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Host species determines egg size in Oriental cuckoo

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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 oometric 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. This constrains cuckoos in maintaining large egg volumes, which are essential for providing a cuckoo chick with the energy required to eject the host eggs and chicks. 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; Krüger & 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 (Schönwetter, 1975–1976)), constituting 8–18% of the female weight. Small egg size of the host presumably determines relatively small egg sizes of the Oriental cuckoo (Chunihin, 1964; Johnsgard, 1997; Krüger & Davies, 2004). While Oriental cuckoo female weight is 75–89 g, the average weight of their eggs is *c*. 1.9 g (Cramp, 1985), which corresponds to 2–2.5% of the body weight. Therefore, the Oriental cuckoo is a good example of an 'ejector' parasite, exploiting hosts which are much smaller than themselves (Krüger & Davies, 2004).

It has been experimentally proven that some of the smallest species among leaf warblers (Hume's warbler *Phylloscopus humei* and yellow-browed warbler *Phylloscopus inornatus*) are likely to reject an egg that is noticeably larger than other eggs in their clutches (Marchetti, 1992, 2000; Meshcheryagina, Golovatin & Bachurin, 2016). One possible mechanism for the rejection was suggested more than a hundred years ago by Latter (1902) as 'an egg projecting far above its fellows in consequence of 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.*, 2011, 2016). 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 & Røskaft, 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 proregulus* (*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; Ryabitsev, 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 (KCZM); 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).

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

Table 1 Number of cuckoo eggs obtained from different sources

Sources of information	*N* cuckoo egg (*N* females) according to eggshell colour phenotypes			
	'*borealis*'	'*collybita*'	'*inornatus*'	'*proregulus*'
Field data	7 (5)	54 (24)	21 (10)	12 (12)
Museum data	2 (2)	17 (17)	4 (2)	19 (16)
Data from literature	9 (9)	22 (22)	2 (2)	4 (4)
Total	18 (16)	93 (63)	27 (14)	35 (32)

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

Sample	*Cuculus optatus* (*Co*) *N* eggs (females)	*Phylloscopus borealis* (*Pb*) *N* clutches	*Phylloscopus collybita tristis* (*Pc*)	*Phylloscopus inornatus* (*Pi*)	*Phylloscopus proregulus* (*Pp*)
Ural	61 (33)	14	58	20	–
Siberia	68 (51)	15	37	128	1
Far East	44 (41)	3	–	13	26
Total	173 (125)	32	95	161	27

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

Region	Location	Coordinates	Breeding seasons	Egg phenotype	*N* egg
Ural	Near Irbit in Sverdlovsk oblast	57°N, 62°E	2002–2014	*Pc*	49
Siberia	Turukhansk district of the Krasnoyarsk Krai	62°N, 88°E	2016	*Pc*	5
				Pb	7
	North-Baikal district of Republic of Buryatia	54°N, 109°E	2005–2007, 2012–2013	*Pi*	21
				Pp	1
Far East	Pozharsky district of Primorsky Krai	46°N, 135°E	1999–2001	*Pp*	3
	Ussuri district of Primorsky Krai	43°N, 131°E	2015	*Pp*	1
	Various locations on Sakhalin island	51°N, 142°E	2008–2011, 2016	*Pp*	7

Table 4 Number of Oriental cuckoo eggs measured from oological collections

Collections	*N* cuckoo egg according to eggshell colour phenotypes			
	'*borealis*'	'*collybita*'	'*inornatus*'	'*proregulus*'
ZM MU	1	4	1	1
Balatsky's collection	–	4	–	7
ZM UrFU	–	1	–	–
Bachurin's oobank[a]	1	8	3	11
Total	2	17	4	19

[a]Eggs not included in Field data.

information about eggshell colour or photographs. If the same eggs were present in oological collections and literature sources, measurements from oological collections were used.

Oometric variables

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

Table 5 Number of Oriental cuckoo eggs from the literature

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

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, measurements from each cuckoo egg were used as they were laid by different females. For this test, we only used the data where host and cuckoo eggs were 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 *Pc* (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 *Pb–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 (*Pb–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*.

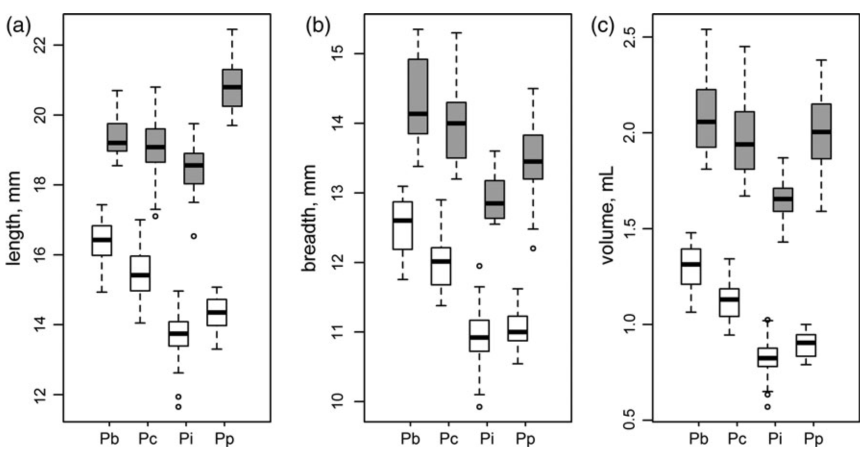

Figure 2 Mean egg length (a), breadth (b) and volume (c) of the host species (*Pb* – *Phylloscopus borealis*, *Pc* – *Phylloscopus collybita tristis*, *Pi* – *Phylloscopus inornatus*, *Pp* – *Phylloscopus proregulus*, white boxes) and corresponding Oriental cuckoo (*Cuculus optatus*) eggshell colour 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, $P < 0.0001$ for breadth–breadth ($t = -5.822$) and breadth–length ($t = -6.157$)]. 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 *Pc*, 1.672 mL for *Pi*) and breadth (13.96 mm for *Pc*, 12.93 mm for *Pi*) 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.

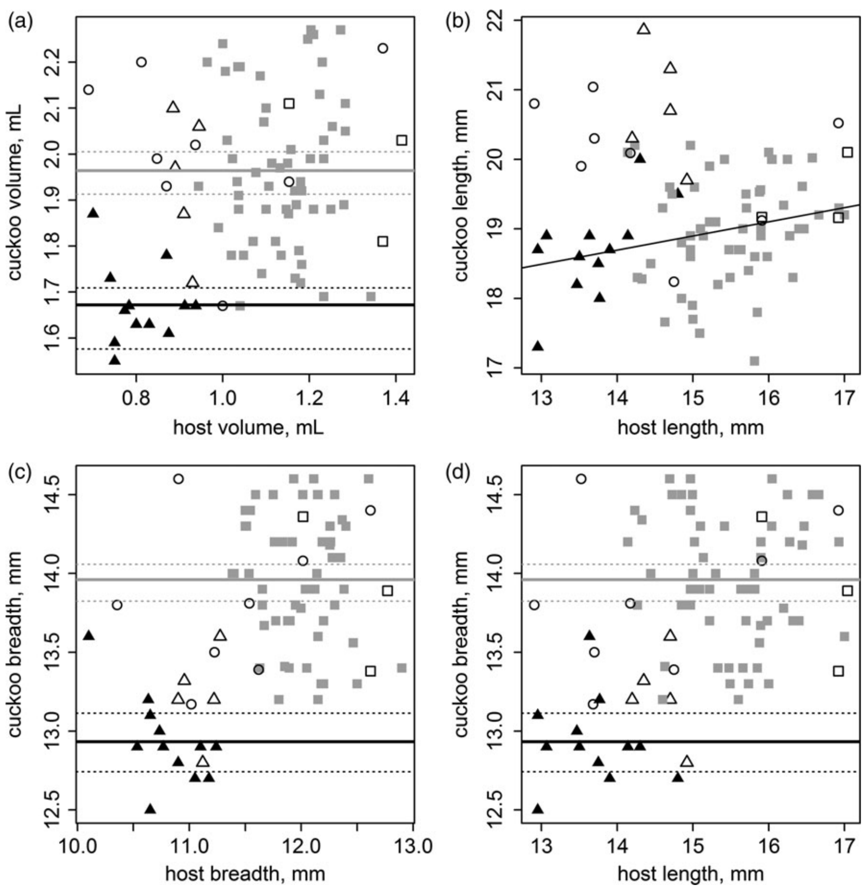

Figure 3 The best-fit models describing the relationship between cuckoo and host egg volume (a), length (b), breadth (c), and cuckoo egg breadth and host egg length (d). The analysis is based on *Pc* (■) and *Pi* (▲) hosts/cuckoo phenotypes. *Pb* (□) and *Pp* (△) are shown for illustrative purposes.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

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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 (*Pb* – arctic warbler; *Pc* – 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).