Female condition, egg shape and hatchability: a study on the grey partridge

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Abstract

Egg features are key components of egg quality that can influence future prospects of survival. Past studies have outlined the importance of egg size, but little is known about egg shape variation, differences among females, influence of external factors on shape and the importance of shape for hatchability. In this study of the grey partridge *Perdix perdix*, we examined shape characteristics (elongation and three indices derived from photographs). There was a significant individual difference in egg shape among females, and shape was influenced by the position in the laying order, with last-laid eggs being less elongated. Egg shape indices were not influenced by food quality (experiment with two diets differing in β-carotene content), nor by an immune challenge (experiment with two groups differing in Newcastle disease virus vaccine treatment). Eggs laid by females in poorer health conditions were more asymmetric and more pointed. Egg hatchability was higher for intermediate egg elongation values.

Introduction

In oviparous animals, clutch production represents a huge investment in terms of energy and reserves allocated to eggs in a limited period of time (Nager, 2006). In avian species, it has been shown that egg mass is highly repeatable and heritable at the individual level (Christians, 2002), suggesting a strong genetic component. Environmental components, for example food availability, and health conditions of the laying female can also play a role in intra-clutch variation in mass and egg composition (Ardia *et al*., 2006).

When we consider within-clutch variation, in several species the well-known phenomenon of hatching asynchrony occurs (Magrath, 1990), and, frequently, the last-laid egg can be smaller and with fewer resources than the first-laid eggs (Lack, 1968; Sockman, 2008). Also, in precocial synchronous species, a pattern of egg size variation with laying order can exist, with either an increase, a decrease or a tendency to increase up to a threshold and to decrease thereafter (Cabezas-Diaz, Virgos & Villafuerte, 2005). Egg size can have important long-term consequences for the survival of offspring (Starck & Ricklefs, 1998; Forbes & Wiebe, 2010) because larger eggs tend to have higher hatching success (Perrins, 1996) and lead to larger hatchlings (Christians, 2002).

In such a life-history context, less attention has been paid to egg shape variability and its possible fitness consequences than to size. The egg shape is a characteristic of each species and can differ markedly within families (Lack, 1968). For all taxonomic groups investigated, egg shape becomes propor-

tionally longer as body weight increases (Olsen, Cunningham & Donnelly, 1994). Concerning the proximate cause of shape differences, developmental biologists have pointed out that egg shape could be the result of the action of the oviduct, with a balance between the expansive forces of the egg components, the resistance of the forming eggshell and the width of the oviduct (Board & Sparks, 1991). From the functional point of view, interspecific egg shape variations have been related to gas and heat exchanges (Rokitka & Rahn, 1987; Deeming & Ferguson, 2004; Mao *et al*., 2007), eggshell characteristics (thickness, pore area and shell density), optimal break out of shell before hatching (Gosler, Higham & Reynolds, 2005), pattern of turning during incubation and efficient use of the brood patch area of the incubating parent (Drent, 1975; Barta & Székely, 1997), and adaptation to avoid danger of eggs rolling off cliff (Cullen, 1957).

Several studies have found that egg morphology (length, width and elongation index) shows high within-clutch repeatability (Hendricks, 1991; Petersen, 1992; Mónus & Barta, 2005). Intraspecific shape variation has been related to local conditions or to geographical distribution changes. In New Zealand, introduced species lay eggs that are different in shape from those of their source population (Congdon & Briskie, 2010). In European populations of great tits *Parus major*, the breadth-to-length ratio was largest at medium latitudes, and eggs were more elongated toward the north and the south (Encabo *et al*., 2002). In the common cuckoo *Cuculus canorus*, the egg shape differed between two distant geographical areas (Hungary and Japan: Bán *et al*., 2011). In England, Gosler

et al. (2005) found that great tit eggs in clutches laid in low-calcium areas were more spherical than those laid in a high-calcium area. The authors suggested that because the strongest shape is a sphere, this might compensate for reduced shell thickness. Moreover, a sphere has the smallest surface area of all three-dimensional solids of a given volume; hence, spherical eggs reduce calcium investment and should therefore be advantageous.

Data on possible direct benefits of a particular egg shape are still sparse. Encabo *et al.* (2001) observed in two passerine species that egg shape did not have fitness consequences in terms of chick survival and, hence, failed to find any evidence for an optimal egg shape. On the contrary, in the turkey *Meleagris gallopavo*, hatchability was highest at intermediate egg shape elongation (Erisir & Ozbey, 2005). In the hen *Gallus domesticus*, the morphology of eggs can serve as an indicator of productivity (Mänd, Nigul & Sein, 1986). In this case, genetic selection has produced eggs that are rounded in shape (Anderson *et al.*, 2004), with an increase in shell strength (Altuntas & Sekeroglu, 2008).

Aside from the commonly used elongation and sphericity indices, other descriptors of egg shape have been proposed with the aim of capturing other characteristics of egg morphology, for instance indices derived from photographs (Mänd *et al.*, 1986; Mónus & Barta, 2005). However, up to now, the variation of these shape descriptors remains unexplored.

In this study, we measured the shape characteristics of grey partridge *Perdix perdix* eggs. Our aims were (1) to test the existence of individual female difference in egg shape; (2) to examine whether external factors (food quality, immune challenge and condition of the laying female) do affect egg shape; and (3) to verify if hatchability is related to egg elongation.

Methods

The study was conducted on grey partridges reared in 2002, 2003, 2004 and 2005 at a game breeding farm in S. Giuliano Nuovo, Alessandria, NW, Italy (Cucco *et al.*, 2006a, 2008; Garcia-Fernandez *et al.*, 2010). In total, 32 breeding pairs in 2002, 32 in 2003, 16 in 2004 and another 25 in 2005 were housed in individual outdoor reproduction cages (4 m long × 1 m wide × 0.5 m high). Throughout the year, the birds were maintained in natural light and temperature conditions, and all of them were of the same age (first year) to avoid possible age effects. Each pair had food and water available *ad libitum*.

When females started laying, all pens were inspected daily to collect eggs. Using a nontoxic marker pen, we marked each egg with the female's code, the position in the laying order and the date of laying. Just after collection, we measured the egg length (L) and breadth (B) with callipers (0.05 mm accuracy) and we weighed the eggs with an electronic balance (± 0.01 g accuracy). From April to June, each female laid a mean of 33.1 eggs, yielding a total of 3476 eggs over the 4 years.

Most of the eggs laid were incubated for 26 days in a commercial incubator at 37.5°C and 60% humidity, while 345 eggs (100 in 2002, 169 in 2003 and 267 in 2005) were brought
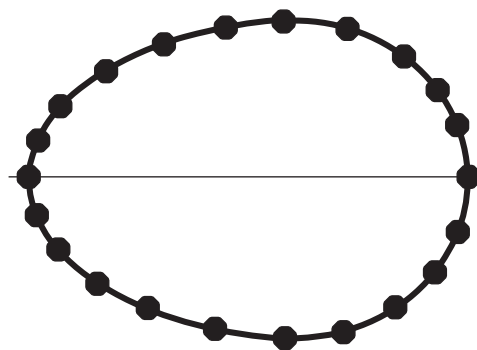

Figure 1 Landmark points along the edge used to calculate egg's morphological parameters, following Mónus & Barta (2005).

to the laboratory for chemical analyses and were analyzed for concurrent studies (Cucco *et al.*, 2006b, 2009).

At the beginning of the laying period, we measured female body mass (1 g accuracy) and blood erythrosedimentation (ES) rate to check whether these were related to egg shape characteristics. Blood was drawn from the brachial vein into 75-mm heparinized capillary tubes to measure the ES rate. The ES rate is diagnostic of many acute and chronic diseases, including infections and rheumatic and inflammatory diseases (Merilä & Svensson, 1995). The ES rate was measured as the ratio between the length of the capillary tube not occupied by blood cells and the total length, after the capillaries stood vertically for 4 h in a refrigerator at 4°C (Cucco *et al.*, 2006b).

In the first three years (2002, 2003 and 2004), egg photographs were not obtained. In this case, we used the L and B measurements taken by callipers in the field to calculate the elongation index L/B.

In 2005, egg shape was assessed by measuring egg's descriptors taken from a photographic image. Following the methods of Mänd *et al.* (1986) and Bridge *et al.* (2007), photographs were taken with a digital camera (Nikon Coolpix 990, Tokyo, Japan) mounted on a custom-built, plywood stand that held the egg and camera in place. The base surface was painted black to increase contrast. A graph paper scale was placed near the egg to use as calibration length when converting pixel-based dimensions into metric units. To compute egg's parameters, we used the image processing software ImageJ (Rasband, 1997–2006).

We applied the method developed by Barta & Székely (1997) and Mónus & Barta (2005) for measuring egg shape parameters from digital pictures based on a circle transformation technique (Todd & Smart, 1984). We marked 22 points around the outline of the egg: two points on the two opposite tips of the eggs, which determined the longitudinal axis of eggs, and 20 roughly equally distributed points along each of the two edges of the shape (Fig. 1). We fitted second-order polynomials to the coordinates of the mark points and used three parameters of the polynomial to describe egg shape (Bán *et al.*, 2011). The first (c_0) parameter is the compression ratio relative to a circle (sphericity): the smaller the c_0, the more elongated the egg. The other two parameters describe the level

Table 1 Egg mass, egg shape characteristics and statistical differences among laying females in the grey partridge *Perdix perdix*

Variable	Values		ANOVA		
	Mean ± SD	CV	F	d.f.	P
Egg mass 2002	14.60 ± 0.89	6.13	63.9	31,1006	0.001***
Egg mass 2003	14.14 ± 0.98	6.96	56.8	31,1003	0.001***
Egg mass 2004	13.14 ± 1.06	8.03	34.4	15,528	0.001***
Egg mass 2005	13.75 ± 0.91	6.58	69.6	24,831	0.001***
Elongation 2002	1.31 ± 0.05	3.77	12.7	31,1007	0.001***
Elongation 2003	1.33 ± 0.07	5.31	24.5	31,1003	0.001***
Elongation 2004	1.33 ± 0.05	3.47	31.1	15,528	0.001***
Elongation 2005	1.43 ± 0.07	5.15	22.6	24,830	0.001***
c0 shape index 2005	0.745 ± 0.036	4.87	6.79	21,173	0.001***
c1 shape index 2005	0.142 ± 0.027	18.82	8.22	21,173	0.001***
c2 shape index 2005	−0.013 ± 0.039	−308.87	3.39	21,173	0.001***

ANOVA, analysis of variance; CV, coefficient of variation; d.f., degrees of freedom; ***, $P < 0.001$.

of asymmetry of the eggs (*c1*: larger value means more asymmetric egg) and roundness of the tips (*c2*: larger value means more blunted tips). The three parameters were highly repeatable within individual eggs, as determined by measuring 12 eggs twice (intra-class coefficient; $c0$: $F_{11,12} = 1474.8$, $r = 0.984$, $P < 0.001$; $c1$: $F_{11,12} = 201.5$, $r = 0.893$, $P < 0.001$; $c2$: $F_{11,24} = 125.5$, $r = 0.838$, $P < 0.001$).

Experimental groups and statistics

In 2002 and 2003, the breeding partridges were randomly assigned to two groups differing in the content of β-carotene in the food, i.e. a rich diet and a poor diet (details in Cucco *et al.*, 2007). In brief, the birds were assigned to two groups raised with different food: the low-carotene group was fed with a standard partridge diet of cereal pellet plus 2.7 mg kg^{-1} of β-carotene, while the high-carotene group received the same standard food plus 27 mg kg^{-1} of β-carotene. The high β-carotene level was chosen to match the values usually provided in Italian grey partridge breeding farms (near the highest value used in poultry, NRC 1994). The low β-carotene level was one-tenth of the β + amount, nearly equal to the minimum nutrient requirement reported by NRC (1994). We chose β-carotene because of its known effect on egg content (Tengerdy, Lacetera & Nockels, 1990; Haq, Bailey & Chinnah, 1995; Cucco *et al.*, 2007).

In 2005, the breeding partridges were randomly assigned to two groups differing in immune challenge, i.e. a vaccinated group and a control group (details in Cucco, Pellegrino & Malacarne, 2010). In brief, females were immunized orally with Newcastle disease virus live vaccine (Bio-Vac NDV 1000 doses made by Fatro in Ozzano Emilia, Italy) in accordance with the procedure of Kiss *et al.* (2003). In 2004, breeding females were not subjected to experimental treatments.

We analyzed egg characteristics using linear mixed models with egg mass and the egg shape descriptors as dependent variables. Among-female variation was controlled by including female identity as a random effect. The independent factors included the diet treatment in the 2002 and 2003 dataset, and the vaccine treatment in the 2005 dataset. The

possible effect of female condition was tested by inserting their mass and blood ES rate in the models as covariates. The effect of egg position in the laying order was tested by inserting laying order as a covariate. In all the models, we included only the eggs with an intermediate position in the laying order (4th–20th). We excluded the first-laid (1st–3rd) and last-laid eggs (>20th) because it is known that the first-laid eggs are usually of low quality (grey partridge usually lay two or three eggs in different places before choosing the exact location of the nest: Cramp & Simmons, 1980; Potts, 1986; Aufradet, 1996) and the eggs laid after the 20th are out of the range occurring in natural conditions (del Hoyo, Elliott & Sargatal, 1994).

Initially, we entered simultaneously all variables in the mixed models. Afterward, we used a stepwise backward procedure of selection of independent variables by eliminating, at each step, the variable that had the smallest predictive power. The stepwise backward procedure led to a final model containing only the variables reaching the 0.05 level of significance.

We used a logistic regression model to determine if any of these variables (clutch, egg mass, position in the laying order, elongation and elongation^2) predicted which eggs would hatch. Elongation was inserted both as a linear and a quadratic term to allow a U-shaped pattern of variation. The analyses used the dataset of 2002, 2003 and 2004, when egg photographs were not available and only elongation and sphericity could be calculated. The dataset of 2005 could not be used in this analysis because the incubator suffered an electric power problem that caused a severe decrease in hatching rate.

Results

There were statistically significant differences in egg mass and egg shape descriptors in relation to female identity, i.e. each female laid eggs that differed in mass and shape from other females (Table 1; all eggs laid by each female were included).

We found a small variation in egg mass [coefficient of variation (CV) = 6.1–8.0%] and the *c0* and *c1* shape descriptors.

Table 2 Multivariate mixed-model analysis of egg mass and egg shape indices, with vaccine as factor, and female mass, erythrosedimentation rate and position in the laying order of the focal egg as covariates. Year 2005

Variable*	Complete model		Coefficient (SE)	Stepwise model	
	F	P		F	P
Egg mass ($n = 380$)					
Vaccine	3.921	**0.048**	−0.677 (0.342)	4.130	**0.043**
Female mass	0.285	0.59	0.004 (0.008)	–	–
Erythrosedimentation	0.149	0.70	0.515 (1.333)	–	–
Position laying order	2.189	0.14	0.007 (0.005)	–	–
Elongation ($n = 380$)					
Vaccine	0.012	0.91	0.002 (0.022)	–	–
Female mass	1.058	0.30	0.001 (0.001)	–	–
Erythrosedimentation	2.474	0.12	0.136 (0.086)	–	–
Position laying order	1.237	0.27	−0.001 (0.001)	–	–
Egg mass	1.406	0.24	0.006 (0.005)	–	–
$c0$ shape index ($n = 125$)					
Vaccine	0.753	0.39	0.010 (0.011)	–	–
Female mass	1.522	0.22	0.001 (0.001)	–	–
Erythrosedimentation	7.556	**0.007**	−0.116 (0.042)	6.149	**0.015**
Position laying order	1.670	0.20	0.001 (0.001)	–	–
Egg mass	6.835	**0.01**	0.013 (0.005)	5.236	**0.024**
$c1$ shape index ($n = 125$)					
Vaccine	2.686	0.10	−0.014 (0.008)	–	–
Female mass	0.029	0.87	0.001 (0.001)	–	–
Erythrosedimentation	8.664	**0.004**	0.094 (0.032)	5.826	**0.018**
Position laying order	0.059	0.81	0.001 (0.001)	–	–
Egg mass	4.780	**0.031**	−0.008 (0.003)	–	–
$c2$ shape index ($n = 125$)					
Vaccine	0.056	0.81	0.002 (0.009)	–	–
Female mass	0.356	0.55	0.001 (0.001)	–	–
Erythrosedimentation	1.731	0.19	−0.046 (0.035)	–	–
Position laying order	1.084	0.30	0.001 (0.001)	–	–
Egg mass	1.317	0.25	0.006 (0.005)	–	–

*In the models, the female identity was inserted as a random factor.

However, a high variation was observed for the $c2$ index (Table 1).

Influence of female condition and laying order

Table 2 shows the results of linear mixed models with egg mass and egg shape descriptors as dependent variables. The analyses used the dataset of 2005, when egg photographs were available and computation of all shape indicators was possible.

Egg mass was related only to vaccination, with a significant difference between eggs laid by vaccinated females (13.46 g ± 0.035 SE) and eggs laid by control females (14.10 g ± 0.036 SE).

Elongation and the $c2$ index were not significantly related to any independent variable. The $c0$ and $c1$ indices were significantly related to female's ES rate (Table 2). In particular, females in worse condition (higher ES rate) laid eggs with lower $c0$ values, while the $c1$ index increased (Fig. 2).

Tables 3 and 4 show the results of linear mixed models with egg mass and egg elongation as dependent variables. The analyses used the dataset of 2002, 2003 and 2004, when egg photographs were not available and only elongation
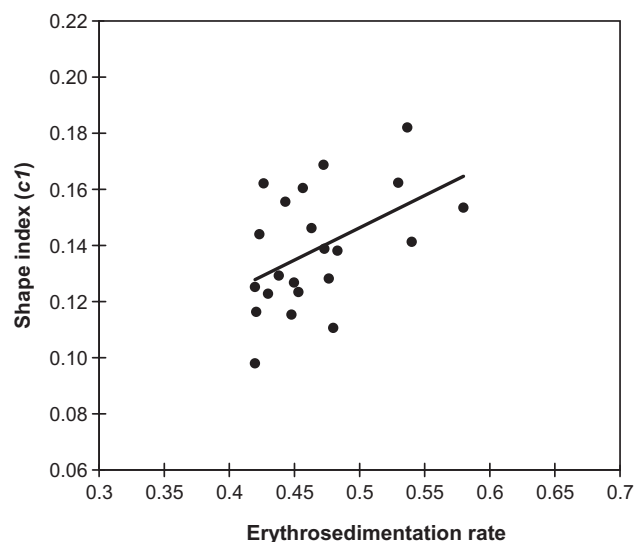

Figure 2 Mean $c1$ index of eggs in relation to erythrosedimentation rate of laying female. Larger $c1$ value means more pointed egg. Erythrosedimentation rate is the ratio between the length of the capillary tube not occupied by blood cells and the total length.

Table 3 Multivariate mixed-model analysis of egg mass and elongation, with nutrition as factor, and female mass, erythrosedimentation rate and position in the laying order of the focal egg as covariates. Years 2002–2003

| Variable	Complete model			Stepwise model	
	F	P	Coefficient (SE)	F	P
Egg mass (n = 969)					
Nutrition	0.661	0.42	0.169 (0.208)	–	–
Year	0.243	0.62	0.199 (0.403)	–	–
Female mass	1.029	0.31	0.004 (0.004)	–	–
Erythrosedimentation	0.370	0.54	−0.589 (0.968)	4.680	**0.031**
Position laying order	5.056	**0.025**	−0.007 (0.003)	5.120	**0.024**
Elongation (n = 968)					
Nutrition	2.456	0.12	0.015 (0.010)	–	–
Year	0.864	0.35	0.017 (0.018)	–	–
Female mass	3.591	0.06	0.001 (0.001)	–	–
Erythrosedimentation	0.10	0.74	−0.015 (0.044)	–	–
Position laying order	25.129	**0.001**	−0.002 (0.001)	26.179	**0.001**
Egg mass	1.440	0.20	0.003 (0.003)	–	–

Table 4 Multivariate mixed-model analysis of egg mass and elongation, with female mass, erythrosedimentation rate and position in the laying order of the focal egg as covariates. Year 2004

Variable	Complete model			Stepwise model	
	F	P	Coefficient (SE)	F	P
Egg mass (n = 240)					
Female mass	0.184	0.67	−0.003 (0.008)	–	–
Erythrosedimentation	1.951	0.16	3.975 (2.845)	–	–
Position laying order	7.208	**0.008**	−0.023 (0.009)	7.736	**0.006**
Elongation (n = 240)					
Female mass	7.720	**0.006**	−0.001 (0.001)	7.083	**0.008**
Erythrosedimentation	0.003	0.96	0.006 (0.114)	–	–
Position laying order	0.474	0.49	0.001 (0.001)	–	–
Egg mass	3.146	0.08	0.005 (0.003)	–	–

could be calculated. The hen nutrition did not influence egg mass and shape (Table 3). In contrast with the dataset of 2005, there was a difference related to the position in the laying order, with a progressive decrease in egg mass and elongation. The negative relationship between egg mass and position in the laying order was also found in 2004 (Table 4). A mixed-model analysis combining data from all four study years confirmed that elongation was related to laying order (mixed model with elongation as dependent variable, year as a fixed effect, female mass, ES rate and position in the laying order as covariates, and female identity as a random effect: $F_{1,1483} = 4.359$, $P < 0.001$, coefficient = −0.003 ± 0.001 SE). This negative relationship between elongation and position in the laying order occurred along the laying sequence of eggs 4–20 (Fig. 3). The eggs excluded from the analysis (first three eggs and eggs beyond number 20) showed an increasing dispersion of elongation values.

Relationship between shape and hatchability

Logistic regression indicated that egg elongation and position in the laying order significantly contribute to the model
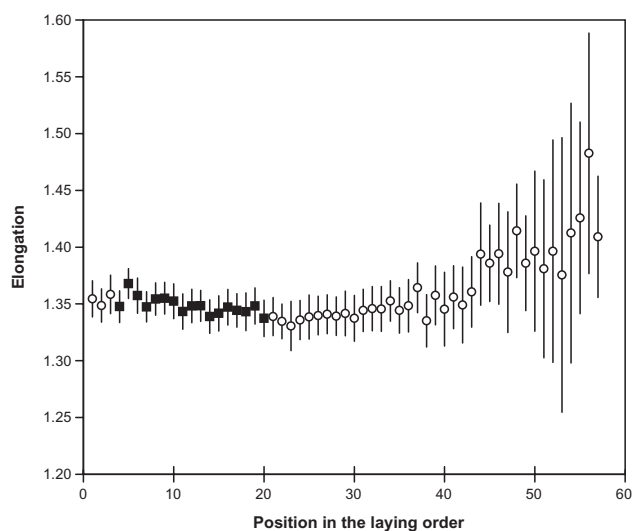
Figure 3 Elongation (length/breadth) of eggs along the laying sequence. Black squares: eggs (4–20) included in the multivariate analyses; open circles: eggs not included in the multivariate analyses.
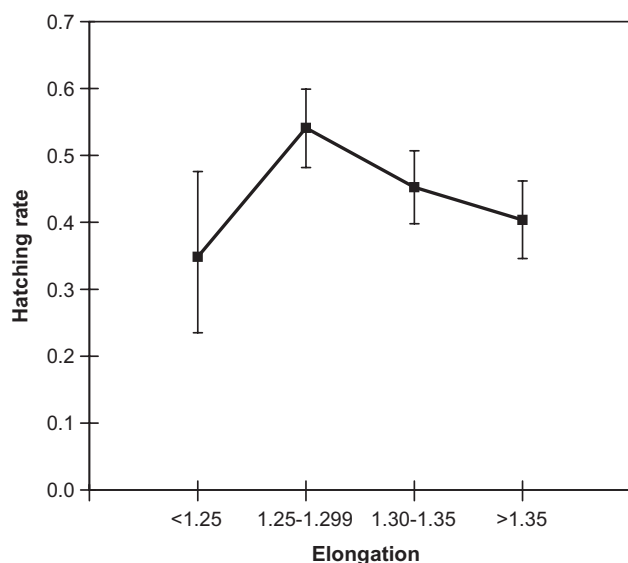
Figure 4 Relationship between hatchability and egg elongation (length/breadth).

Table 5 Logistic regression analysis of hatching success in relation to egg laying order, egg mass, position in the laying order and egg elongation

	Coefficient (SE)	Wald	P
Constant	−86.266 (53.48)	2.602	0.11
Egg mass	0.170 (0.137)	1.553	0.21
Elongation	130.646 (47.93)	7.431	**0.006****
Elongation × Elongation	−51.279 (18.17)	7.969	**0.005****
Position laying order	−0.036 (0.015)	5.655	**0.02***

Overall predictive success = 59.4% (n = 980).
Naglekerke's R^2 = 0.246; *, $P < 0.05$; **, $P < 0.01$.

predicting hatching success (Table 5; Naglekerke R^2 = 0.246; 2 log likelihood = 204.7; 59.4% of the cases correctly classified). The negative quadratic coefficient determines an inverse U-shaped pattern of variation (Fig. 4), with higher hatchability for the intermediate egg elongations (index = 1.250–1.299).

Discussion

In this study, the application of multiple egg shape descriptors in the grey partridge can help enhance the knowledge of the significance of external egg morphology variation. The most important findings were that hatching success was higher with intermediate egg elongation, and that egg shape characteristics can be influenced by female condition.

Eggs laid by each female were very similar in mass, elongation and the $c0$ shape descriptor, while there was a higher variation in the other egg shape indices. The low variation coefficient of elongation was in line with the previous data on ducks (Petersen, 1992), shorebirds (Thomas, Thompson & Galbraith, 1989), galliforms (Kul & Seker, 2004) and passe-

rines (Tryjanowski *et al.*, 2001; Surmacki, Stepniewski & Zduniak, 2003; Mónus & Barta, 2005). Little is known about the variability of the other shape descriptors, but our results are similar to those reported in the tree sparrow *Passer montanus*, where there was also a low variability of egg descriptors (Mónus & Barta, 2005).

In our study, shape was influenced by position in the laying order, with last-laid eggs being less elongated. This trend was accompanied by a decrease in egg mass; hence, the last-laid eggs were both lighter and more spherical. It is noticeable that the variation in egg shape with laying order has been little studied, even though the variation in egg mass has been the subject of several previous studies (Christians, 2002), and patterns of favoritism or cainism toward young that hatch from last-laid or from smaller eggs have been considered in detail for the discussion of the phenomenon of hatching asynchrony (Magrath, 1990). The decrease in egg mass observed in our species is similar to that reported in the red-legged partridge *Alectoris rufa* (Cabezas-Diaz *et al.*, 2005) and in several other bird species (Lack, 1968).

With reference to shape, a seasonal reduction in egg length but not mass, implying a change of shape, was reported in the greater rhea (Fernandez & Reboreda, 2008). In the least flycatcher *Empidonax minimus*, egg volume increased with laying sequence, but egg elongation was similar along the laying sequence (Briskie & Sealy, 1990). A negative correlation between egg weight and shape sphericity index has been reported in the Japanese quail *Coturnix coturnix japonica* (Kul & Seker, 2004) and in hens (Poyraz, 1989), and in the coot *Fulica atra*, egg length increased much faster than the breath with increasing egg mass (Uzun, Uzun & Kopij, 2010). In the hooded crow *Corvus corone cornix*, there were differences in egg shape in relation to clutch size, with more spherical eggs in two-egg clutches and progressively more elongated eggs toward six-egg clutches (Dolenec, 2006).

In our species, egg elongation index was not influenced by food quality (experiment with two diets differing in β-carotene content), nor there was a significant effect of an immune challenge (experiment with two groups differing in NDV vaccine treatment). More interestingly, we found a significant relationship between some shape indices and female health condition. The $c1$ index increased, while the $c0$ index decreased, in eggs laid by females with higher ES rates. Hence, females in poorer health condition laid sharper eggs. The absence of effects on elongation index is in line with those reported for the starling (*Sturnus vulgaris*; Dolenec *et al.*, 2008), where no correlation was found between female condition (body mass/wing length) and egg elongation. To the best of our knowledge, no data are available for other shape indices. It is conceivable that these traits have been undervalued in avian studies. It should be noted that recent work showed that female condition can influence external egg characteristics, such as egg shell pigmentation, as females in better body condition laid more colorful eggs (Moreno & Osorno, 2003; Siefferman, Navara & Hill, 2006) and/or eggs with better distribution of pigment spots (Sanz & Garcia-Navas, 2009; Martinez-Padilla *et al.*, 2010).

To better evaluate the meaning of intraspecific egg shape variation, it is important to know whether shape has fitness consequence in terms of egg hatchability and future chick survival. In our study, eggs with higher or lower elongation hatched at a lower rate. Our result is in accord with the findings in the turkey, where hatchability was highest in intermediate egg shape elongation (Erisir & Ozbey, 2005). In contrast, in the great tit and the blackbird *Turdus merula* (Encabo *et al.*, 2001), egg shape did not have fitness consequences in terms of chick survival; hence, these authors suggested that there was no evidence for an optimal egg shape. In the Japanese quail, there is evidence both against (Copur, Baylan & Canogullari, 2010) and in favor (Baspinar *et al.*, 1997) of a correlation between shape and hatchability. In some studies, even if shape index is not specifically tested against hatchability or survival, there are indications that the morphology of eggs can serve as an indicator of productivity (Mänd *et al.*, 1986), and shapes with extreme values have detrimental effects on hatching rate. In the domestic fowl, a negative correlation between shape index (sphericity) and shell deformation has been reported (Mašić *et al.*, 1972). In the rock partridge, more spherical eggs hatched less (Özbey & Esen, 2007), and in the Muscovy duck *Cairina moschata* breeding farms, the eggs with ducklings that required assistance in hatching were more rounded (Harun, Veeneklaas & Van Kampen, 2001).

Our and most other studies have taken the opportunity to analyze a large number of eggs offered by the conditions of captivity. In general, artificial incubation cannot duplicate the success of incubation by the parent (Eycleshymer, 1907; Klimstra *et al.*, 2009), although no data are available on possible effects of artificial incubation on egg shape.

In conclusion, although models of optimal egg shape have been proposed (Barta & Székely, 1997; Encabo *et al.*, 2001; see also Hutchinson 2000 for a discussion on using two-dimensional analysis), few studies have investigated this argument (Encabo *et al.*, 2001). More data are needed because available research gives conflicting evidence of support for the idea that egg shape may affect fitness. As the simpler shape index (elongation) seems to be less informative (Mónus & Barta, 2005) and oomorphology can now be easily quantified from digital photographs (Mänd *et al.*, 1986; Bridge *et al.*, 2007; Bán *et al.*, 2011), future studies considering other shape indices are likely to shed light on this trait of bird reproduction.

Acknowledgments

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