Host species determines egg size in Oriental cuckoo

S. G. Meshcheryagina, A. Mashanova, G. N. Bachurin, I. S. Mitiay & M. G. Golovatin

1 Institute of Plant and Animal Ecology, Ural branch of the Russian Academy of Sciences, Ekaterinburg, Russia
2 University of Hertfordshire, Hatfield, UK
3 Scientific and Practical Center of Biodiversity, Irbit, Russia
4 National University of Life and Environmental Science of Ukraine, Kyiv, Ukraine

Abstract

The Oriental cuckoo Cuculus optatus is an obligate brood parasite associated with species of the genus Phylloscopus. Four distinct phenotypes of Oriental cuckoo eggs, matching eggshell colour patterns of Arctic warbler Phylloscopus borealis, common chiffchaff (Siberian) P. collybita tristis, yellow-browed warbler P. inornatus and Pallas’s leaf warbler P. proregulus, have been identified in the Russian part of its breeding area. We compared egg length, breadth and volume of Oriental cuckoo egg phenotypes with eggs of the corresponding hosts from three geographical regions in Russia: the Urals, Siberia and the Far East. We found significant ommetric differences between Oriental cuckoo egg phenotypes. Egg breadth of each cuckoo group matched the egg breadth of the host species, while the length of cuckoo eggs did not match egg length in host species. Our results can be explained in terms of clutch geometry. An egg sticking out above the clutch is likely to be rejected by the host and so breadth should match the host’s egg. An increased egg length might compensate for breadth constraints. We suggest that the size of cuckoo eggs might also be affected by parental care - when only one parent is involved in feeding, eggs need to be larger. This might explain why the longest cuckoo eggs belonged to the phenotype parasitizing the smallest host, Pallas’s leaf warbler, where only one parent feeds the chicks. In our view, differences in egg sizes of Oriental cuckoo phenotypes provide evidence of their adaptations to brood parasitism on small leaf warbler species.

Introduction

The Oriental cuckoo Cuculus optatus Gould, 1845 is an obligate avian brood parasite, widely distributed in the Northern Palaearctic (Payne, 2005; Xia et al., 2016). It is very similar to the Himalayan cuckoo Cuculus saturatus Blyth, 1843 and until recently both were treated as subspecies, C. s. horsfieldi and C. s. saturatus, of the polytypic species C. saturatus (Cramp, 1985; Numerov, 1993, 2003; Johnsgard, 1997). Other junior synonyms include: C. horsfieldi (Payne, 1997; King, 2005), and C. saturatus optatus (Erritzøe et al., 2012). Based on their distributions (saturatus has an Asian distribution compared to the Palaearctic optatus, Johnsgard, 1997; Erritzøe et al., 2012) and song features (King, 2005; Payne, 2005), species status was adopted by the International Ornithological Congress (Gill & Donsker, 2016). Recently, Xia et al. (2016) provided further support for separating C. optatus and C. saturatus into distinct species because of song differences.

Similar to the common cuckoo Cuculus canorus Linnaeus, 1758, females of the Oriental cuckoo lay their eggs into the nests of host species that carry out all aspects of parental care from incubation to fledging. Two to three days after hatching, a cuckoo chick ejects all other eggs or nestlings from the host nest (Cramp, 1985; Numerov, 1993, 2003; Johnsgard, 1997; Payne, 1997; Kruger & Davies, 2004), completely eliminating the reproductive success of the foster parents. It is expected that the host-cuckoo interaction has led to a co-evolutionary arms race (Dawkins & Krebs, 1979). Brood parasites develop morphological and behavioural adaptations to minimize detection by hosts. In turn, hosts develop sensory and cognitive responses to recognize and reject foreign eggs (Davies, 2011).

It is well known that the Oriental cuckoo often exploits leaf warblers from the genus Phylloscopus (Cramp, 1985; Numerov, 1993, 2003; Johnsgard, 1997; Payne, 1997, 2005; Erritzøe et al., 2012). Species of this genus are characterized by small body size (weight 4.5-16.0 g for species breeding in Russia (Cramp & Brooks, 1992; Ryabitsev, 2014)) and correspondingly small egg sizes (0.8-1.4 g (Schonwetter, 1975-1976)), constituting 8-18% of the female weight. Small egg size of the host presumably determines relatively small egg
sized greater breadth would probably inconvenience the sitter.' Meshcheryagina et al. (2016) confirmed that yellow-browed warblers rejected eggs that were broader than a particular threshold. Therefore, we expect that there might be differences in oometric characteristics, in particular in breadth, between Oriental cuckoos parasitizing hosts of different sizes.

It has been genetically proven that races (or gentes) exist in the common cuckoo, with each race specializing on a particular host species (Gibbs et al., 2000; Fossøy et al., 2010, 2011). Females of each race lay eggs matching the hosts’ eggs in eggshell colour and pattern, which are used to distinguish the races (e.g. Moksnes & Roskaft, 1995; Yang et al., 2010; Vikan et al., 2011). It has been suggested that host-specific gentes also exist in the Oriental cuckoo (Kislenko & Naumov, 1967; Balatsky, 1998; Balatsky & Bachurin, 1999).

Using oological material, four eggshell colour phenotypes have been described for the Oriental cuckoo in Russia (Chunihin, 1964; Kislenko & Naumov, 1967; Balatsky, 1991a,b, 1998; Balatsky & Bachurin, 1999; Pukinsky, 2003; Egorov, 2013; Bachurin & Kapitonova, 2014). These phenotypes correspond to the eggs of Arctic warbler Phylloscopus borealis (Pb), common chiffchaff (Siberian) Phylloscopus collybita tristis (Pc), yellow-browed warbler P. inornatus (Pi) and Pallas’s leaf warbler Phylloscopus prorregulus (Pp; see Fig. S1, S2). These host species differ significantly in body weight (Table S1), egg size, and parental involvement in rearing chicks (Gaston, 1974; Schönwetter, 1975-1976; Cramp & Brooks, 1992; Brazil, 2009; Ryabitshev, 2014). In this work, we, for the first time, explored oometric parameters in Oriental cuckoo egg phenotypes in relation to their hosts’ egg sizes. We suggest that the breadth of cuckoo eggs is constrained by the host egg breadth, but their length might also be affected by the level of parental care.

Materials and methods

Study site and species

We used eggs of the Oriental cuckoo and its hosts collected in the eastern part of Russia, including the Urals, Siberia, the Far East and adjacent areas of Kazakhstan (Fig. 1). Cuckoo eggs used in this study were found in the nests of 17 host species (see Table S2 for the full list of host species). Here, we focus on four species of leaf warbler [Arctic warbler, common chiffchaff (Siberian), yellow-browed warbler and Pallas’s leaf warbler] for which the Oriental cuckoo has four mimetic egg phenotypes, differing in colour and pattern of their eggshells. These four species accounted for 71% of parasitic eggs. In our study, we compared Oriental cuckoo eggs only to the host eggs with corresponding eggshell colours. We did not compare cuckoo eggs with other hosts’ eggs (leaf warblers with pure white eggs or eggs with differently coloured spots; species of the genus Sylvia, Tarsiger, Carpodacus, Emberiza).

Data were obtained from field studies, measurements from museum collections, and from the available literature (Table 1). Cuckoo eggs were grouped according to the eggshell colour phenotypes (Table 1).

To check for geographical differences, the data were grouped into three areas: Urals, Siberia and Far East (Table 2). ‘Urals’ included data from Komi Republic, Perm Krai, Sverdlovsk and Chelyabinsk Oblasts. ‘Siberia’ included data from Yamalo-Nenets Autonomous Okrug, Omsk, Novosibirsk, Tomsk and Kemerovo Oblasts, Krasnoyarsk, Altai and Zabaykalsky Krai, Republic of Altai, Khakassia, Tyva, Buryatia and Sakha (Yakutia) as well as adjacent areas of Kazakhstan. ‘Far East’ included data from Chukotka, Magadan, Amur and Sakhalin Oblasts, Khabarovsk and Primorsky Krai (Fig. 1).

General methods

We assigned cuckoo eggs to the same female based on Moksnes et al. (2008). This takes into account the remoteness of nest locations, frequency of egg-laying (laying on the same or the following day indicates that the eggs belong to different females), cases of multiple parasitism (i.e. each female lays only one egg in the same nest) and external egg features (the similarity of ovoid contour, eggshell pattern and, where possible, weight of the dry eggshell).

Latin and English names are given according to Clements et al. (2017).

Field data

Oriental cuckoo eggs (n = 94) were studied between 1999 and 2016 in six locations across all three geographical areas (Table 3).

Museum data

In addition to the field data, we used the Oriental cuckoo eggs and host eggs from the clutches in Russian oological collections: Zoological Museum of The Moscow State University (ZM MU), The State Darwin Museum (SDM, Moscow); Kirov City Zoological Museum (KCMZ); Novosibirsk State Museum of Local History & Nature (NSMLHN), the private collection of N.N. Balatsky (Balatsky’s collection, Novosibirsk); Institute of Plant and Animal Ecology, Ural branch of the Russian Academy of Sciences (IPAE URAN), Zoological Museum of The Urals Federal University (ZM UrFU, Ekaterinburg); private collection ‘Oological bank of cuckoos’ of G.N. Bachurin (Bachurin’s oobank, Irbit).
Oriental cuckoo eggs from oological collections \((n = 42\), Table 4\) were collected in 22 reproductive seasons since 1958 (Meshcheryagina, Bachurin & Bourski, 2017).

**Data from literature**

We obtained further data on Oriental cuckoo eggs \((n = 37)\) and its host species from the available literature and personal field diaries (Table 5). We included only data which had...
Table 2 Sample sizes of Oriental cuckoo eggs and host clutches according to geographical regions

<table>
<thead>
<tr>
<th>Region</th>
<th>Location</th>
<th>Coordinates</th>
<th>Breeding seasons</th>
<th>Egg phenotype</th>
<th>N egg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ural</td>
<td>Near Irbit in Sverdlovsk oblast</td>
<td>57°N, 62°E</td>
<td>2002-2014</td>
<td>Pc</td>
<td>49</td>
</tr>
<tr>
<td>Siberia</td>
<td>Turukhansk district of the Krasnoyarsk Krai</td>
<td>62°N, 88°E</td>
<td>2016</td>
<td>Pc</td>
<td>5</td>
</tr>
<tr>
<td>Far East</td>
<td>Pozharsky district of Primorsky Krai</td>
<td>46°N, 135°E</td>
<td>1999-2001</td>
<td>Pp</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Ussuri district of Primorsky Krai</td>
<td>43°N, 131°E</td>
<td>2015</td>
<td>Pp</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Various locations on Sakhalin island</td>
<td>51°N, 142°E</td>
<td>2008-2011, 2016</td>
<td>Pp</td>
<td>7</td>
</tr>
</tbody>
</table>

Table 3 Number of Oriental cuckoo eggs measured at different locations in the field

<table>
<thead>
<tr>
<th>Region</th>
<th>Location</th>
<th>Coordinates</th>
<th>Breeding seasons</th>
<th>Egg phenotype</th>
<th>N egg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ural</td>
<td>Near Irbit in Sverdlovsk oblast</td>
<td>57°N, 62°E</td>
<td>2002-2014</td>
<td>Pc</td>
<td>49</td>
</tr>
<tr>
<td>Siberia</td>
<td>Turukhansk district of the Krasnoyarsk Krai</td>
<td>62°N, 88°E</td>
<td>2016</td>
<td>Pc</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Ussuri district of Primorsky Krai</td>
<td>43°N, 131°E</td>
<td>2015</td>
<td>Pp</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Various locations on Sakhalin island</td>
<td>51°N, 142°E</td>
<td>2008-2011, 2016</td>
<td>Pp</td>
<td>7</td>
</tr>
</tbody>
</table>

Table 4 Number of Oriental cuckoo eggs measured from oological collections

<table>
<thead>
<tr>
<th>Collections</th>
<th>N cuckoo egg according to eggshell colour phenotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZM MU</td>
<td>ℬ' borealis'              ℬ' colllybita'  ℬ' inornatus' ℬ' proregulus'</td>
</tr>
<tr>
<td>Balatsky's</td>
<td>1                      4                      1                      1</td>
</tr>
<tr>
<td>collection</td>
<td></td>
</tr>
<tr>
<td>ZM UrFU</td>
<td>-                          1                      -                      -</td>
</tr>
<tr>
<td>Bachurin's</td>
<td>1                      8                      3                      11</td>
</tr>
<tr>
<td>oobank</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2                          17                     4                      19</td>
</tr>
</tbody>
</table>

Table 5 Number of Oriental cuckoo eggs from the literature

<table>
<thead>
<tr>
<th>Source</th>
<th>N cuckoo egg</th>
<th>Eggshell colour phenotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field diaries of W. Forstmeier from 1997 to 1999 (Max Planck Institute for Ornithology, Germany)</td>
<td>9</td>
<td>ℬ' borealis'</td>
</tr>
<tr>
<td>Balatsky (1991b, 1998), Zaharov (2006), Kislenko &amp; Naumov (1967), Korelov (1970), Kuzikov (2005), field diaries of S.P. Chunin from 1961 to 1965 (State Darwin Museum, Russia; one of these eggs was described by Makatsch, 1976)</td>
<td>22</td>
<td>ℬ' colllybita'</td>
</tr>
<tr>
<td>Sokolov &amp; Sokolov (1986), Schcherbakov (2012)</td>
<td>2</td>
<td>ℬ' inornatus'</td>
</tr>
<tr>
<td>Kislenko, Leonovich &amp; Nikolaevskij(1990), Litvinenko &amp; Shibaev (1971), field diaries of W. Forstmeier from 1997 to 1999 (Max Planck Institute for Ornithology, Germany)</td>
<td>4</td>
<td>ℬ' proregulus'</td>
</tr>
</tbody>
</table>

Each egg was measured using the Egg Scanner Beta software (Mitiay, 2009). Where measurements were obtained from the literature, the egg volume was calculated using formula \( V = \frac{1}{6} \pi \times b^2 \times l \) (Murav'ev, Suhova & Yudin, 2008).

Statistical analysis

Egg length, breadth and volume of the host species were compared using one-way ANOVA in \( r^3.2.2 \) (R Core Team, 2015). One-way ANOVA was also used to compare egg length, breadth and volume between Oriental cuckoo eggshell colour phenotypes. To avoid pseudo-replication and to reduce the amount of variation within species, the mean values per female were used (Logan, 2010). Initially, we tested the effect of species and region on egg parameters. The effect of region was not significant either on its own or in interaction with species and was removed from the analysis (the details of two-way ANOVA and model comparisons are provided in Table S3). Residuals in the final models were checked for normality using Shapiro-Wilk tests. One cuckoo female had an exceptionally large egg affecting the normality of the residuals. This egg was removed from the analysis and the residuals from all models became normal. Pairwise comparisons were done using Tukey tests. The ratios between the parameters of each egg using the Egg Scanner Beta software (Mitiay, 2009).
cuckoo eggs and corresponding host eggs were calculated using the mean values from the corresponding groups.

To disentangle the effect of host egg size from the effect of host species, ANCOVA was used to investigate the relationships between cuckoo egg breadth and host egg breadth, cuckoo egg length and host egg length, cuckoo egg volume and host egg volume, and cuckoo egg breadth and host egg length. The mean values for host egg size in the nest were used in ANCOVA. Where more than one cuckoo egg was found in the same nest (81 nests, including four with multiple parasitism). We removed the nest with an exceptionally large cuckoo egg and the nests where the cuckoo egg phenotype did not match the host species (n = 8). As there were only three nests for Pb and five nests for Pp, these nests were only used for plotting, while the ANCOVA was done for Pp (n = 56) and Pi (n = 12). After testing the effect of both host egg size and host species, non-significant terms were removed and the models were compared using ANOVA to establish the best-fit model (Crawley, 2005).

Results

Egg length, breadth and volume in host species

All variables differed significantly in host species (length - d.f. = 3, F = 272.9, P < 0.0001, breadth - d.f. = 3, F = 342.3, P < 0.0001, volume - d.f. = 3, F = 431, P < 0.0001). Shapiro-Wilk normality tests of the residuals confirmed that the models were a ‘good fit’ to the data (length - W = 0.996, P = 0.541, breadth - W = 0.996, P = 0.703, volume - W = 0.997, P = 0.811). Pairwise, all four species differed significantly in egg length and egg volume (P < 0.0001 for all pairs for length, and for all but Pp-Pi pair for volume with P = 0.002). For egg breadth, Pp-Pi was the only pair where the difference was not significant (P = 0.234, all other pairs P < 0.0001). All the variables reduced in the order Pb > Pc > Pp > Pi (Fig. 2, Table S4).

Egg length, breadth and volume in oriental cuckoo eggshell colour phenotypes

In cuckoo phenotypes, all variables also differed significantly (length - d.f. = 3, F = 51.77, P < 0.0001, breadth - d.f. = 3, F = 28.2, P < 0.0001, volume - d.f. = 3, F = 17.7, P < 0.0001) with the residuals normally distributed (length - W = 0.994, P = 0.859, breadth - W = 0.986, P = 0.227, volume - W = 0.983, P = 0.119). Pairwise comparison was not consistent between the variables. Breadth was significantly different in all the cuckoo phenotypes (P < 0.0001 for each pair) and the values followed the same order as their host species Pb > Pc > Pp > Pi (Fig. 2). For length, the Pp-Pc pair was not significantly different (P = 0.365), while all other pairs were significantly different (Pc-Pi P = 0.029, P < 0.0001 for all others). The Pp phenotype had the longest eggs, while the length in the other three phenotypes reduced in the same order as in the host species. For volume, Pp was not significantly different from Pb (P = 0.342) and Pc (P = 0.637) while other pairs were significantly different (Pp-Pc P = 0.034, P < 0.0001 for all others).

Ratios between host and cuckoo egg sizes

The ratio between the mean breadth of cuckoo phenotypes eggs and their corresponding host eggs was fairly consistent: 1.22 in Pp, 1.18 in Pi, 1.16 in Pc and 1.15 in Pb. The length of Pp phenotype eggs was disproportionally large compared to those of all other phenotypes with ratios between the mean length of cuckoo eggs and corresponding host eggs as follows: 1.46 in Pp, 1.34 in Pi, 1.23 in Pc and 1.18 in Pb. The ratios between the volumes followed the pattern observed for the ratios of the lengths: 2.25 in Pp, 1.98 in Pi, 1.74 in Pc and 1.62 in Pb.

Figure 2 Mean egg length (a), breadth (b) and volume (c) of the host species (Pb - Phylloscopus borealis, Pc - Phylloscopus collybita tristis, Pi - Phylloscopus inornatus, Pp - Phylloscopus prregrilus, white boxes) and corresponding Oriental cuckoo (Cuculus optatus) eggshell colour phenotypes (grey boxes). The means and confidence intervals are provided in Table S4.
The effect of host egg size and host species on cuckoo egg size

For all four relationships (between cuckoo egg volume and host egg volume, cuckoo egg length and host egg length, cuckoo egg breadth and host egg breadth, cuckoo egg breadth and host egg length), interactions were not significant and were removed from the models (see Table S5 for details). In the relationship between egg lengths, the effect of host species was not significant \( t = 0.408, P = 0.685 \), while the effect of the host egg length was marginally significant \( t = 1.846, P = 0.069 \) (Fig. 3b). After removal of the host species from the model, the effect of the host egg length became significant \( t = 2.24, P = 0.029 \). For the other three relationships, the effect of host egg sizes was not significant (volume-volume: \( t = -0.148, P = 0.883 \) (Fig. 3a); breadth-breadth: \( t = -1.329, P = 0.188 \) (Fig. 3c); breadth-length: \( t = -0.586, P = 0.56 \) (Fig. 3d), while the effect of host species was highly significant \( t = -3.52, P = 0.001 \) for volume-volume, \( t = -5.822 \) for breadth-breadth and \( t = -6.157 \) for breadth-length). After removal of the host egg size parameter from the model, the effect of host species remained highly significant in all three models \( P < 0.0001, t = -5.853 \) for volume-volume, \( t = -8.255 \) for breadth-breadth and breadth-length). In all four models, the reduced model was not significantly different from the full model \( (P = 0.883 \) for volume-volume, \( P = 0.685 \) for length-length, \( P = 0.188 \) for breadth-breadth and \( P = 0.56 \) for breadth-length). Distribution of the residuals in the final models was not different from normal at 95% significance level \( (W = 0.969, P = 0.084 \) for volume-volume, \( W = 0.989, P = 0.81 \) for length-length, \( W = 0.967, P = 0.072 \) for breadth-breadth and breadth-length).

The intercept values for volume (1.964 mL for \( P_c \), 1.672 mL for \( P_i \)) and breadth (13.96 mm for \( P_c \), 12.93 mm for \( P_i \)) of cuckoo eggs fit well within the confidence intervals calculated for the corresponding cuckoo egg phenotypes using all measured eggs (Table S4).

Discussion

We have found that all four host species differed in egg length and volume, while egg breadth in the two smaller leaf warblers (yellow-browed warbler and Pallas’s leaf warbler) was similar.

Figure 3 The best-fit models describing the relationship between cuckoo and host egg volume (a), length (b), breadth (c), and cuckoo egg breadth and host egg length (d). The analysis is based on \( P_c \) and \( P_i \) hosts/cuckoo phenotypes. \( P_b \) and \( P_p \) are shown for illustrative purposes. Circles mark the nests where cuckoo eggs did not match the host egg colour. Dotted lines show confidence intervals estimated for the whole set of cuckoo eggs.
However, egg volume of Pallas’s leaf warbler was significantly larger than that of yellow-browed warbler due to the increased length. A bigger egg containing more nutrients improves offspring quality (Krist, 2011), which is especially important for Pallas’s leaf warbler since only the female feeds the young.

All four egg colour phenotypes in *C. optatus* differed in egg breadth. We suggest that a match between cuckoo and host egg breadth could have evolved as a response to host rejection behavior. It has been shown that a host is likely to reject an egg larger than the rest of the clutch (Marchetti, 1992, 2000). In addition, Meshcheryagina et al. (2016) showed that yellow-browed warbler rejected eggs broader than a certain threshold. The difference in breadth could potentially be identified during incubation using tactile stimuli because a broader egg would stick out above the clutch. We are not aware of behavioral studies investigating which type of stimuli the host uses to detect a broader egg, but our finding of a good match between breadth of the host and the parasite eggs supports the suggestion by Latter (1902) that breadth is an important component of egg mimicry.

Cuckoo eggs of the two larger egg phenotypes parasitizing Arctic warbler and common chiffchaff (Siberian) did not differ significantly in length but differed significantly in volume. Thus, the egg phenotype parasitizing the largest host (Arctic warbler) produced the largest egg to match the size of the host egg. Surprisingly, egg length of an egg phenotype parasitizing the smallest host species (Pallas’s leaf warbler) was significantly larger than in any other egg phenotype, and 46% larger than the host egg length. This was the largest increase in egg length over that of the host; it compares with 34% in yellow-browed warbler (also a small species) and around 20% in larger Arctic warbler and common chiffchaff (Siberian). We suggest that this increase in length compensates for the restriction on egg breadth and allows cuckoos to increase egg volume, thus providing a young cuckoo chick with a good starting weight. Similar differences in egg sizes were found in shiny cowbird *Molothrus bonariensis* (Tuero et al., 2012).

Large egg volume and other egg properties (Krist, 2011) are not the only conditions for providing a young cuckoo chick with sufficient strength to eject the host eggs and chicks. Ejection typically happens 2-3 days after cuckoo chick hatching (Numerov, 1993, 2003) and during this period the cuckoo chick needs to gain weight (Kruger & Davies, 2004). The final weight depends both on the egg properties (Hargitai et al., 2010) and on the feeding intensity. We found that the smallest difference in egg volume between the host and the cuckoo eggs (cuckoo egg 1.62 times larger) was in the egg phenotype parasitizing Arctic warbler, in which both parents feed the young (Cramp & Brooks, 1992; Ryabitsyev, 2014). The largest difference was in the egg phenotype parasitizing Pallas’s leaf warbler (cuckoo egg 2.25 times larger) where only female feeds the young. Yellow-browed warbler is very similar in weight to Pallas’s leaf warbler but, in this case, the male also feeds the young and this is reflected in the ratio of the volumes of cuckoo and host eggs (cuckoo egg 1.98 times larger). In common, chiffchaff (Siberian) feeding might sometimes be provided by both parents and sometimes by the female only, and the ratio between volumes of the cuckoo and host egg volume was intermediate (cuckoo egg 1.74 times larger).

Comparison of the host and cuckoo eggs laid in the same nest showed that the length of cuckoo eggs was increasing with the length of the host egg in common chiffchaff (Siberian) and yellow-browed warbler. This is different from the relationships between breadths and volumes, which were best described as having mean values depending on the host species irrespective of whether host eggs in particular nests were smaller or larger than the mean values. This correlation might be explained by either regional or seasonal differences in both host and cuckoo egg sizes.

We have not found geographical differences in egg sizes either in cuckoo egg phenotypes or in host species. Bán et al. (2011) found differences in the shape of common cuckoo eggs from Hungary and Japan. In our case, populations were not completely isolated from each other and we compared the same phenotypes, while Bán et al. (2011) compared distinct races of common cuckoo separated by a very long distance. Increasing number of locations and sample sizes might lead to identifying distinct local variations in egg sizes within the same cuckoo egg phenotypes.

In conclusion, we collected a large volume of oometric data on Oriental cuckoo egg phenotypes and statistically compared these with the host species oometric data. We have found cuckoo egg breadth to be determined by the host egg breadth, while cuckoo egg length is more closely related to the pattern of care exhibited by host parents. This is a clear example of the co-evolutionary arms race where cuckoo must strictly mimic host species egg colour pattern and breadth but exploits the host’s inability to detect differences in length between its own eggs and those laid by the cuckoo.

**Acknowledgements**

The authors express sincere gratitude to Irina F. Vurdova, Aleksandr A. Ananin, Oleg V. Bourski for the help in field works; to Wolfgang Forstmeier for providing diary data; to Pavel S. Tomkovich, Yaroslav A. Red’ kin, Igor’ V. Fadeev, Ol’ga S. Zaganova for the organization of work in Museum collections, and to Ian Denholm for carefully checking the manuscript. This study was performed within the frameworks of state contract with the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (project no 18-9-4-22).

**References**


Balatsky, N.N. (1991a). Глухая кукушка и её воспитатели в заповеднике Кедровая Падь и его окрестностях [Oriental cuckoo and its hosts in the Kedrovaya Pad nature reserve and the surrounding area]. *Urags* 1, 4-11.


Meshcheryagina, S.G., Golovatin, M.G. & Bachurin, G.N. (2016). Experimental study of discrimination behavior in the yellow-browed warbler (Phylloscopus inornatus) brood-


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

Figure S1. Examples of egg variation in Oriental cuckoo phenotypes (top) and corresponding host species (bottom). I: cuckoo phenotype 'borealis' and *P. borealis*; II: cuckoo phenotype 'collybita' and *P. collybita tristis*; III: cuckoo phenotype 'inornatus' and *P. inornatus*; IV: cuckoo phenotype 'proregulus' and *P. proregulus*.

Figure S2. Oriental cuckoo egg laid in a nest of yellow-browed warbler containing two host’s eggs.

Table S1. Body weight of the host leaf warblers (*Ph - arctic warbler; Pe - common chiffchaff (Siberian); Pi - yellow-browed warbler; Pp - Pallas’s leaf warbler*).

Table S2. The full list of host species in the nests of which eggs of *Cuculus optatus* were found.

Table S3. The effect of region and species on egg length, breadth and volume in Oriental cuckoo and its hosts (two-way ANOVA and model reduction).

Table S4. The means, SD and confidence intervals of cuckoo eggshell phenotypes and their hosts (calculations are based on the average values per female).

Table S5. The effect of host egg parameters and host species on cuckoo egg parameters (ANCOVA with interactions and model reduction).
Table S1 Body weight of the host leaf warblers (*Pb* - arctic warbler; *Pc* - common Chiffchaff (Siberian); *Pi* - yellow-browed warbler; *Pp* - Pallas’s leaf warbler).

<table>
<thead>
<tr>
<th>Source</th>
<th>Mean body weight (*by females during the breeding season), g</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Pb</em></td>
</tr>
<tr>
<td>Brazil, 2009</td>
<td>11.2</td>
</tr>
<tr>
<td>Cramp &amp; Brooks, 1992</td>
<td>9.3*</td>
</tr>
<tr>
<td>Gaston, 1974</td>
<td>10.6</td>
</tr>
<tr>
<td>Ryabitsev, 2014</td>
<td>11.0</td>
</tr>
<tr>
<td>Shaw, 1936</td>
<td>10.0*</td>
</tr>
<tr>
<td>range (all sources)</td>
<td>7.0 - 15.0</td>
</tr>
</tbody>
</table>
Table S2 The full list of host species in the nests of which eggs of *Cuculus optatus* were found.

<table>
<thead>
<tr>
<th>Host species</th>
<th>N clutches (including N clutches with multiple parasitism)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Field data</td>
<td>Museum data</td>
</tr>
<tr>
<td><em>Phylloscopus borealis</em></td>
<td>4 (2)</td>
<td>-</td>
</tr>
<tr>
<td><em>Ph. collybita tristis</em></td>
<td>46 (1)</td>
<td>14</td>
</tr>
<tr>
<td><em>Ph. inornatus</em></td>
<td>22 (2)</td>
<td>4</td>
</tr>
<tr>
<td><em>Ph. proregulus</em></td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td><em>Ph. fuscatus</em></td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td><em>Ph. coronatus</em></td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td><em>Ph. tenellipes</em></td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><em>Ph. schwarzi</em></td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td><em>Ph. trochiloides</em></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Ph. trochilus</em></td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><em>Sylvia curruca</em></td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Tarsiger cyanurus</em></td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><em>Carpodacus erythrinus</em></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>C. roseus</em></td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><em>Emberiza spodocephala</em></td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><em>Emberiza tristrami</em></td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Emberiza rutila</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>outside the host nest</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>
Table S3 The effect of region and species on egg length, breadth and volume in Oriental cuckoo and its hosts (two-way ANOVA and model reduction)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Hosts</th>
<th>Cuckoo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>length</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>269.095</td>
</tr>
<tr>
<td></td>
<td>region</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>species*region</td>
<td>4</td>
</tr>
<tr>
<td>breadth</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>344.696</td>
</tr>
<tr>
<td></td>
<td>region</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>species*region</td>
<td>4</td>
</tr>
<tr>
<td>volume</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>431.215</td>
</tr>
<tr>
<td></td>
<td>region</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>species*region</td>
<td>4</td>
</tr>
</tbody>
</table>

Comparison of models including species, region and interaction between species and region with models including only species (ANOVA, see Crawley, 2005 for details).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Hosts</th>
<th>Cuckoo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>length</td>
<td>0.2856</td>
<td>0.9436</td>
</tr>
<tr>
<td>breadth</td>
<td>1.3571</td>
<td>0.2317</td>
</tr>
<tr>
<td>volume</td>
<td>1.0296</td>
<td>0.406</td>
</tr>
</tbody>
</table>
**Table S4** The means, SD and confidence intervals of cuckoo eggshell phenotypes and their hosts (calculations are based on the average values per female).

<table>
<thead>
<tr>
<th>Species/phenotypes</th>
<th>Length, mm</th>
<th>Breadth, mm</th>
<th>Volume, ml</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>mean</td>
<td>SD</td>
</tr>
<tr>
<td><strong>Host Pb</strong></td>
<td>32</td>
<td>16.39 ±0.61</td>
<td>16.17, 16.61</td>
</tr>
<tr>
<td><strong>Host Pc</strong></td>
<td>95</td>
<td>15.43 ±0.68</td>
<td>15.30, 15.57</td>
</tr>
<tr>
<td><strong>Host Pi</strong></td>
<td>161</td>
<td>13.73 ±0.55</td>
<td>13.65, 13.82</td>
</tr>
<tr>
<td><strong>Host Pp</strong></td>
<td>27</td>
<td>14.31 ±0.51</td>
<td>14.11, 14.51</td>
</tr>
<tr>
<td><strong>Parasite Pb</strong></td>
<td>16</td>
<td>19.40 ±0.61</td>
<td>19.08, 19.73</td>
</tr>
<tr>
<td><strong>Parasite Pc</strong></td>
<td>62</td>
<td>19.06 ±0.78</td>
<td>18.86, 19.26</td>
</tr>
<tr>
<td><strong>Parasite Pi</strong></td>
<td>14</td>
<td>18.44 ±0.77</td>
<td>18.00, 18.88</td>
</tr>
<tr>
<td><strong>Parasite Pp</strong></td>
<td>32</td>
<td>20.86 ±0.73</td>
<td>20.59, 21.12</td>
</tr>
</tbody>
</table>
**Table S5** The effect of host egg parameters and host species on cuckoo egg parameters (ANOVA with interactions and model reduction).

Cuckoo egg volume - host egg volume, species, and interaction between volume and species

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>volume</td>
<td>-0.052</td>
<td>0.958</td>
</tr>
<tr>
<td>species</td>
<td>-0.262</td>
<td>0.794</td>
</tr>
<tr>
<td>volume*species</td>
<td>-0.258</td>
<td>0.797</td>
</tr>
</tbody>
</table>

Cuckoo egg length - host egg length, species, and interaction between length and species

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>length</td>
<td>1.254</td>
<td>0.214</td>
</tr>
<tr>
<td>species</td>
<td>-1.491</td>
<td>0.141</td>
</tr>
<tr>
<td>length*species</td>
<td>1.517</td>
<td>0.134</td>
</tr>
</tbody>
</table>

Cuckoo egg breadth - host egg breadth, species, and interaction between breadth and species

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>breadth</td>
<td>-0.763</td>
<td>0.448</td>
</tr>
<tr>
<td>species</td>
<td>0.84</td>
<td>0.404</td>
</tr>
<tr>
<td>breadth *species</td>
<td>-1.13</td>
<td>0.263</td>
</tr>
</tbody>
</table>

Comparison of the models including egg parameters, species, and interaction between species and parameters with models not including interactions (ANOVA, see Crawley, 2005 for details).

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cuckoo volume - host volume</td>
<td>0.067</td>
<td>0.797</td>
</tr>
<tr>
<td>Cuckoo length - host length</td>
<td>2.301</td>
<td>0.134</td>
</tr>
<tr>
<td>Cuckoo breadth - host breadth</td>
<td>1.277</td>
<td>0.263</td>
</tr>
<tr>
<td>Cuckoo breadth - host length</td>
<td>0.001</td>
<td>0.98</td>
</tr>
</tbody>
</table>