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Research Paper

Clues and cues in a Japanese quail egg: What individual variable parameters can be used to identify the hen that laid it?

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ABSTRACT

Variability in eggs laid by the same bird is well known but remarkably understudied. Ecological, physiological and genetic mechanisms clearly play a role; however, the reasons for the high/low variability of some parameters remain a mystery. Here, with the aim of identifying a wider range of data for analysis of their individual variability, the variability of several egg parameters in F_2 Japanese quail (*Coturnix japonica*) hens was studied. The highest variability was noted for the parameters of shell strength (21.4–27.1%), suggesting its unsuitability as an identifier of a single hen. The highest reproducibility (i.e., the lowest variability of 1.5%) was observed for the ratio of egg surface area to volume (S/V). This indicator can indirectly characterise the level of embryonic metabolism and be used as an adaptive feature of the hen body targeted towards maintaining the stability of the S/V value. Excessive formation of the yolk component leads to an "adjustment" of the shell, ensuring low variability of the total egg weight. These findings can be taken into account to advance our understanding of the ecological, physiological, and genetic underpinnings for developing promising intraclutch "signatures" of quail egg production. It could find application in the field of preincubation egg sorting, with artificial intelligence (AI)-assisted classification of individually identified eggs to tailored incubation regimes. Moreover, given that the S/V value is also related to egg contents parameters, identifying laying hens by this feature might allow breeders to categorise separate groups of females, each of which lay eggs of identified nutritional value.

Nomenclature

Abbreviations	
AI	Artificial intelligence
DL	Deep learning
ML	Machine learning
Symbols	
B	Egg maximum breadth (cm)
D	Egg density (W/V) (g cm^{-3})
D_p	Egg diameter at the distance of $L/4$ from the pointed end (cm)
F	Shell strength (kg)
L	Egg length (cm)
S	Egg surface area (cm^2)
T	Shell thickness (cm)
V	Egg volume (cm^3)
w	Variable that conforms to a distance between two vertical axes, one of which coincides with B and the other one transects the egg at the point of $L/2$ (cm)
W	Egg weight (g)
W_s	Egg shell weight (g)
W_y	Egg yolk weight (g)
Greek symbols	
δ_{max}	Shell maximum deformation at failure (mm)

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1. Introduction

A bird's egg is a unique structure providing all necessary needs for the developing embryo to form a fully-fledged chick. Due to physiological, genetic and adaptive features and mechanisms, birds have developed a certain species-specific "standard" for the formation of particular egg parameters. Such a "standard", however, has intraspecific differences, that may be habitat-unique. Thus, for an oologist, it is relatively easy to link a specific egg to the particular species of the laying hen. Also, geometric, shell colouration and/or morphological features of the egg can provide the necessary information when solving issues of evolutionary ecology, taxonomy, phylogeny and physiology of birds (e.g., Mityay et al., 2015; Mityay & Matsyura, 2014; Montgomerie et al., 2021; Stevens, 2013; Stoddard et al., 2017, 2019). On the other hand, the issue of intraspecific identification of the egg (i.e., which particular hen laid it) has been studied somewhat superficially. Indeed, the eggs are typically of a similar size, colour and geometric shape. The question thus arises of whether there are certain features that a specific hen's body incorporates into the structure of the egg being laid and that are "signatures" of that particular mother.

Studies conducted historically amongst poultry species have mainly aimed at identifying a certain group of layers combined with certain parameters, such as breed (Sokołowicz et al., 2019), bird weight (Lacin et al., 2008), genetic characteristics (Yang et al., 2023), age (Kraus et al., 2020), housing conditions (Oke et al., 2014) and some others. In any event, individual recording and analysis of egg parameters from a specific layer are generally not involved in these studies.

Investigations in wild avian species have been more fruitful as some have allowed for precise identification of a specific mother bird and measurement of a number of egg parameters within a single clutch. Sometimes it is possible to perform such measurements over several years. For instance, Petersen (1992) assessed the intraspecific (conspecific) brood parasitism and individual intraclutch characteristics among the emperor geese (*Chen canagicus*) eggs over five years and concluded that a female lays eggs of the same shape. In studying the shape criteria, Petersen (1992) went on to use a set of different geometric indices, among which the ratio of the egg maximum breadth (B) to its length (L) or its inverse form (L/B) had the highest reproducibility. According to that study, this featured individual characteristic of the goose can be associated with the identification of conspecific parasitic eggs laid in her nest by other females. That is, it is assumed that this ratio (B/L), which received its name more than 100 years ago as the *shape index* (Dunn & Schneider, 1923), is so individual that the goose can easily distinguish an alien egg within her nest. At the same time, it is extremely difficult for a conspecific parasitic female to readjust her egg formation system to suit the egg shape of her neighbouring nest hosts. In the case of interspecific (heterospecific) parasitic egg laying, negative frequency dependence has been proposed to play a significant role in developing host counter-adaptations to brood parasitism, since cuckoos and their hosts are also subject to intense coevolutionary dynamics (first of all, in terms of egg appearance), which are frequently compared to arms-races (Dall, 2006). In addition, other studies (as reviewed by Shizuka & Lyon, 2011) established that there seems to be natural selection in hosts of avian brood parasites, such that the information they use to identify their own eggs is more reliable. This requires a respective evolutionary adaptation when mothers, in effect, "sign" their eggs using certain visually identifiable characteristics (Dall, 2006). On the other hand, when liberated from the fear of rearing the offspring of diederik cuckoos (*Chrsococcyx caprius*) that imitate host eggs, African village weaver birds (*Ploceus cucullatus*) exhibit reduced individuality in this aspect of their eggs (Dall, 2006; Lahti, 2005).

The reproducibility of egg shape nuances was also confirmed by Mónus and Barta (2005) who studied the eggs of the tree sparrow (*Passer montanus*). The authors paid closer attention to shape criteria, proposing a method for their assessment by calculating the coefficients included in the mathematical model describing the egg shape proposed by Preston (1953). The authors focused most of their studies on the methodical approach to assessing the egg geometry adequately. However, in the discussion they also paid due attention to the assumptions of Petersen (1992) about the possible adaptation of the bird to the formation of eggs with a unique size ratio for recognising parasitic eggs. These authors also suggested that the observed variability of the measured egg parameters in their studies is precisely due to the possible inclusion of eggs laid by parasitic species in the experimental sample. It is feasible that the bird's ability to form eggs that are similar in size dimensions and/or their ratios helps to identify alien objects, but this fact appears to be secondary. The results of the research by Montgomerie et al. (2021) enabled the authors to conclude that egg size is determined by the peculiarities of the internal structure of the bird, in particular its oviduct, body structure and pelvic anatomy, as well as the locomotor component.

Another individual characteristic of the mother bird that is reflected in the laid egg is considered by many authors to be the pigmentation of the eggshell (e.g., Wisocki et al., 2020). According to a study on Japanese quail (*Coturnix japonica*) camouflage (Lovell et al., 2013; Stevens, 2013), individual birds in the wild can recognise the appearance of their own eggs and choose an appropriate nest background that will best conceal them. Lovell et al. (2013) stated that "*quail 'know' their individual egg patterning.*" It was demonstrated that Japanese quails vary greatly in the shape, size, colour and maculation patterns of their eggs between females, but very little within them (Pike, 2011). Undoubtedly, the unique colouration of the eggs helps the female to identify and "neutralise" the eggs of parasitic species, despite their mimicry skills (Brooke & Davies, 1988; Stoddard & Stevens, 2010, 2011). However, the distinctive eggshell colouration is due exclusively to the physiological features of the female uterus, although "*the precise mechanism responsible for the elaborate patterns on bird eggs remains mysterious*" (Stoddard, 2022).

Thus, it can be inferred that the identification of the bird that laid a particular egg can be carried out by the ratio of its sizes, mainly L and B, or by the unique shell colouration/pattern, if, of course, the egg has some pigmentation. Herewith, the genetically transmitted egg features can be assumed to be not only of an adaptive nature, but also depend entirely on the internal structure and physiological characteristics of the female.

Summarising the results of previous studies, the most convenient parameters, easily measured and effective, in terms of interrelation with other indicators, are indices, in other words, ratios of different geometric sizes of eggs. Accordingly, we decided to focus on revisiting the possibility of their use for carrying out the current studies. Perhaps, the earliest and most widely used indicator served as a geometric characteristic of an egg is the above mentioned shape index (B/L). However, the features of the egg shape cannot be reduced only to such "truncated" descriptors as the ratio of just egg breadth and length. In this regard, a number of authors have tried to expand the list of these indices. Preston (1968, 1969) published the most straightforward and reasonable ones: egg asymmetry, or the degree to which one end is greater than the other; and bicone, ascertained by measuring the radius of curvature at the blunt and pointed ends. In subsequent studies, geometric indices were complemented, for instance, by the pointedness index (Troscianko, 2014) or the conicity index (Hays et al., 2020; Hays & Hauber, 2018; Narushin, 2001). Additionally, the formulae used to calculate them were changed or marginally altered (Mänd et al., 1986; Montgomerie et al., 2021; Mytiai & Matsyura, 2017). Narushin et al. (2024c) came to the conclusion that the shape index (B/L), the displacement (or asymmetry) index (w/L), and the conicity index (D_p/B) are the three primary geometric indices that best describe the egg profile. In two latter indices, w is the parameter that displays the separation between two vertical lines representing the egg's maximum breadth (B) and half length ($L/2$), while D_p is the egg's diameter at a location that is $L/4$ away from the pointed end.

As part of an ongoing project to study the physiological, genetic and ecological bases for determining promising phenotypes of egg production in Japanese quails, the list of examined egg parameters and indices was expanded to the maximum extent possible. The goal of this investigation was thus to identify and analyse individual variability in a wider range of data for eggs produced by single hens using these egg parameters and indices. This may serve as an impetus for alternative hypotheses about the relationship between the hen and the egg formed by it as an embryo "capsule", as well as a deeper understanding of the physiological, genetic and ecological mechanisms of egg formation.

Recently, engineering mechanisms serving various biological and agricultural systems have begun to actively use the unique features of artificial intelligence (AI), its deep learning (DL) and machine learning (ML) technologies. In particular, these include engineering solutions related to the recognition of various objects (e.g., Zhang, 2024). In this regard, a deeper understanding of the physiological features of the geometric and physical parameters of eggs, and, in particular, their interrelationship, will improve the efficiency of DL and ML, which will enable AI to perform technological operations both in poultry industry and in the implementation of various research programs for the study of bird eggs (Narushin et al., 2025). Therefore, the long-term goal of these studies is to find egg parameters suitable for measurements and the possibilities of further use of AI, which would be effective markers for identifying the biological chain from egg laying to the results of hatching embryo development.

2. Materials and methods

2.1. Experimental model and subject details

One of the factors limiting the conduct of the given studies is the ethical regulation of destructive methods when assessing the parameters of eggs of wild species. In this regard, it is advisable to carry out such experiments using domestic bird eggs, which, moreover, can be used unfertilised. Since, among other parameters, we were also interested in the shell pigmentation, we executed the experiment on quail eggs, the only poultry species that is distinguished by a wide range of colouration in its eggs. For this purpose, 166 eggs from seventeen 11-month-old female quails that were collected over 18 days. The birds came from an F_2 model resource population that was created by the interbreeding of layer (Japanese) and meat-type (Texas) breeds (Narushin et al., 2024a, 2024b, 2024f, 2024g; Volkova et al., 2023, 2024).

2.2. Egg measurements and calculations

Electronic scales were used to weigh (W) each egg precisely to within 0.01 g. The length (L) and maximum breadth (B) of the egg were measured using a calliper, with the precision of 0.1 mm. Every egg was photographed (according to Narushin et al., 2020a). Using egg photos and Microsoft Picture Manager software, the L and B values, along with the distance w for the B axis deviation from the egg centre (Narushin et al., 2020b) and the egg diameter (D_p) at the distance of $L/4$ from the pointed end (Narushin et al., 2021, 2023), were identified with an accuracy of 1 pixel. The geometric parameters B, w and D_p were translated to the metric system of measurement after it was determined how big L was in millimetres and pixels, respectively.

The following universal equations were used to compute the egg volume (V) and surface area (S) (Narushin et al., 2024b):

$$V = \frac{\pi}{128}\left[\left(8.917 - 29.998\frac{w}{L}\right)\left(\frac{D_p}{B}\right)^2 + \left(2.459 + 88.647\frac{w}{L}\right)\frac{D_p}{B} - 36.26\frac{w}{L} + 12.453\right]LB^2 \quad (1)$$

$$S = \pi BL\left(0.389 + 0.188\frac{B}{L} - 0.063\frac{w}{L} + 0.365\frac{D_p}{B} + 0.114\frac{D_p}{L} - 0.168\frac{w}{L}\cdot\frac{B}{L} + 0.46\frac{w}{L}\cdot\frac{D_p}{B} + 0.484\frac{w}{L}\cdot\frac{D_p}{L}\right), \quad (2)$$

where V is measured in cm^3, S in cm^2, and other geometric variables are expressed in cm.

There is a fairly wide range of alternative equations for calculating V and S of bird eggs, many of which have been summarised in the relevant reviews (e.g., Narushin, 1997; Narushin et al., 2025). However, Eqns (1) and (2) were chosen because (i) when deriving them, the authors (Narushin et al., 2024b) used a universal formula (Narushin et al., 2023) that accurately describes all the geometric nuances of the egg profile and, moreover, has been tested in experiments, including the description of various shapes of quail eggs (Narushin et al., 2024a); (ii) these formulae (Eqns (1) and (2)) contain a set of indices (B/L, w/L and D_p/B) that can be very informative in describing the geometry of egg profiles; and (iii) when deriving (Eqns (1) and (2)), the authors (Narushin et al., 2024b) used a test of their adequacy using a sample of quail eggs from F_2 progenies of a Japanese and Texas breed cross, whose eggs were also used in this experiment.

These formulae were previously generated, and their suitability was evaluated using quail eggs, among other species (Narushin et al., 2024b). The ratio of W to V was used to compute the egg density (D).

Shell strength (F) and the degree of its maximum deflection at failure (δ_{max}) were measured with an accuracy of 0.001 kg and 0.01 mm, respectively, using the Egg Quality Testing System measurement complex (Stable Micro Systems, Godalming, Surrey, UK).

A broken egg's shell was carefully washed from the insides without removing the subshell membrane. After a 24-h air drying period, it was weighed (W_s) with a precision of 0.01 g. Shell thickness (T) was measured using a micrometre that was part of the Egg Quality Testing System (Stable Micro Systems), with the three measuring points being close to the egg equator, at the pointed and blunt ends. The value was then averaged. The yolk was carefully separated from the albumen and weighed (W_y) with an accuracy of 0.01 g. The similarity of egg pigmentation was assessed visually by analysing the main colour of the shell pigment, as well as the location and size of spots (if present) along the surface.

2.3. Variability assessment

As a statistical assessment in such studies, other authors (e.g., Mónus & Barta, 2005; Petersen, 1992) used the *repeatability index*, referring to the calculation method presented in detail in the work of Lessels and Boag (1987). However, despite the fact that the name of this index is logical for the purposes of the described studies, its physical essence does not meet the conditions of the present experiment. Lessels and Boag (1987), revealing the essence of this statistical parameter in their work, clearly made it clear that for its calculation it is necessary to have both within-group and among-group variances. Perhaps, such an approach is relevant when it is possible to evaluate the eggs of individual laying hens, for example, by years. In the current study, we had the results of measurements of eggs laid by individuals over a certain short period of time. That is, the assessment was carried out only within individual and unrelated clutches. In this case, one can focus on variations of the measured parameters around the mean, i.e., the ratio of the standard deviation to the mean value multiplied by 100%. For instance, such an approach was used in similar studies by Arnold (1991).

2.4. Statistical tests

The data was processed using a number of relevant statistical and mathematical techniques that are available in the Microsoft Excel applications and the STATISTICA 5.5 program (StatSoft, Inc./TIBCO, Palo Alto, CA, USA). Regression models using the coefficient of determination (R^2) and the Pearson correlation coefficient (R) were used to evaluate the validity of the discovered relationships, with their significance confirmed at the $p < 0.05$ level.

3. Results and discussion

As a result of the evaluation of the clutch data for a total of 166 eggs collected from 17 hens studied over 18 days, two females laid only one egg during this period. Therefore, their data were included in the calculation of the average values for the entire sampling but were not taken into account in the statistical analysis of variations in clutches. The remaining 15 quails laid 6–14 eggs during the 18 days in which they were evaluated.

Even the most superficial visual comparative analysis of the shell colouration among eggs laid by the same quail demonstrated that the variability of their pigmentation was pronounced, and this parameter can be safely excluded from the number of traits repeatable from egg to egg within one clutch. Fig. 1 shows photographs of three eggs laid in succession by the same bird over five days. This preliminary observation, however, contradicts that of other authors (e.g., Pike, 2011) calling for a more detailed and sophisticated exploration.

The mean values of the morphometrical measured and calculated egg parameters, as well as the average values of variability observed for each clutch of eggs from a specific quail involved in the experiment, are presented in Table 1.

The egg parameters varied slightly between clutches but had a similar tendency to vary around the mean intragroup value. In this regard, it can be argued that the average values of variation were completely suitable for the analysis of each clutch of eggs laid by the quails.

As can be seen in Table 1, the highest variability was observed in shell strength (27.1%) and shell maximum deformation (21.4%). Therefore, these parameters can be excluded from the number of parameters repeating from egg to egg.

The lowest variability was recorded for the S/V index, i.e., the ratio of egg surface area (S) to its volume (V), with an average value being ±1.5% and with its limits across clutches being ±0.4 … ±3.9%. Almost the same variability, with an average value of ±1.5% and its limits across clutches of ±0.7 … ±2.4%, was noted for the D_p/B indicator, or the ratio of egg diameter at the distance of length quarter from the pointed end (D_p) to B. At the same time, if the intraclutch variability of the parameters that formed these ratios were separately considered, their variability turned out to be higher, and for some it was significantly

Table 1
Mean values of Japanese quail egg parameters and variability averaged across the quails used in the experiment.

Parameters	Mean	Variance (±), %
Egg weight, W (g)	11.33	4.4
Length, L (cm)	3.25	2.4
Maximum breadth, B (cm)	2.51	2.0
Ratio B/L	0.77	2.1
Distance of the B axis offset from the egg centre, w (cm)	0.21	18.3
Ratio w/L	0.06	17.7
Egg diameter at the distance of $L/4$ from the pointed end, D_p (cm)	1.95	2.2
Ratio D_p/B	0.78	1.5
Egg volume, V (cm^3)	10.37	4.6
Shell surface area, S (cm^2)	23.41	3.2
Ratio S/V (cm^2 cm^{-3})	2.27	1.5
Egg density, D (g cm^{-3})	1.093	2.6
Shell weight, W_s (g)	0.95	10.9
Ratio W_s/W (%)	8.45	12.0
Ratio W_s/S (g cm^{-2})	0.041	11.5
Shell thickness, T (cm)	0.025	7.8
Ratio T/S (μm cm^{-2})	10.71	8.2
Shell strength, F (kg)	1.63	27.1
Shell maximum deformation, δ_{max} (mm)	0.317	21.4
Yolk weight, W_y (g)	3.49	10.8
Ratio W_y/W (%)	30.78	9.6

higher (Table 1). For example, the variation limits across clutches were ±1.2 … ±7.4% for the S value, and ±1.7 … ±10.9% for V.

It has been repeatedly demonstrated in previous studies, including those conducted on quail eggs (Narushin et al., 2024a, 2024c, 2024d, 2024e, 2024f, 2024g), that combining egg parameters into some logical indices provides opportunities for a much more effective analysis of their impact on the physiological and/or structural features of embryonic development. In this regard, the S/V and D_p/B ratios are explicitly indicative. The S/V value can be conditionally considered a *metabolic index* (Narushin et al., 2024c, 2024d, 2024e). This index appears to be the basis for successful embryonic development of the offspring. In addition, Narushin et al. (2024c, 2024d) have shown that this index also affects the duration of the incubation period. Thus, it can be assumed that one of the main physiological tasks of the female is to maintain the S/V value at a constant level. Therefore, despite the rather large differences in the volume of eggs, the quail has to "contrive", varying the surface area in such a way that the ratio of these parameters remains practically unchanged. How the hen achieves this effect is a matter for further study and conjecture.

In the previous studies on the possible reasons for the formation of pyriform (i.e., pear-shaped) eggs, Narushin et al. (2024c) examined some Alcidae species. As was shown, through mathematical analysis, this shape allows for an increase in the S/V ratio, which, accordingly, leads to an increase in the metabolic rate. The indicator of the level of pear-shapedness (or conicity) of eggs is the D_p/B value that was also called the *conicity index* (Narushin et al., 2024c), the degree of which is somehow genetically programmed in a specific bird species. Thus, the bird tries to give the egg a certain shape based on the degree of its conicity in order to ensure the optimal S/V value for the eggs of its

Fig. 1. Images of eggs laid successively by the same Japanese quail over five days.

offspring. Since both indices (S/V and D_p/B) have equally low variability, it is quite difficult, at first glance, to assume which of them is primary. Most likely, due to the female oviduct structure, as well as the physiological characteristics of the muscular efforts aimed at forming an egg of a certain shape (e.g., Gilbert, 1979; Smart, 1991), the mother bird cannot ensure high variability of the conicity index. The consistency of the D_p/B value within a clutch of eggs laid by the same female leads to the fact that the metabolic index S/V also remains practically unchanged from egg to egg. In this respect, we decided to consider interclutch differences in these indices between the layers involved in the current experiment in order to assess the extent to which both indicators are unique characteristic features for each individual.

To do this, the S/V values were ranked in ascending order, conditionally designating the quails as numbers 1 … 17 (Fig. 2). The trend line in Fig. 2 does not carry any semantic load and was used by us only to present clearly the degree of variability of the intraclutch data.

The respective analysis of D_p/B values did not demonstrate a similar relationship with S/V (Fig. 3), which is quite obvious, since the value of the metabolic index is also somewhat influenced by the B/L and w/L ratios, where w is the distance of the B axis shift from the egg centre (Narushin et al., 2024c).

Overall, the S/V index is an integral indicator, the value of which depends on the values of three ratios of egg parameters: B/L, w/L and D_p/B. At the same time, S/V had the highest reproducibility within all the studied clutches of eggs laid by the same quail. In this regard, it is recommended to use this index as a characteristic individual feature of the mother bird, which makes, following the concept described by Dall (2006), the imprint (or "signature") of her individuality in the formation of her eggs. Despite the differences in the degree of variation of various geometric parameters of the egg, as well as their relationships, the adaptive feature of the quail's body is apparently configured in such a way as to take into account possible fluctuations in the size of the egg and its shape. This, in turn, may maintain the stability of the S/V value, thus providing a certain guaranteed and genetically determined consistency in the level of metabolism of her developing offspring.

The analysis of the variability of the data within the clutches of eggs laid by each quail (Table 1) demonstrated a fairly high consistency of the geometric parameters, and vice versa, regarding the structural components of the egg. For example, the percentage of yolk in the egg structure (W_y/W) varied on average at the level of ±9.6% and by clutches from ±6.7 to ±13.1%, whereas the shell content (W_s/W) was, on average, at the level of ±12.0% and by clutches from ±8.1 to ±15.9%. In all likelihood, the laying hen's anatomy and physiology "pay more attention" to the geometry of the egg profile that, according to our assumption, is related to the level of embryonic metabolism. However, the female produces the yolk, most likely, according to the principle of excess reserves and this can vary extensively from egg to egg. Moreover, part of the yolk is utilised after hatching. Unfortunately, there is insufficient research on this physiological process in quails (e.g., van der Wagt et al., 2020); however, by analogy with broiler chickens, it can be suggested that the utilisation of the residual yolk continues for another five days after hatching (Lamot, 2017).

Based on the fact that the weight of the whole egg varies significantly less among clutches than the structural components (on average at the level of ±4.4%, with limits from ±1.0 to ±8.0%), the quail presumably regulates the content of the laid shell, taking into account the already formed yolk, maintaining the weight of the whole egg to within the desired range. Herewith, judging from the sufficiently high values of the variation of the parameters characterising the shell strength, maintaining this characteristic at a constant level is not a priority.

Returning to the minimum variability and maximum reproducibility of the S/V index values within a clutch, we can support Dall's (2006) opinion that a female generates a "signature" of eggs that are not only distinct from other females' eggs but also consistently produced by that specific female. By doing this, a female minimises the chance of confusing her own eggs for foreign ones, while receiving an advantage due to their uniqueness, regardless of whether the recognition process is a set template coded for by alleles linked to those determining egg features or a learned "search image" for her own eggs (Dall, 2006). The analysis reported here suggests that the egg formation prioritises parameters that relate to the success of embryonic development from the viewpoint of the physiological and genetic capabilities of the mother's body. Whether this has arisen via evolution through natural selection (Dall, 2006) will form the basis of future analysis.

4. Conclusions

Japanese quail eggs can be considered a model for studying the adaptive and evolutionary processes of embryonic development in birds. The physiological and genetic mechanisms of formation, development

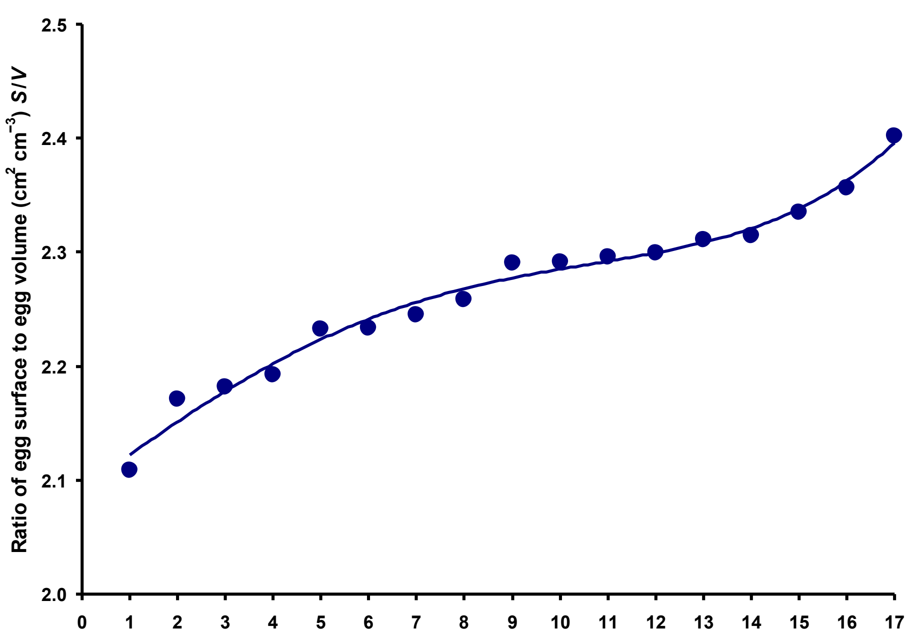

Fig. 2. Mean values of egg surface to egg volume (S/V) ratio for clutches of eggs laid by the same quail (1 … 17) as ranked from minimum to maximum.

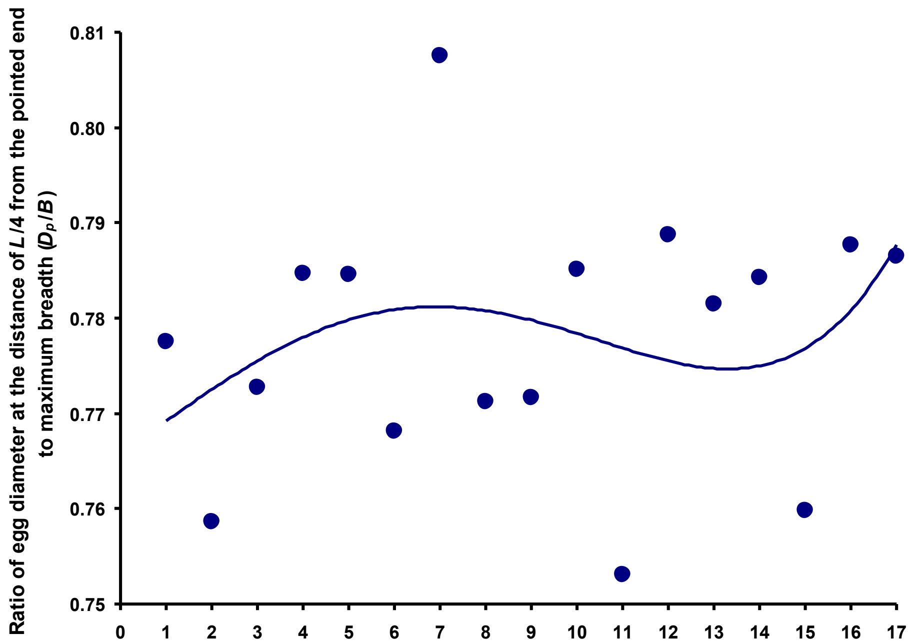

Fig. 3. Mean values of egg diameter at the distance of $L/4$ from the pointed end to maximum breadth (D_p/B) ratio for clutches of eggs laid by the same quail (1 … 17) in accordance with the ranked S/V values presented in Fig. 2.

and manifestation of promising phenotypes pertaining egg production, including shell pigment, can be examined without ethical concerns of destructive evaluation methods since the birds are commercial in nature.

Having rejected the excessively variable features of shell strength, it was established that the most consistent parameter, relatively accurately duplicated by quail from egg to egg, is the S/V ratio, indirectly characterising the level of embryonic metabolism. The average variability for the 15 clutches of eggs studied, each laid by one individual, was ±1.5%. Taking into account previously conducted studies, including mathematical calculations of the relationship of the S/V value with other egg parameters, the quail seems to achieve such S/V uniformity by varying the egg's geometric shape. Hereby, a few indices expressing the ratios of various geometric parameters of the egg had greater stability (S/V and D_p/B), some, in contrast, are distinguished by high variability (w/L). Nevertheless, they all contribute to maintaining the level of metabolism at a certain level that is characteristic of a particular quail. The S/V values for the quails used in this experiment, although close between individuals, did not completely match each other. Thus, the S/V ratio value may become a significant criterion for identifying a single mother bird. It would be interesting to evaluate the possibility of a similar approach for other species to see if this evolutionary adaptative feature is present across the total avian realm.

A sufficiently high variability of the structural components of the egg, i.e., the yolk and the shell, allows one to assume the excessive production of the former, and the corresponding "adjustment" of the latter. The found variations of different parameters of eggs generally provide low within-clutch variability of the majority of eggs laid by one female. This seems to be one of the important physiological, genetic and ecological aspects in the formation of egg production traits in Japanese quails. From the viewpoint of general biological laws, it is recommended to use major findings of the present research for deeper understanding interclutch "signatures" of eggs laid by a single mother bird as an adaptive tactics to address certain risk-posing environmental factors (e.g., conspecific and heterospecific brood parasitism).

Distribution of eggs by their metabolic index (S/V) can have both scientific merits and real-world applications. In the field of pre-incubation sorting, use of S/V values might help tailor corresponding optimization of incubation regimes for individual eggs. In this regard, the use of AI with its preliminary DL for sorting eggs by S/V value might prove to be an indispensable technological solution for both production engineering systems and the design of laboratory equipment such as precision incubators. Looking further into the future, since the S/V value is also related to the parameters of the egg contents, identifying laying hens by S/V value (AI/DL assisted) might even allow breeders to categorise hens into separate groups that lay eggs of different nutritional values.

CRediT authorship contribution statement

Valeriy G. Narushin: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Natalia A. Volkova:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation. **Alan Yu. Dzhagaev:** Visualization, Validation, Investigation. **Zarina V. Gagieva:** Investigation. **Ludmila A. Volkova:** Validation, Investigation. **Darren K. Griffin:** Writing – review & editing, Supervision. **Michael N. Romanov:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration. **Natalia A. Zinovieva:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Ethical approval

Only manipulating eggs was done for this study; no direct experiments on animals were used.

Data availability

All the data reported in this paper will be shared by the lead contact upon request. This paper does not report original code. Any additional information required to reanalyse the data reported in this paper is available from the lead contacts upon request. This study did not generate new materials. Further information and requests for resources should be directed to, and will be fulfilled by, the lead contacts Valeriy G. Narushin and corresponding author Michael N. Romanov.

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Declaration of competing interest

The authors declare that they have no conflicts of interest.

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