Optimal egg shape in waders

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Wader eggs deviate markedly from the spherical shape, which should be optimal in several important respects. It is suggested that the marked pear-shape in wader eggs is mainly an adaptation for increasing the egg volume in a four-egg clutch occupying an area limited by the brood patch of the incubating adult. Using a simple model, it is shown that the maximum-volume eggs for clutches of four have 8 % larger volume than four spherical eggs covering the same area. Other factors influencing egg shape in waders are discussed.

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Introduction

There is a remarkable variation in egg shape among bird families, a variation which probably reflects adaptations to different selective pressures. In the classical case of the Guillemot *Uria aalge,* TSCHANTZ et al. (1969) have shown that the marked pear-shape reduces the risk that the egg will fall off the cliff-ledge used for breeding. In most other cases the egg shapes have remained unexplained, and LACK (1968) noted that "virtually no research has been carried out on their significance". A recent exception is VON HAARTMAN's (1971) study of the trend in the length/width ratio with increasing egg size.

The eggs of waders (mainly Charadriidae and Scolopacidae) deviate markedly from the spherical form, which should be optimal in at least two important respects: it is the strongest, and it has the smallest surface area in relation to volume, which minimizes heat loss (LACK 1968). I here suggest that wader eggs derive their pear-shape mainly from selection for maximizing volume without increasing the area covered by the incubating bird. Most wader chicks are precocial, being sufficiently advanced to gather food when they hatch. This calls for large, nutrient-rich eggs, which is probably why waders limit their clutch to three or four (LACK 1968). The limit might be set by the laying capacity of the female (e.g. LACK 1954), by the number of chicks she can raise (SAFRIEL 1975), or by the number of eggs that the adult can brood (LACK 1954). In small waders, the clutch may weight as much as the female (LACK 1968), yet in some species she produces two four-egg clutches in succession; the male broods the first one, and the female the second (e.g. HILDÉN 1975). In these cases therefore the clutch is not limited to four by the laying capacity of the female, or by the productivity of the habitat. The constraint is probably imposed by the limited brood patch area, which determines the number of eggs of a given size that the adult can incubate, a hypothesis which can easily be tested (ANDERSSON 1976).

Model

Given a clutch of four eggs occupying a certain maximum area, we will try to find the shape which yields the egg with the maximum volume. One of several admirable solutions would be an egg shaped as a quarter sphere, a clutch of four fitting together like wedges in an orange. However, for the convenience of the female, we will assume that the egg must be rotationally symmetric about the length axis, and without discontinuities like edges or corners, except perhaps for pointed ends.

Assume the brooding bird can efficiently cover an area of maximum width w (Fig. 1). With four spherical eggs, this limits their radius to $r = w/4$, and the volume to $Vs = 4\pi r^3/3$. Does any other rotationally symmetric solid of larger volume fit into the same space? Obviously, by elongating the eggs, we can utilize the empty space between them (Fig. 1a). To use a geometrical image, elongating the eggs corresponds to removing a segment from each sphere and replacing it with a cone (Fig. 2a). The volume of the cone increases with its height h (see appendix and Fig. 2a), which should therefore be maximized. The height will attain its maximum value

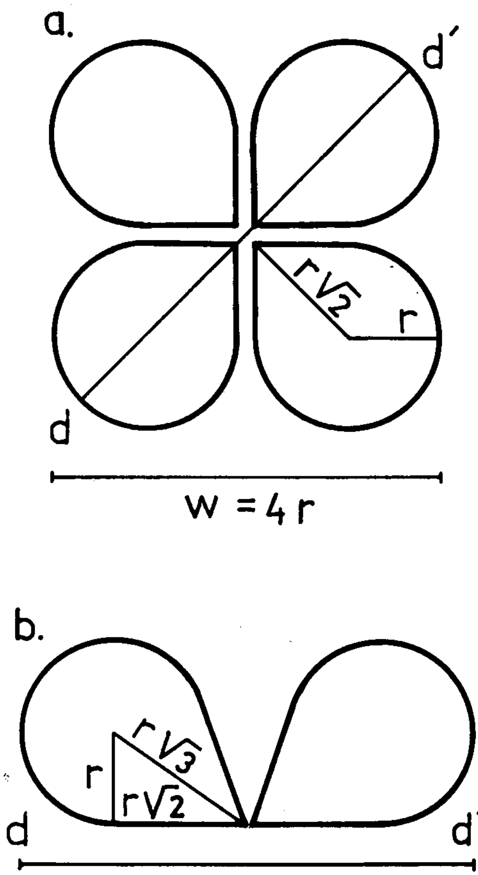

FIGURE 1. (a) A four-egg clutch of maximum-volume eggs, each with diameter 2r and length $r(1+\sqrt{3})$. The maximum-volume eggs, which fit into the same area w • w as four spherical eggs with radius r, have 8 % larger volume. (b) Vertical section along the diameter d—d' through two of the eggs in Fig. 1a.

when the eggs are tilted, the pointed ends meeting as in Fig. 1b. Without increasing the area covered by the incubating bird, the volume can be increased from that of the spherical egg by 8 % (see appendix). This gain should be important, since it would permit the chick to hatch at a more advanced stage, and/or provide it with greater energy reserves at hatching. The extra volume could supply the newborn chick with nutrition for one or a few days, an important reserve in case of inclement weather and food scarcity at hatching.

Most waders have clutches of four, but some species lay only three eggs. Using the previous approach, the maximum-volume egg with three-egg clutches can be shown to be 5 % larger than the corresponding spherical egg (Fig. 2b).

Discussion

Compared to other selective pressures on egg shape, volume maximization should be the most important when egg size approaches the limit set by brooding efficiency, as may happen in species with large eggs relative to female body mass. This prediction is born out among waders: it is in such species we find eggs whose shape is most similar to that giving maximum volume, whereas species with smaller relative egg size have more rounded eggs (see e.g. MAKATSCH 1974). The main difference between our model egg and real wader eggs is that the latter are less sharply pointed. This deviation is not surprising, because egg shape is certainly also subject to other selective pressures than brooding efficiency. A clutch of four wader eggs may contain twice as much calcium as the female, so that she must ingest large amounts of extra calcium during the laying period (MACLEAN 1974). As the pointed vertex region requires much more shell material per unit volume than the remainder of the egg, this is one possible reason why it is less sharply pointed than in the model egg; two others are increase of shell strength and reduction of heat loss from the vertex region.

There may be several other reasons for the deviations from maximum-volume shape. Wader eggs are not usually situated on a perfectly plane substrate, but rather in a rounded nest-cup. The pointed ends of the eggs then tend to lean more vertically than in Fig. 1b, which might influence the optimal shape. This arrangement might permit longer eggs, and hence further reduction of the incubation area in relation to egg volume.

In species which normally lay four eggs, clutches of three occur more or less regularly (MAKATSCH 1974). If clutch size partly depends on the (variable) food abundance at laying time (LACK 1968), the maximum-volume shape for clutches of four should not be optimal. The best shape would rather be some compromise between the optimal shapes for clutches of different sizes, weighted by the probability of their occurrence. The most common alternative to four eggs in waders seems to be three. Because the corresponding maximum-volume egg is shorter than that for clutches of

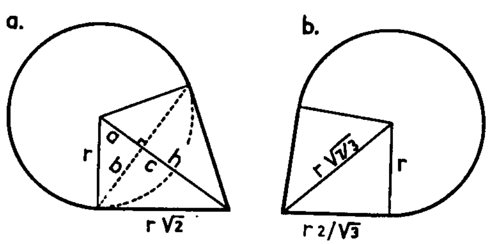

FIGURE 2. (a) Dimensional relations of the maximum-volume egg for a four-egg clutch. The egg can be viewed as consisting of two parts; 1) a sphere where a segment (dotted) has been replaced by 2) a cone with height h and basal diameter 2b. Because $a+h = r\sqrt{3}$, the length of the egg is $r(1+\sqrt{3})$.
(b) Maximum-volume egg for a three-egg clutch. The length in this case is $r(1+\sqrt{7/3})$.

four (see appendix), the optimal compromise egg should also be shorter, as most wader eggs seem to be (see MAKATSCH 1974).

Besides, there is considerable inter- and intra-clutch variation in egg shape (VÄISÄNEN et al. 1972). If in a species some females are hereditarily disposed to lay three eggs, whereas others lay four, the present hypothesis predicts that three-egg layers should have larger and relatively shorter eggs than four-egg layers.

At least one further selective pressure might contribute to the pear-shape of wader eggs. NORTON (1970, cited in DRENT 1975) showed that the cooling rate of eggs in a wader clutch increased drastically if one of the four eggs was removed. He suggested that thermal efficiency might be one of the selective pressures behind four-egg clutches in waders. Probably the pear-shape contributes to decrease the cooling rate, because when the pointed ends meet, as in Fig. 1, the egg mass per unit volume occupied by the clutch is higher than with spherical eggs. Further, the entire additional mass is located at the "interior" of the clutch, which is advantageous with respect to heat conservation. Whether the pear-shape does actually reduce the cooling rate could be tested by comparing clutches of model eggs of identical volume, but ranging in shape from spherical to "maximum-volume".

It might be possible to relate variations in egg shape among certain other bird families to particular selective pressures. In species with a clutch of one, or with several eggs of small relative size, egg shape should tend towards the spherical form, which is optimal with respect to shell strength, heat conservation and saving of shell material. The almost spherical eggs in Procellariiformes and owls are possible examples. Due to the elongated body shape of most birds, the width of the brood patch may be smaller than the length, which could partly explain the elongated egg shape in many species with clutches of two, for example cranes (Gruidae), doves (Columbidae) and divers (Gavidae) (see LACK 1968).

To summarize, egg shape in waders apparently comes close to the optimum with respect to volume maximization. Several other selective pressures have probably caused the existing deviation from maximum-volume shape.

Selostus: **Kahlaajanmunan edullisin muoto**

Kahlaajien munat poikkeavat huomattavasti soikeasta perusmuodosta, jonka pitäisi olla edullisin ainakin kahdelta tärkeältä kannalta: se on lujin ja sen pinta-ala on pienin tilavuuteen nähden. Kahlaajanmunan kartiomainen tai päärynämäinen muoto tulkitaan sopeutumaksi, joka lisää nelimunaisen pesyeen munien tilavuutta laajentamatta hautovan linnun peitettävää pinta-alaa. Matemaattisen kaavan avulla osoitetaan, että neljä päärynämäistä munaa ovat tilavuudeltaan 8 % suurempia kuin saman pinta-alan vievät neljä soikeaa munaa. Munan suuremman tilavuuden ansiosta poikanen kuoriutuu kehittyneempänä ja/tai sillä on enemmän vararavintoa käytettävissään ensimmäisinä elinpäivinään. Tällä on ilmeisesti suuri merkitys silloin kun kuoriutumishetkellä on huono sää ja ravinto vähissä. Kirjoituksessa pohditaan myös muita kahlaajien munanmuodon kehitykseen vaikuttaneita tekijöitä.

Appendix: **The maximum-volume egg**

The volume of the "maximum-volume egg" (Fig. 1) is obtained as the sum of two volumes (Fig. 2); a) a sphere from which a segment has been removed; b) a right circular cone. From Fig. 1b, and from similar triangles in Fig. 2a, we obtain $a/r = r/r\sqrt{3}$; hence $a = r/\sqrt{3}$. Further, $b = \sqrt{r^2 - a^2} = r\sqrt{2/3}$. The height c of the segment removed is $c = r - a = r(1 - 1/\sqrt{3})$, and the height h of the cone is $h = r\sqrt{3} - a = r2/\sqrt{3}$. Let V_s = the volume of the sphere with radius r; V_{ca} = the volume of the segment removed, and V_{co} = the volume of the cone. The volume V_{m4} of the maximum-volume egg is

$$V_{m4} = V_s + V_{co} - V_{ca} = \frac{4\pi r^3}{3} + \frac{\pi b^2 h}{3} - \frac{\pi c}{6}(3b^2+c^2) =$$

$$= \frac{4\pi r^3}{3}\left[1 + \frac{1}{3\sqrt{3}} - \frac{1}{4}(1-\frac{1}{\sqrt{3}}) - \frac{1}{8}(1-\frac{1}{\sqrt{3}})^3\right] \approx 1.08\frac{4\pi r^3}{3}$$

The volume is therefore about 8 % larger than that of the corresponding sphere with radius r. The length of the maximum-volume egg is $r(1+\sqrt{3}) \approx 2.73$ r, i.e. 37 % larger than the diameter of the spherical egg.

By the same arguments, the maximum-volume egg with three-egg clutches (Fig. 2b) has the length $r(1+\sqrt{7/3}) \approx 2.53$ r, and its volume is

$$V_{m3} = \frac{4\pi r^3}{3} + \frac{8\pi r^3}{21}(\frac{1}{\sqrt{3}} - \frac{1}{\sqrt{7}}) - \frac{\pi r^3}{6}\left[\frac{4}{7}(1-\sqrt{\frac{3}{7}}) + (1-\sqrt{\frac{3}{7}})^3\right] \approx 1.05\frac{4\pi r^3}{3}$$

i.e. 5 % larger than the volume of the spherical egg.

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