al. 1985) are included for comparison (Fig. 2). We could not count individual fish in White-chinned Petrel stomachs after 4 h (Fig. 3). Initial digestion of krill was slower