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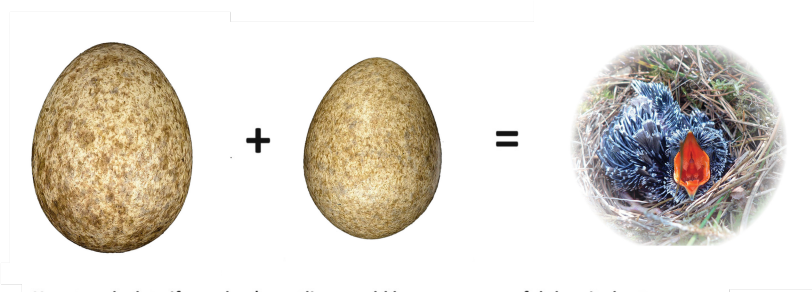
How to calculate if a cuckoo's nestling would be more successful than its host

1 **Brood parasitism and host-parasite relationships: Cuckoos adapt to reduce the**

2 **time of hatching ahead of host nestlings by increasing egg thickness**

3

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Abstract

The phenomenon of cuckoos' brood parasitism is well known and can be investigated using applied mathematical techniques. Among adaptive features of this phenomenon are certain egg parameters that ensure their shortened incubation period (I) and thus the successful survival of their offspring. In particular, the volume of a cuckoo egg is not less than, or exceeds, that of the host species, which should, in theory, increase I. Also, cuckoo eggs have thicker shell than that of nest hosts. Here, we analyzed the available geometric dimensions of eggs in 447 species and found an inverse correlation (-0.585, $p < 0.05$) between I and the shell thickness-to-egg surface area ratio (T/S). A mathematical relationship was derived to calculate I depending on T/S. This premise was confirmed by comparative calculations using egg images of two parasitic species, common (*Cuculus canorus*) and plaintive cuckoo (*Cacomantis merulinus*) and their hosts: great reed warbler (*Acrocephalus arundinaceus*), European robin (*Erithacus rubecula*), rufescent prinia (*Prinia rufescens*), and common tailorbird (*Orthotomus sutorius*). An average calculated I value for cuckoo eggs was one day less than that for host eggs. Our findings unravel additional details of how cuckoos adapt to brood parasitism and specific host-parasite relationships.

Key words: avian eggs; cuckoo's brood parasitism; egg incubation period; shell thickness; egg surface area and volume; metabolic rate; host-parasite relationships

1. Introduction

The brood parasitism of cuckoos is a well-described concept present beyond the peer-reviewed zoological literature (e.g., Wang et al., 2016; Pradeep et al., 2016). "Cuckoo in the nest" is a commonly used idiom in popular culture, universally taken to mean an unwanted intruder in any given situation or location. By disguising their eggs as those of other birds, cuckoos devolve the efforts of parental care, i.e. hatching, feeding and raising of their offspring, to parents of other species. Moreover, hatched cuckoo chicks either eject eggs and/or chicks of the real (natural) progenies of their adoptive parents from the nest, or else make them starve by aggressively competing for food resources (Honza et al., 2007; Anderson et al., 2009; Schulze-Hagen et al., 2009; Moksnes et al., 2013; Canestrari et al., 2014). In turn, host species often evolve to recognize abandoned cuckoo eggs and thus can neutralize the worst of the parasitic effects (Davies and Brooke, 1988; Grim, 2008; Antonov et al., 2008; Feeney et al., 2014). Indeed, some host species are so successful in such identification that they eject almost 100% of parasitic cuckoo eggs (e.g., Yang et al., 2022). As part of the evolutionary "arms race", the mother cuckoo does her best to make her eggs as similar as possible to those of the host species (Brooke and Davies, 1988; Stoddard and Stevens, 2010, 2011; see also Fig. 1).

It is nonetheless evolutionarily advantageous for the cuckoo egg to be slightly larger in size than that of its host (Fig. 1), instantly providing a weight advantage for the cuckoo hatchling (Alvarez, 1994, 2000; Moksnes and Røskaft, 1995; Krüger and Davies, 2004). At the same time, it is also evolutionarily advantageous to be incubated faster than its egg neighbors in the nest. Given that there is a direct relationship between the incubation time and the egg weight (W) or size (Rahn and Ar, 1974; Ar and Rahn, 1978; Deeming et al., 2006) and thus a larger egg should spend more time till the hatch, a paradox exists. That is, it is both evolutionarily advantageous and disadvantageous for cuckoos to have larger eggs than that of their hosts. In nature cuckoo chicks do indeed hatch ahead of their nestmates (Gill, 1980; Briskie and Sealy, 1990; Strausberger, 1998; Birkhead et al., 2011; Igic et al., 2015; Cao et al.,

62 2018). Many studies have been devoted to uncovering the causes for this phenomenon, with its most

63 studied and popular prerequisite being accelerated cuckoo chick embryo development in an already

64 formed but not yet laid egg, i.e. located in the mother cuckoo's body (Liversidge, 1961; Perrins, 1967;

65 Birkhead et al., 2011). Applied mathematical modelling approaches have also been used to explore the

66 brood parasitism phenomenon (e.g., Wang et al., 2016; Pradeep et al., 2016).

67 Such an adaptive feature of brood parasitism in cuckoos, i.e., the egg incubation beginning while still in

68 the mother's body, is crucial for reducing I in the host nest; however, it is not always feasible in practice.

69 Indeed, the cuckoo has to adapt to the egg's adoptive parents, synchronizing the laying of its eggs with

70 those already in the nest (e.g., Moskàt et al., 2006). Such a synchronization requires the cuckoo to make

71 a prompt decision to lay an egg in an "emergency", which does not always include a sufficiently long

72 incubation of the egg inside the mother's body.

73 In this respect, other (alternative) prerequisites should be considered to explain the possible reasons for

74 the reduction in I for eggs of brood parasite species. One possibility in this regard involves adaptive

75 changes in the structure of the yolk, as it is the main source of vital substances, including energy reserves

76 (Török et al., 2004; Igic et al., 2015; Cao et al., 2018). Geltsch et al. (2016) provided evidence that the

77 explanation may be relatively simple in that the majority of cuckoo eggs are laid before host incubation

78 begins; however, this may only be a contributory factor, among several others.

79 In studies to assess the differences between the eggs of brood parasites and their hosts, many researchers

80 have noted that the shell thickness (T) of the former is somewhat greater than that of the latter (Spaw and

81 Rohwer, 1987; Brooker and Brooker, 1991; Antonov et al., 2006; Pujol and Mermoz, 2011; Igic et al.,

82 2011, 2017; Holleley et al., 2022). Moreover, such an excess in T is observed even when the eggs of both

83 species are of the same size. It would seem, given the fierce struggle for the survival of parasitic species,

84 the most likely hypothesis of a thicker shell of parasite eggs is protection from damage to such an egg by

85 the hosts trying to break, or at least puncture, it (Spaw and Rohwer, 1987; López et al., 2023) leading to

4

86   proposition of the '*puncture resistance hypothesis*' (e.g., Holleley et al., 2022). A number of authors

87   have, however, suggested that, to a greater extent, the thicker shells of brood parasites are associated not

88   with protection from damage to the eggs by the beak of the nest owners, but in order to reduce risk of

89   damage to the eggs "when eggs are dropped into nests" (Holleley et al., 2022), or "to protect the parasite's

90   egg from damage if the nest is multiply parasitized" (Brooker and Brooker, 1991). Igic et al. (2017)

91   suggested that a thicker shell enables developing embryos to consume more calcium and other minerals

92   contained in its structure. However, as a result of the research, this version was rejected due to the fact

93   that the decalcification of the shell in cuckoo eggs was no different from the eggs of the hosts.

94   Another hypothesis was put forward by Ian Wyllie (1981) suggesting that, either before or during

95   incubation, a cuckoo's thick eggshell may help to prevent heat loss, which could hasten the development

96   of the embryo. Yang et al. (2018) agreed with Wyllie's assumption by stating that "the unusually thick-

97   shelled eggs laid by parasitic cuckoos retain more heat for the developing embryo and thus facilitate early

98   hatching." To test this supposition, Yang et al. (2018) measured shell temperature during incubation of

99   host and cuckoos' eggs. As a result, the authors confirmed that the shell temperature of cuckoo eggs was

100 higher than that of host eggs.

101 Confirmation of this hypothesis was also found in studies conducted on poultry eggs. For example,

102 Lourens et al. (2007) demonstrated that higher shell temperatures in chicken eggs decreased hatch time.

103 In a study conducted by Yamak et al. (2016) when incubating eggs of chukar partridge (*Alectoris chukar*),

104 the authors, although not finding significant differences in I, noted, however, that "thin-shelled eggs had

105 a relatively longer hatching period than medium- and thick-shelled eggs." Undoubtedly, this premise

106 requires a more thorough analysis by involving in research as many eggs of different species as possible.

107 In a series of our previous studies (Narushin et al., 2024a,b,c), we demonstrated that I of eggs in various

108 bird species is associated not only with their W or volume (V), but also with the ratio of different

109 geometric parameters. For example, this can be the egg surface area-to-volume ratio (S/V), the value of

110 which can conditionally characterize the metabolism of the developing embryo. It is unlikely that the S/V

111 value can be used in relation to the shortened I of cuckoo eggs. Most often, these eggs either correspond

112 to, or exceed, the S and V values of the host eggs. According to our results (Narushin et al., 2024b), the

113 larger the egg size, the lower the S/V value and, therefore, the longer I. It is possible that other parameters,

114 especially the relationships between these indicators, also influence the period of incubation

115 development.

116 Considering the promising direction of research into the possible effect of T on I, a more thorough study

117 of this relationship, taking into account other egg characteristics, could be of special interest. In

118 particular, this can include the ratio of T with other egg parameters. Many works have shown sufficient

119 effectiveness of this relationship. For instance, the ratios of T^2/W (Juang et al., 2017) or T/R (where R is

120 the egg curvature radius) or some mathematically transformed set of geometric dimensions (Macleod et

121 al., 2006; Ma et al., 2008; Zhang et al., 2017) can characterize the shell strength traits.

122 The objective of this study, therefore, was to assess the relationship between the duration of incubation

123 of bird eggs depending on the ratio of their morphological parameters. This was followed by

124 substantiation of their possible effect on the shortened development time of the cuckoo embryo and/or

125 other parasitic species.

126

2. Material and methods

128 The experimental work was carried out in two stages. Initially, we assessed the possibility of predicting

129 the value of I depending on the geometric and/or physical egg parameters of wild bird species.

130 Methodologically, work on measuring parameters such as shell thickness (T) and its weight (W_s) requires

131 destructive approaches, which is unacceptable in view of the existing wildlife protection regulations. In

132 this regard, we decided to use published data, with the most extensive database of oomorphological

133 information being contained in the reference book by Schönwetter (1960–1992). Particularly important

134 is the fact that Schönwetter (1960–1992), in addition to oomorphological parameters, also placed many

135 images of bird eggs. This enabled to carry out the necessary geometric measurements of the required

136 parameters as follows: the egg's length (L), maximum breadth (B), diameter (D_p) at the point where the

137 pointed end is $L/4$ away from the egg's center, and the distance w that the B axis is moved from the egg's

138 center to the point where the egg is $L/2$ away (Narushin et al., 2021, 2023). The measured values allowed

139 us to calculate the volume (V) and surface area (S) of the eggs using the formulae from Narushin et al.

140 (2024d):

141

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

(1)

143

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

145

146 The procedure for measuring images of bird eggs was described in detail by us in the results of our

147 previous studies (Narushin et al., 2024a,b). Briefly, the egg image was measured in pixels using an

148 electronic ruler in Microsoft Office Picture Manager. The pixel measurements were then converted to

149 cm according to the metric egg length data given in the tables of Schönwetter (1960–1992).

150 In addition to geometric dimensions, data from Schönwetter (1960–1992) on egg weight (W), shell

151 thickness (T) and shell weight (W_s) were used in the present analysis.

152 Information on I values was gathered from publicly accessible ornithological websites located online

153 (e.g., Avibase 2003, Celebrate Urban Birds 2016, Animal Diversity Web 2020, Project FeederWatch

154 2021, eBird 2023, Macaulay Library 2023, Bird Academy 2024, Birds of the World 2024, Great

155 Backyard Bird Count 2024, NestWatch 2024).

156 Schönwetter included pictures of 434 eggs from 433 bird species in his oological reference book (1960–

157 1992). The relatively narrow egg weight (*W*) range of eggs with available images—from 1 to 100 g—

158 was a limitation of Schönwetter's investigation, despite the vast diversity of data he was able to gather.

159 We were missing data on birds laying eggs with larger *W* values, which would have allowed for a more

160 thorough examination. In these cases, we relied on photos of these eggs that we retrieved from other

161 sources, such as the digitized collection of images of bird eggs from the Natural History Collections of

162 the Museum Wiesbaden (Wikimedia Commons, 2014), while using the numerical values of these eggs

163 from the reference book by Schönwetter (1960–1992). This resulted in 454 eggs altogether, representing

164 447 bird species, 95 families, and 13 orders.

165 Correlation analysis made it possible to evaluate the most significant relationships between the *I* value

166 depending on combinations of *T* and other parameters of avian eggs. The data that showed the closest

167 correlation were approximated by formulae for calculating *I*.

168 The task of the second research stage was to practically test the equations for calculating *I* obtained in

169 the first stage. For these purposes, in the available scientific publications, we selected photographs of

170 cuckoo eggs along with host eggs, allowing us to measure their geometric parameters. To conduct a

171 comparative analysis, we used images of eggs of the following parasitic species and their hosts from the

172 respective sources:

173 1. Common cuckoo (*Cuculus canorus*) eggs were compared with great reed warbler (*Acrocephalus*

174 *arundinaceus*) eggs depicted by Moskàt et al. (2009, 2012) and Bán et al. (2011).

175 2. Common cuckoo (*Cuculus canorus*) eggs were compared with European robin (*Erithacus rubecula*)

176 eggs as reported by Bán et al. (2011).

177   3. Plaintive cuckoo (*Cacomantis merulinus*) eggs were compared with rufescent prinia (*Prinia*

178   *rufescens*) eggs presented by Liang et al. (2017) and Yang et al. (2021).

179   4. Plaintive cuckoo (*Cacomantis merulinus*) eggs were compared with those of the common tailorbird

180   (*Orthotomus sutorius*) reported by Yang et al. (2021).

181   To convert pixels into cm, we used the reference of the host egg to its real size, presented either by the

182   authors of the respective publication, or, in the absence of such data, in the handbook by Schönwetter

183   (1960–1992) or in another source. Information about *T* of both types of eggs was taken from the same

184   sources. This approach made it possible to maintain the proportions between specific eggs of the cuckoo

185   and the hosts when converting them into metric measurement systems.

186   A number of statistical and mathematical procedures, which can be found in the STATISTICA 5.5

187   program (StatSoft, Inc./TIBCO, Palo Alto, CA, USA) and applications for the Microsoft Excel program,

188   were utilized to process the data. Here, the Pearson correlation coefficient (*R*) and regression models

189   employing the coefficient of determination (R^2) were used to evaluate the validity of the found

190   associations, with significance being confirmed at the $p < 0.05$ level.

191

192   **3. Results and discussion**

193   *3.1. Effects of T on I of bird eggs*

194   When performing correlation analysis of various egg traits, our main attention was focused on the

195   relationship between egg parameters that indirectly characterize certain physiological, biological and/or

196   physical processes that influence embryonic development. As expected, the strongest relationship was

197   observed between the incubation period (*I*) and the *S*/*V* ratio, which indirectly characterizes the

198   metabolism level of the developing embryo (Narushin et al. 2024a,b). Despite the fact that the present

199   research used a different database of egg images from the reference book by Schönwetter (1960–1992)

than that from Museum Wiesbaden images (Wikimedia Commons, 2014) in the previous study (Narushin et al. 2024b), the nature of the relationship between I and S/V (Fig. 2) and the resultant calculation formula echoed the outcome produced by Narushin et al. (2024b).

In particular, according to Narushin et al. (2024b) who used the Museum Wiesbaden images (Wikimedia Commons, 2014):

$$I = 32.638\left(\frac{S}{V}\right)^{-0.635}, \tag{3}$$

with $R^2 = 0.725$ ($p < 0.05$),

where I is measured in days, S in cm^2, and V in cm^3.

The current investigation based on the egg images from the reference book by Schönwetter (1960–1992) resulted in the following similar mathematical dependence (shown as a yellow line in Fig. 2):

$$I = 31.071\left(\frac{S}{V}\right)^{-0.598}, \tag{4}$$

with $R^2 = 0.726$ ($p < 0.05$).

To create a single mathematical calculation algorithm, we decided to combine both above equations (Eqns 3 and 4). As a result, a universal dependence was obtained, the practical use of which did not affect the decrease in the accuracy of the calculations, both current and previous (Narushin et al. 2024b) data:

220

$$I = 32\left(\frac{S}{V}\right)^{-0.6} \tag{5}$$

with $R^2 = 0.726$ ($p < 0.05$).

Furthermore, we paid the closest attention to the analysis of ratios containing T and revealed their inverse relationship with the value of I, i.e., reducing I when increasing T. Among these, we selected the ratios of T/S ($R = -0.585$, $p < 0.05$) and T/V ($R = -0.565$, $p < 0.05$) and the geometric mean between the main dimensional characteristics of the egg, i.e., $T/(SV)^{0.5}$ ($R = -0.579$, $p < 0.05$). The highest correlation was noted between I and T/S (Fig. 3), based on of which the following calculation formula was derived:

$$I = 99\left(\frac{T}{S}\right)^{-0.91} \tag{6}$$

with $R^2 = 0.602$ ($p < 0.05$),

where I is measured in days, S in cm^2, and T in μm.

Considering the hypothesis suggested by Yang et al. (2018) to explain the reasons for thicker shells in eggs of cuckoos and/or other parasitic species, i.e., as a way to keep more heat inside the egg, it can be assumed that the T/S index characterizes the physical feature of the egg in retaining heat along its outer surface.

3.2. Comparative analysis of the parameters of cuckoo eggs and their hosts

Using the T values taken from Schönwetter (1960–1992) and after averaging the results presented there, this parameter equaled 0.098 and 0.08 mm for the shells of two parasitic species, common cuckoo (*Cuculus canorus*) plaintive cuckoo (*Cacomantis merulinus*), respectively. Among four host species, it was equal to 0.082 mm in the great reed warbler (*Acrocephalus arundinaceus*), being almost completely consistent with the values given by Picman and Honza (2020); 0.08 mm in the European robin (*Erithacus rubecula*); 0.063 mm in the rufescent prinia (*Prinia rufescens*); and 0.0563 mm in the common tailorbird (*Orthotomus sutorius*). The results of the calculation of the averaged main parameters pertaining to the compared species, their eggs and incubation time are given in Table 1.

The limited sampling of available images of cuckoo eggs and hosts that would allow for a full comparative analysis prevented us from unambiguously judging the significance of the differences between a number of parameters and their relationships. However, the following general trends can be observed for all parasite–host pairs of the species considered:

1. The average value of V, although in some cases not by much, still exceeded that of the hosts.
2. The S/V ratio in cuckoo eggs was lower than that in host eggs, which, according to our previous studies (Narushin et al., 2024b), should lead to an increase in incubation time in comparison with host eggs.
3. The T/S ratio of cuckoo eggs was greater than that of hosts, despite the fact that the S value was greater than that of hosts. That is, this effect occurred due to the thicker shell of cuckoo eggs.
4. The calculated value of I for cuckoo eggs was approximately 0.5 to 1.5 days less than that for host eggs.

Thus, there seems to be a certain fine line in the mother cuckoo's ability to form the "correct" egg, from the viewpoint of nest parasitism. A skew in the egg's characteristics, either in one direction or the other, is undesirable, as it calls into question the survival of her offspring. It is inconceivable that the cuckoo

12

264 subjects its actions to complex mathematical calculations and analyses that help her form an egg with

265 clearly defined parameters suitable for a specific host nest. However, we do believe that most likely her

266 reproductive behavior is instinctively "guided" by the evolutionarily fixed experience of many past

267 generations adapted to nest parasitism. Since we do not have such an ability to judge this directly, herein

268 are our efforts to follow a similar analytical path using strict mathematical logic.

269

270 *3.3. Evolutionary adaptation or a clear mathematical calculation?*

271 In addition to achieving similarity in the shell pigmentation with the eggs of the owners of the nest, the

272 mother cuckoo faces another dilemma: how to shape the egg in such a way that it is the same size or

273 slightly larger in size than that of the hosts. This thereby provides the cuckoo with an evolutionary

274 advantage in nestling weight after hatching, and, at the same time, reduces the period of its incubation.

275 Considering this problem from a mathematical point of view, we have the value of *I*, i.e., the standard

276 incubation time of eggs, depending on their size, or rather, on the *S*/*V* ratio, which indirectly characterizes

277 embryonic metabolism (Narushin et al., 2024b). The calculation of the standard value of *I* can be done

278 according to formula (5). For the convenience of further analysis, we will slightly transform Eqn5,

279 expressing the value of *S* via *V*. Undoubtedly, the accuracy of the calculation will be somewhat reduced,

280 however, this fact will not affect the reliability of consequent mathematical logic.

281 In our previous work (Narushin et al., 2024d), we derived a universal relationship between *S* and *V* that

282 is characteristic of an egg of any shape found in nature:

283

284 $$S = \left[6.438 - 2.666\frac{B}{L} + 1.867\frac{w}{L} - 0.44\frac{D_p}{B} - 0.134\frac{D_p}{L} - 0.683\frac{B}{L}\cdot\frac{w}{L} - 2.578\frac{w}{L}\cdot\frac{D_p}{B} + 1.29\frac{w}{L}\cdot\frac{D_p}{L} + 1.369\left(\frac{B}{L}\right)^2 + 0.336\left(\frac{w}{L}\right)^2 + 0.233\left(\frac{D_p}{B}\right)^2 \right] V^{\frac{2}{3}}$$

285 (7)

286

287   where B is the egg's breadth, L is its length, w is the distance that the B axis is moved away from the egg's

288   center to the point $L/2$, and D_p is diameter at the point where the pointed end is $L/4$ away.

289   Simplifying Eqn7 and substituting the following average values of the respective coefficients: $B/L =$

290   0.736; $w/L = 0.05$; $D_p/B = 0.794$, obtained as a result of our measurements of bird egg images. Then,

291   Eqn7 will take the following form:

292

293    $$S = 4.941V^{\frac{2}{3}}.$$ (8)

294

295   Taking into account the resultant formula (8), Eqn5 is transformed into the following:

296

297    $$I = 12.27V^{0.2},$$ (9)

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

299

300   In a similar way, we transform another dependence to predict the I value, according to formula (6):

301

302    $$I = 423.65T^{-0.91}V^{0.61},$$ (10)

303   where T is measured in μm.

304

305   Conventionally, Eqns 9 and 10 reflect the standard dependence of I relevant to the size (V) and T of a

306   specific egg, in particular, within the framework of our conditions, the host egg.

14

307   Now considering the following "endeavor" of the mother cuckoo:

308   (i) Assume that she wants to reduce the value of I by at least 1 day.

309   (ii) In this case, the size (volume) of her egg should be greater than the volume of the host egg (V). Let

310   us express this condition in such a way that the volume of a cuckoo egg is equal to $K_V V$, where K_V is

311   a certain coefficient whose value is greater than 1.

312   (iii)   The only way for the cuckoo to achieve the above conditions is to increase the shell thickness

313   in comparison with the shell thickness (T) of the host eggs. Again, this condition can be written

314   mathematically as the product of T by a certain coefficient K_T, the value of which is also greater than

315   1.

316   Mathematically, the cuckoo's "endeavor" to shorten I can be expressed by the following relationship

317   based on Eqn10:

318

319     $$I - 1 = 423.65 (K_T T)^{-0.91} (K_V V)^{0.61} \qquad (11)$$

320

321   The difference and some mathematical transformations of formulae (10) and (11) allows us to obtain the

322   relationship between the coefficients K_T and K_V:

323

324     $$K_T = \left(1 - 0.00236 T^{0.91} V^{-0.61}\right)^{-1.1} K_V^{0.67} \qquad (12)$$

325

326   Again, for simplicity of analyzing formula (12), we express the T value in terms of V using the calculation

327   data for egg images from the oological reference book by Schönwetter (1960–1992):

15

328

329 $$T = 51.06 V^{0.45},\tag{13}$$

330 with $R^2 = 0.970$ ($p < 0.05$),

331 where T is measured in μm, and V in cm^3.

332

333 Substituting Eqn13 into formula (12), we obtain:

334

335 $$K_T = \left(1 - 0.085 V^{-0.2}\right)^{-1.1} K_V^{0.67}.\tag{14}$$

336

337 Then, dependence (14) can be presented graphically as shown in Fig. 4 where, for example, we chose

338 three options for V: 1, 2, and 3 cm^3.

339

340 Despite some possible errors in the dependence of the coefficients K_T and K_V caused by the assumptions

341 we made in the prediction calculations of the values S (Eqn8), I (Eqn10) and T (Eqn13), it can be

342 unequivocally stated that in order to shorten the incubation time I, the cuckoo needs to lay eggs with

343 thicker shells. In our example, a reduction in the I value by 1 day, even when laying an egg with the same

344 V value as that of the hosts of the nest, requires an increase in T by 8-10% depending on the size of the

345 egg (V). At the same time, the analysis of Eqn14 and Fig. 4 suggests that changing V by 2- or even 3-

346 fold did not significantly change the numerical values of K_T relative to the values of K_V,. All three lines

347 of functional relationship practically coincide (Fig. 4). In this case, the coefficient of T increase (K_T) is

348 approximately proportional to the coefficient of V increase (K_V) to the power of 2/3. This relationship

349 warrants that the cuckoo nestling hatching 1 day earlier than the chick (or chicks) of the nest owners.

350   Considering that our comparative calculations of the *I* value for cuckoo eggs and their hosts (section

351   "*Comparative analysis of the parameters of cuckoo eggs and their hosts*") demonstrated an average 1

352   day difference in *I*, we can test the adequacy of the derived dependence (14) for the coefficients K_T on

353   K_V. Taking, for example, the data on the calculation for eggs of the common cuckoo (*Cuculus canorus*)

354   and its host, the great reed warbler (*Acrocephalus arundinaceus*), due to the greater representativeness

355   of this sample, numbering 21 eggs in each species. The average *V* value of great reed warbler eggs,

356   according to our measurements, was 3.0 cm^3, and that of the common cuckoo was 3.3 cm^3, or 1.1 times

357   more, i.e., the value of $K_V = 1.1$. The *T* value for the great reed warbler was taken to be 82 μm, and that

358   for the common cuckoo 96 μm (Schönwetter, 1960–1992). Thus, the K_T value was 1.17. Recalculation

359   of the theoretical value of K_T according to Eqn14 gave a similar result $K_T = 1.15$. Such ratios of

360   parameters led to the fact that the estimated incubation time of common cuckoo eggs was 13.6 days,

361   while that of great reed warbler was 15 days.

362

363   *3.4. Calculation of I for avian eggs*

364   Thus, based on both previous (Narushin et al., 2024a,b) and current studies, it can be argued that the

365   duration of incubation of bird eggs depends on two indices expressed by the ratio *S*/*V* and *T*/*S*. Our natural

366   instinct was to combine the results of current and previous calculations, proposing a single, most adequate

367   dependence that enables to predict the *I* value most accurately. As a result of approximation of the

368   obtained measurements and/or calculations of the values of *V*, *S* and *T*, we derived the following

369   relationship:

370

371   $$I = 33.83\left(\frac{S}{V}\right)^{-0.56} \cdot \left(\frac{T}{S}\right)^{-0.06} \tag{15}$$

17

372   with $R^2 = 0.727$ ($p < 0.05$),

373   in which I is measured in days, S in cm^2, V in cm^3, and T in μm.

374

375   The results of the present research and subsequent theoretical analysis suggested that T can have a

376   significant impact on the duration of incubation. To a greater extent, the value of I is determined not even

377   by T, but by the T/S ratio. The higher the value of this ratio, the less time the bird spends incubating

378   future chicks. The T/S index seems to have multiple effects on the bird's egg. In addition to the effect on

379   I, T/S indirectly expresses the strength properties of the shell, whereas many researchers prefer to use in

380   this ratio a complex of geometric dimensions of the egg instead of just the S value (Macleod et al., 2006;

381   Ma et al., 2008; Zhang et al., 2017). The mother cuckoo seems to have adapted to skillfully use the T/S

382   indicator with maximum efficiency, increasing its value in her eggs. A stronger shell prevents mechanical

383   damage to the egg when laid in another nest (Holleley et al., 2022), or in case of possible aggression

384   from the hosts (Spaw and Rohwer, 1987; López et al., 2023). At the same time, early hatching makes it

385   possible for the cuckoo nestling to eliminate competition from the host chicks by force. Namely, in view

386   of the use of force by the cuckoo nestling to neutralize competitors, the mother cuckoo is possibly

387   inclined to increase the T/S ratio not at the expense of reducing S, which affects the size of the egg, but

388   by increasing T. After all, to use a force ejection action, the cuckoo chick should be no smaller than, and,

389   if possible, somewhat larger in size than other host nestlings.

390   As part of our measurements and further calculations (Table 1), we discovered that I for eggs of two

391   cuckoo species, common cuckoo (*Cuculus canorus*) and plaintive cuckoo (*Cacomantis merulinus*), was

392   0.5 to 1.5 days less than that for eggs of four hosts: great reed warbler (*Acrocephalus arundinaceus*),

393   European robin (*Erithacus rubecula*), rufescent prinia (*Prinia rufescens*), and common tailorbird

394   (*Orthotomus sutorius*).

395

4. Conclusions

Collectively, the following suggestions can be drawn from the results of our research. Firstly, the *T*/*S* index, reflecting the ratio of eggshell thickness to its surface area, is an indirect indicator of the duration of incubation of bird eggs. At the same time, an increase in this indicator leads to a decrease in hatching time. Secondly, based on geometric measurements of egg images from 447 species and information on the value of *T* from the oological reference book by Schönwetter (1960–1992), we derived an empirical relationship that enabled to calculate the value of *I* (Eqn6). Thirdly, through a comparative analysis of cuckoo eggs and their hosts, we confirmed the hypothesis that *I* of cuckoo eggs is reduced due to the greater *T*/*S* value. Most likely, the adaptive ability of cuckoos somehow to adjust this indicator is only one on the list of "tricks" used by cuckoos to hatch their offspring earlier. Fourthly, considering the presence of a few indicators based on the parameters of a bird's egg to predict the *I* value, we proposed an empirical calculated dependence of *I* on the ratios *S*/*V* and *T*/*S* (Eqn15). Our findings provide more insight into the ways in which cuckoos adapt to specific brood parasitism and host-parasite relationships.

Ethical aspects

Importantly, due to the currently existing protection and research ethics restrictions aimed to prevent human impact on wildlife, we did not directly examine the nests and eggs of wild avian species in the natural conditions. Instead, we used the previously published data available in the ornithological literature and web resources.

CRediT authorship contribution statement

V.G. Narushin: Conceptualization, Methodology, Investigation, Visualization, Project administration, Writing – original draft, Writing – review & editing. **M.N. Romanov:** Visualization, Project

418 administration, Writing – original draft, Writing – review & editing. **N. Avni-Magen:** Writing – review

419 & editing. **D.K. Griffin:** Validation, Visualization, Supervision, Writing – review & editing.

420 **Declaration of competing interest**

421 Authors declare that they have no competing interests.

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427

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607

608   **Table 1.** Values of the main egg parameters and their incubation periods for four pairwise cuckoo–host

609   species comparisons.

Parameters	Cuckoo	Host
Comparison 1	Common cuckoo (*Cuculus canorus*) $n = 21$	Great reed warbler (*Acrocephalus arundinaceus*) $n = 21$
Egg volume, V (cm^3)	3.3	3.0
Egg surface area, S (cm^2)	10.9	10.3
S/V (cm^2/cm^3)	3.3[a]	3.5[a]
T/S (µm/cm^2)	8.9[a]	8.0[a]
Estimated incubation period according to Eqn6, I (days)	13.6[a]	15.0[a]
Standard average incubation period for host eggs according to Planet of Birds (2011)		14
Comparison 2	Common cuckoo (*Cuculus canorus*) $n = 1$	European robin (*Erithacus rubecula*) $n = 1$
Egg volume, V (cm^3)	2.4	2.3
Egg surface area, S (cm^2)	8.8	8.5
S/V (cm^2/cm^3)	3.7	3.7

T/S (μm/cm^2)	10.2	9.4
Estimated incubation period according to Eqn6, I (days)	12.0	12.9
Standard average incubation period for host eggs according to Bouglouan (2024)		13

Comparison 3	Plaintive cuckoo (*Cacomantis merulinus*) $n = 4$	Rufescent prinia (*Prinia rufescens*) $n = 8$
Egg volume, V (cm^3)	1.7[a]	1.3[a]
Egg surface area, S (cm^2)	7.0[a]	5.8[a]
S/V (cm^2/cm^3)	4.1[a]	4.6[a]
T/S (μm/cm^2)	11.4	10.9
Estimated incubation period according to Eqn6, I (days)	10.8	11.3
Standard average incubation period for host eggs according to Krishnan (2021)		12

Comparison 4	Plaintive cuckoo (*Cacomantis merulinus*) $n = 2$	Common tailorbird (*Orthotomus sutorius*) $n = 2$

Egg volume, V (cm^3)	1.6	1.1
Egg surface area, S (cm^2)	6.7	5.3
S/V (cm^2/cm^3)	4.3	4.8
T/S (μm/cm^2)	12.0	10.7
Estimated incubation period according to Eqn6, I (days)	10.3	11.5
Standard average incubation period for host eggs according to Chan (2012)		12

610   n is the quantity of egg images taken for the analysis.

611   [a] Significance of pairwise parameter comparisons ($p < 0.05$); the values without superscript index are

612   insignificant.

613

Figure legends

Fig. 1. A mimicking egg of the common cuckoo nominate subspecies (*Cuculus canorus canorus*; left) in a clutch of Marmora's warbler (*Curruca sarda*; right). Image source: https://commons.wikimedia.org/wiki/File:Cuculus_canorus_canorus_MHNT.ZOO.2010.11.150.36.jpg; collection of Jacques Perrin de Brichambaut, Muséum de Toulouse, France; by Ercé, CC-BY-SA-4.0.

Fig. 2. Visualization of data approximation of the relationship between the incubation period value (I) and the egg surface area-to-volume ratio (S/V).

Fig. 3. Visualization of data approximation of the relationship between the incubation period value (I) and the shell thickness-to-egg surface area ratio (T/S) according to Eqn6.

Fig. 4. Visualization of the mathematical relationship between the coefficients K_T and K_V depending on the volume of host eggs: $V = 1, 2$ and 3 cm^3.
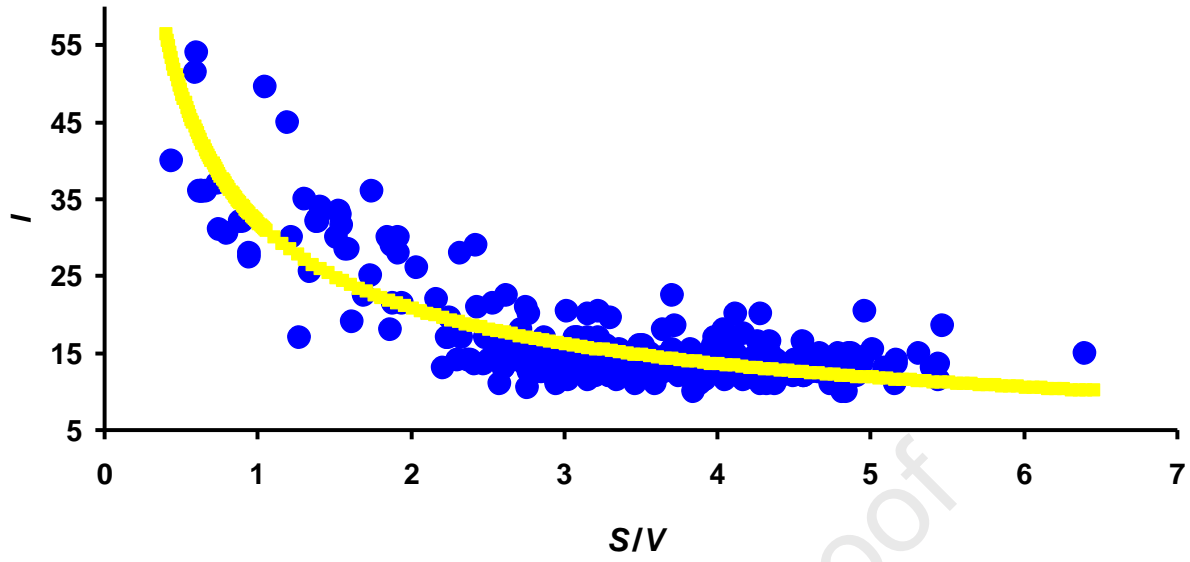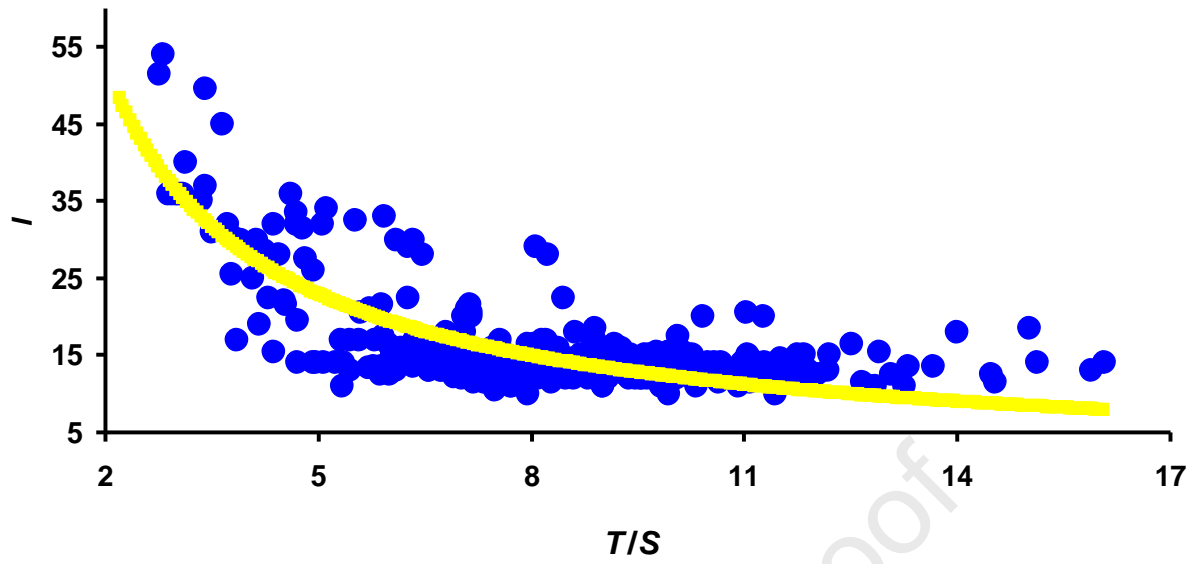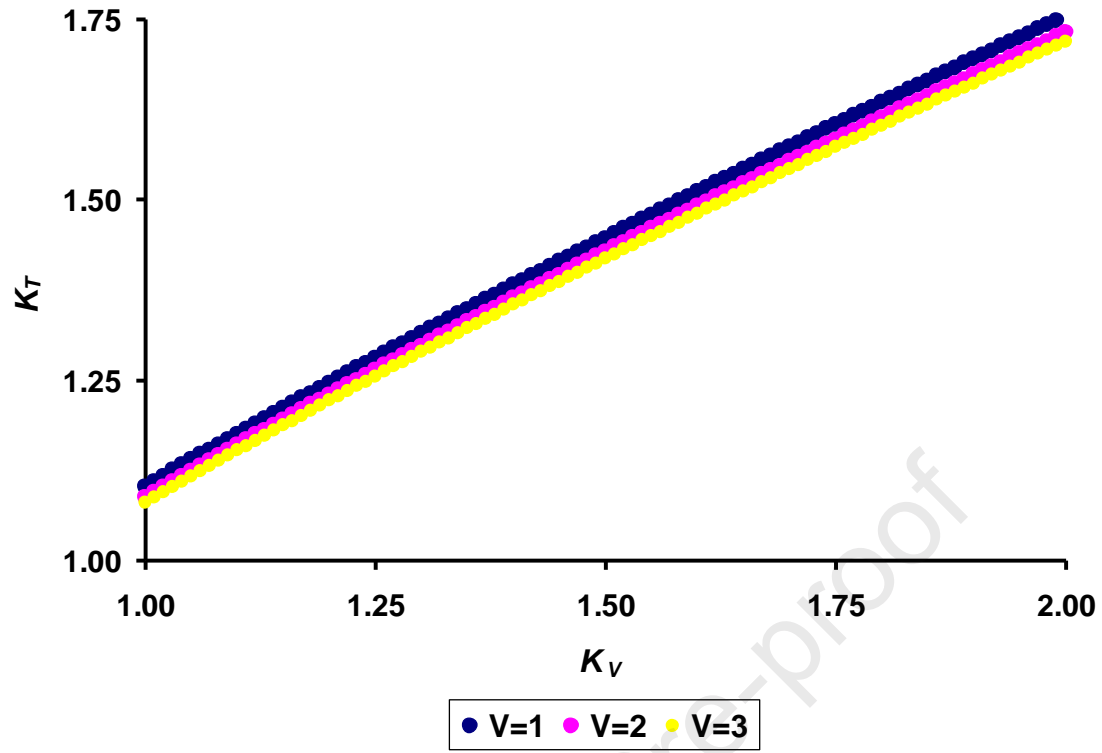
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Fig. 1.

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Fig. 2.

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Fig. 3.

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637   **Fig. 4.**

- We assumed that cuckoo eggs have shorter incubation time (*I*) due to thicker shells.
- To test this, we analyzed published data for 454 eggs from 447 bird species.
- We found that *I* can be determined by shell thickness-to surface area ratio (*T/S*).
- Mother cuckoo seems to be adapted to increasing the *T/S* ratio by increasing *T*.
- We derived empirical formulae for calculating *I* based on *S/V* and *T/S* ratios.

Conflict of interest

Authors declare that they have no competing interests.