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# The optimal shape of avian eggs

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## Summary

**1.** The shape of avian eggs is often explained by involving the mechanical properties of eggshell such as resistance to breakage or invoking physiological forces operating during egg development.

**2.** Here we take a different approach and investigate the efficient use of space. According to this approach the optimal egg shape is the one that produces the most compact fit under the incubating parent.

**3.** We extend the model of Andersson (1978) and use a numerical technique to investigate egg shapes in clutches of 1 to 10 eggs. In our model the shape of eggs is described by four parameters in a two-dimensional space. These parameters are free to vary – but eggs cannot be concave**.**

**4.** The optimal egg shape for each clutch size was found by a genetic algorithm.

**5.** The model predicts that egg shape should depend on clutch size. In particular, if the clutch consists of one egg then this egg should be spherical; whereas in clutches of two or three eggs the eggs should be biconical. In clutches of four the eggs should be pointed. The model also predicts that in clutches of over seven eggs the optimal egg shape should be approximately spherical.

**6.** These predictions are valuable because they point out that some of the variation in avian egg shapes may be explained solely by the efficient use of the brood patch area of the incubating parent.

*Key-words:* Birds, clutch size, egg shape, genetic algorithm, incubation

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## Introduction

The avian egg has a hard shell which gives a permanent shape for the egg materials. A typical avian egg is symmetric along the long axis and one of its ends is often more pointed than the other. Yet within these features egg shape varies greatly among avian taxa (Lack 1968; Walters 1994). For example, owls *Strigidae* lay spherical eggs, alcids *Alcidae* often have oval eggs and most shorebirds *Charadrii* have pointed eggs (Lack 1968; Walters 1994).

Three approaches have been used to investigate the shape of avian eggs. First, the egg is formed in the isthmus of the female oviduct and developmental biologists pointed out that egg shape could be the result of the action of the isthmus wall (Smart 1991; Solomon 1991). The egg is motionless when the calcareous shell is secreted by the cells of the isthmus wall and it floats in the fluid viscera and fat of the abdominal cavity. Under conditions of neutral buoyancy the egg would obtain a spherical shape. To produce a non-spherical egg the muscle coat of isthmus wall should press the egg along its long axis (Gilbert 1979). Thus females may control the shape of their eggs by using the muscles in their isthmus wall.

Second, egg shape has been often considered from a mechanical point of view. According to this approach, egg shape may be significant because it may increase the resistance to breakage (Bain 1991; Bain & Solomon 1991). This approach suggests that the optimal egg shape should be spherical, because this would provide the highest resistance against external forces (Bain 1991). Spherical shape would also provide the best gas transfer between the embryo and the outside environment (Ar *et al.* 1974). Clearly, these two approaches on their own are not adequate to explain the diversity of avian egg shapes found in nature.

Third, egg shape may be an adaptation to utilize the area of brood patch(es) of the parents through which the heat of incubation is transmitted (Thompson 1942; Lack 1968; Drent 1975). Andersson (1978) presented a geometric model to explain why shorebirds lay pointed eggs in clutches of four eggs. His model showed that pointed eggs fitted into the brood patch area more efficiently than spherical eggs. This is

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because pointed eggs provided 8% larger eggs for a given brood patch area than spherical eggs. If the survival of offspring increases with the size or mass of young at hatching (Clutton-Brock 1991; Williams 1994; Blomqvist, Johansson & Götmark 1997), then the extra egg material would give a survival advantage to chicks hatched from pointed eggs. On the other hand, if incubation efficiency is reduced (for example by enlarging the clutch with an extra egg), then the development of embryos slows down (Hills 1983) and the duration of incubation expands (Hills 1983; Székely, Karsai & Williams 1994).

However, Andersson's model was limited to four eggs and it was constrained to use two geometric shapes; spheres and cones. Here we extend his approach by a computational model and do not limit the egg shapes to some geometric shapes – except that eggs cannot be concave. By using this simple approach we show that the optimal shape of eggs should depend on clutch size.

## The model

### DESCRIPTION OF EGGS

Many birds nest on a flat surface such as ground or cliffs and in such nests the eggs typically lie on their sides (Drent 1975). Although the pointed end (or the blunt end) of some eggs may stick out of this two-dimensional space, this may be infrequent. Therefore, the egg shape and the incubation surface of the parents, i.e. their brood patch area, are considered as two-dimensional objects and it is assumed that the heat of incubation is transferred through this area which lacks down feathers.

Following Todd & Smart (1984) we describe the shape of the eggs as

$$Y = \pm\sqrt{a^2 - X^2} \times f(x), \qquad \text{eqn 1}$$

where $-a \le X \le a$. $Y = \pm\sqrt{a^2 - X^2}$ is the equation of a circle with radius $a$, which was modified by a factor

$$f(x) = c_0 + c_1 \times x + c_2 \times x^2 + c_3 \times x^3, \qquad \text{eqn 2}$$

with $x = X/a$ (Fig. 1). Each egg was represented by 22 coordinates in a two-dimensional space (Fig. 1a). Two of these coordinates defined each end of the egg, while the rest of the coordinates described the shape of the egg. The length of the egg ($2a$) was constant throughout this study (Fig. 1a). Egg shapes were generated by changing the parameters of the function $f(x)$ (Fig. 1b). With increasing $c_0$ the egg approached a circle and with increasing $c_1$ the egg became more pointed. $c_2$ and $c_3$ influenced the shape at each end of the egg (Fig. 2b).

The centre of gravity of an egg was on the main axis of the egg. The distance between the centre of gravity and the blunt end was calculated as

$$a\left(1 - \frac{3c_3 + 7c_1}{35c_0 + 7c_2}\right)$$

(Bronstejn & Szemengyajev 1987).

### GENETIC ALGORITHM

A genetic algorithm procedure was used to find the optimal egg shape. The genetic algorithm is a simulated evolutionary process which acts on a population of chromosomes (Holland 1975; Sumida *et al.* 1990). The chromosomes code for the input parameters. First, the chromosomes reproduce and their coded values are randomly altered, imitating the effect of mutation and recombination. Second, the chromosomes are selected based on their performance, i.e. fitness. The number of chromosomes is kept constant by excluding the chromosomes with the lowest fitness from the population. By repeating these two steps, genetic algorithms often reach a global maximum (Davis 1991).

In our model the chromosomes coded the egg-shape parameters and the position of eggs in the clutch. Each chromosome represented a clutch. The first four loci described the shape of eggs by coding the egg-shape parameters ($c_0$, …, $c_3$). This assumes that all eggs in a modelled clutch had the same shape. The next $n - 1$ pair of loci ($\varphi_i$, $\omega_i$) were used to determine the position of eggs in a clutch (Fig. 2, see below). These $n - 1$ pair of loci gave the initial position of the eggs. Thus a chromosome that coded a clutch of $n$ eggs had $4 + 2(n - 1)$ loci. Clutch size ($n$) was kept constant over the iterations.

The first egg was always placed in the centre of the coordinate system (Fig. 2a). The second and subsequent eggs were placed at a constant distance from the centre of the coordinate system. The direction of egg $i + 1$ ($i = 1, 2\ldots, n - 1$) was given by $\omega_i$ (Fig. 2b). The angle between the main axis of egg $i + 1$ and axis $X$ was given by $\varphi_i$. Then egg $i + 1$ was moved by coordinate transformation towards the centre of gravity of the clutch. The centre of gravity of the clutch was calculated by taking the mean centre of gravity of the eggs. The direction of the movement was given by a vector pointing from the centre gravity of egg $i + 1$ to that of the clutch (Fig. 2b). Egg $i + 1$ was moved until it touched an egg which was already in the clutch.

After all eggs were in the nest the algorithm calculated the fitness of the chromosomes. The fitness was based on the radius of the smallest circle which completely covered all eggs. This circle was defined as the brood patch area. Then the area covered by the eggs ($A_E$) and the area of the brood patch ($A_{BP}$) were evaluated. The ratio of these two measures ($A_E/A_{BP}$) gave the efficiency of brood patch use. $A_E/A_{BP}$ was used as the fitness of the chromosomes, except the fitness of clutches which contained concave eggs were set to zero. Those chromosomes that had high fitness (top 83·3%) were allowed to enter the next generation and reproduce whereas the worst chromosomes (bottom 16·7**%**) were excluded**.** Since mechanical and physiological studies considered a sphere to be the optimal egg shape, clutches were

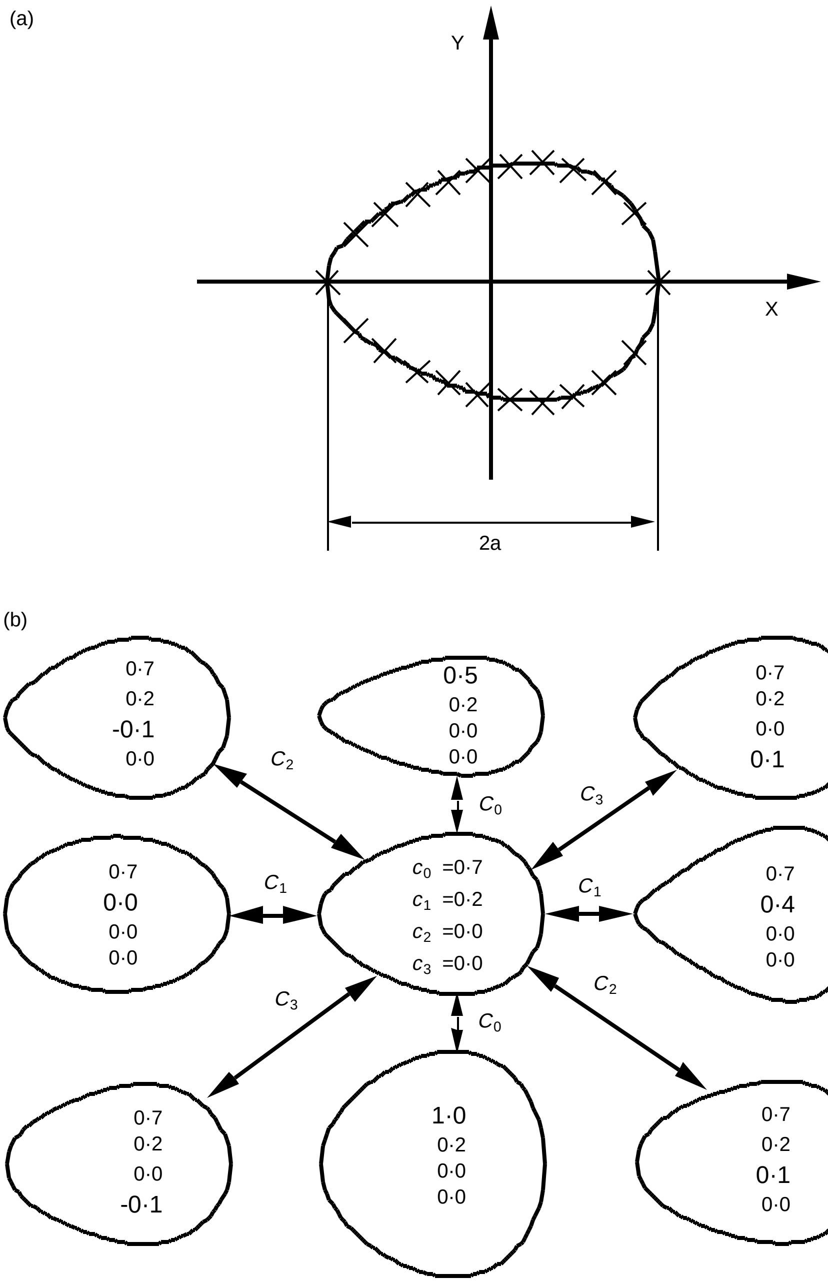

**Fig. 1.** The description of an avian egg. (a) Coordinates of 22 points (*X*) defined the shape of the egg in a two-dimensional space. The length of the egg is fixed at *2a*. (b) The influence of egg-shape parameters. The arrows indicate the direction of changes when the value of a single parameter is altered.

also constructed from spheres. These spheres were packed as close as possible and the efficiency of brood patch use was calculated ($A_E/A_{BP}$) as described above.

The genetic algorithm acted on a population of 72 chromosomes and the number of generation was 500. The population size and generation time were chosen as a rational compromise between computer storage capacity, running time and computational precision. $c_0$ and $c_1$ varied between 0·0 and 1·0, $c_2$ and $c_3$ varied between –0·1 and 0·1. Both $\varphi_i$ and $\omega_i$ varied between 0 and $2\pi$. The chromosomes were initialized with random values of shape parameters, $\varphi_i$ and $\omega_i$. The recombination rate was 0·5 and it was the probability that some of the shape or position parameters were swapped between two chromosomes (Davis 1991). A randomly selected pair of chromosomes were involved in recombination. The mutation rate was 0·05 and it gave the probability that the value of a locus change to any other possible value within the given range. The computer simulations were repeated 30 times for each clutch size and the statistics of these 30 simulations are given. Robust statistical measures are used, such as median, and upper and lower quartiles. Coefficients of Spearman rank correlation ($r_S$) and two-tailed probabilities are given.

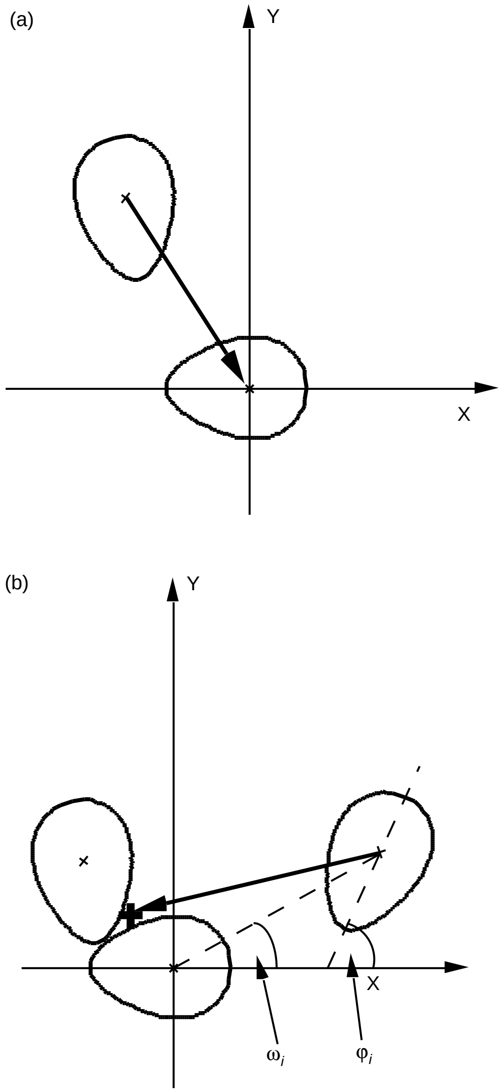

**Fig. 2.** The process of egg-packing. The arrows indicate the movement vectors of the eggs. The crosses give the centre of gravity of each egg (×) or the centre of gravity of the clutch (+). (a) Direction of the movement of the second egg. (b) Movement of the third egg towards the clutch. $\varphi_i$ and $\omega_i$ describe the position of eggs (see 'The model' section for details).

## Results

### THE EFFICIENT USE OF BROOD PATCH AREA

Efficiency of brood patch use decreased with clutch size ($r_S = -0{\cdot}952$, $n = 10$, $P < 0{\cdot}001$, Fig. 3a). It is unlikely that this reduction was caused by the inability of the genetic algorithm to find the best egg shapes, because the variations in efficiency between simulations, i.e. interquartile ranges of efficiency of brood patch use were unrelated to clutch size ($r_S = 0{\cdot}430$, $n = 10$, NS). In 6 out of 10 clutch sizes the eggs fitted the brood patch area significantly better than the spheres (Fig. 3b).

### THE OPTIMAL EGG SHAPE

All egg-shape parameters were significantly influenced by clutch size, that is the optimal egg shapes were different among clutches of different sizes (Table 1, Fig. 4). In clutches of one egg the optimal shape was nearly spherical (Figs 4 and 5). In clutches of two and three the eggs were biconical (Figs 4 and 5). The most pointed eggs were found in clutches of four eggs in which both $c_0$ and $c_1$ were high (Figs 4 and 5). In clutches of more than five eggs the optimal egg shape tended to be close to spherical (Figs 4 and 5).

## Discussion

In this paper we investigate egg shapes that result from maximizing the area of the heat transfer between the incubating parent and the eggs. By using this criterion the model predicts that egg shape should depend on clutch size. First, the model predicts that eggs should be pointed in those species in which the female lays clutches of four eggs. This result is in agreement with the prediction of Andersson's (1978) geometric model. Second, in species in which the female lays one egg or more than five eggs, the eggs should be approximately spherical. Third, if parents incubate two eggs these eggs should have biconical shapes. The predicted relation between egg shape and clutch size is supported by a preliminary survey in several avian taxa. The most common clutch size in albatrosses, fulmars and storm-petrels *Procellariidae* is one egg and this egg is typically spherical (Walters 1994). Two eggs are laid by divers *Gaviidae*, pigeons *Columbidae* and cranes *Gruidae* and these eggs are often ellipsoid. Many sandpipers *Scolopacidae* and plovers *Charadriidae* lay four eggs and these eggs are pointed. However, proper tests of these predictions across several avian taxa require quantitative descriptions of egg shapes and should take into account the phylogenetic relatedness among species, because the shape of eggs is likely to be similar in closely related species.

The predictions of our model could also be tested by using intraspecific variation in egg shape. Egg shape is highly variable among clutches of Pied Flycatchers, *Ficedula hypoleuca*, since some eggs are almost spherical whereas others are ellipsoidal or pointed (Kern & Cowie 1996). Our model predicts that these egg shapes should relate to clutch size in a particular way (Fig. 4).

Heat transfer between the incubating parent and the eggs may not be the only adaptive explanation for egg shapes. Eggs that fit together may also reduce heat loss. Norton (1970, in Drent 1975) experimentally showed that a compact clutch of four eggs in the Dunlin *Calidris alpina* lost heat at a slower rate than a single egg, whereas three eggs lost heat at approximately the same rate as a single egg. Von Tschanz, Ingold & Lengacher (1969) showed that the pear shape of Common Murre *Uria aalge* eggs is advantageous for preventing the egg from rolling down from the edge of cliffs. Furthermore, resistance to breakage

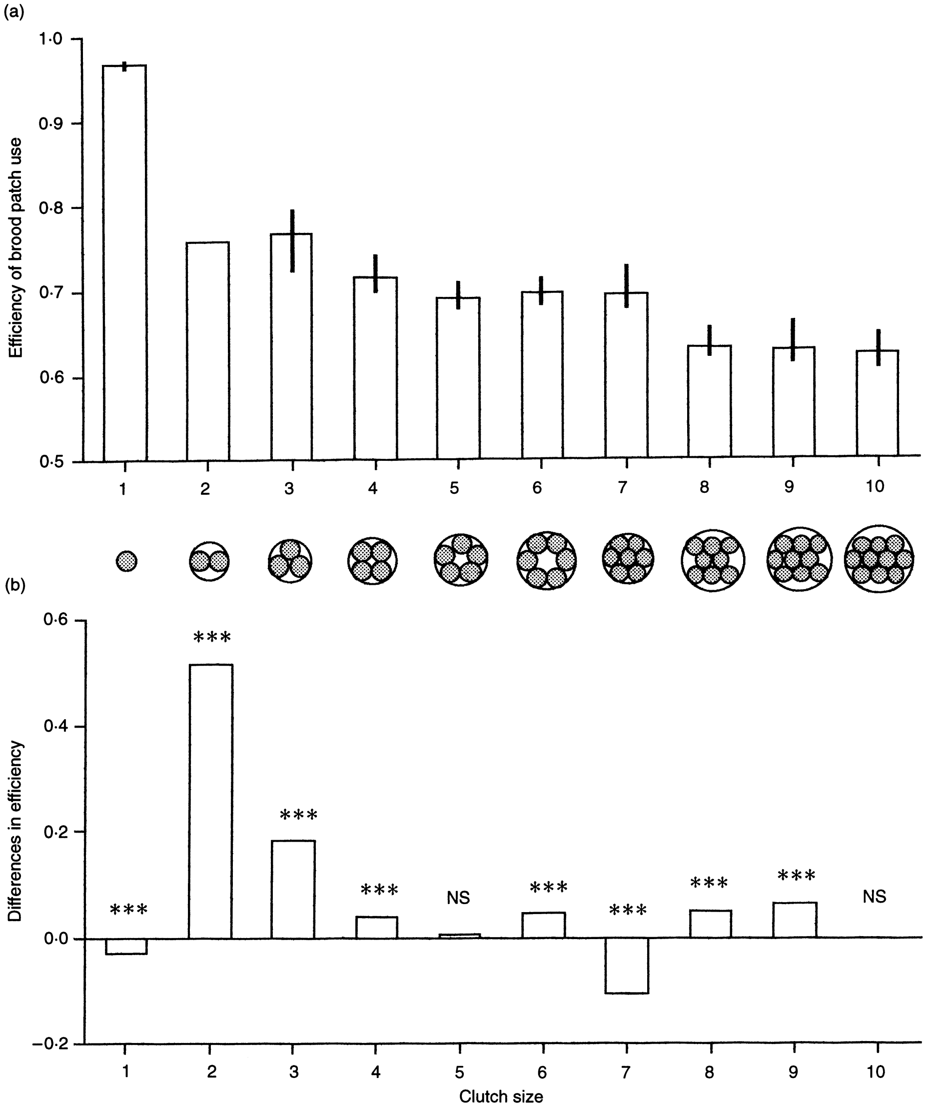

**Fig. 3.** (a) Efficiency of brood patch use by modelled eggs at various clutch sizes. The median and interquartile ranges of 30 simulations are given. (b) Differences between the median efficiency of brood patch use of modelled eggs ($E_{BP}$) and that of the circles ($E_C$). Best fit of spheres are indicated above each bar. Differences in efficiency were calculated as $(E_{BP} - E_C)/E_C$. Wilcoxon one sample signed-ranks tests; *** $P < 0{\cdot}001$; NS $P > 0{\cdot}05$.

**Table 1.** The influence of clutch size on shape parameters of eggs (Kruskal–Wallis tests, $c_0$: $\chi^2 = 155{\cdot}09$, $P < 0{\cdot}001$; $c_1$: $\chi^2 = 114{\cdot}92$, $P < 0{\cdot}001$; $c_2$: $\chi^2 = 91{\cdot}68$, $P < 0{\cdot}001$; $c_3$: $\chi^2 = 38{\cdot}50$, $P < 0{\cdot}001$, $n = 30$ for each egg-shape parameter). Lower quartiles (LQ), median and upper quartiles (UQ) are given. 30 simulations were carried out for each clutch size

| | Egg-shape parameters | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $c_0$ | | | $c_1$ | | | $c_2$ | | | $c_3$ | | |
| Clutch size | LQ | Median | UQ | LQ | Median | UQ | LQ | Median | UQ | LQ | Median | UQ |
| 1 | 0·994 | 0·997 | 0·999 | 0·003 | 0·004 | 0·011 | –0·000 | 0·004 | 0·009 | –0·018 | –0·008 | –0·004 |
| 2 | 0·541 | 0·544 | 0·548 | 0·007 | 0·019 | 0·038 | –0·100 | –0·098 | –0·097 | –0·083 | –0·061 | –0·031 |
| 3 | 0·611 | 0·644 | 0·738 | 0·057 | 0·104 | 0·194 | –0·094 | –0·087 | –0·018 | –0·061 | –0·006 | 0·054 |
| 4 | 0·713 | 0·865 | 0·951 | 0·075 | 0·272 | 0·388 | –0·062 | 0·014 | 0·069 | –0·068 | 0·005 | 0·064 |
| 5 | 0·548 | 0·622 | 0·840 | 0·066 | 0·135 | 0·257 | –0·058 | –0·008 | 0·059 | –0·042 | 0·031 | 0·072 |
| 6 | 0·736 | 0·830 | 0·944 | 0·071 | 0·112 | 0·195 | –0·044 | 0·011 | 0·057 | –0·077 | –0·058 | 0·015 |
| 7 | 0·733 | 0·868 | 0·961 | 0·076 | 0·131 | 0·229 | –0·069 | –0·002 | 0·070 | –0·060 | –0·016 | 0·054 |
| 8 | 0·663 | 0·732 | 0·883 | 0·075 | 0·144 | 0·266 | –0·063 | –0·023 | 0·066 | –0·017 | 0·026 | 0·072 |
| 9 | 0·723 | 0·798 | 0·868 | 0·023 | 0·078 | 0·141 | –0·083 | –0·029 | 0·053 | –0·068 | –0·020 | 0·040 |
| 10 | 0·774 | 0·855 | 0·934 | 0·036 | 0·119 | 0·210 | –0·062 | 0·001 | 0·047 | –0·050 | 0·044 | 0·082 |

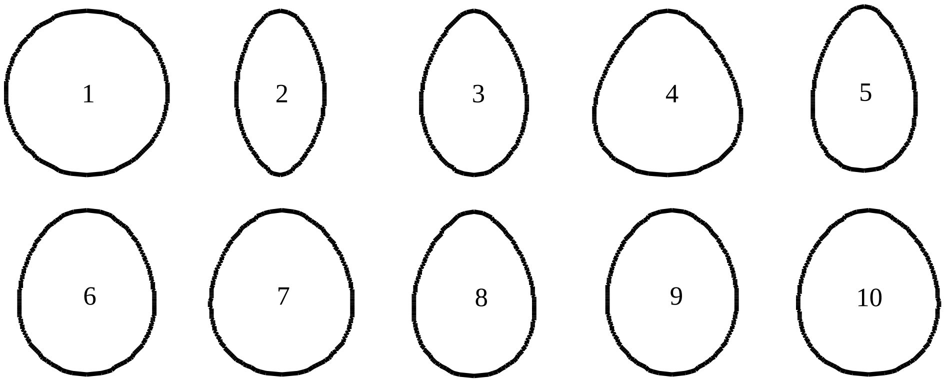

**Fig. 4.** The optimal egg shape in various clutch sizes. Eggs are given by the median egg-shape parameters of 30 simulations (Table 1). Clutch sizes are indicated inside each egg.

may be important in species in which the body mass of parents is substantial. Female Ostriches *Struthio camelus* lay almost spherical eggs and these eggs have a thick shell (Walters 1994). The spherical shape of the eggs may contribute to the strength of egg, enabling it to withstand the considerable weight of incubating birds (Bertram 1992).

We are aware of the limitations of our simple model. For example, the model assumes that incubation heat is transferred through a single, circular brood patch. First, not all birds possess a brood patch, thus a potential relation between egg shape and clutch size in such birds could be fortuitous. Megapodes lay their eggs in incubation mounds and the eggs develop inside such mounds (Drent 1975). Penguins use brooding pouches to keep their eggs warm and pelecaniform birds use their webbed feet to incubate their eggs (Drent 1975). Second, the shape of brood patch is highly variable among birds (Drent 1975; Wiebe & Bortolotti 1993) and the shape of brood patch may influence egg shape. Andersson (1978) suggested that the elongated shape of the brood patch may explain elongated egg shapes in some birds. However, parents may change position during incubation so that the total surface covered during incubating may still be close to a circle. Third, several species of pigeons, gulls, falcons and shorebirds possess a certain number (two or three) brood patches (Wiebe & Bortolotti 1993). It has been suggested that the number of brood patches may have coevolved with clutch size (Winkler & Walters 1983; Székely *et al.* 1994). The variation in shape and number of brood patches may indeed be adaptations to circumvent the limitations of egg shape. Thus, shape of eggs may have influenced the shape and number of brood patches over the evolution, whereas brood patches may have influenced the number, size and shape of eggs. Clearly, future models should investigate both of these evolutionary relations, perhaps by adopting a similar approach to that advocated here.

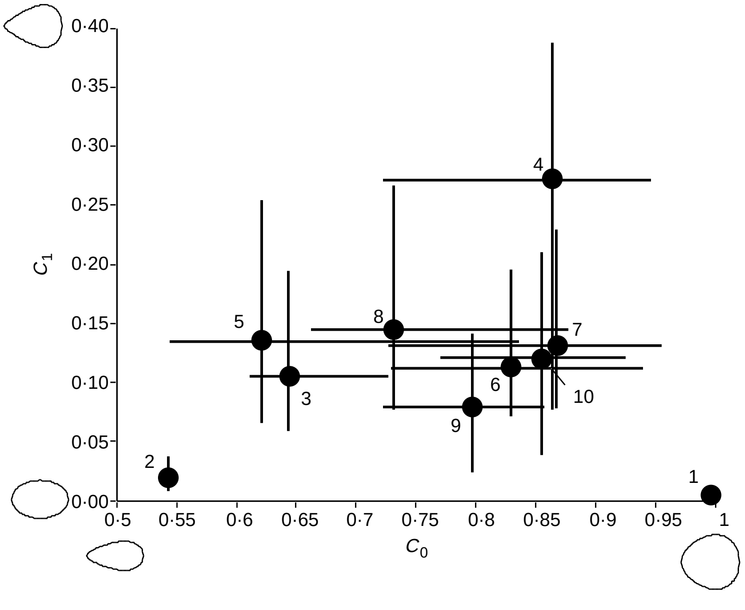

**Fig. 5.** The optimal eggs in relation to egg-shape parameters $c_0$ and $c_1$. The median and interquartile ranges of both egg-shape parameters are given. The numbers refer to clutch size.

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