



Kent Academic Repository

Narushin, Valeriy G., Romanov, Michael N, Avni-Magen, Nili and Griffin, Darren K. (2026) *Avian egg incubation period: Revisiting existing allometric relationships via surface area-to-volume ratio of an egg*. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 320 . ISSN 1095-6433.

Downloaded from

<https://kar.kent.ac.uk/116479/> The University of Kent's Academic Repository KAR

The version of record is available from

<https://doi.org/10.1016/j.cbpa.2026.112066>

This document version

Author's Accepted Manuscript

DOI for this version

Licence for this version

CC BY (Attribution)

Additional information

For the purpose of open access, the author(s) has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising.

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in **Title of Journal** , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our [Take Down policy](https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies) (available from <https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies>).

Avian egg incubation period: revisiting existing allometric relationships via surface area-to-volume ratio of an egg

Valeriy G. Narushin¹, Michael N. Romanov^{2,3,*}, Nili Avni-Magen⁴, Darren K. Griffin^{2,3,5}

¹ Independent Scientist, Zaporizhya, Ukraine

² School of Natural Sciences, University of Kent, Canterbury, Kent, UK

³ Animal Genomics and Bioresource Research Unit (AGB Research Unit), Faculty of Science, Kasetsart University, Bangkok, Thailand

⁴ Tisch Family Zoological Gardens in Jerusalem, West Jerusalem, Israel

⁵ University College London, London WC1E 6BT, UK

Running title: ***S/V* ratio as a new but old egg parameter**

*Correspondence: m.romanov@kent.ac.uk

Valeriy G. Narushin: <https://orcid.org/0000-0001-6799-6605>, e-mail: valnarushin@gmail.com

Michael N. Romanov: <https://orcid.org/0000-0003-3584-4644>, e-mail: m.romanov@kent.ac.uk

Nili Avni-Magen: <https://orcid.org/0009-0000-4885-2243>, e-mail: niliavnimagen@gmail.com

Darren K. Griffin: <https://orcid.org/0000-0001-7595-3226>, e-mail: D.K.Griffin@kent.ac.uk

Abstract: The incubation period (I) for bird eggs varies among species and is used in establishing allometric relationships. Research on variations in I shed light on the evolutionary mechanisms that gave rise to the differentiation of embryonic development in distinct taxa of birds. Here, using a sampling of 444 images from 444 avian species, 89 families and 30 orders, we calculated their major geometric dimensions: volume (V) and surface area (S). An assessment of the relationship between I and the measured and calculated egg parameters demonstrated the closest and most significant correlation ($R = -0.760$) between I and the S/V ratio that was adopted as a conditional indicator and reflects the embryo's metabolic rate. Approximation of the values of these parameters made it possible to derive a power-law dependence for the prediction of I depending on the S/V value of a particular egg ($R^2 = 0.757$). The prediction accuracy was higher ($R^2 = 0.783$) if the eggs of the family Procellariiformes (petrels), whose I value is characterized by a longer time, were removed from the general sampling computation. We conclude that the value of the S/V ratio can characterize both the metabolism of an embryo and the conditional thermal conductivity of an egg, which aids in ensuring the temperature regime of egg incubation.

Key words: Avian eggs, Incubation period, Allometric relationships, Egg surface area (S) and volume (V), Metabolic rate, S -to- V ratio, Thermal conductivity

1. Introduction

The duration of egg incubation (usually denoted by the letter “ I ”) varies among birds and is a reproductive trait unique to each species. It is also the topic of numerous studies establishing the allometric relationships that can be derived from certain physical characteristics of eggs pertaining to weight or size (Deeming et al., 2006; Atanasov, 2019). Although predicted (calculated) I values can serve as a certain standard for any given species, these do not always correspond to ones observed in nature. Indeed, comparing a species standard I value with an observed one in an individual bird or population may help assess the impact, for example, of environmental factors that may be compromising (or possibly even improving) reproductive performance. Interspecific comparisons indicate that different species of birds that have comparable egg weight (W) and size parameters such as volume (V) and/or surface area (S) can have quite different I values. Studies of such I differences help provide insight into the evolutionary processes that led to the differentiation of embryonic development in varying taxonomic groups. Doing this is not a straightforward task, however, as the predictive equations for species standard I obtained by different authors (Rahn and Ar, 1974; Ar and Rahn, 1978; Deeming et al., 2006) are usually based on W alone. In this regard, the standard I values for eggs of similar W should be consistent for all species. In practice, however, this rule is not always observed, and the practical application of such formulae is thus extremely problematic due to the significant errors that are introduced as a result. Without a doubt, I is also essentially affected by the belonging of a bird to the group of different patterns of development, altricial vs. precocial. In this respect, along with a single allometric dependence uniting both groups of birds, researchers have proposed a few separate equations derived relative to these developmental features (Rahn and Ar, 1974; Ar and Rahn, 1978; Deeming et al., 2006).

In addition to the difficulties in establishing a standard species-specific I value, there are a number of limitations that hinder the practical application of establishing allometric dependencies. The main issue here is the need for an accurate and timely measurement of W , which can be an extremely difficult procedure to carry out in field studies while ensuring minimal disturbance to the hatching process (e.g., Grant et al., 1982). Moreover, the egg is subject to weight reduction (so called “shrinkage”) during incubation (Shomina et al., 2009; Narushin et al., 2024a; Chekh et al., 2025) and thus the weight of a freshly laid egg is somewhat different, even the next day after laying. For this reason, often the W value given by various authors does not always correspond to the W of a freshly laid egg. Indeed, W is often calculated using approximate methods based on its volume (V), which remains unchanged throughout the entire incubation period. In preliminary recent studies, we used calculations based on V to establish why some eggs are pyriform (Narushin et al., 2025) and this served as a prerequisite for the current investigation where we considered possible calculation errors in more detail (see subsection Prediction of W Based on V below).

A second limitation in conducting reliable analyses pertaining to I and interspecific allometric studies of bird eggs is the availability of samples; in this case, images of bird eggs to carry out the required measurements. A third is that, according to the results of many studies (e.g., Petersen, 1992; Barta and Székely, 1997; Mónus and Barta, 2005; Duursma et al., 2018; Hays et al., 2020; Liu et al., 2023), intraspecific variability of the geometric parameters of avian eggs is not large, but it does exist and needs to be taken into account.

With the above caveats for practical purposes, the variation in I within one species can be considered negligible unless external factors change it. In other words, I will not vary between individuals of the same species, when incubated in the same environment. For this reason, to predict I through mathematical calculation a standard reference characteristic of a given bird species is

essential if allometric relationships are to be generated accurately. Research in this direction has been carried out for decades but, thus far, only for domestic species. For example, Romanoff and Romanoff (1949) reported the standard parameters of chicken eggs; however, such studies for the diversity of wild bird species existing in nature are yet to be established.

1.1. Prediction of W based on V

In principle, a possible approach is to determine the volume of an egg and then convert it into weight using the same allometric relationships. A group of researchers led by Hermann Rahn (as reviewed by Pappenheimer, 1996) published a number of results based on several studies aimed at the development of allometric relationships that mathematically describe the relationships between various parameters of bird eggs. Unfortunately, some fairly popular equations were not taken into account. For example, we (Narushin et al., 2025) recently examined the relationship between eggs laid by birds of the Alcidae family (auks, guillemots, puffins and related species), their W and their metabolic status expressed by the ratio of their surface area (S) to V (i.e., S/V). In this study, we faced the need to recalculate the value of W depending on V . Despite the apparent simplicity of such a recalculation (because for this, it would be enough to have at our disposal only the corresponding dependence for egg density, D), such a functional relationship has not been described. Paganelli et al. (1974), however, demonstrated several mathematical formulae that could be transformed into the needed relationship between W and V . For instance, these authors presented two relationships for calculating S :

$$S = 4.835W^{0.662} \tag{1}$$

and

$$S = 4.951V^{0.666} . \tag{2}$$

By equating Eqns 1 and 2, we can obtain the following relationship to describe egg weight:

$$W = 1.036V^{1.006}, \quad (3)$$

where W is measured in g and V in cm^3 .

In addition to Eqns 1 and 2, Paganelli et al. (1974) also presented a formula for calculating D :

$$D = 1.038W^{0.006}, \quad (4)$$

where D is measured in g/cm^3 and W in g.

Multiplying Eqn 4 by V and equating it to W , we obtain:

$$W = 1.038V^{1.006}. \quad (5)$$

Some disagreement between Eqns 3 and 5 forced us to carry out another test using the following formulae from Paganelli et al. (1974) for the weight (W_s) and volume (V_s) of the shell:

$$W_s = 0.0482W^{1.132}, \quad (6)$$

$$V_s = 0.0248W^{1.118}, \quad (7)$$

where V_s is measured in cm^3 , and W_s and W in g.

In our previous work (Narushin et al., 2023a), we showed a theoretical relationship between W and other egg parameters:

$$W = W_s + (V - V_s)D_i, \quad (8)$$

where D_i is the density of the egg contents (in g/cm^3).

Based on their own and others' data, Rahn and Paganelli (1989) provided D_i values for the eggs of both domestic and wild avian species. The authors suggested employing the value 1.031 for D_i as a significant constant because the average value of this indicator, which ranged from 1.027 to 1.038 g/cm^3 , was the same for subgroups of domestic and wild species. Substituting this value, along with Eqns 6 and 7 into Eqn8, we can rewrite it in the following form:

$$V = 0.97W - 0.04675W^{1.132} + 0.0248W^{1.118}. \quad (9)$$

Substituting W values from 0.5 to 1000 g, approximately corresponding to the entire range of eggs existing in nature, into Eqn8, calculating V and approximating the obtained data with the function $W = f(V)$, we obtained the following equation:

$$W = 1.0448V^{1.0072}, \quad (10)$$

Thus, based on the results of Rahn and colleagues, three different approaches led to three different outcomes (Eqns 3, 5 and 10). Some of these were quite close to one another, some were not; however, it was not possible to obtain a single calculated relationship, perhaps because of discrepancies associated with the approximate values of the initial data. For instance, the authors took the entire array of initial data from the Schönwetter oological reference book (1960–1992) and, according to Maurer et al. (2010), a number of inaccuracies and assumptions were made in its compilation. It should also be noted that, in similar studies, Worth (1940) expressed the feasibility,

and demonstrated the effectiveness, of using V for a mathematical prediction of I . It is achievable that, for most studies, any of the obtained relationships (Eqns 3, 5, and 10) may be sufficient to produce relatively accurate data on egg mass from its volume. With the above theoretical overview, we merely wanted to demonstrate the feasibility and research validity of using V as a fundamental and more adequate parameter in deriving and evaluating allometric relationships for calculating various parameters (both physical and biological) of bird eggs.

Considering the above, we hypothesized that using V values when obtaining allometric and/or other empirical dependencies instead of W values might be more expedient. Such advantages are that: (i) V , in contrast to W , does not change over time due to shrinkage; (ii) the value of V is quite simple to calculate, having images of eggs with their geometric dimensions linked to actual metric units; (iii) the use of V will allow us to move away from the indices of the egg's structural components (e.g., shell thickness, shell density and/or weight of the contents), all these factors that may cause errors in calculations.

Another approach to increasing the accuracy of I value prediction is to make use of other egg parameters. In our previous work (Narushin et al., 2025), we suggested that, in addition to W , S/V can directly affect I and that the S/V value can indirectly characterize the metabolic level of the developing embryo. For more suitable use of this indicator and in order to make it universal for eggs of any size and geometric shape nuances, we developed a mathematical index that we named the egg metabolic rate (EMR ; Narushin et al., 2024b, 2025). This hypothesis was tested on eggs of the Alcidae family birds, as a result of which, its adequacy was confirmed.

Taking into account the above premise and assumptions, and using V and egg images, the goal of the present study was to explore, and expand as much as possible, the relationship between I and various geometric and physical parameters of the entire diversity of bird eggs existing in nature.

2. Materials and methods

2.1. Study species

One of the most suitable resources for working with images of bird eggs is the digitized collection of the Natural History Museum of Wiesbaden, Germany (Wikimedia Commons, 2014a). The collection includes a total of 615 images, each of which is equipped with a metric scale, allowing for accurate geometric measurements. Since, among the presented images, a number of them belong to the same species, and some were not linked to real metric sizes, as a result, we selected 442 eggs plus photographs of the eggs of the common ostrich (*Struthio camelus*) and antillean crested hummingbird (*Orthorhyncus cristatus*) from the collection of the Muséum de Toulouse, France (Wikimedia Commons, 2019) to represent upper and lower extremes of size. As a result, we had at our disposal the geometric parameters of 444 eggs belonging to 444 avian species, 89 families and 30 orders, respectively representing approximately 4%, 36% and 73% of the entire biodiversity of species, families and orders worldwide.

2.2. Egg image analyses and traits measured and calculated

Each egg image selected for subsequent analysis was analysed as follows: Measurements of geometric parameters were carried out in pixels using the Microsoft Office Picture Manager program. We measured the breadth (B) and length (L) of the egg, the diameter of the egg (D_p) at the point corresponding to the $L/4$ distance from the pointed end, as well as the distance (w) by which

the B axis is shifted from the centre of the egg corresponding to the point $L/2$ (Narushin et al., 2021, 2023b). Using the ruler with metric units presented next to the image, we made the appropriate conversion of pixels to centimetres for all measured geometric parameters.

A schematic representation of the measured geometric parameters using the example of an image of a song thrush (*Turdus philomelos*) egg is shown in Fig. 1.

(Position of Fig. 1)

For each egg, its V (in cm^3), S (in cm^2), their ratio, S/V (in cm^2/cm^3), and EMR (in %) were calculated. The following corresponding formula from Narushin et al. (2024b, 2025) were used:

$$V = \frac{\pi}{128} \left[\left(8.917 - 29.998 \frac{w}{L} \right) \left(\frac{D_p}{B} \right)^2 + \left(2.459 + 88.647 \frac{w}{L} \right) \frac{D_p}{B} - 36.26 \frac{w}{L} + 12.453 \right] LB^2 \quad (11)$$

$$S = \pi BL \left(0.389 + 0.188 \frac{B}{L} - 0.063 \frac{w}{L} + 0.365 \frac{D_p}{B} + 0.114 \frac{D_p}{L} - 0.168 \frac{w}{L} \cdot \frac{B}{L} + 0.46 \frac{w}{L} \cdot \frac{D_p}{B} + 0.484 \frac{w}{L} \cdot \frac{D_p}{L} \right) \quad (12)$$

$$EMR = \frac{0.362 + 0.175 \frac{B}{L} - 0.059 \frac{w}{L} + 0.34 \frac{D_p}{B} + 0.106 \frac{D_p}{B} \cdot \frac{B}{L} - 0.156 \frac{w}{L} \cdot \frac{B}{L} + 0.428 \frac{w}{L} \cdot \frac{D_p}{B} + 0.45 \frac{w}{L} \cdot \frac{D_p}{B} \cdot \frac{B}{L}}{\left[\left(0.716 - 2.409 \frac{w}{L} \right) \left(\frac{D_p}{B} \right)^2 + \left(0.197 + 7.119 \frac{w}{L} \right) \frac{D_p}{B} - 2.914 \frac{w}{L} + 1 \right] \frac{B}{L}} \cdot 100 \quad (13)$$

Data on I values were obtained from open ornithological resources available on the Internet elsewhere (e.g., Avibase, 2003; Celebrate Urban Birds, 2016; Animal Diversity Web, Project FeederWatch, 2021; eBird, 2023; Bird Academy, 2024; Birds of the World, 2024; Great Backyard Bird Count, 2024; Macaulay Library, 2024; NestWatch, 2024). Unfortunately, there is no single methodological approach to determining the incubation time (Nice, 1954). In addition, the value of I is directly dependent on weather conditions. Therefore, the above reference databases provide a

range of parameters from their minimum to maximum values. In this regard, for our further calculations we used average values of I .

2.3. Statistical analyses

The strength of the relationship between the parameters was assessed using the value of the Pearson correlation coefficient R , with confirmation of their significance at the level of $p < 0.05$. The experimental data were approximated by regression equations using the ‘Non-linear estimation’ subfunction in STATISTICA 5.5 program (StatSoft, Inc./TIBCO, Palo Alto, CA, USA). The validity of the obtained regression models was estimated using the coefficient of determination (R^2), with confirmation of their significance at the level of $p < 0.05$.

3. Results

Correlation analysis of the obtained data demonstrated the following results: The highest value of $R = -0.760$ ($p < 0.05$) was observed between the I value and the S/V ratio. A negative correlation confirmed our hypothesis that an increase in S/V , which indirectly indicates an increase in the level of embryonic metabolism, would lead to a decrease in incubation time. At the same time, the values of V and S , included in this ratio, showed a slightly lower and, quite logically, positive correlation with the duration of incubation: $R = 0.585$ ($p < 0.05$) for V , and $R = 0.728$ ($p < 0.05$) for S , respectively. Visualization of the marked correlation dependencies is presented in Fig. 2.

(Position of Fig. 2)

The dependencies presented in Fig. 2 were approximated by power equations:

$$I = 32.638 \left(\frac{S}{V} \right)^{-0.635}, \quad (14)$$

with $R^2 = 0.757$ ($p < 0.05$);

$$I = 11.839 V^{0.211}, \quad (15)$$

with $R^2 = 0.755$ ($p < 0.05$);

$$I = 7.153 S^{0.316}, \quad (16)$$

with $R^2 = 0.755$ ($p < 0.05$).

In Eqns 14 to 16, the value of I is expressed in days, V in cm^3 , and S in cm^2 .

Despite the sufficiently similar coefficients of determination in all three approximated equations (Eqns 14 to 16), data visualization indicated a more uniform distribution along the S/V axis (Fig. 2a) than in the case of using the values of individual components, V (Fig. 2b) or S (Fig. 2c). This fact suggested that S/V was a more accurate and, therefore, appropriate parameter for predicting the value of I .

Despite the uniform distribution of S/V values obtained as a result of our calculations along the trend line expressed by Eqn14, such uniformity was violated by a number of data points that did not fit into the general array and were located slightly above the trend line. Analysis of these data that did not fit into the general outline made it possible to identify their belonging to the order Procellariiformes (albatrosses, petrels etc.). Visually, the selection of data for Procellariiformes will look as shown in Fig. 3.

(Position of Fig. 3)

The dependence between the incubation period of Procellariiformes eggs and the S/V ratio (Eqn14) was defined as follows:

$$I_p = 55.821 \left(\frac{S}{V} \right)^{-0.319}, \quad (17)$$

with $R^2 = 0.796$ ($p < 0.05$).

In Eqn17, I_p is the incubation period of Procellariiformes eggs in days.

We also recalculated the value of I for the entire array of bird eggs available to us, excluding those from the order Procellariiformes. As a result, Eqn14 was slightly modified and was expressed as follows:

$$I = 32.154 \left(\frac{S}{V} \right)^{-0.627}, \quad (18)$$

with $R^2 = 0.783$ ($p < 0.05$).

Relationship of the EMR magnitude, which value corresponds to the percentage of the actual S/V value in the structure of its maximum possible value for a given egg, relative to the incubation period (I) is shown in Fig. 4.

(Position of Fig. 4)

The correlation between I and EMR demonstrated an extremely weak and insignificant relationship ($R = 0.112$).

In their work, Deeming et al. (2006) examined a number of scientific premises to refine the possible allometric prediction of incubation time. In their opinion, the bird taxon has a special influence on the I value. In this respect, they presented graphical dependences of I on W in various avian families. We used a similar approach when assessing the influence of the EMR value on the value of I , which implied dividing the parameters of interest into certain intervals and analysing each of them accordingly.

Considering that the intraspecific structure of eggs practically does not differ depending on the species of birds, we evaluated the possibility of a more accurate prediction of I when distributing eggs into groups according to different I values. Thus, all eggs involved in our studies were conditionally divided into the following categories: (1) $I < 20$ days, (2) $I = 20 \dots 40$ days, and (3) $I > 40$ days of incubation. Analysis of these subgroups demonstrated the results presented in Figs. 5 and 6.

Previously, we also demonstrated (Narushin et al., 2025) that the best prediction of incubation time was noted when using two parameters, i.e., W and the value of egg's EMR . Since the W was obtained by recalculation using Eqn5 from the V value, we carried out a similar recalculation of the results of our measurements for the entire variety of bird eggs in order to obtain the mathematical relationship $I = f(V, EMR)$. The result of this approximation was expressed by the following dependence:

$$I = 200.863 \frac{V^{0.214}}{EMR^{0.664}}, \quad (19)$$

with $R^2 = 0.707$ ($p < 0.05$),

where I is measured in days, V in cm^3 , and EMR in %.

4. Discussion

Previously, Atanasov (2012) demonstrated a close relationship (with $R^2 = 0.931$) of the inversed V/S ratio with the lifespan of many organisms (unicellular organisms, poikilotherms, mammals, and birds). Similar studies conducted by him as a result of the analysis of published data on eggs of various avian species, Atanasov (2019) found a similar relationship between V/S and the duration of egg incubation. However, the correlation coefficient, in this case, was much lower ($R = 0.561$) than in his previous studies for other living organisms (2012). Also, the R value in the Atanasov (2019) studies was lower than in our studies here for S/V . It is possible that the reason for a lower accuracy lies in the insufficiently accurate method for calculating the values of V and S , the data of which were taken by Atanasov (2019) from the work of Hoyt (1976) and/or due to the limited experimental sampling that consisted of 28 eggs.

The phenomenon of extended incubation period in Procellariiformes has been studied by many authors (e.g., Wilbur, 1969; Ricklefs and Rahn, 1979; Boersma, 1982; Rahn and Huntington, 1988; Minguez, 1998; Borg and Sultana, 2010). Incubation temperature, egg-nest water vapor pressure differences, relative yolk weight, oxygen uptake, and behavioural factors were discussed as possible reasons. For example, nesting in predator-free places contributes to the safety of eggs, allowing parents to leave the nest for a longer time, thereby increasing I .

Regardless of the possible reasons, if we consider the eggs of Procellariiformes birds separately (Fig. 3), the pattern of changes in the timing of their incubation was the same as for the eggs of all other species. That is, an increase in the level of egg metabolism expressed by the S/V ratio led to a decrease in their incubation time. The only thing was that this dependence had a slightly different mathematical expression that distinguished it from the equation for the entire array of bird eggs (Eqn14).

In our previous studies (Narushin et al., 2025) conducted on eggs of the Alcidae family, we demonstrated that a methodologically more adequate criterion for assessing the level of metabolism can be not so much the S/V ratio, but its derivative, EMR . The EMR value corresponds to the percentage of the actual S/V value in the structure of its maximum possible value for a given egg under study. However, analysis of this parameter (EMR) for the entire avian egg data set did not demonstrate the same predictive potential that we obtained from our analysis of Alcidae eggs (Fig. 4). The weak relationship and the fact that, if anything, a rise in EMR had a slight tendency to increase, and not to decrease, the incubation time I (as was noted in Alcidae by Narushin et al., 2025) prompted us to carry out a more thorough investigation of EMR and I .

The resultant trend lines (Fig. 5) suggested that the trend of the relationship between I and EMR depended on groups of eggs with different I values. Of the I values we identified, an increase in EMR led to a slight decline in I only for a group of eggs whose I ranged from 20 to 40 days. It was to this period that the eggs of the Alcidae family belong, which explained and confirmed our previously obtained results (Narushin et al., 2025). For eggs with a period of embryonic development of up to 20 days, the EMR value was stable and did not have any effect on I . On the other hand, for the group of eggs whose incubation time exceeds 40 days, an inverse relationship was observed, according to which an increase in EMR led to a longer incubation time.

(Position of Fig. 5)

Thus, a more preferable factor for predicting the value of I and an indirect indicator of the metabolic level was the S/V ratio, with the nature of its change being not affected by the duration of the egg incubation (Fig. 6).

(Position of Fig. 6)

Analysis of the multiparameter equation (19), which uses V and EMR values to predict the incubation time, showed that the interaction of these two parameters did not lead to an increase in the accuracy of the prediction of the I value in comparison with the use of the S/V ratio (Eqn14).

The objective of this study was to establish interspecific patterns in incubation time and predict them based on other egg parameters. The sample size used is sufficient to identify and describe large-scale interspecific patterns, although it does not allow for the assessment of intraspecific variability or conclusions about the variability of I within each individual species. In this regard, the lack of repeated measurements within each species limits intraspecific conclusions, although it does not make it impossible to analyze interspecific patterns. Therefore, intraspecific analysis of the relationship between I and the S/V ratio could be the focus of further, more extensive research in this area.

5. Conclusions

As an output of this computational investigation, we can categorically state that I of bird eggs is directly influenced by the S/V value. This ratio can have a direct impact on the incubation temperature due to a direct effect on thermal conductivity (e.g., Planinšič and Vollmer, 2008). If we accept the validity of the statement that this ratio is an indirect indicator of metabolism (e.g., Cohen et al., 1999; Cragg, 2016; Harris and Theriot, 2018; Lewis, 2023), we may conclude that the S/V value also affects the physiological characteristics of the developing embryo. Namely, these two factors named in the comprehensive paper by Martin et al. (2018) as '*intrinsic (physiological) and extrinsic (e.g., temperature)*' are fundamental causes of the difference in I among species.

Author contributions statement

Conceptualization, data curation, formal analysis, methodology, resources, investigation, software, visualization: VGN. Writing – original draft: VGN and MNR. Writing – review and editing: VGN, MNR, NAM, and DKG. Project administration: MNR. Supervision: DKG.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Data and materials availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics statement

This study involved only images of the eggs from the electronic sources. No live animals or natural eggs were used. No compliance with ARRIVE or other relevant guidelines were needed.

Funding statement

Not available.

References

- Animal Diversity Web (2020). Regents of the University of Michigan, Ann Arbor, MI USA [online]. Website <https://animaldiversity.org/> [accessed 14 May 2026].
- Ar A, Rahn H. (1978). Interdependence of gas conductance, incubation length, and weight of the avian egg. In: Piiper J (editor). *Respiratory Function in Birds, Adult and Embryonic; Proceedings in Life Sciences*. Berlin, Heidelberg, Germany: Springer, pp. 227–236. https://doi.org/10.1007/978-3-642-66894-4_31
- Atanasov AT (2012). Scaling of biological space and time: Volume to surface ratio in living organisms is proportional to lifespan. *Trakia Journal of Sciences* 10 (2): 36–47 [online]. Website http://tru.uni-sz.bg/tsj/Vol10N2_%202012/At.Atanasov.pdf [accessed 14 May 2026].
- Atanasov AT (2019). Allometric relationship between volume to surface ratio and incubation days in bird's eggs. In: *Proceedings of the International Conference of Computational Methods in Sciences and Engineering 2019 (ICCMSE-2019); AIP Conference Proceedings*. Rhodes, Greece: AIP Publishing LLC, Vol. 2186, No. 1, p. 110002. <https://doi.org/10.1063/1.5138021>
- Avibase (2003). Denis Lepage, Data Science and Technology, Birds Canada, Port Rowan, ON, Canada [online]. Website <https://avibase.bsc-eoc.org/> [accessed 14 May 2026].
- Barta Z, Székely T (1997). The optimal shape of avian eggs. *Functional Ecology* 11: 656–662. <https://doi.org/10.1046/j.1365-2435.1997.00136.x>
- Bird Academy (2024). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <https://academy.allaboutbirds.org/> [accessed 14 May 2026].
- Birds of the World (2024). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <http://birdsoftheworld.org/> [accessed 14 May 2026].

- Boersma DP (1982). Why some birds take so long to hatch. *The American Naturalist* 120: 733–750.
<https://doi.org/10.1086/284027>
- Borg JJ, Sultana J. (2010). Extended laying period by the European Storm-petrel *Hydrobates pelagicus melitensis* on Filfla island. *Il-Merill* 32: 15–21 [online]. Website
<https://www.um.edu.mt/library/oar/handle/123456789/36398> [accessed 14 May 2026].
- Celebrate Urban Birds (2016). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <https://celebrateurbanbirds.org/> [accessed 14 May 2026].
- Chekh OO, Bondarenko YuV and Bordunova O (2025). Influence of pre-incubation storage conditions and calibration of eggs on differential mortality of embryos of different sex. *Bulletin of Sumy National Agrarian University Series Livestock* 1: 105–110.
<https://doi.org/10.32782/bsnau.lvst.2025.1.14>
- Cohen A, Moreh AB, Chayoth R (1999). Hands-on method for teaching the concept of the ratio between surface area & volume. *The American Biology Teacher* 61: 691–695.
<https://doi.org/10.2307/4450805>
- Cragg SM (2016). Chapter 2 – Biology and ecology of scallop larvae. In: Shumway SE, Parsons GJ (editors). *Scallops – Biology Ecology Aquaculture and Fisheries*. 3rd ed. Amsterdam, The Netherlands: Elsevier. *Developments in Aquaculture and Fisheries Science* 40: 31–83.
<https://doi.org/10.1016/B978-0-444-62710-0.00002-X>
- Deeming DC, Birchard GF, Crafer R, Eady PE (2006). Egg mass and incubation period allometry in birds and reptiles: effects of phylogeny. *Journal of Zoology* 270: 209–218.
<https://doi.org/10.1111/j.1469-7998.2006.00131.x>
- Duursma ED, Gallagher RV, Price JJ, Griffith SC (2018). Variation in avian egg shape and nest structure is explained by climatic conditions. *Scientific Reports* 8: 4141.
<https://doi.org/10.1038/s41598-018-22436-0>

eBird (2023). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online].

Website <https://ebird.org/> [accessed 14 May 2026].

Grant GS, Paganelli CV, Pettit TN, Whittow GC, Rahn H (1982). Determination of fresh egg mass during natural incubation. *The Condor* 84: 121–122. <https://doi.org/10.2307/1367835>

Great Backyard Bird Count (2024). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <https://www.birdcount.org/> [accessed 14 May 2026].

Harris LK, Theriot JA (2018). Surface area to volume ratio: a natural variable for bacterial morphogenesis. *Trends in Microbiology* 26: 815–832. <https://doi.org/10.1016/j.tim.2018.04.008>

Hays IR, Ljubičić I, Hauber ME (2020). The shape of avian eggs: Assessment of a novel metric for quantifying eggshell comicality. *The Auk* 137: ukaa021. <https://doi.org/10.1093/auk/ukaa021>

Hoyt DF (1976). The effect of shape on the surface-volume relationships of birds' eggs. *The Condor* 78: 343–349. <https://doi.org/10.2307/1367694>

Lewis M (2023). Chapter 6 – Physical concepts. In: *Food Process Engineering Principles and Data*. Amsterdam, The Netherlands: Woodhead Publishing, Elsevier, pp. 37–46. <https://doi.org/10.1016/B978-0-12-821182-3.00030-3>

Liu J, Chai Z, Wang H, Ivanov A, Kubelka V, et al. (2023). Egg characteristics vary longitudinally in Arctic shorebirds. *iScience* 26: 106928. <https://doi.org/10.1016/j.isci.2023.106928>

Macaulay Library (2023). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <https://www.macaulaylibrary.org/> [accessed 14 May 2026].

Martin TE, Ton R, Oteyza JC (2018). Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines. *The Auk* 135: 101–113. <https://doi.org/10.1642/AUK-17-124.1>

Maurer C, Russell DG, Cassey P (2010). Interpreting the lists and equations of egg dimensions in Schönwetter's *Handbuch der Oologie*. *The Auk* 127: 940–947. <https://doi.org/10.1525/auk.2010.09260>

- Minguez E (1998). The costs of incubation in the British Storm-petrel: an experimental study in a single-egg layer. *Journal of Avian Biology* 29: 183–189. <https://doi.org/10.2307/3677197>
- Mónus F, Barta Z (2005). Repeatability analysis of egg shape in a wild Tree Sparrow (*Passer montanus*) population: A sensitive method for egg shape description. *Acta Zoologica Academiae Scientiarum Hungaricae* 51: 151–162 [online]. Website <https://www.researchgate.net/publication/288544879> [accessed 14 May 2026].
- NestWatch (2024). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <https://nestwatch.org/> [accessed 14 May 2026].
- Narushin VG, Romanov MN, Griffin DK (2021). Egg and math: introducing a universal formula for egg shape. *Annals of the New York Academy of Sciences* 1505: 169–177. <https://doi.org/10.1111/nyas.14680>
- Narushin VG, Kent JP, Salamon A, Romanov MN, Griffin DK (2023a). A simulation-based insight into the interrelationships between density and other physical parameters of the egg. *Journal of Food Engineering* 358: 111679. <https://doi.org/10.1016/j.jfoodeng.2023.111679>
- Narushin VG, Orszulik ST, Romanov MN, Griffin DK (2023b). A novel approach to egg and math: Improved geometrical standardization of any avian egg profile. *Annals of the New York Academy of Sciences* 1529:61–71. <https://doi.org/10.1111/nyas.15059>
- Narushin VG, Romanov MN, Salamon A, Kent JP (2024a). An innovative non-destructive technology for controlling the storage period of chicken eggs using egg parameters. *Food and Bioprocess Technology* 17: 2770–2781. <https://doi.org/10.1007/s11947-023-03290-z>
- Narushin VG, Volkova NA, Vetokh AN, Dzhagaev AY, Sotnikov DA, et al. (2024b). Reimagining Archimedes: an innovative and accurate calculation of volumes and asserting another standard method for defining the surface area of quail and any avian eggs. *Food and Bioprocess Technology* 147: 327–334. <https://doi.org/10.1016/j.fbp.2024.07.013>

- Narushin VG, Romanov MN, Griffin DK (2025). Pear-shaped eggs evolved to maximize the surface area-to-volume ratio, increase metabolism, and shorten incubation time in birds. *Integrative Zoology* 20: 1098–1109. <https://doi.org/10.1111/1749-4877.12936>
- Nice MM (1954). Incubation periods throughout the ages. *Centaurus* 3: 311–359. <https://doi.org/10.1111/j.1600-0498.1954.tb00462.x>
- Petersen MR (1992). Intraspecific variation in egg shape among individual Emperor Geese. *Journal of Field Ornithology* 63: 344–354 [online]. Website <http://www.jstor.org/stable/4513717> [accessed 14 May 2026].
- Paganelli CV, Olszowka A, Ar A (1974). The avian egg: surface area, volume, and density. *The Condor* 76: 319–325. <https://doi.org/10.2307/1366345>
- Pappenheimer J (1996). Hermann Rahn 1912—1990: Biographical Memoir. Washington D.C., USA: National Academies Press [online]. Website <https://www.nasonline.org/publications/biographical-memoirs/memoir-pdfs/rahn-hermann.pdf> [accessed 14 May 2026].
- Planinšič G, Vollmer M (2008). The surface-to-volume ratio in thermal physics: from cheese cube physics to animal metabolism. *European Journal of Physics* 29: 369–384. <https://doi.org/10.1088/0143-0807/29/2/017>
- Project FeederWatch (2021). The Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA [online]. Website <https://feederwatch.org/> [accessed 14 May 2026].
- Rahn H, Ar A (1974). The avian egg: incubation time and water loss. *The Condor* 76: 147–152. <https://doi.org/10.2307/1366724>
- Rahn H, Huntington CE (1988). Eggs of leach's storm petrel: O₂ uptake, water loss, and microclimate of the nest. *Comparative Biochemistry and Physiology Part A: Physiology* 91: 519–521. [https://doi.org/10.1016/0300-9629\(88\)90628-7](https://doi.org/10.1016/0300-9629(88)90628-7)

- Rahn H, Paganelli CV. (1989). The initial density of avian eggs derived from the tables of Schönwetter. *Journal of Ornithology* 130: 207–215. <https://doi.org/10.1007/BF01649755>
- Romanoff AL, Romanoff AJ (1949). *The Avian Egg*. New York, NY, USA: John Wiley & Sons Inc. [online]. Website <https://archive.org/details/avianegg0000alex> [accessed 14 May 2026].
- Ricklefs RE, Rahn H (1979). The incubation temperature of Leach's Storm-Petrel. *The Auk* 96: 625–627. <https://doi.org/10.1093/auk/96.3.625>
- Schönwetter M (1960–1992). *Handbuch der Oologie*. Meise W (editor). Berlin, Germany: Akademie Verlag, Vol. 1–4. [online]. Website <https://archive.org/details/handbuchderoolog16schn> [accessed 14 May 2026].
- Shomina NV, Tkachenko SM, Tagirov MT and Tereshchenko OV (2009). Monitoring the quality of hatching eggs during storage. *Efektivne Ptakhivnytstvo* 11: 29–33.
- Wikimedia Commons (2014a). Category: Eggs of the Natural History Collections of the Museum Wiesbaden [online]. Website https://commons.wikimedia.org/wiki/Category:Eggs_of_the_Natural_History_Collections_of_the_Museum_Wiesbaden [accessed 14 May 2026].
- Wikimedia Commons (2014b). Song thrush *Turdus philomelos*, egg, Coll. Museum Wiesbaden, Origin: Aßling, Bavaria, 24.04.1973, leg. W. Abelmann; by Klaus Rassinger and Gerhard Cammerer, 2012; CC-BY-SA-3.0 [online]. Website https://commons.wikimedia.org/wiki/File:Turdus_philomelos_MWNH_2235.JPG [accessed 14 May 2026].
- Wikimedia Commons (2019). Category: Bird eggs of the Muséum de Toulouse [online]. Website https://commons.wikimedia.org/wiki/Category:Bird_eggs_of_the_Mus%C3%A9um_de_Toulouse [accessed 14 May 2026].
- Wilbur HM (1969). The breeding biology of Leach's Petrel, *Oceanodroma leucorhoa*. *The Auk* 86: 433–442. <https://doi.org/10.2307/4083406>

Worth CB (1940). Egg volumes and incubation periods. *The Auk* 57: 44–60.

<https://doi.org/10.2307/4078847>

Figure captions

Fig. 1. Schematic representation of the measured geometric parameters using the example of the song thrush egg image (*Turdus philomelos*; CC-BY-SA-3.0; Wikimedia Commons, 2014b).

Fig. 2. Graphical visualization of the correlations between the incubation period (I) and the S/V ratio (a), egg volume, V (b), and its surface area, S (c).

Fig. 3. Graphical visualization of the correlations between the incubation period (I) and the S/V ratio, highlighting data for species from the order Procellariiformes (pink dots and trend line).

Fig. 4. Graphical visualization of the correlations between the incubation period (I) and the egg metabolic rate (EMR) value.

Fig. 5. Graphical visualization of correlations between different incubation period (I) and EMR values.

Fig. 6. Graphical visualization of correlations between various incubation periods (I) and the S/V ratio.