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Fitness consequences of egg shape variation: a study on two passerines and comments on the optimal egg shape model

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A model has been proposed that predicts a relationship between egg shape and fitness, arguing that eggs will be shaped to fit within the brood patch in an arrangement that is optimal for incubation. Deviations from the "optimal egg shape" would therefore entail a decrease of fitness of the parents. We explored the fitness consequences of egg shape variation, using data on egg characteristics and breeding performance of 354 Great Tit *Parus major* and 150 Blackbird *Turdus merula* clutches. "Optimal egg shape" for a particular clutch size was defined as the mean of the shape index for each clutch size. For each clutch, mean egg shape, an index of shape deviation from the optimal egg shape, and the coefficient of variation of the shape deviation index, were computed ("egg shape variables"). We found that (1) mean egg shape did not vary with clutch size; (2) hatching and breeding success, and weight of nestlings at 15 days of age, were not related to egg shape variables, even after controlling for the effects of clutch size and egg size; and (3) within a clutch, the relative shape of an egg did not affect its hatchability. Therefore, within the range found in natural populations, the shape of eggs does not seem to have fitness consequences, a conclusion that does not support the optimal egg shape model.

1. Introduction

In a review of the effects of avian egg characteristics on fitness, Williams (1994) only considered egg size (volume or mass) and egg composition. This was not surprising, since few published studies offered information about egg shape and its variability within a species, and none related egg shape to any measure of fitness. Why should we look for such a relationship?

Barta and Székely (1997) developed a model to predict egg shape, based on the assumption that eggs will be shaped to fit within the area of the brood patch in an arrangement that is optimal for incubation. A prediction of the model was that the optimal egg shape within a species would change with clutch size, since the optimal arrangement of the eggs within the brood patch should change with the addition of new eggs (see Fig. 3 in Barta & Székely 1997).

If there were an "optimal egg shape" for each particular clutch size, females producing eggs of the "wrong" shape will have their fitness reduced, i.e., egg shape would have fitness consequences. Effects of non-optimal egg shape on fitness would be mediated by inefficient incubation, since a "wrong" shape may affect the amount of heat received by particular eggs. A strong, immediate negative effect would be that eggs poorly incubated might not hatch (Webb 1987). However, more subtle effects could be expected if differences in the heat received do not affect hatchability, but alter the hatching pattern (Stoleson & Beissinger 1995). The degree of hatching asynchrony may affect chick survival during the nestling phase (e.g. Slagsvold 1986, Mock & Ploger 1987). Moreover, final fledgling size could be affected by the hatching pattern (Slagsvold 1986, Slagsvold *et al.* 1995), and weight at fledging is important for post-fledging survival in many species (e.g. Tinbergen & Boerlijst 1990, Magrath 1991).

We examined the fitness consequences of egg shape variation, using data on egg characteristics and breeding performance of Great Tits *Parus major* and Blackbirds *Turdus merula*. Specifically, we studied (1) the variability of egg shape with clutch size; (2) the relationships between egg shape and its deviation from an estimated "optimum", with hatching success, breeding success, and nestling weight just before normal fledging age; and (3) the hatchability of particular eggs in relation to their shape. The results were discussed in the context of the optimal egg shape model.

2. Material and methods

The measurements of the eggs were taken during long-term studies of a Great Tit and a Blackbird population in eastern Spain (e.g. Barba *et al.* 1995, Gil-Delgado & Lacort 1996). The study area was located within an extensive orange monoculture near Sagunto, eastern Spain (39°42´N, 0°15´W, 30 m above sea level).

Nestboxes have been available in this area since 1986, and basic breeding parameters of the Great Tit (laying date, clutch size, number of eggs hatched and number of fledglings per nest) were recorded each year through periodic inspections. From 1992 onwards, nestlings were weighed on day 15 (i.e. just prior to normal fledging age) and the mean weight and coefficient of variation (CV) were estimated for each clutch. Hatching success (percentage of eggs hatched) and breeding success (percentage of fledglings from eggs laid) were also calculated for each clutch; these were arcsine transformed, using the Anscombe correction, to achieve normality (Zar 1996), and transformed values used in all the analyses. Hatching and breeding success, mean nestling weight, and its CV, will be referred to as the "fitness variables" hereafter. Eggs were measured from 1986 until 1988 and from 1990 until 1999. All the eggs of 76 clutches were individually marked, and the hatchability of each particular egg was assessed.

Blackbird nests were located each breeding season since 1975, using the mapping method and searching for nests in each tree within a 17 ha plot (Gil-Delgado & Lacort 1996). Each particular tree was inspected at least once every 15 days, and more often early in the season. The same breeding parameters as for Great Tits were recorded, but nestlings were not weighed. Eggs were measured in 1976 and 1998.

Length (L) and breadth (B) of eggs were measured to the nearest 0.1 mm in 354 Great Tit and 150 Blackbird complete clutches. All the measures of each species were taken by the same author (EB for great tits; JAG-D for blackbirds). As females were not individually marked during part of the study, it was possible that more than one clutch per female was included in the analyses. However, not all the clutches were measured each year, some of the ones measured were excluded from some analyses (see below), and the same female could have laid clutches of different sizes. Therefore, we think that the level of pseudoreplication in the data set was low, and no systematic error would be expected.

As a measure of egg shape, we calculated the sphericity index (S) for each egg as

$$S = B/L \qquad (1)$$

(e.g. Hõrak *et al.* 1995). The volume of each egg was calculated from linear dimensions using the equation

$$V = (0.4673\ L\ B^2) + 0.042, \qquad (2)$$

for Great Tits (Ojanen *et al.* 1978), and

$$V = 0.507\ L\ B^2, \qquad (3)$$

for Blackbirds (Hoyt 1979). For each clutch, mean egg shape and mean egg volume were calculated and used in the analyses.

Clutches lost to predation or deserted were included up to the point of failure, but excluded afterwards. We considered that these causes of failure were independent of egg shape. Also, some clutches were manipulated for other purposes at different stages, and were included up to the point of manipulation, but excluded afterwards (e.g. broods manipulated after hatching were not included in analyses concerning breeding success or fledging weight). Therefore, sample sizes decreased throughout the nesting period.

The model proposed by Barta and Székely (1997) assumed that, for each clutch size, all the eggs should have the same "optimal" shape. Therefore, the optimal egg shape for a particular clutch size will refer hereafter to the optimal egg shape of all the eggs within a clutch of this size. We assumed here that the mean egg shape for a particular clutch size (calculated over the clutch means of the population) would be equal to the optimal egg shape for this clutch size.

To explore the effects of deviations from the optimal egg shape, a value quantifying this deviation was computed for each clutch. The deviation was defined as the absolute value of the difference between the sphericity index of each egg and the optimal egg shape for the clutch size. The mean of the absolute values for each clutch (shape deviation) was taken as a measure of the deviance between the egg shape of a clutch and the optimal egg shape for this clutch size. This assumed that more rounded eggs do not compensate for more elongated eggs within a clutch, and a shape deviation of zero would mean that all the eggs of the clutch were optimally shaped. Also, for each clutch, the coefficient of variation of the shape deviation was also used as an independent variable, to check whether the within-clutch variability of egg shape itself could affect fitness. Egg shape, shape deviation, and the CV of shape deviation will be referred as the "shape variables" hereafter.

The optimal egg shape model, as proposed by Barta and Székely (1997), assumed stabilising selection, i.e., both deviations towards more rounded or more elongated eggs would be bad, and therefore we used absolute values of the differences in our main analyses. Directional selection, however, might also occur, i.e., either more rounded or more elongated eggs than the mean could be bad, but the opposite may not be. To test for this directional selection we selected those clutches where all the eggs deviated in the same direction from the optimal shape. Then, we compared the fitness variables between clutches where all the eggs were more rounded than the optimal and those where all the eggs were more elongated than the optimal. If there were directional selections, we would expect to find differences between the two groups. These analyses were performed only with Great Tits, since there were more data for this species.

Finally, the model did not consider that some bird species usually lay clutches of more eggs than could be accommodated within the brood patch. For these species, the optimal egg shape would probably be that of the maximum number of eggs that could be fitted within the brood patch, independently of the actual clutch size. We also explored this possibility with the Great Tit data, since this species usually lays large clutches relative to the body size of the female. As an example, we considered that a maximum of 5 eggs could be touching the brood patch (see photograph in Löhrl 1986: Fig. 2). Therefore, we analysed the consequences of deviations from this optimal egg shape for all the clutches independently of their size.

Other factors, such as egg volume or clutch size, could affect the fitness variables considered here (e.g. Murphy & Haukioja 1986, Williams 1994). To remove their possible effects, we checked whether clutch size and egg size had a significant effect on each of the fitness related factors examined and, if they did, the residuals were taken and regressed against the shape variable considered.

Ideally, the optimal egg shape should be calculated by taking into account brood patch size and shape of the species or, even better, of each individual. These data are not available but, given the individual optimisation hypothesis, it could be predicted that the more an egg deviated from the mean egg shape of its clutch, the lower its hatchability would be. We therefore calculated the difference between the shape of each egg and the mean for its clutch in these Great Tit clutches where eggs were individually marked. We then compared the hatchability of the egg closest to the mean value and that of (a) the more elongated egg, (b) the more rounded egg, and (c) the egg which is more different in either direction.

We have used our data on egg shape for different tests, under different assumptions, trying

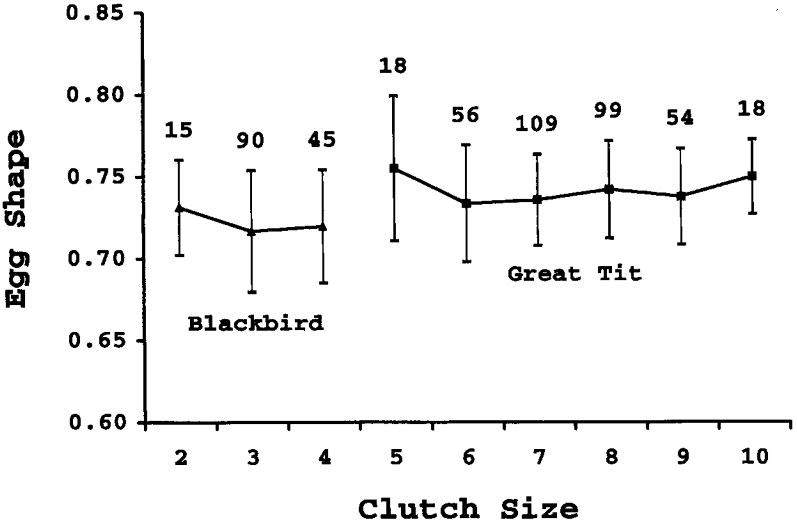

Figure 1. The relationship between egg shape and clutch size in Great Tits and Blackbirds. Mean egg shape (sphericity index), its standard deviation, and number of clutches (numbers above bars) are shown for each clutch size. Clutch sizes outside the range shown were too rare (< 5 nests for each clutch size) to analyse.

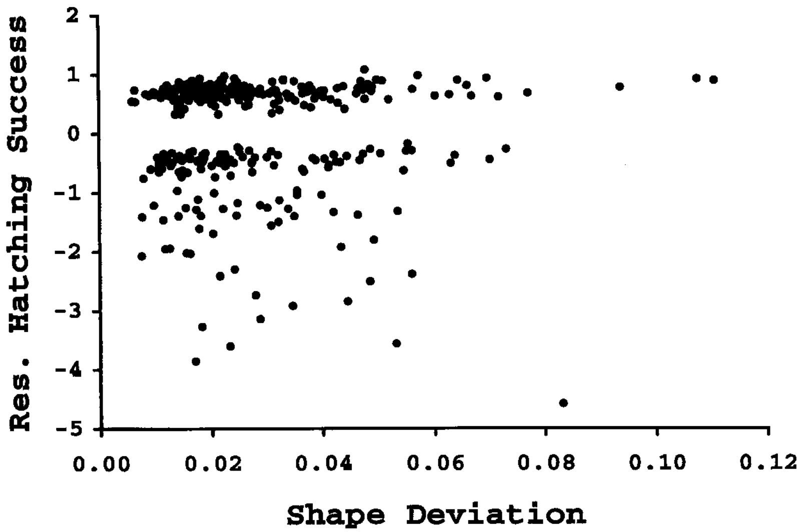

Figure 2. The relationship between residual hatching success (after removing the effects of egg volume and clutch size) and shape deviation in Great Tits. $r^2 < 0.001$, $F_{1,313} = 0.02$, $P = 0.89$. Hatching success was arcsine transformed to achieve normality.

to find some support for the optimal egg shape model. This might have increased the probability of finding significant relationships by chance alone (see e.g. Rice 1989). Since virtually none of the tests performed was significant, we think that this caveat of the analyses did not affect our conclusions.

3. Results

The sphericity index for Great Tit eggs ranged between 0.58 and 0.88, while that for Blackbirds ranged between 0.56 and 0.99 (Fig. 1). The differences in egg shape among clutches of different size were not significant for Blackbirds ($F_{2,147} = 1.07$, $P = 0.34$). For Great Tits, the differences were marginally significant ($F_{5,348} = 2.27$, $P = 0.047$). However none of the post-hoc tests used (Scheffe, Student-Newman-Keuls, Tukey) found differences between groups. Given the large number of tests performed (see Methods), the high p-value, and the absence of significance in the post-hoc tests, we conclude that the differences in egg shape among clutch sizes were probably caused by chance alone.

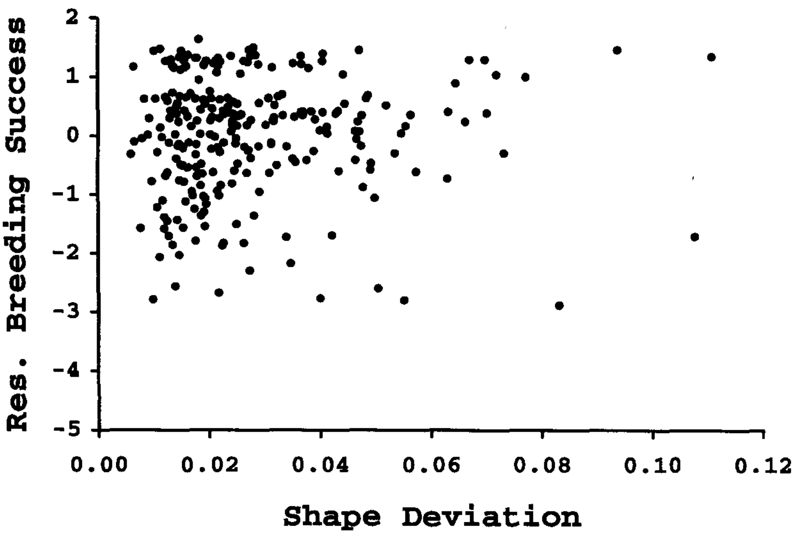

Figure 3. The relationship between residual breeding success (after removing the effects of egg volume) and shape deviation in Great Tits. $r^2 = 0.003$, $F_{1,247} = 0.67$, $P = 0.41$. Breeding success was arcsine transformed to achieve normality.

For Great Tits, no significant effect of egg shape ($r^2 = 0.002$, $F_{1,313} = 0.76$, $P = 0.38$), shape deviation ($r^2 = 0.003$, $F_{1,313} = 0.90$, $P = 0.34$), or CV of shape deviation ($r^2 = 0.001$, $F_{1,313} = 0.45$, $P = 0.50$) on hatching success was detected. The hatching success of Great Tits was positively related to egg volume and clutch size (multiple regression, $r^2 = 0.042$, $F_{2,311} = 6.82$, $P = 0.001$). After removing the effects of these two variables, no significant effect of egg shape ($r^2 = 0.002$, $F_{1,313} = 0.69$, $P = 0.41$), shape deviation (Fig. 2) or CV of shape deviation ($r^2 < 0.001$, $F_{1,313} = 0.12$, $P = 0.73$) on residual hatching success was detected (for brevity, only a sample of relationships are plotted throughout).

For Blackbirds, no significant effect of egg shape ($r^2 = 0.007$, $F_{1,119} = 0.88$, $P = 0.35$), shape deviation ($r^2 = 0.024$, $F_{1,119} = 2.94$, $P = 0.089$) or CV of shape deviation ($r^2 = 0.005$, $F_{1,119} = 0.64$, $P = 0.43$) on hatching success was found. The hatching success of Blackbirds was not related to egg or clutch size.

We found no significant effect of egg shape ($r^2 = 0.004$, $F_{1,247} = 0.90$, $P = 0.34$), shape deviation ($r^2 = 0.001$, $F_{1,247} = 0.16$, $P = 0.69$) or CV of shape deviation ($r^2 = 0.004$, $F_{1,247} = 0.96$, $P = 0.33$) on breeding success in the Great Tit. Breeding success of Great Tits was positively related to egg volume ($r^2 = 0.019$, $F_{1,247} = 4.68$, $P = 0.031$), but not to clutch size. After removing the effect of egg volume, no significant effect of egg shape ($r^2 = 0.003$, $F_{1,247} = 0.70$, $P = 0.41$), shape deviation (Fig. 3) or CV of shape deviation ($r^2 = 0.007$, $F_{1,247} = 1.72$, $P = 0.19$) on residual breeding success was detected.

In the Blackbird, no significant effect of egg shape ($r^2 < 0.001$, $F_{1,78} < 0.001$, $P = 0.995$), shape deviation ($r^2 < 0.001$, $F_{1,78} = 0.002$, $P = 0.96$), or CV of shape deviation ($r^2 = 0.005$, $F_{1,78} = 0.36$, $P = 0.55$) on breeding success was found. Breeding success was not related to egg volume or clutch size in Blackbirds.

For Great Tits, no significant effect of egg shape ($r^2 = 0.007$, $F_{1,163} = 1.09$, $P = 0.30$), shape deviation (Fig. 4) or CV of shape deviation ($r^2 < 0.001$, $F_{1,163} = 0.003$, $P = 0.96$) on mean nestling weight at day 15 was detected. Similarly, we found no significant effect of egg shape ($r^2 = 0.013$, $F_{1,163} = 2.11$, $P = 0.15$), shape deviation (Fig. 5) or CV of shape deviation ($r^2 = 0.011$, $F_{1,163} = 1.84$, $P = 0.18$) on the CV of nestling weight. Mean nestling weight and its CV were not related to clutch size or egg volume.

Any of the fitness variables considered for Great Tits differed significantly between clutches where all the eggs were more rounded than the optimal and those where all the eggs were more elongated (hatching success: $t_{129} = 0.69$, $P = 0.50$; breeding success: $t_{100} = 0.88$, $P = 0.38$; mean nestling weight: $t_{69} = 1.76$, $P = 0.08$; CV of mean nestling weight: $t_{69} = 0.58$, $P = 0.56$). Therefore, the possible existence of directional selection was not supported.

Assuming that the optimal egg shape for Great

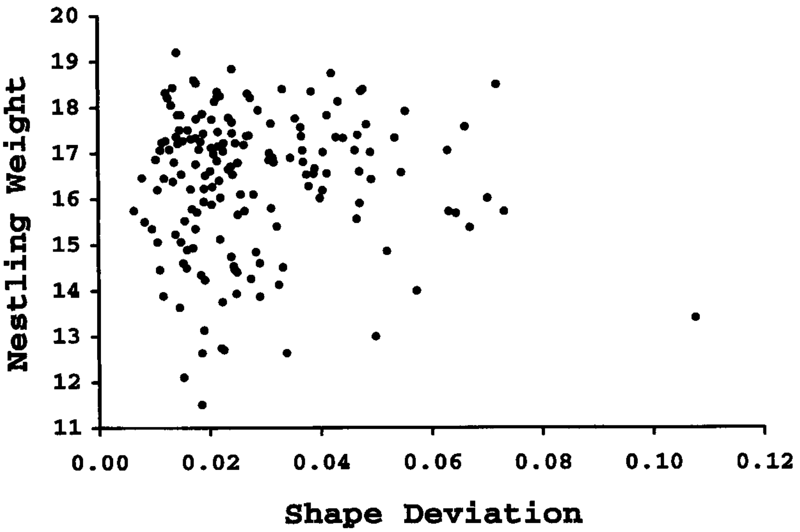

Figure 4. The relationship between nestling weight and shape deviation in Great Tits. $r^2 < 0.001$, $F_{1,163} = 0.02$, $P = 0.90$.

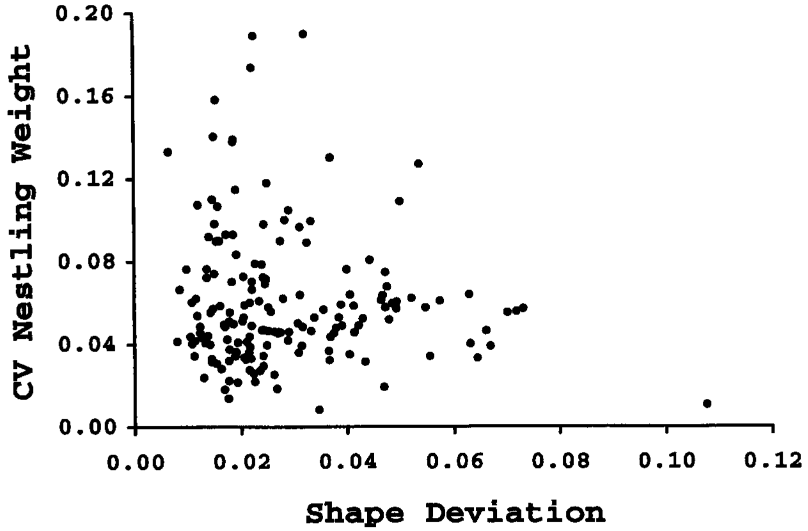

Figure 5. The relationship between CV of nestling weight and shape deviation in Great Tits. $r^2 = 0.010$, $F_{1,163} = 1.58$, $P = 0.21$.

Tits was that of 5-egg clutches, we found no effect of shape deviation on hatching success ($r^2 = 0.003$, $F_{1,312} = 0.80$, $P = 0.37$), breeding success ($r^2 = 0.001$, $F_{1,312} = 0.30$, $P = 0.59$), mean nestling weight ($r^2 = 0.003$, $F_{1,163} = 0.47$, $P = 0.49$), or CV of mean nestling weight ($r^2 = 0.001$, $F_{1,163} = 0.23$, $P = 0.64$).

Within Great Tit clutches, there were no differences in the hatching probabilities between the egg more similar to the mean of the clutch and that more rounded ($\chi^2_1 = 1.19$, $P = 0.28$), more elongated ($\chi^2_1 = 0.08$, $P = 0.78$) or more different in absolute value ($\chi^2_1 = 0.47$, $P = 0.49$). Therefore, within a clutch, the shape of individual eggs does not seem to affect their hatchability.

4. Discussion

4.1. Egg shape and clutch size

Although many studies have reported the egg dimensions of Great Tits (e.g. Hõrak *et al.* 1995) and Blackbirds (e.g. Magrath 1992), few have attempted to relate egg shape and clutch size. Among these, conclusions differed greatly, as illustrated by the following examples on Great Tits. Yoo (1993) did not find any relationship between egg shape and clutch size. Ojanen *et al.* (1978) found that the egg shape index (defined as L/B × 100) decreased from 4-egg clutches (C4) to C6, increased from C6 to C8, and decreased again from C8 to C13. They used linear regression analyses to test for the significance of each increase or decrease; only the decrease from C8 to C13 was significant. They suggested that producing rounded eggs in large clutches could save calcium (more rounded eggs would have lower surface/volume ratio), and that rounded eggs would be better covered by the incubating female. Nevertheless, they stated that "The ecological significance of the variation of egg shape with clutch size is not clear." Finally, Haftorn (1985), also using a linear regression, but including all the clutch sizes in a single analysis, found that the egg shape index (calculated as in Ojanen *et al.* 1978) increased significantly with clutch size (clutches from 6 to 13 eggs included). No explanation for these results was given, but they clearly contradicted those proposed by Ojanen *et al.* (1978). Our results showed that egg shape did not vary significantly among clutches of different size. All these studies suggest that there is not a consistent pattern of egg-shape variation with clutch size among populations of Great Tits, nor clear explanations for positive or negative relationships when they have been found.

We are not aware of any study relating egg shape and clutch size in Blackbirds. However, in most other species where this relationship has been examined, [Willow Grouse *Lagopus lagopus* (Myrberget 1977), Pied Flycatcher *Ficedula hypoleuca*, Redstart *Phoenicurus phoenicurus*, Starling *Sturnus vulgaris* (Ojanen *et al.* 1978), Least Flycatcher *Empidonax minimus* (Briskie and Sealy 1990) American Pipit *Anthus rubescens* (Hendricks 1991), and Blue Tit *Parus caeruleus* (Yoo 1993)], no significant relationship has been found. To our knowledge, the only study reporting a significant effect of clutch size on egg shape, apart from the Great Tit ones mentioned above, is that of Suárez (1991) on Black-eared Wheatear *Oenanthe hispanica*, where eggs were more rounded in 4-egg than in 5-egg clutches. Again, no explanation was given for this pattern.

The results presented here, and those from published studies on several species, do not show any pattern of egg shape variation with clutch size and, therefore, do not support the optimal egg shape model.

4.2. Egg shape and breeding performance

A positive relationship between egg size and the probability of offspring survival during the first few days after hatching seems well established (reviewed by Williams 1994), although its later influence on nestlings is not clear (e.g. Reed *et al.* 1999). However, we have reviewed a large number of papers dealing with egg dimensions in several species (including all 40 references given by Williams 1994: Table 1) and, though some of them have shown that, within a population, egg shape can vary with female age (Robertson *et al.* 1994) or laying sequence (Haftorn 1985), none looked for relationships between egg shape and any measure of fitness. As far as we know, this is the first attempt to relate egg shape and breeding performance in any bird.

We did not find any significant relationship between egg shape and any of the fitness factors examined. Also, clutches where the mean egg shape deviates more from the optimum (large shape deviation), or those where the shape of the eggs were more variable (large CV of shape deviation) did not suffer any decrease of fitness. Finally, within a clutch, eggs which differ more from the mean egg shape did not have their hatchability reduced. Our sample sizes and the range of clutch sizes were large, so we think it is safe to conclude that egg shape, at least within the range observed in the populations studied, does not have a significant effect on the breeding performance of great tits or blackbirds.

4.3. Is the "optimal egg shape model" a general model?

Our results suggested that the shape of the eggs, or its variability within a clutch, had no appreciable effect on the efficiency of the incubation in the two species examined. This result does not agree with the predictions of the optimal egg shape model. We think that this lack of agreement could be attributed partly to technical difficulties in quantifying egg shape, and partly to deficiencies of the model, at least for some species.

Firstly, the method we used to estimate the shape of eggs was crude compared with that proposed by Barta and Székely (1997). Eggs with the same length and width could have different shapes, a fact that could not be detected with the method used here but could be with that proposed by Barta and Székely (1997). Although the sphericity index used here, or the elongation index used in other studies (e.g. Ojanen *et al.* 1978), seems appropriate to detect shape differences between eggs (Smart 1991, Hõrak *et al.* 1995, present study), a proper test of the model should be done following the method proposed by Barta and Székely (1997).

Secondly, it might be argued that each female has a particular optimum egg shape depending on the particular size and shape of her brood patch and, therefore, assuming a single optimum for each clutch size is not appropriate. We have approached this problem considering the hatching probability of individual eggs as a function of their deviation from the mean shape of their clutch. However, a further study of individual optimisation, actually measuring brood patch size and shape, may be an interesting approach to this problem. Also, experimental approaches could be devised to overcome the difficulties of measuring the brood patch size and shape in the field. For example, if each female had her optimal egg shape for a particular clutch size, exchanging complete clutches between females with equal clutch sizes and different egg shapes should entail a reduction in fitness.

Thirdly, the model proposed by Barta and Székely (1997) raised some problems at the intraspecific level in species with variable clutch size. For example, it would be difficult to apply to indeterminate layers, e.g. species for which clutch size is not determined before the first egg is laid (e.g. Haywood 1993). To shape all the eggs adequately, the female should know the number of eggs she will lay before producing the first egg.

Fourthly, the optimal egg shape model proposed that the eggs should have a particular shape to best fit within the brood patch. If the brood patch is able to accommodate all the eggs from the largest clutch size that the female is able to produce under normal circumstances, there should be ample space for eggs within the brood patch in clutches smaller than the maximum. Therefore, it is unlikely that there would be much pressure for eggs in smaller clutches to have a specific shape to fit into the brood patch. On the other hand, some species seem able to incubate successfully clutches enlarged experimentally (e.g. Baltz & Thompson 1988, Moreno & Carlson 1989, Sanz 1997).

Fifthly, it is evident from the clutch sizes laid by some species and the size of the bird, that not all the eggs could be accommodated within the brood patch at the same time. Photographs clearly showing this were provided by Löhrl (1986: Fig. 2), where a dead Great Tit sat on a clutch of 9 eggs and only a few of them were in contact with the body, not to mention the brood patch. Clutches of 9 eggs or even larger are common in Great Tits (Perrins 1979), and the eggs are frequently found in two layers when clutches are large (pers. obs.). These birds should frequently move all the eggs to incubate them properly (see Fig. 3 in Löhrl 1986). In this case, and modifying the predictions of the original model, it could be predicted that the optimal egg shape, for all clutch sizes, would be that of the clutch size which could be actually accommodated within the brood patch. Our approach to this question, considering that a maximum of 5 eggs could be accommodated within a Great Tit brood patch, did not support this prediction.

Finally, the temperatures of the eggs within a clutch vary greatly depending on their position (e.g. Huggins 1941, Mertens 1970 in Drent 1975, Haftorn 1983), so it is probable that even in small clutches which could be accommodated into the brood patch, the eggs are moved frequently to give them a similar amount of heat. Thus, with all the eggs being continually moved around, the pressure for a particular egg shape probably would not be very strong.

In conclusion, although the model proposed by Barta and Székely (1997) seems logical, we have found no evidence to support that egg shape affects fitness in the manner predicted by the optimal egg shape model. The possibility that the natural range of egg shape would fall within a broad optimum, and selection against shapes outside this optimum have been so severe that virtually no egg has a "wrong" shape, could not be rejected. In this case, although the model would be valid, it would be of little use to explain the observed variation in egg shape.

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Selostus: **Vaikuttaako linnunmunan muoto emojen kelpoisuuteen: tutkimus espanjalaisilla talitiaisilla ja mustarastailla**

Kirjoittajat arvioivat Bartan ja Székelyn (1997) esittämän optimaalisen munan muodon mallin soveltuvuutta selittämään talitiaisten ja mustarastaiden munan muotoa. Mallin oletusten mukaisesti, munan muodon tulisi olla optimaalinen haudonnan kannalta ja optimaalinen muoto voisi muuttua munaluvun muuttuessa. Poikkeamat optimaalisesta muodosta johtaisivat emojen kelpoisuuden alenemiseen. Kirjoittajat tutkivat munan muodon vaihtelun vaikutusta talitiaisemojen (354 pesyettä) ja mustarastasemojen (150 pesyettä) kelpoisuuteen Itä-Espanjassa. Optimaalisena munan muotoindeksinä kussakin pesyekokoluokassa käytettiin munan keskimääräistä muotoa. Tulosten mukaan: 1) keskimääräisessä munan muodossa ei ollut eroja eri pesyekokoluokkien välillä, 2) munan muoto ei vaikuttanut haudontamenestykseen (tarkasteltu muuttuja: % munista haudottu), pesimämenestykseen (% munista lentopoikasiksi) tai poikasten painoon senkään jälkeen, kun kirjoittajat kontrolloivat analyyseissään mahdolliset pesyekoon ja munan koon vaikutukset munan muotoindeksiin ja 3) munan muoto ei vaikuttanut sen haudottavuuteen pesyeen sisällä. Aineisto antaa siis viitteitä siihen, ettei munan muodolla ole vaikutusta emojen kelpoisuuteen eivätkä saadut tulokset tue optimaalisen munan muodon mallia. Tutkijat esittävät kirjoituksensa lopussa useita mahdollisia syitä siihen, miksi heidän tuloksensa eivät tukeneet Bartan ja Székelyn esittämää mallia.

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