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1 HOST SPECIES DETERMINES EGG SIZES IN ORIENTAL CUCKOO

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12 Host species determines egg size in Oriental cuckoo

13

1 **Abstract**

2 The Oriental cuckoo *Cuculus optatus* is an obligate brood parasite associated with species
3 of the genus *Phylloscopus*. Four distinct phenotypes of Oriental cuckoo eggs, matching eggshell
4 colour patterns of Arctic warbler *P. borealis*, common chiffchaff (Siberian) *P. collybita tristis*,
5 yellow-browed warbler *P. inornatus* and Pallas's leaf warbler *P. proregulus*, have been
6 identified in the Russian part of its breeding area. We compared egg length, breadth, and volume
7 of Oriental cuckoo egg phenotypes with eggs of the corresponding hosts from three geographical
8 regions in Russia: the Urals, Siberia and the Far East. We found significant oometric differences
9 between Oriental cuckoo egg phenotypes. Egg breadth of each cuckoo group matched the egg
10 breadth of the host species, while the length of cuckoo eggs did not match egg length in host
11 species. Our results can be explained in terms of clutch geometry. An egg sticking out above the
12 clutch is likely to be rejected by the host and so breadth should match the host's egg. This
13 constrains cuckoos in maintaining large egg volumes, which are essential for providing a cuckoo
14 chick with the energy required to eject the host eggs and chicks. An increased egg length might
15 compensate for breadth constraints. We suggest that the size of cuckoo eggs might also be
16 affected by parental care – when only one parent is involved in feeding, eggs need to be larger.
17 This might explain why the longest cuckoo eggs belonged to the phenotype parasitizing the
18 smallest host, Pallas's leaf warbler, where only one parent feeds the chicks. In our view,
19 differences in egg sizes of Oriental cuckoo phenotypes provide evidence of their adaptations to
20 brood parasitism on small leaf warbler species.

21 **Keywords** *Cuculus optatus*; brood parasitism; *Phylloscopus*; adaptation; egg size.

22 **Introduction**

23 The Oriental cuckoo *Cuculus optatus* Gould, 1845 is an obligate avian brood parasite,
24 widely distributed in the Northern Palaearctic (Payne, 2005; Xia *et al.*, 2016). It is very similar to
25 the Himalayan cuckoo *Cuculus saturatus* Blyth, 1843 and until recently both were treated as
26 subspecies, *C. s. horsfieldi* and *C. s. saturatus*, of the polytypic species *C. saturatus* (Cramp,

1 1985; Numerov, 1993, 2003; Johnsgard, 1997). Other junior synonyms include: *C. horsfieldi*
2 (*Payne, 1997; King, 2005*), and *C. s. optatus* (*Erritzøe et al., 2012*). Based on their distributions
3 (*saturatus* has an Asian distribution compared to the Palaearctic *optatus*, Johnsgard, 1997;
4 Erritzøe et al., 2012) and song features (King, 2005; Payne, 2005) species status was adopted by
5 the International Ornithological Congress (Gill & Donsker, 2014). Recently, Xia et al. (2016)
6 provided further support for separating *C. optatus* and *C. saturatus* into distinct species because
7 of song differences.

8 Similar to the common cuckoo *C. canorus* Linnaeus, 1758, females of the Oriental
9 cuckoo lay their eggs into the nests of host species that carry out all aspects of parental care from
10 incubation to fledging. Two-three days after hatching a cuckoo chick ejects all other eggs or
11 nestlings from the host nest (Cramp, 1985; Johnsgard, 1997; Krüger & Davies, 2004; Numerov,
12 1993, 2003; Payne, 1997), completely eliminating the reproductive success of the foster parents.
13 It is expected that the host-cuckoo interaction has led to a co-evolutionary arms race (Dawkins &
14 Krebs, 1979). Brood parasites develop morphological and behavioural adaptations to minimize
15 detection by hosts. In turn, hosts develop sensory and cognitive responses to recognize and reject
16 foreign eggs (Davies, 2011).

17 It is well known that the Oriental cuckoo often exploits leaf warblers from the genus
18 *Phylloscopus* (Cramp, 1985; Erritzøe et al., 2012; Johnsgard, 1997; Numerov, 1993, 2003;
19 Payne, 1997, 2005). Species of this genus are characterized by small body size (weight 4.5–16.0
20 g for species breeding in Russia (Cramp & Brooks, 1992; Ryabitsev, 2014)) and correspondingly
21 small egg sizes (0.8–1.4 g (Schönwetter, 1975-1976)), constituting 8–18% of the female weight.
22 Small egg size of the host presumably determines relatively small egg sizes of the Oriental
23 cuckoo (Chunihin, 1964; Johnsgard, 1997; Krüger & Davies, 2004). While Oriental cuckoo
24 female weight is 75-89 g, the average weight of their eggs is ~1.9 g (Cramp, 1985), which
25 corresponds to 2-2.5% of the body weight. Therefore the Oriental cuckoo is a good example of

1 an “ejector” parasite, exploiting hosts which are much smaller than themselves (Krüger &
2 Davies, 2004).

3 It has been experimentally proven that some of the smallest species among leaf warblers
4 (Hume’s warbler *P. humei* and yellow-browed warbler *P. inornatus*) are likely to reject an egg
5 that is noticeably larger than other eggs in their clutches (Marchetti, 1992, 2000,
6 Meshcheryagina *et al.*, 2016). One possible mechanism for the rejection was suggested more
7 than a hundred years ago by Latter, 1902 as “an egg projecting far above its fellows in
8 consequence of greater breadth would probably inconvenience the sitter.” Meshcheryagina *et al.*,
9 2016 confirmed that yellow-browed warblers rejected eggs that were broader than a particular
10 threshold. Therefore, we expect that there might be differences in oometric characteristics, in
11 particular in breadth, between Oriental cuckoos parasitizing hosts of different sizes.

12 It has been genetically proven that races (or gentes) exist in the common cuckoo, with
13 each race specialising on a particular host species (Gibbs *et al.*, 2000; Fossøy *et al.*, 2011, 2016).
14 Females of each race lay eggs matching the hosts’ eggs in eggshell colour and pattern, which are
15 used to distinguish the races (e.g., Moksnes & Røskaft, 1995; Yang *et al.*, 2010; Vikan *et al.*,
16 2011). It has been suggested that host-specific gentes also exist in the Oriental cuckoo (Balatsky,
17 1998; Balatsky & Bachurin, 1999; Kislenko & Naumov, 1967).

18 Using oological material, four eggshell-colour phenotypes have been described for the
19 Oriental cuckoo in Russia (Bachurin & Kapitonova, 2014; Balatsky, 1991a, 1991b, 1998;
20 Balatsky & Bachurin, 1999; Chunihin, 1964; Egorov, 2013; Kislenko & Naumov, 1967;
21 Pukinsky, 2003). These phenotypes correspond to the eggs of Arctic warbler *P. borealis* (*Pb*),
22 common chiffchaff (Siberian) *P. collybita tristis* (*Pc*), yellow-browed warbler *P. inornatus* (*Pi*)
23 and Pallas’s leaf warbler *P. proregulus* (*Pp*) (see Fig. S1). These host species differ significantly
24 in body weight (Table S1), egg size, and parental involvement in rearing chicks (Brazil, 2009;
25 Cramp & Brooks, 1992; Gaston, 1974; Ryabitsev, 2014; Schönwetter, 1975-1976). In this work,
26 we, for the first time, explored oometric parameters in Oriental cuckoo egg phenotypes in

1 relation to their hosts' egg sizes. We suggest that the breadth of cuckoo eggs is constrained by
2 the host egg breadth, but their length might also be affected by the level of parental care.

3 **Materials and methods**

4 **Study site and species**

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

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

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

25 **General methods**

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

6 Latin and English names are given according to Clements *et al.*, 2017.

7 **Field data**

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

10 **Museum data**

11 In addition to the field data, we used the Oriental cuckoo eggs and host eggs from the
12 clutches in Russian oological collections: Zoological Museum of The Moscow State University
13 (ZM MU), The State Darwin Museum (SDM, Moscow); Kirov City Zoological Museum
14 (KCZM); Novosibirsk State Museum of Local History & Nature (NSMLHN), the private
15 collection of N.N. Balatsky (Balatsky's collection, Novosibirsk); Institute of Plant and Animal
16 Ecology, Ural branch of the Russian Academy of Sciences (IPAE URAN), Zoological Museum
17 of The Urals Federal University (ZM UrFU, Ekaterinburg); private collection "Oological bank of
18 cuckoos" of G.N. Bachurin (Bachurin's oobank, Irbit).

19 Oriental cuckoo eggs from oological collections (n=42, Table 4) were collected in 22
20 reproductive seasons since 1958 (Meshcheryagina *et al.*, 2017).

21 **Data from literature**

22 We obtained further data on Oriental cuckoo eggs (n=37) and its host species from the
23 available literature and personal field diaries (Table 5). We included only data which had
24 information about eggshell colour or photographs. If the same eggs were present in oological
25 collections and literature sources, measurements from oological collections were used.

26 **Oometric variables**

1 Egg length (l) and breadth (b) were measured using digital callipers (10 μ m resolution).
2 These measurements and digital photographs of the eggs were used to calculate the volume of
3 each egg using the Egg Scanner Beta software (Mitiay, 2009). Where measurements were
4 obtained from the literature, the egg volume was calculated using formula $V=(1/6\times\pi\times b^2\times l)$
5 (Murav'ev *et al.*, 2008).

6 **Statistical analysis**

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

20 To disentangle the effect of host egg size from the effect of host species, ANCOVA was
21 used to investigate the relationships between cuckoo egg breadth and host egg breadth, cuckoo
22 egg length and host egg length, cuckoo egg volume and host egg volume, and cuckoo egg
23 breadth and host egg length. The mean values for host egg size in the nest were used in
24 ANCOVA. Where more than one cuckoo egg was found in the same nest, measurements from
25 each cuckoo egg were used as they were laid by different females. For this test we only used the

1 data where host and cuckoo eggs were found in the same nest (81 nests, including 4 with
2 multiple parasitism). We removed the nest with an exceptionally large cuckoo egg and the nests
3 where the cuckoo egg phenotype did not match the host species (n=8). As there were only three
4 nests for *Pb* and five nests for *Pp* these nests were only used for plotting, while the ANCOVA
5 was done for *Pc* (n=56) and *Pi* (n=12). After testing the effect of both host egg size and host
6 species, non-significant terms were removed and the models were compared using ANOVA to
7 establish the best-fit model (Crawley, 2005).

8 **Results**

9 **Egg length, breadth and volume in host species**

10 All variables differed significantly in host species (length – df = 3, $F = 272.9$, $P < 0.0001$,
11 breadth – df = 3, $F = 342.3$, $P < 0.0001$, volume – df = 3, $F = 431$, $P < 0.0001$). Shapiro-Wilk
12 normality tests of the residuals confirmed that the models were a “good fit” to the data (length –
13 $W = 0.996$, $P = 0.541$, breadth – $W = 0.996$, $P = 0.703$, volume – $W = 0.997$, $P = 0.811$).
14 Pairwise, all four species differed significantly in egg length and egg volume ($P < 0.0001$ for all
15 pairs for length, and for all but *Pp-Pi* pair for volume with $P = 0.002$). For egg breadth *Pp-Pi*
16 was the only pair where the difference was not significant ($P = 0.234$, all other pairs $P < 0.0001$).
17 All the variables reduced in the order $Pb > Pc > Pp > Pi$ (Fig. 2, Table S4).

18 **Egg length, breadth and volume in Oriental cuckoo eggshell colour phenotypes**

19 In cuckoo phenotypes all variables also differed significantly (length – df = 3, $F = 51.77$,
20 $P < 0.0001$, breadth – df = 3, $F = 28.2$, $P < 0.0001$, volume – df = 3, $F = 17.7$, $P < 0.0001$) with
21 the residuals normally distributed (length – $W = 0.994$, $P = 0.859$, breadth – $W = 0.986$, $P =$
22 0.227 , volume – $W = 0.983$, $P = 0.119$). Pairwise comparison was not consistent between the
23 variables. Breadth was significantly different in all the cuckoo phenotypes ($P < 0.0001$ for each
24 pair) and the values followed the same order as their host species $Pb > Pc > Pp > Pi$ (Fig. 2). For
25 length, the *Pb-Pc* pair was not significantly different ($P = 0.365$), while all other pairs were

1 significantly different (P_c-P_i $P = 0.029$, $P < 0.0001$ for all others). The P_p phenotype had the
2 longest eggs, while the length in the other three phenotypes reduced in the same order as in the
3 host species. For volume, P_p was not significantly different from P_b ($P = 0.342$) and P_c ($P =$
4 0.637) while other pairs were significantly different (P_b-P_c $P = 0.034$, $P < 0.0001$ for all others).

5 **Ratios between host and cuckoo egg sizes**

6 The ratio between the mean breadth of cuckoo phenotypes eggs and their corresponding
7 host eggs was fairly consistent: 1.22 in P_p , 1.18 in P_i , 1.16 in P_c and 1.15 in P_b . The length of
8 P_p phenotype eggs was disproportionally large compared to those of all other phenotypes with
9 ratios between the mean length of cuckoo eggs and corresponding host eggs as follows: 1.46 in
10 P_p , 1.34 in P_i , 1.23 in P_c and 1.18 in P_b . The ratios between the volumes followed the pattern
11 observed for the ratios of the lengths: 2.25 in P_p , 1.98 in P_i , 1.74 in P_c and 1.62 in P_b .

12 **The effect of host egg size and host species on cuckoo egg size**

13 For all four relationships (between cuckoo egg volume and host egg volume, cuckoo egg
14 length and host egg length, cuckoo egg breadth and host egg breadth, cuckoo egg breadth and
15 host egg length) interactions were not significant and were removed from the models (see Table
16 S5 for details). In the relationship between egg lengths the effect of host species was not
17 significant ($t = 0.408$, $P = 0.685$), while the effect of the host egg length was marginally
18 significant ($t = 1.846$, $P = 0.069$, Fig. 3b). After removal of the host species from the model the
19 effect of the host egg length became significant ($t = 2.24$, $P = 0.029$). For the other three
20 relationships the effect of host egg sizes was not significant (volume-volume: $t = -0.148$, $P =$
21 0.883 , Fig. 3a; breadth-breadth: $t = -1.329$, $P = 0.188$, Fig. 3c; breadth-length: $t = -0.586$, $P =$
22 0.56 , Fig. 3d), while the effect of host species was highly significant ($t = -3.52$, $P = 0.001$ for
23 volume-volume, $P < 0.0001$ for breadth-breadth ($t = -5.822$) and breadth-length ($t = -6.157$)).
24 After removal of the host egg size parameter from the model the effect of host-species remained
25 highly significant in all three models ($P < 0.0001$, $t = -5.853$ for volume-volume, $t = -8.255$ for
26 breadth-breadth and breadth-length). In all four models the reduced model was not significantly

1 different from the full model ($P = 0.883$ for volume-volume, $P = 0.685$ for length-length, $P =$
2 0.188 for breadth-breadth and $P = 0.56$ for breadth-length). Distribution of the residuals in the
3 final models was not different from normal at 95% significance level ($W = 0.969$, $P = 0.084$ for
4 volume-volume, $W = 0.989$, $P = 0.81$ for length-length, $W = 0.967$, $P = 0.072$ for breadth-breadth
5 and breadth-length).

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

9 Discussion

10 We have found that all four host species differed in egg length and volume, while egg
11 breadth in the two smaller leaf warblers (yellow-browed warbler and Pallas's leaf warbler) was
12 similar. However, egg volume of Pallas's leaf warbler was significantly bigger than that of
13 yellow-browed warbler due to the increased length. A bigger egg containing more nutrients
14 improves offspring quality (Krist, 2011), which is especially important for Pallas's leaf warbler
15 since only the female feeds the young.

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

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

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

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

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

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

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3

4 **References**

- 5 Bachurin, G.N. & Kapitonova, L.V. (2014). Aspects of biological compatibility between the
6 Oriental cuckoo *Cuculus (saturatus) optatus* and its host-species on Sakhalin Island,
7 Russia. *Far East. J. Orn.* **4**, 42-56.
- 8 Balatsky, N.N. (1991a). Глухая кукушка и её воспитатели в заповеднике Кедровая Падь и
9 его окрестностях [Oriental cuckoo and its hosts in the Kedrovaya Pad nature reserve and
10 the surrounding area]. *Uragus* **1**, 4-11.
- 11 Balatsky, N.N. (1991b). Глухая кукушка и теньковка в Новосибирской области [Oriental
12 cuckoo and chiffchaff in Novosibirsk region]. *Biologicheskie Nauki* **5**, 56-62.
- 13 Balatsky, N.N. (1998). Ооморфологические характеристики глухой кукушки *Cuculus*
14 *saturatus* в Северной Азии [Oomorphological characteristics of Oriental cuckoo *Cuculus*
15 *saturatus* in northern Asia]. In *Current problem of oology*. Lipetsk: LGPU, 21-22.
- 16 Balatsky, N.N. & Bachurin, G.N. (1999). The cuckoos of the West Siberia and adjoining areas.
17 *Berkut* **8**, 172-182.
- 18 Bán, M., Barta, Z., Muñoz, A.R., Takasu F., Nakamura H. & Moskát C. (2011) The analysis of
19 common cuckoo's egg shape in relation to its hosts' in two geographically distant areas.
20 *J. Zool.* **284**, 77-83.
- 21 Brazil, M. (2009). *Birds of East Asia: China, Taiwan, Korea, Japan, and Russia*. London:
22 Christopher Helm.

- 1 Chunihin, S.P. (1964). Об особенностях гнездового паразитизма глухой кукушки *Cuculus*
2 *saturatus* [About features of brood parasitism in Oriental cuckoo]. *Zoologicheskii*
3 *Zhurnal* **43**, 1249-1250.
- 4 Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L. &
5 Wood C.L. (2017). The eBird/Clements checklist of birds of the world: v2017.
6 Downloaded from <http://www.birds.cornell.edu/clementschecklist/download/>
- 7 Cramp, S. (ed.) (1985). *Cuculus saturatus* Oriental cuckoo. In *Handbook or the Birds of Europe,*
8 *the Middle East and North Africa: the Birds of the Western Palearctic*. Oxford – New
9 York. **4**: Terns to Woodpeckers, 417-422.
- 10 Cramp, S. & Brooks, D.J. (eds.) (1992). *Handbook or the Birds of Europe, the Middle East and*
11 *North Africa: the Birds of the Western Palearctic*. Oxford – New York. **6**: Warblers.
- 12 Crawley, M.J. (2005). *Statistics: An introduction using R*. Chichester: Wiley
- 13 Davies, N.B. (2011). Cuckoo adaptations: trickery and tuning. *J. Zool.* **284**, 1-14.
- 14 Dawkins, N.B. & Krebs, J.R. (1979). Arms races between and within species. *Proc. R. Soc.*
15 *Lond. B Biol. Sci.* **205**, 489-511.
- 16 Egorov, N.N. (2013). Data on the brood parasitism in Oriental cuckoo (*Cuculus optatus* Gould,
17 1845) in Yakutia. *Amurian Zool. J.* **4**, 471-472.
- 18 Erritzøe, J., Mann, C.F., Brammer, F., & Fuller, R.A. (2012). *Cuckoos of the World (Helm*
19 *Identification Guide)*. London: Christopher Helm.
- 20 Fossøy F., Antonov A., Moksnes A., Røskaft E., Vikan J.R., Møller A.P., Shykoff J.A., Stokke
21 B.G. (2011). Genetic differentiation among sympatric cuckoo host races: males matter.
22 *Proc. R. Soc. Lond. B Biol. Sci.* **278**, 1639–1645.

- 1 Fossøy, F., Sorenson, M.D., Liang, W., Ekrem, T., Moksnes, A., Møller, A.P., Rutila, J.,
2 Røskaft, E., Takasu, F., Yang, C. & Stokke, B.G. (2016). Ancient origin and maternal
3 inheritance of blue cuckoo eggs. *Nat. Commun.* **7**, 10272.
- 4 Gaston, A.J. (1974). Adaptation in the genus *Phylloscopus*. *Ibis* **116**, 432-450.
- 5 Gill, F. & Donsker, D. (eds.) (2016) IOC World Bird List (v 6.3). doi
6 10.14344/IOC.ML.6.3. <http://www.worldbirdnames.org/>
- 7 Hargitai, R., Moskát, C., Bán, M., Gil, D., López-Rull, I. & Solymos, E. (2010). Eggshell
8 characteristics and yolk composition in the common cuckoo *Cuculus canorus*: are they
9 adapted to brood parasitism? *J. Avian Biol.* **41**, 177–185.
- 10 Johnsgard, P.A. (1997). *The avian brood parasites: Deception at the nest*. New York: Oxford
11 University Press.
- 12 King, B. (2005). The taxonomic status of the three subspecies of *Cuculus saturatus*. *Bull. Br.*
13 *Orn. Club* **125**, 48-55.
- 14 Kislenko, G.S., Leonovich, V.V. & Nikolaevskij, L.A. (1990). Материалы по изучению птиц
15 Амурской области [Materials on studying of birds of the Amur oblast]. In *Ehkologiya i*
16 *rasprostranenie ptic yuga Dal'nego Vostoka*. Vladivostok. 90-105.
- 17 Kislenko, G.S. & Naumov, P.L. (1967). Паразитизм и экологические расы обыкновенной и
18 глухой кукушек в азиатской части СССР [Parasitism and ecological races of the
19 common cuckoo and the Oriental cuckoo in the Asian part of the USSR]. *Ornitologiya* **8**,
20 79-97.
- 21 Korelov, M.N. (1970). Order *Cuculiformes*. In Птицы Казахстана [*Birds of Kazakhstan*].
22 Almaty. **3**, 9-21.
- 23 Krist, M. (2011). Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* **86**, 692-716.

- 1 Krüger, O. & Davies, N.B. (2004). The evolution of egg size in the brood parasitic cuckoos.
2 *Behav. Ecol.* **15**, 210-218.
- 3 Kuzikov, I.V. (2005). К фауне птиц окрестностей поселка Мыс [On the avifauna the
4 surroundings of the village Mys]. *Fauna of the Urals and Siberia* **10**, 155-161.
- 5 Latter, O.H. (1902). The egg of *Cuculus canorus*. *Biometrika* **1**, 164-176.
- 6 Litvinenko, N.M. & Shibaev, Yu.V. (1971). К орнитофауне Судзухинского заповедника и
7 долины реки Судзухэ [On the avifauna Sudzuhinskogo Reserve and the valley of the
8 Suzuha river]. *Trudy zapovednika "Kedrovaya pad"* **2**, 127-186.
- 9 Logan, M. (2010). *Biostatistical Design and analysis using R*. Chichester: Wiley-Blackwell.
- 10 Makatsch, W. (1976). *Die Eier der Vogel Europas 2*. Leipzig – Radebeul: Neumann Verlag. **2**.
- 11 Marchetti, K. (1992). Costs to host defence and the persistence of parasitic cuckoos. *Proc. R.*
12 *Soc. Lond. B Biol. Sci.* **248**, 41-45.
- 13 Marchetti, K. (2000). Egg rejection in a passerine bird: size does matter. *Anim. Behav.* **59**, 877-
14 883.
- 15 Meshcheryagina, S.G., Bachurin, G.N. & Bourski, O.V. (2017). The distribution of Oriental
16 cuckoo gentes in Russia: review of registration of brood parasitism on host-species.
17 *Fauna of the Urals and Siberia* **2**, 139-163.
- 18 Meshcheryagina, S.G., Golovatin M.G. & Bachurin G.N. (2016). Experimental study of
19 discrimination behavior in the yellow-browed warbler (*Phylloscopus inornatus*) brood-
20 parasitized by the Oriental cuckoo (*Cuculus (saturatus) optatus*). *Russ. J. Ecol.* **47**, 88-90.
- 21 Mitiay, I.S. (2009). Modern approach to description of volume and surface area of bird eggs.
22 *Branta* **12**, 148-156.

- 1 Moksnes, A. & Røskaft, E. (1995). Egg-morphs and host preference in the common cuckoo
2 (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum
3 collections. *J. Zool.* **236**, 625-648.
- 4 Moksnes, A., Røskaft, E., Rudolfson, G., Skjelseth, S., Stokke, B.G., Kleven, O., Gibbs, H.L.,
5 Honza, M., Taborsky, B., Teuschl, Y., Vogl, W. & Taborsky, M. (2008). Individual
6 female common cuckoos *Cuculus canorus* lay constant egg types but egg appearance
7 cannot be used to assign eggs to females. *J. Avian Biol.* **39**, 238-241.
- 8 Murav'ev, I.V., Suhova, O.V. & Yudin, K.I. (2008). Принцип «золотого сечения» при расчете
9 геометрических показателей в оологических исследованиях [The principle of
10 "Golden section" when calculating the geometric parameters in oological studies]. *Izv.*
11 *Penz. gos. pedagog. univ. im.i V. G. Belinskogo.* **6**, 194-199.
- 12 Numerov, A.D. (1993). Oriental cuckoo. In *The birds of Russia and contiguous Regions:*
13 *Pteroclitiformes, Columbiformes, Cuculiformes, Strigiformes.* Moscow: Science. 225-236.
- 14 Numerov, A.D. (2003). *Interspecific and intraspecific brood parasitism in birds.* Vonorezh:
15 Federal state unitary enterprise publish & polygraph corporation.
- 16 Payne, R.B. (1997). Family *Cuculidae* (cuckoos). In *Handbook of the birds of the world.*
17 Barcelona: Lynx Edicions. **4**, 508-607.
- 18 Payne, R.B. (2005). *The Cuckoos.* Oxford University Press.
- 19 Pukinsky, Y.B. (2003). [The breeding birds of the Bikin river basin]. *Trudy Sankt-*
20 *Peterburgskogo Obshchestva Estestvoispytatelej. Ser. 4: Zoological.* **86**, 1-316.
- 21 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
22 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 23 Ryabitsev, V.K. (2014). *Birds of Siberia: Field Guide in two Volumes.* Moscow – Ekaterinburg:
24 Armchair Scientist.

- 1 Schönwetter, M. (1975-1976). Familie *Sylviidae*. In *Handbuch der Oologie. Band II*. Berlin:
2 Akademie-Verlag. **22-25**, 545-732.
- 3 Shcherbakov, B.V. (2012). Глухая кукушка *Cuculus saturatus* на Западном Алтае [Oriental
4 cuckoo *Cuculus saturatus* in the Western Altai]. *Russ. J. Ornithol.* **21**, 1112-1114.
- 5 Sokolov, E.P. & Sokolov, A.M. (1986). Новые виды птиц-воспитателей кукушки *Cuculus*
6 *canorus* [New species of cuckoo hosts *Cuculus canorus*]. *Trudy Zoologicheskogo*
7 *instituta AN SSSR* **147**, 145-146.
- 8 Tuero, D.T., Fiorini, V.D., Mahler, B., & Reboreda, J.C. (2012). Shiny cowbird *Molothrus*
9 *bonariensis* egg size and chick growth vary between two hosts that differ markedly in
10 body size. *J. Avian Biol.* **43**, 227-233.
- 11 Vikan, J.R., Fossøy, F., Huhta, E., Moksnes, A., Røskft, E., & Stokke, B.G. (2011). Outcomes
12 of brood parasite–host interactions mediated by egg matching: common cuckoos *Cuculus*
13 *canorus* versus *Fringilla* finches. *PloS one.* **6**, e19288.
- 14 Xia, C., Liang, W., Carey, G. J. & Zhang, Y. (2016). Song characteristic of Oriental cuckoo
15 *Cuculus optatus* and Himalayan cuckoo *Cuculus saturatus* and implications for
16 distribution and taxonomy. *Zool. Studies* **55**, 38.
- 17 Yang, C., Liang, W., Cai, Y., Shi, S., Takasu, F., Møller, A.P., Antonov, A., Fossøy, F.,
18 Moksnes, A., Røskft, E. & Stokke, B.G. (2010). Coevolution in action: disruptive
19 selection on egg colour in an avian brood parasite and its host. *PLoS ONE* **5**, e10816.
- 20 Zaharov, V.D. (2006). Птицы Южного Урала (видовой состав, распространение,
21 численность) [*Birds of South Ural: specific structure, distribution, population size*].
22 Ekaterinburg – Miass.
- 23

1 **Table 1** Number of cuckoo eggs obtained from different sources.

2 **Table 2** Sample sizes of Oriental cuckoo eggs and host clutches according to geographical
3 regions.

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

5 **Table 4** Number of Oriental cuckoo eggs measured from oological collections.

6 **Table 5** Number of Oriental cuckoo eggs from the literature.

7 **Figure 1** Breeding range of Oriental cuckoo in Russia (dotted area) and the sample sizes of
8 cuckoo (a) and warbler eggs (b) from different locations. Warbler species are shown as: PB –
9 black circle, PC – black quadrat, PI – grey circle, PP – grey quadrat. Dotted lines show the
10 boundaries between Ural, Siberia and Far East regions. Location abbreviations: Ural - Komi
11 Republic (**KR**), Perm Krai (**PK**), Sverdlovsk Oblasts (**SvO**), Chelyabinsk Oblasts (**CO**); Siberia
12 - Yamalo-Nenets Autonomous Okrug (**YN**), Omsk Oblasts (**OO**), Novosibirsk Oblasts (**NO**),
13 Tomsk Oblasts (**TO**), Kemerovo Oblasts (**KO**), Krasnoyarsk Krai (**KK**), Altai Krai (**AK**),
14 Republic of Altai (**RA**), Republic of Khakassia (**RK**), Republic of Tyva (**RT**), Republic of
15 Buryatia (**RB**), Zabaykalsky Krai (**ZK**), Republic of Sakha (**RS**) as well as adjacent areas of
16 Kazakhstan (**Kz**); Far East - Chukotka Oblasts (**CkO**), Magadan Oblasts (**MO**), Amur Oblasts
17 (**AO**), Khabarovsk Krai (**KhK**), Primorsky Krai (**PK**), Sakhalin Oblasts (**SO**).

18 **Figure 2** Mean egg length (a), breadth (b) and volume (c) of the host species (*Pb* – *Phylloscopus*
19 *borealis*, *Pc* – *P. collybita tristis*, *Pi* – *P. inornatus*, *Pp* – *P. proregulus*, white boxes) and
20 corresponding Oriental cuckoo (*Cuculus optatus*) eggshell colour phenotypes (grey boxes). The
21 means and confidence intervals are provided in Table S4.

22 **Figure 3** The best-fit models describing the relationship between cuckoo and host egg volume
23 (a), length (b), breadth (c), and cuckoo egg breadth and host egg length (d). The analysis is based
24 on *Pc* (■) and *Pi* (▲) hosts / cuckoo phenotypes. *Pb* (□) and *Pp* (△) are shown for illustrative

1 purposes. Circles mark the nests where cuckoo eggs did not match the host egg colour. Dotted
2 lines show confidence intervals estimated for the whole set of cuckoo eggs.

3

4 **Supporting Information**

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

9 **Table S1** Body weight of the host leaf warblers (*Pb* - arctic warbler; *Pc* - common chiffchaff
10 (Siberian); *Pi* - yellow-browed warbler; *Pp* - Pallas's leaf warbler).

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

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

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

16 **Table S5** The effect of host egg parameters and host species on cuckoo egg parameters
17 (ANCOVA with interactions and model reduction).