Original Article

Common cuckoos do not mimic the size and shape of host eggs

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Often considered a textbook example of coevolution, common cuckoo (*Cuculus canorus*) eggs are among the best-studied eggs in the world. Female cuckoos belong to genetically distinct host-races, each laying a specific egg type. When host species evolved to reject cuckoo eggs from their nests, cuckoos evolved better egg color and pattern mimicry. In this study, we asked: have cuckoos also evolved eggs that are well matched to host eggs in size and shape, and is the match better for highly discriminating hosts? We used digital image analysis to quantify the sizes and shapes of ~1230 eggs laid by ten European host species and their respective cuckoo host-races. We found that there is some variation in egg size and shape among host species. By contrast, different cuckoo host-races lay eggs that are—on average—similar in size and shape. This generic "one size and shape fits all" cuckoo egg morph is a poor match to most host egg sizes but a good match to most host egg shapes. Overall, we showed that host discrimination behavior was not correlated with the degree of egg size or shape similarity. We concluded that cuckoo females have not evolved egg size or shape mimicry. Alternative explanations for egg shape similarity include biophysical constraints associated with egg formation and selection for incubation efficiency. Finally, to place our results in a broader context, we compared the egg shapes of the common cuckoo and its hosts to those of three Australian parasitic cuckoo species and their hosts.

Key words: brood parasitism, coevolution, *Cuculus canorus*, egg shape, egg size, mimicry.

INTRODUCTION

In the coevolutionary arms race between avian brood parasites and their hosts, parasites evolve better tricks and hosts evolve tougher defenses. One outcome of this perpetual struggle is egg mimicry (Brooke and Davies 1988; Davies 2011; Langmore and Spottiswoode 2012; Stoddard and Hauber 2017). In response to hosts' rejection of odd eggs, many parasites have evolved eggs that more closely resemble those of their hosts. Although diverse parasites have evolved egg mimicry, the common cuckoo (*Cuculus canorus*) is noteworthy for its extraordinary range of egg morphs (Moksnes and Røskaft 1995). Female common cuckoos belong to genetically distinct host-races, each of which lays a distinctive egg morph and targets a particular host species (Gibbs et al. 2000). Often the cuckoo egg is a good match to the host's eggs with respect to color and pattern. Moreover, the degree of color and pattern mimicry is correlated with host defenses. For host species exhibiting strong egg rejection, cuckoo females (of the corresponding host-race) have evolved refined color and pattern egg mimicry (Brooke and Davies 1988; Stoddard and Stevens 2010, 2011). For host species

like the dunnock (*Prunella modularis*), which lays bright blue eggs and does not show strong rejection defenses, cuckoo females have not evolved egg mimicry: they lay speckled beige eggs in dunnock nests. Cuckoo females are nevertheless capable of laying blue eggs; those parasitizing the redstart (*Phoenicurus phoenicurus*) have evolved a relatively close color match to the redstart's blue eggs (Stoddard and Stevens 2011), even though redstarts show only modest rejection defenses and do not typically reject natural cuckoo eggs (Avilés et al. 2005).

Most work on egg mimicry—in brood parasites generally, but also in common cuckoos—has focused on color and pattern (Langmore and Spottiswoode 2012; Stoddard and Hauber 2017; Stoddard 2022). Indeed, these features seem to be critical for egg recognition and rejection by many host species (Langmore and Spottiswoode 2012; Stoddard and Hauber 2017). What about the size and shape of eggs? The question of whether parasitic eggs resemble host eggs in these respects, as opposed to color and pattern, has received relatively little research attention. In a recent synthesis of the existing work on this topic, Stokke et al. (2017) reviewed the evidence for egg size and shape mimicry. In some parasite–host systems, hosts reject foreign eggs on the basis of size and shape differences—suggesting that parasitic eggs in these systems are under strong selection for size and shape mimicry. Yellow-browed leaf warblers (*Phylloscopus humei*), which are parasitized by the lesser cuckoo (*Cuculus poliocephalus*), reject model eggs that are about 75%

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larger than their own (Marchetti 2000). Rufous horneros (*Furnarius rufus*) reject shiny cowbird (*Molothrus bonariensis*) eggs if they are not well matched to their own in width (Mason and Rothstein 1986). Similarly, superb fairy-wrens (*Malurus cyaneus*) are more likely to abandon Horsfield's bronze-cuckoo (*Chalcites basalis*) eggs that are short and round (as opposed to long and narrow) (Taylor and Langmore 2020). Greater honeyguides (*Indicator indicator*), which parasitize a variety of host species, use size and shape information to identify and selectively remove other parasitic honeyguide eggs from host nests (Spottiswoode 2013). In this twist on the classic scenario, it is the honeyguide parasites (rather than the hosts) that select for egg mimicry. In the warbler, hornero, fairy-wren and honeyguide cases, host birds nest in dark cavities or domes, where color and pattern information might be less helpful than size and shape cues, which can be potentially be assessed by touch.

However, egg size and shape mimicry are not necessarily limited to—or exacerbated in—dark nests. A recent study of Australian cuckoo-host systems (Attard et al. 2017) showed that eggs laid by cuckoos that exploit open, cup-nesting host species more closely resemble the size and shape of those of their own hosts, relative to hosts of other cuckoo species. The authors attributed this result to the improved ability of open-nesting hosts to recognize parasitic eggs using visual cues. Further support for the idea that open-nesting hosts can reject oddly sized and shaped eggs comes from American robins (*Turdus migratorius*), which are more likely to reject artificial egg-like objects that diverge from natural eggs in width and angularity (Hauber et al. 2021). Taken together, these studies—in both closed and open nests—suggest that differences in egg size and shape can influence host rejection behavior. Consistent with this view, parasitic cuckoos generally lay eggs that are well matched in size to host eggs (Krüger and Davies 2004) and—compared with nonparasitic cuckoos—lay eggs that are smaller for their body size (Krüger and Davies 2004) and more quickly evolving (in terms of egg size) (Medina and Langmore 2015), presumably due to selection by hosts against substantially size-mismatched eggs.

The story appears more nuanced when we turn to hosts of the common cuckoo. On the one hand, some hosts do appear to reject eggs that differ in size (Davies and Brooke 1988; Moksnes and Røskaft 1992; Roncalli et al. 2017) or shape (Zölei et al. 2012). Eventually, this could lead to the emergence of common cuckoo egg morphs (laid by the different cuckoo host-races) with different sizes and shapes, each well matched to eggs of the typical hosts. Some support for this comes from Moksnes and Røskaft (1995), who found a positive correlation in size between cuckoo egg morphs and their respective host eggs; Antonov et al. (2010) observed a similar trend. Intriguingly, Berkowic et al. (2015) detected a decrease in the egg size of common cuckoos parasitizing the Eurasian reed warbler (or reed warbler, *Acrocephalus scirpaceus*) over a nine-decade span, potentially due to selection pressure from the hosts. On the other hand, some hosts ignore differences in egg size when determining whether to reject a foreign egg (Antonov et al. 2006; Stokke et al. 2010), and there appears to be little differentiation in the shapes (Antonov et al. 2010; Drobniak et al. 2014) and sizes (Drobniak et al. 2014) of some cuckoo egg morphs. In an analysis of three common cuckoo egg morphs in Japan and three in Hungary, Bán et al. (2011) found differences in the shapes of cuckoo egg morphs between, but not within, geographic locales. The authors suggested that this difference has more to do with geographic isolation than adaptation to specific hosts. We currently lack a more extensive analysis of egg size and shape in the common cuckoo and its frequently used European host species.

To investigate egg shape mimicry, it is important to use the right quantitative tools. Many previous studies used simple metrics to describe egg shape, like the ratio of egg length to egg breadth. This approach might mask important aspects of egg shape (Troscianko 2014; Stoddard et al. 2017; Biggins et al. 2018, 2022; Montgomerie et al. 2021; Narushin et al. 2021). In a recent study, Biggins et al. (2018) compared common egg shape metrics and demonstrated that a four-parameter model, first proposed by Preston (1953), provided the best fit for the most egg shapes, especially for highly pyriform eggs. For eggs that are not highly pyriform, two sets of indices (representing pointedness/polar asymmetry and elongation, respectively) provide a general description of egg shape (Stoddard et al. 2017, 2019; Biggins et al. 2018; Baker 2002). A variety of tools now exist for quantifying shape from photographs: for freely available software, see Troscianko (2014), Stoddard et al. (2017), and Biggins et al. (2018). Additional geometric morphometric approaches have been proposed to quantify egg shape in 2D (Deeming and Ruta 2014) and 3D (Attard et al. 2018).

Here, we perform a detailed analysis of egg size and shape in the common cuckoo and ten of its European host species. Using museum specimens and new tools for assessing egg shape, we ask the following questions: 1) Are there size and shape differences among eggs of the host species? 2) Are there size and shape differences among the cuckoo egg morphs? 3) How different are cuckoo egg morphs from eggs of their respective hosts in size and shape? 4) Are differences in egg size and shape correlated with rejection defenses evolved by hosts? If cuckoo eggs have evolved to mimic the size and shape of host eggs to escape host defenses, we predict that cuckoo egg morphs will be a better match in size or shape to the eggs of highly discriminating host species. An alternative explanation for size and shape similarity is that size and shape are associated with incubation efficiency (Davies and Brooke 1988; Krüger and Davies 2004; Bán et al. 2011). In this case, oddly sized or shaped eggs would not develop properly, so cuckoos would be under strong selection pressure to match the size and shape of host eggs. Therefore, we might detect similarities between the eggs of cuckoos and their respective hosts, but we would not observe a positive correlation between egg similarity and host rejection defenses. Finally, we might also detect similarities in egg size and shape if hosts and cuckoos experience broadly similar physiological constraints associated with egg laying.

MATERIALS AND METHODS
Data collection and photography

We analyzed the sizes and shapes of 1231 eggs in 285 digital photographs of parasitized clutches representing ten European host-species of the common cuckoo. Eggs were from the collections of the Natural History Museum (NHM) in Tring (Hertfordshire, UK). Subsets of this dataset have been used in previous studies (Stoddard and Stevens 2010, 2011; Stoddard et al. 2014). We provide a brief overview of the dataset here but direct readers to these papers for additional details. Table 1 provides a summary of the eggs used in our analyses, including details on host species, cuckoo host-races, and sample sizes. Most eggs were collected between 1880 and 1940. Where possible, clutches for a given host species were selected from different localities to avoid pseudoreplication (measuring more than one cuckoo egg laid by the same female); for more information about geographic localities, see Stoddard and Stevens (2010). All eggs in a clutch were placed in a similar orientation and

Summary of the data used in this study

Host abbreviation	Cuckoo host-race abbreviation	Host species	Host species common name	Number of clutches	Number of host eggs	Number of cuckoo eggs
AA	AA-C	*Acrocephalus arundinaceus*	Great reed warbler	30	87	30
AS	AS-C	*Acrocephalus scirpaceus*	Reed warbler	32	94	32
AP	AP-C	*Anthus pratensis*	Meadow pipit	32	108	32
ER	ER-C	*Erithacus rubecula*	Robin	30	104	30
FM	FM-C	*Fringilla montifringilla*	Brambling	14	54	14
LC	LC-C	*Lanius collurio*	Red-backed shrike	32	104	32
MA	MA-C	*Motacilla alba*	Pied wagtail	31	120	31
PM	PM-C	*Prunella modularis*	Dunnock	30	96	30
PP	PP-C	*Phoenicurus phoenicurus*	Redstart	22	95	22
SB	SB-C	*Sylvia borin*	Garden warbler	32	84	32

photographed using a Fujifilm IS Pro ultraviolet-sensitive digital camera, using the image acquisition procedure previously described in Stoddard and Stevens (2010). All the images included a ruler. We visually identified the cuckoo egg in each clutch, consulting the museum information cards when the egg was difficult to distinguish from the host eggs (Stoddard and Stevens 2010, 2011; Stoddard et al. 2014). If there was more than one cuckoo egg in a clutch, only one (selected at random) was retained for analysis. Cuckoo eggs were attributed to host-race based on the host species' clutch in which they were found. This is likely to be an oversimplification because cuckoos can lay eggs in the nests of secondary host species (Moksnes and Røskaft 1995). However, our approach avoids the complex process of assigning eggs to cuckoo host-races based on subjective visual criteria.

Image analyses

To analyze each egg's shape from photographs, we used the *EggxTractor* toolbox (Stoddard et al. 2017) written in MATLAB (Mathworks, Inc., Natick, MA). We obtained two measures of egg shape: asymmetry, which captures how pointy an egg is, and ellipticity, which captures how elongated an egg is. When the image contrast was too low for the automatic thresholding to capture the boundaries of an egg accurately, we performed image segmentation (removal of the egg image from the background) manually. Asymmetry and ellipticity are weakly correlated (see Supplementary Figure S3). In addition, we extracted the egg shape indices pointedness, elongation, and polar asymmetry using the software provided by Biggins et al. (2018). To estimate egg size, we measured the major axis length of each egg in pixels and calculated the egg's absolute length in centimeters using the ruler in each image. We used the length of the major axis of the egg as a proxy for egg size instead of its volume because we were able to measure length directly from 2D photographs. The volume and length of the major axis of an egg have an approximately cubic relationship, but for the small magnitudes of length in our dataset (around 2 cm or less), an approximately linear relationship can be assumed (Stoddard et al. 2017).

Statistical analyses

We carried out all the statistical analyses in MATLAB using two different sets of shape indices (asymmetry and ellipticity; and pointedness, elongation, and polar asymmetry), both of which yielded similar overall results. For ease of visualization in two dimensions, we report asymmetry and ellipticity in the main text and the other indices in the Supplementary Materials. Since there was generally more than one host egg in each clutch, we calculated the average length, asymmetry, and ellipticity (and standard deviation) for each clutch of host eggs and used these "per clutch" averages in subsequent analyses.

To test for statistically significant differences in egg size and shape (among host species, and among cuckoo host-races), we used a one-way analysis of variance (ANOVA). If differences were identified at the $P \leq 0.01$ level, we performed a Tukey's honestly significant difference post hoc test. Next, we tested for a difference of means between the average host egg and cuckoo egg distributions for length, asymmetry, and ellipticity. Since our data did not conform to the assumptions of parametric tests, we used a two-tailed t-test with a permutation approach, for 10,000 permutations and using a significance threshold of $P \leq 0.01$. We also calculated an effect size (Cohen's d) for each cuckoo-host species pair, which describes the overlap between distributions of each index between cuckoos and hosts. To do so, we computed average length, asymmetry, and ellipticity across all host eggs in each clutch and obtained an "average host egg" for the clutch. For a given host species, we then computed Cohen's d by comparing the distribution of all average host eggs to the distribution of all cuckoo eggs in those clutches. A large value ($d \geq 0.8$) indicates a large effect size (Cohen 1988; Stoddard and Stevens 2010); there is a small overlap in the distributions and a weaker size or shape match. A smaller d value ($d < 0.8$) indicates a stronger size or shape match.

We used three additional metrics for assessing the degree of match between cuckoo and host egg indices. 1) First, we quantified the degree of overlap between cuckoos and hosts in an egg morphospace defined by asymmetry and ellipticity. This comparison does not take into account differences in egg size. Specifically, we calculated the area of the 2D convex hull (the minimum convex polygon containing all points) for a given host species and for its corresponding cuckoo host-race. We then quantified similarity, or match, between the cuckoo-host pairs as the percentage of area (A) overlap relative to the area covered by the host species:

$$percent\ area\ overlap = \frac{A_{host} \cap A_{cuckoo}}{A_{host}} \times 100 \tag{1}$$

Table 2

Rejection rates compiled from Soler (2016) and Cohen's d values (standardized mean difference) calculated for egg length, asymmetry, and ellipticity for cuckoo-host pairs. A large d magnitude represents a small overlap in distributions of a given trait and therefore a poor match, whereas a small d magnitude represents a large overlap in distributions and a good match. Following Cohen (1988), we consider smaller effect sizes ($d < 0.8$) to indicate a "match" between cuckoo and host traits. Large effects, indicating a poor match or a difference, are shown in bold

				Cohen's d values		
Host abbreviation	Species name	Common name	Rejection rates (%)	Length	Asymmetry	Ellipticity
AA	*Acrocephalus arundinaceus*	Great reed warbler	42.4	0.68	0.61	**1.06**
AS	*Acrocephalus scirpaceus*	Reed warbler	43.6	**3.65**	0.02	**0.99**
AP	*Anthus pratensis*	Meadow pipit	36.6	**2.78**	0.52	0.59
ER	*Erithacus rubecula*	Robin	16.1	**2.13**	**0.86**	0.64
FM	*Fringilla montifringilla*	Brambling	88.1	**3.29**	0.79	**0.86**
LC	*Lanius collurio*	Red-backed shrike	95.1	0.23	0.11	0.21
MA	*Motacilla alba*	Pied wagtail	75.0	**2.07**	0.58	0.43
PM	*Prunella modularis*	Dunnock	3.1	**2.79**	0.19	0.47
PP	*Phoenicurus phoenicurus*	Redstart	37.9	**4.34**	0.55	0.21
SB	*Sylvia borin*	Garden warbler	66.7	**3.34**	0.04	0.03

where ∩ represents intersection (overlap). A larger percentage of area overlap indicates higher similarity between cuckoo and host egg shapes.

2) Second, we calculated the percentage difference of the means of each index independently (asymmetry, ellipticity, length):

$$percent\ difference\ of\ means = \frac{|\eta_{host} - \eta_{cuckoo}|}{\eta_{host}} \times 100 \tag{2}$$

where η represents the mean. A larger difference indicates higher dissimilarity.

3) Third, for each host species and cuckoo-host race, we calculated the average asymmetry and ellipticity coordinates (centroid) defining their convex hulls. If the egg shape centroids of a host species and a cuckoo host-race are close to one another, the *average* egg shapes of the host and cuckoo are similar.

Finally, we used linear regressions to compare egg size and shape similarity metrics to egg rejection rates by the different host species, using a significance threshold of $P \leq 0.01$. Reported egg rejection rates by host species vary widely, but here we follow Soler (2016), who compiled rejection rates of non-mimetic eggs from the literature. We report these rejection rates in Table 2. To account for the phylogenetic non-independence of the host species, we repeated these regression analyses using phylogenetic generalized least squares (PGLS). Using BirdTree (Jetz et al. 2012) following the procedure outlined by Rubolini et al. (2015), we obtained a consensus tree for the ten host species. We then fitted PGLS models using the "gls" function in R (R Core Team, 2020). For each regression, we fitted three alternative models for the error structures (1: none, equivalent to ordinary least squares; 2: Brownian Motion using the "ape" package "corBrownian" function; and 3: Lambda using the "ape" package "corPagel" function) (Paradis and Schliep 2018).

Egg volume estimation

To estimate the volume of each egg, we used the formula from Baker (2002):

$$V = \frac{\pi L^3}{8} \int_{-1}^{1} y^2 dx \tag{3}$$

Here, y is the equation of a path curve that describes the shape of the egg, which is parameterized by λ and T as follows:

$$y = T(1+x)^{\frac{1}{1+\lambda}} (1-x)^{\frac{\lambda}{1+\lambda}} \tag{4}$$

Where the parameters λ and T are related to asymmetry and ellipticity as $\lambda = A + 1$, and $T = 1/(E + 1)$, respectively.

Comparison to Australian parasitic cuckoos

Attard et al. (2017) recently quantified the egg shapes of three Australian cuckoos—the pallid cuckoo (*Cuculus pallidus*), brush cuckoo (*Cacomantis variolosus*), and fan-tailed cuckoo (*Cacomantis flabelliformis*)—and their hosts. To compare these egg shapes to those of the common cuckoo and its hosts, we reanalyzed the data from Attard et al. (2017), who reported Cartesian XY coordinates (derived from egg images) for all the egg shapes in their supplementary material. Using these coordinates, we reconstructed the egg shapes and calculated each egg's asymmetry and ellipticity. We focused on the eggs of the pallid and brush cuckoos and their hosts, since Attard et al. (2017) found evidence of egg shape mimicry in these systems. Additional details about the Attard et al. (2017) dataset can be found in the Supplementary Materials. Overall, our goal was to evaluate the eggs of different cuckoo species—and their respective hosts—in a common egg shape morphospace.

RESULTS

Figures 1–3 provide a visual summary of our results. Figure 1A shows example eggs from our dataset representing each cuckoo host-race and its corresponding host species. For most host species, cuckoo eggs (of the corresponding host-race) are larger than hosts' (on average 10%), but egg sizes of the great reed warbler (*Acrocephalus arundinaceus*)-cuckoo and red-backed shrike (*Lanius collurio*)-cuckoo do not differ from those of their hosts (Table 2; Figure 2A). Figure 1B shows the egg shapes of each host species and its corresponding cuckoo host-race in the morphospace defined by Stoddard et al. (2017) (gray areas in each subplot). Host and cuckoo egg shapes occupy the same general region of morphospace but exhibit varying degrees of shape similarity (overlap in morphospace). Figure 2 shows the distributions of egg size and shape values for each host and its corresponding cuckoo
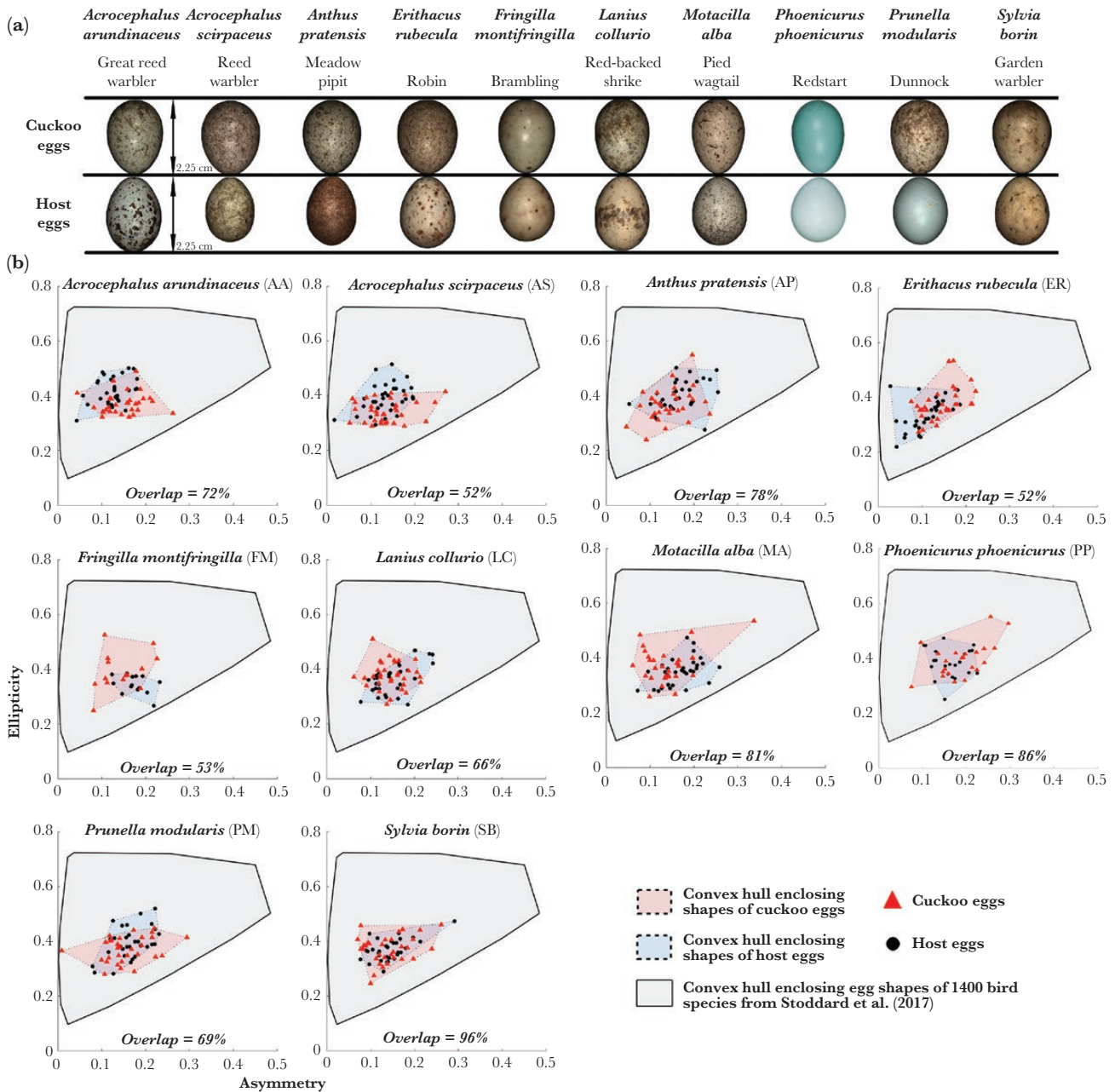
Figure 1

(A) Representative eggs from the ten cuckoo host-races and their respective hosts analyzed in this study. Eggs are scaled (while keeping their aspect ratio the same) relative to the largest egg in our dataset— that of the great reed warbler (*Acrocephalus arundinaceus*), with an average length of 2.25 cm. Egg photographs were taken by M.C. Stoddard and are copyright of the NHM. (B) The egg shapes of ten cuckoo-host pairs are plotted in the morphospace (gray shaded area) obtained from the average egg shapes of 1400 species from Stoddard et al. (2017). Each black dot represents the "per clutch" average shape of host eggs, while each red triangle represents the shape of one parasitic cuckoo egg. For all species studied here, at least 50% of the area occupied by host eggs is overlapped by cuckoo eggs.

host-race. For both size and shape, variation among the different host species appears to be greater than variation among the cuckoo host-races. Whereas Figure 1B shows the egg shapes of each host and cuckoo host-race in separate morphospaces, Figure 3A depicts the centroids of egg shapes for all cuckoo-host pairs in a single morphospace. Figure 3B,C shows that there is no correlation between host rejection defenses and the degree of egg shape and size similarity between cuckoo host-races and their respective hosts. We

elaborate on the key results below and provide extended results in the Supplementary Material (Supplementary Figures S1–S3, Supplementary Tables S1–S8).

(1)Are there size and shape differences among eggs of the host species?

The eggs of different host species differ from each other in size (ANOVA length: $F_{8,254} = 80.21$, $P < 0.001$) (Figures 1A and 2A). A
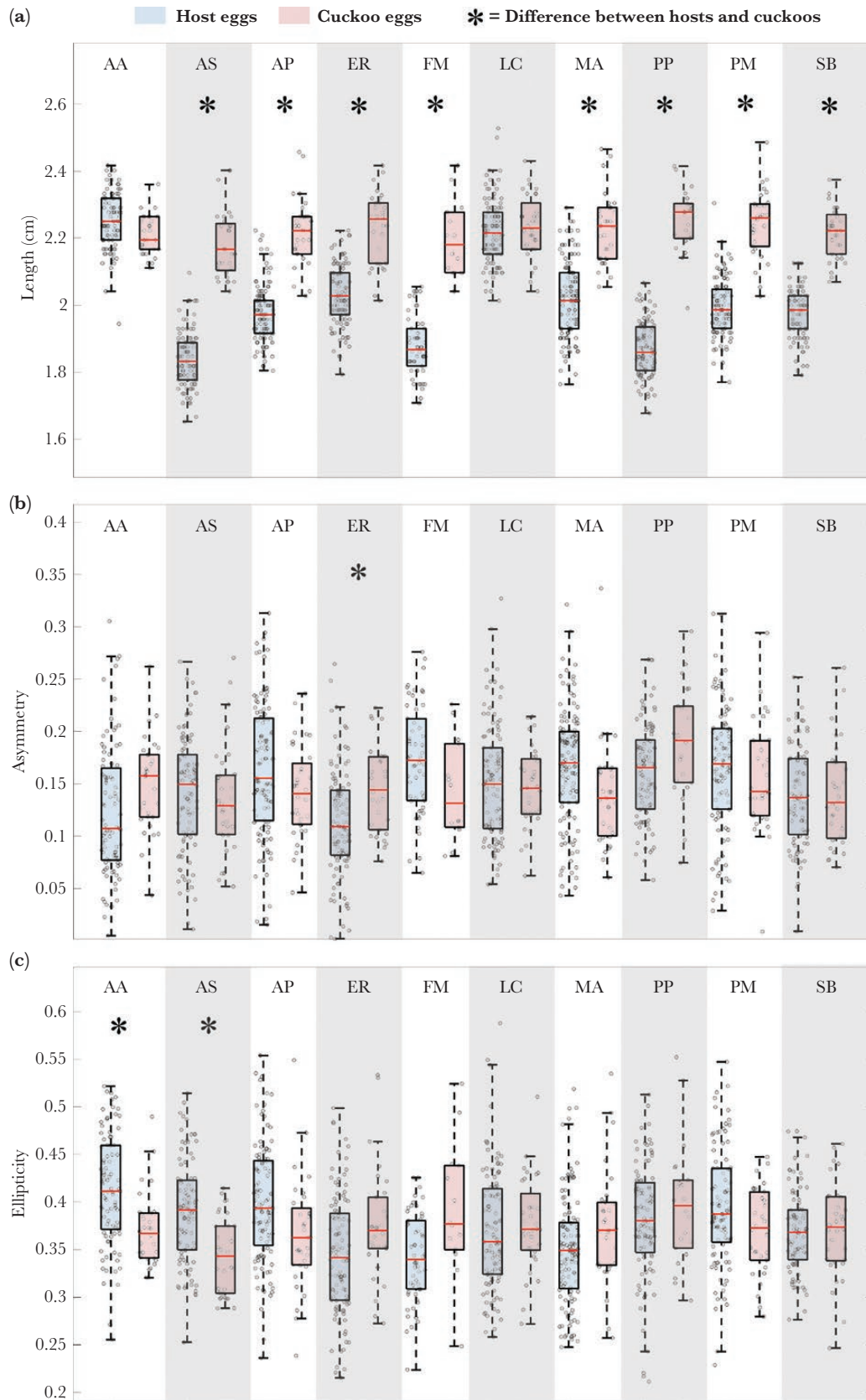
Figure 2
Distributions of major axis length (in cm), asymmetry, and ellipticity for all individual eggs (gray dots) in our dataset, with the distribution of host eggs shown next to the eggs of the corresponding cuckoo host-race in standard box plots (see Data S1 in the Supplementary Materials). Red lines represent means, and for host eggs, means shown here are calculated considering all host eggs (i.e., not clutch-averaged). Distributions that are statistically different according to a two-tailed t-test at a significance level of $P \leq 0.01$ are marked with * (using "per clutch" host egg averages).
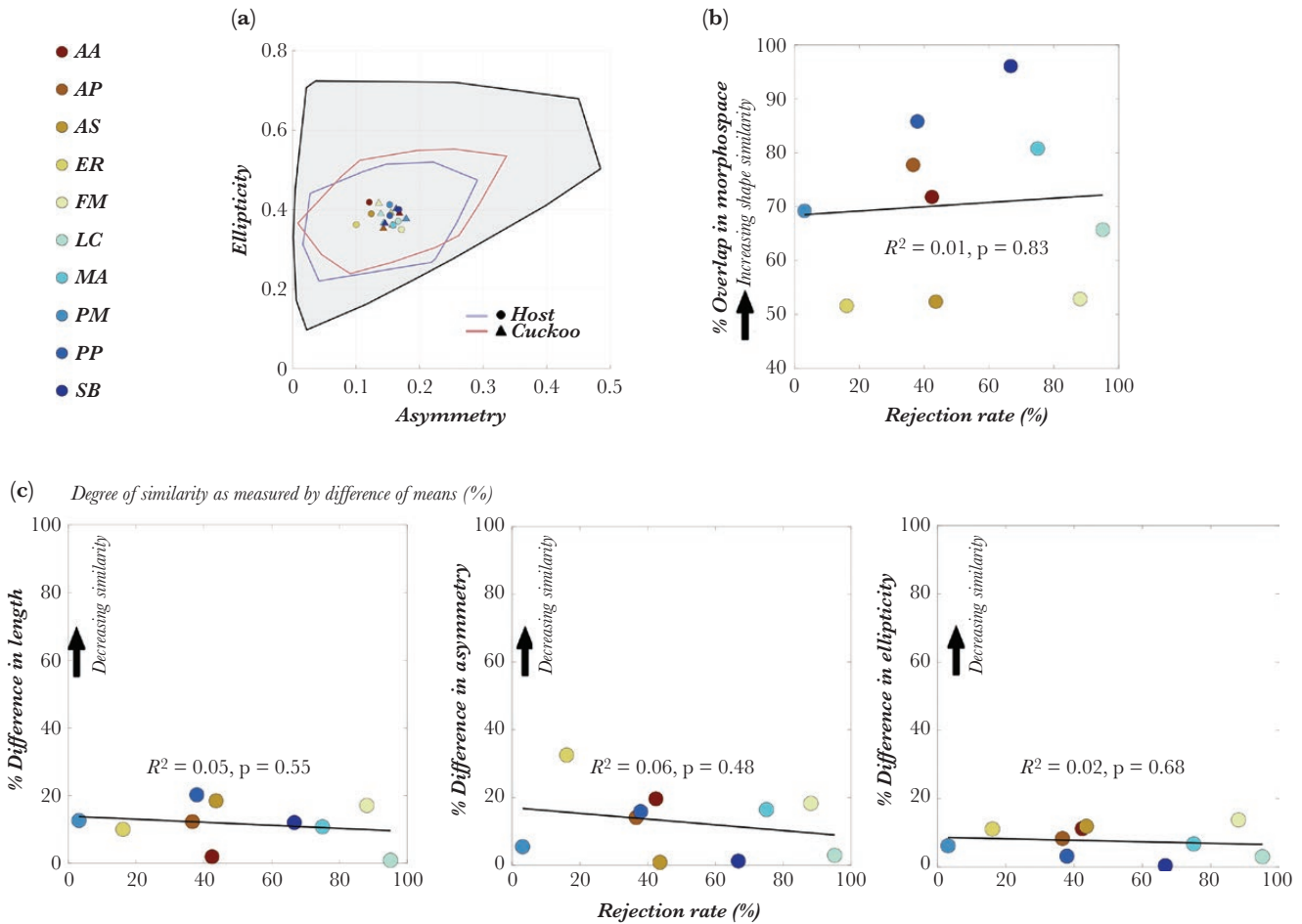
Figure 3
(A) The centroids for all host species and cuckoo host-races are plotted against the morphospace (gray shaded area) of the average shapes of eggs from 1400 species from Stoddard et al. (2017). Color coding of species is the same throughout all parts of the figure. The overall ranges of host and cuckoo egg shapes are indicated by the blue and red boundaries. While the egg shapes of some host species differ statistically from others, none of the cuckoo host-races differ from one another in terms of egg shape (see main text for details and Fig. S1 for individual eggs). (B) Rejection behavior of the different host species is not correlated with egg shape similarity between common cuckoo host-races and their hosts, when egg shape similarity is measured as percent overlap in shape space. (C) Rejection behavior of the different host species is not correlated with egg size and shape similarity between common cuckoo host-races and their hosts, when size and shape similarity are measured as percent difference of the means in egg length, asymmetry, or ellipticity.

post hoc Tukey test (Supplementary Table S1) shows that the egg sizes of the great reed warbler and red-backed shrike differ from all other species but not from each other. Similarly, the reed warbler, brambling (*Fringilla montifringilla*), and redstart differ from all other species but not from each other; and the remaining species [meadow pipit (*Anthus pratensis*), robin (*Erithacus rubecula*), pied wagtail (*Motacilla alba*), dunnock, and garden warbler (*Sylvia borin*)] all differ from the great reed warbler, reed warbler, red-backed shrike, and redstart eggs, but not from each other. In addition, there are no significant size differences between meadow pipit and brambling eggs.

The eggs of different host species also differ statistically in shape (ANOVA asymmetry: $F_{8,254} = 7.68$, $P < 0.001$; ANOVA ellipticity: $F_{8,254} = 7.12$, $P < 0.001$) (Figures 1B and 2B,C). A post hoc Tukey test (Supplementary Table S1) shows that the eggs of the great reed warbler are significantly different in both asymmetry and ellipticity from the eggs of the pied wagtail. The eggs of the robin also differ significantly in both asymmetry and ellipticity from the eggs of the dunnock and meadow pipit. The

remaining species do not differ from each other, or only differ from others in either asymmetry or ellipticity but not both. Figure 1B shows that some hosts appear to occupy different regions in shape morphospace. Compare, for example, the shapes of great reed warbler eggs to those of the brambling and the pied wagtail, which tend to be more asymmetric and less elliptical than great reed warbler eggs. Despite some differences, the average egg shapes of different host species are fairly similar, occupying the same general region of morphospace (Figure 3A). In summary, we detect some differences in size and shape among eggs of the host species.

(2) Are there size and shape differences among the common cuckoo egg morphs?

Eggs of different cuckoo host-races do not differ statistically in size (ANOVA length: $F_{8,254} = 1.46$, $P = 0.161$) (Figures 1A and 2A), when the significance threshold is $P \leq 0.01$ (see **Materials and Methods**). Eggs of different cuckoo host-races also do not differ statistically in shape (ANOVA asymmetry: $F_{8,254} = 2.39$, $P = 0.013$;

ANOVA ellipticity: $F_{8,254} = 1.82$, $P = 0.064$) (Figures 1B and 2B,C). Cuckoo host-races have extremely similar average egg shapes (Figures 1–3A). Specifically, as Figure 3A shows, whereas host eggs have centroids that are close to each other in shape morphospace (average distance of 0.04), the centroids of the different cuckoo host-races are 25% closer to each other (average distance of 0.03). In summary, we do not detect significant differences in size and shape among the cuckoo egg morphs: the cuckoo appears to be making one type of egg (in terms of size and shape).

(3)How different are common cuckoo egg morphs from eggs of their respective hosts in size and shape?

In general, eggs laid by a given cuckoo host-race and those of its target host differ in size but not in shape (Figures 1–2; Table 1). In the terms of egg size, cuckoo eggs tend to be larger than the eggs of their corresponding hosts (Figure 2A) by an average of 10%. Some cuckoo eggs are much larger: the reed warbler-cuckoo lays an egg that is, on average, 18.5% larger than the reed warbler host eggs. The great reed warbler-cuckoo and red-backed shrike-cuckoo lay eggs that are better matched to those of their hosts; here, the smaller effect size ($d < 0.8$) (Table 1) suggests a better match. Consistent with this, a two-tailed t-test (with the significance threshold defined as $P \leq 0.01$) indicates no difference between the egg sizes of the great reed warbler and red-backed shrike and their cuckoo host-races ($P = 0.012$ and $P = 0.370$, respectively; Figure 2). The close match in egg size achieved by these cuckoo host-races occurs because their hosts, the great reed warbler and red-backed shrike, lay the largest eggs among the ten hosts in our dataset; they are also the largest host species, with adults weighing 27.2 and 28.2 grams on average, respectively (Soler 2016). The remaining hosts in our dataset are about 30% smaller in body mass on average, ranging from 12.3 to 19.7 grams (Soler 2016).

In terms of egg shape, eggs of the different cuckoo host-races are generally like those of their hosts, overlapping the areas covered by their respective hosts in the shape morphospace by a minimum of 52% and up to 96% (Figure 1B). Based on effect size (Table 2), cuckoo egg shapes only differ from those of their respective hosts as follows: with the robin in asymmetry, and with the great reed warbler, reed warbler, and brambling in ellipticity. None of the cuckoo host-races lay eggs that, on average, differ from their respective hosts in both asymmetry and ellipticity (Table 1; Figure 2). Despite this general similarity in egg shape, the common cuckoo tends to lay eggs that are slightly more variable in shape than those of all hosts considered collectively (Figure 3A). However, the centroids of the different cuckoo host-races vary less than those of the different hosts (Figure 3A). For all but two cuckoo host-races, the area of shape morphospace occupied by each cuckoo egg morph exceeds that of its host (reed warbler-cuckoo and robin-cuckoo occupy 7.2% and 3.6% less area than their respective hosts). We can see this more generally when we consider the region of morphospace occupied by all cuckoo host-races collectively, which is slightly larger than the region occupied by all host species (Figure 3A). In total, 88% of the entire host region (all eggs of all host species) of morphospace is overlapped by the common cuckoo (all eggs of all host-races) (Figure 3A). In summary, cuckoo eggs are generally not well matched to host eggs in size but are well matched in shape.

(4)Are differences in size and shape correlated with rejection defenses evolved by hosts?

Regression analyses using PGLS revealed nonsignificant correlations (see Supplementary Materials); here, we report the non-phylogenetically corrected ordinary least squares results (Figure 3B,C). We do not find any evidence of a correlation between species-level rejection rates (Soler 2016) and the degree of egg size or shape similarity (or difference) between cuckoo egg morphs and the corresponding host eggs when similarity is quantified according to Equation 1 (percentage of area overlap in morphospace; Figure 3B; $R^2 = 0.01$, $P = 0.829$) or Equation 2 (percentage of difference of means; Figure 3C; $R^2 = 0.05$, $P = 0.553$ for length; $R^2 = 0.06$, $P = 0.480$ for asymmetry; $R^2 = 0.02$, $P = 0.682$ for ellipticity). In summary, cuckoos do not appear to lay eggs that are a closer match in size or shape for host species that are more likely to reject parasitic eggs.

We also tested the hypothesis that increased intraclutch variation in the host egg traits might be correlated with reduced egg rejection behavior. In this scenario, we would expect that the variance (or standard deviation) in host egg size or shape would be inversely correlated with rejection defenses. We investigated whether the standard deviation of egg size and shape across host eggs in each clutch was correlated with rejection rates, but we found no correlations ($R^2 = 0.03$, $P = 0.662$ for length, $R^2 = 0.01$, $P = 0.829$ for asymmetry, and $R^2 = 0.03$, $P = 0.664$ for ellipticity). Standard deviation values for host egg traits, along with information about how they were calculated, can be found in the Supplementary Tables S7 and S8.

(5)Comparison to Australian parasitic cuckoos

We reanalyzed data from Attard et al. (2017) in order to compare the egg shapes of the common cuckoo and its hosts to several Australian cuckoo species and their hosts (see additional details in the Supplementary Materials). The pallid cuckoo, brush cuckoo, and fan-tailed cuckoo appear to have different egg shapes, with little overlap in the egg shape morphospace defined by asymmetry and ellipticity (Figure 4A). The common cuckoo lays eggs that are nearly as variable in shape as the three Australian cuckoos combined (Figure 4A). The pallid cuckoo and brush cuckoo lay eggs that resemble the shapes of those of their hosts (Figure 4B), consistent with the suggestion of egg shape mimicry by Attard et al. (2017). The host-race of pallid cuckoo that parasitizes the black-headed honeyeater (*Melithreptus affinis*) matches host eggs fairly well in terms of shape (Figure 4C); this cuckoo host-race is also known to mimic host eggshell color (Starling 2006). However, other pallid cuckoo host-races do not appear to lay eggs that are well matched to those of hosts, as there is little overlap between these cuckoo-host pairs in the egg shape morphospace (Figure 4C).

DISCUSSION

While many of the common cuckoo's European host species lay eggs of variable sizes and shapes, the different cuckoo host-races lay eggs that are—at least on average—generally similar to one another in size and shape. This generic "one size and shape fits all" cuckoo egg is a poor match to the most host eggs in size but a good match to most host eggs in shape. Our results are broadly consistent with previous studies on select common cuckoo host-races showing limited differentiation in egg shape (Antonov et al. 2010; Bán et al. 2011; Drobniak et al. 2014), at least within a shared geographic region (Bán et al. 2011). Why have the various common cuckoo egg morphs not diverged in size and shape? There are three possibilities, which are not mutually exclusive. The first is that physiological constraints on cuckoo egg size (e.g., the egg must be sufficiently large to support chick development) and shape (e.g., the
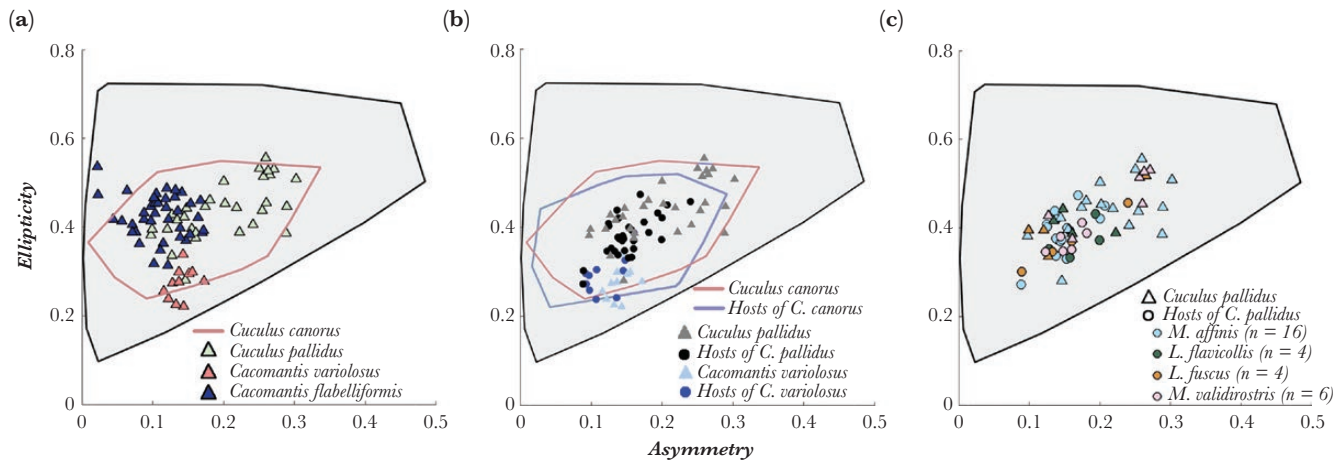
Figure 4

(A) Reanalysis of Attard et al. (2017) data shows that the eggs of the pallid cuckoo (*Cuculus pallidus*), brush cuckoo (*Cacomantis variolosus*), and fan-tailed cuckoo (*Cacomantis flabelliformis*) appear to be occupying distinct parts of the morphospace with little overlap. In comparison to these three Australian cuckoo species, the common cuckoo (*Cuculus canorus*) appears to make eggs that are more variable in shape, nearly encompassing the area occupied by the three Australian cuckoo species combined. (B) Attard et al. (2017) suggested that the pallid and brush cuckoos evolved to mimic the egg shapes of their open, cup-nesting hosts. Our reanalysis does indeed show that these two cuckoo species appear to lay more similarly shaped eggs to those of their own hosts. It is interesting to note that the host eggs occupy different regions of the morphospace with little overlap. (C) The host-race of the pallid cuckoo that parasitizes the black-headed honeyeater (*Melithreptus affinis*) is known to mimic the eggshell color of its host well (Starling et al. 2006). Here, we see that this host-race lays eggs that are also similar in shape to those of black-headed honeyeaters, with considerable overlap in morphospace. In contrast, the other pallid cuckoo-host races do not appear to lay similarly shaped eggs to those of their hosts, indicated by the lack of major overlap of cuckoo eggs with those its other hosts.

egg-shaping process in the oviduct may restrict shape variation) prevent cuckoos from evolving eggs that are well matched to host eggs. A second possibility is that host species do not discriminate on the basis of egg size or shape, so cuckoos are not under strong selection to match these features. A third possibility is that any benefit to closely matching egg size and shape to improve incubation efficiency is small, so cuckoos have not evolved perfectly matched eggs.

Let us first consider egg size in the context of these three hypotheses. Consistent with previous studies (Davies and Brooke 1988; Moksnes and Røskaft 1995), we found that common cuckoos generally lay slightly larger eggs than those of their hosts. That cuckoo eggs approach the ballpark size of host eggs is remarkable given that cuckoo adults weigh four to nine times more (Krüger and Davies 2004) than their corresponding hosts (Avilés and Garamszegi 2007). Relative to birds of a similar size, the common cuckoo lays the smallest egg for its body size, with the egg accounting for just 2.4% of its body weight (Lack 1968). Clearly, there has been strong selection for reduced egg size in common cuckoos, so that these eggs escape rejection or are more efficiently incubated. But physiological constraints likely place a lower limit on egg size, such that cuckoos cannot lay eggs so small that they pose major costs to the cuckoo chick's development or ability to overthrow host eggs. What is this lower limit? In our dataset, the smallest cuckoo egg is 2.01 cm long, with an estimated volume of 3.15 cm^3, calculated using the equation from Baker (2002). This estimate is consistent with Moksnes and Røskaft (1995), whose smallest recorded common cuckoo eggs have ~3.00 cm^3 volume. When targeting host species laying eggs smaller than ~2 cm long—and many hosts fit this description (Figures 1A and 2A)—it may not be possible for cuckoo host-races to evolve eggs that are well matched in size. However, if the cost to laying a slightly-too-large egg is minor—as in, it does not always trigger host rejection or impede efficient incubation— then common cuckoos might not suffer from laying eggs that are poorly matched in size to host eggs.

Do common cuckoo hosts pay attention to differences in egg size? Although there is evidence suggesting that some host species reject cuckoo eggs on the basis of size (Davies and Brooke 1988; Moksnes and Røskaft 1992; Roncalli et al. 2017), other hosts disregard size differences (Antonov et al. 2006; Stokke et al. 2010). Some hosts appear to tolerate a small size difference. Reed warblers, for example, reject model eggs that are much larger than typical cuckoo eggs, but they do not discriminate between typical reed warbler-sized and (slightly larger) cuckoo-sized model eggs (Davies 2000). Consistent with the idea that some hosts might accept eggs that are relatively similar in size to host eggs, dome-nesting *Phylloscopus* warblers (parasitized by various *Cuculus* species) appear to apply such rules, rejecting eggs that are much larger but not slightly larger than their own (Marchetti 1992, 2000; Meshcheryagina et al. 2016). If this is the norm for common cuckoo hosts, then there may not be enough selection pressure on cuckoos to further reduce egg size.

Do oversized cuckoo eggs run the risk of being inefficiently incubated by the host? A too-large egg might be impossible for small host birds to incubate—or require such long incubation times that the cuckoo chick would hatch too late to eject host young (Davies and Brooke 1988). But perhaps common cuckoo eggs have evolved to be similar enough to host egg size—while still falling short of a perfect match—to avoid these incubation costs. The fact that cuckoos successfully parasitize the hosts examined in this study suggests that this may be the case. Overall, physiological constraints, lack of size-based rejection by hosts (of slightly larger eggs) and minimized incubation costs could together explain the imperfect egg size similarity achieved by cuckoos.

Now, let us consider egg shape. Perhaps the different cuckoo host-races lay eggs of similar shape because the cuckoo's body size and oviduct morphology impose tight constraints on egg shape (Stoddard and Stevens 2011). In other words, perhaps only one egg shape is possible for the different cuckoo host-races, particularly if a

given egg shape is associated with the cuckoo's unusually small (for its body size) egg volume. This hypothesis is broadly consistent with the observation—across a wide variety of bird species—that body and oviduct morphology are correlated with aspects of egg shape (Stoddard et al. 2017; Montgomerie et al 2021), although more work is needed to understand drivers of intraspecific egg shape variation. Although the cuckoo host-races on average lay eggs of broadly similar shape (Figures 1–3), different females within a host-race are capable of laying variable egg shapes (Figure 1B). Cuckoos appear to lay eggs that are at least as variable in shape as those of their respective hosts (Figure 3A); in fact, the area of morphospace occupied by each cuckoo egg morph exceeds that of its corresponding host in all but two cases (reed warbler and robin) (Figure 1B). A hypothesized mechanism for egg shape generation is that pressure in the oviduct and membrane properties both contribute to shaping (Stoddard et al. 2017); here, we would suggest that the cuckoos and hosts have similar egg-shaping mechanisms. Overall, it seems unlikely that cuckoos are physiologically constrained in terms of egg shape. They are capable of making most (if not all) host egg shapes.

It seems more likely that there is not strong selection pressure on cuckoos to evolve an even better matching egg shape, once a generic (perhaps more than 50% overlap) egg shape match has been achieved. Do hosts use egg shape to reject eggs? There is limited evidence that common cuckoo hosts rely on shape cues (Zölei et al. 2012), perhaps because color and pattern are more informative than subtle differences in egg shape. Therefore, the benefit to a close egg shape match may be minimal in terms of evading host rejection. Likewise, the cuckoo's egg shape might be sufficiently similar to hosts' to ensure efficient incubation, so that any advantage to evolving a better-matched egg shape is negligible. Overall, we observe that cuckoo egg morphs are similar in shape to each other and generally well matched to host egg shapes—both on average (Figure 3A) and in terms of variability (Figure 1B). Whether this similarity is purely a consequence of cuckoos and hosts laying broadly generic (and therefore similar) egg shapes or has a functional basis associated with rejection defenses, incubation efficiency, or potentially egg strength (Picman and Honza 2020) is unclear.

Where common cuckoos do have similar egg sizes and shapes to their corresponding hosts (Table 2, Figure 2), this does not appear to be the result of strong selection pressure imposed by host recognition systems (i.e., mimicry) (Figure 3B,C). By contrast, different cuckoo host-races lay eggs that vary spectacularly in pattern (Stoddard and Stevens 2010) and color (Stoddard and Stevens 2011), with eggs well matched to the patterns and colors of eggs laid by highly discriminating hosts. In fact, egg pattern mimicry by some cuckoo host-races may have raised the arms race ante, such that some host species evolved highly recognizable egg pattern signatures on their own eggs (Stoddard et al. 2014). Why these arms races tend to play out in the visual and acoustic—rather than tactile domains (where size and shape could provide additional cues, particularly to dome-nesting hosts)—remains an open question (Stoddard and Hauber 2017). Unraveling the genetic mechanisms underpinning common cuckoo egg color, pattern, size, and shape could provide insights. Cuckoo egg color and pattern genes are hypothesized to be sex-linked, controlled by the female W sex chromosome (reviewed in Stoddard and Hauber 2017; Stokke et al. 2017), as they are in the brood parasitic cuckoo finch (*Anomalospiza imberbis*) (Spottiswoode et al. 2022). If, by contrast, the genes influencing egg size and shape are largely autosomal—as they appear to be in chickens (Goraga 2019)—then this might limit divergence of these traits among cuckoo host-races in the absence of assortative mating

(but see Fossøy et al. 2011, which suggests that some degree of assortative mating may indeed occur).

Another important aim for future work will be to conduct field experiments in common cuckoo hosts to determine how hosts might integrate color, pattern, size, and shape cues when making rejection decisions. One limitation of our study is that the rejection rates compiled by Soler (2016) are based on various studies in which hosts were presented with nonmimetic eggs. The extent to which these nonmimetic eggs differed in terms of color, pattern, size, and shape from host eggs was not recorded in a standardized way across studies, making it difficult to infer how hosts might (or might not) use these cues collectively to make rejection decisions. We used these rejection rates as a proxy for how discriminating the different host species are, but more detailed and carefully controlled experiments could reveal a "hierarchy of cues" used during egg recognition and rejection. An example of such a hierarchy comes from a different parasite–host system: tawny-flanked prinia (*Prinia subflava*) hosts of the cuckoo finch may rely on complex egg pattern cues only when color and simple pattern features provide little information (Stoddard et al. 2019).

Have other cuckoo species (family: Cuculidae) evolved egg size or shape mimicry? Attard and colleagues (2017) recently suggested that two species of Australian cuckoos, the pallid cuckoo and the brush cuckoo, may have evolved egg shape mimicry for open, cup-nesting hosts due to selection by hosts against odd-shaped eggs. For a third Australian species, the fan-tailed cuckoo, which exclusively exploits closed dome-nesting hosts, Attard at al. (2017) found no evidence of egg shape mimicry; the same was true for dome-nesting hosts of the brush cuckoo. In order to compare the egg shapes of Australian cuckoos and their hosts to those of the common cuckoo and its hosts, we reanalyzed data from Attard et al. (2017) by plotting them in a morphospace defined by asymmetry and ellipticity. The three Australian cuckoo species appear to have differently shaped eggs that occupy distinct regions of the morphospace, with little overlap (Figure 4A). Each Australian cuckoo species is less variable in egg shape than the common cuckoo (Figure 4A). Consistent with the suggestion of egg mimicry by Attard et al. (2017), our reanalysis shows that the pallid and brush cuckoos generally overlap the egg shape space of their respective hosts (Figure 4B). By comparison, the hosts of the common cuckoo lay eggs that are collectively more variable in shape than either the hosts of the pallid or brush cuckoo (Figure 4B). The common cuckoo generally overlaps the egg shape space of its hosts (Figure 4B; Supplementary Figure S1); in fact, considering the ten common cuckoo hosts collectively, 88% of the entire host region of morphospace is overlapped by the common cuckoo (Figure 3A). In this sense, common cuckoos (as a species) lay eggs that are highly similar in shape to those of their hosts, like pallid and brush cuckoos.

In our study, we did not assess different European cuckoo species, so we cannot answer the question of whether the common cuckoo lays eggs that are more similar to its hosts than to those of other cuckoo species breeding in Europe, such as the great spotted cuckoo (*Clamator glandarius*). Instead, we investigated the extent to which the host-races of a single species—the common cuckoo—may have evolved egg shape similarity. Attard et al. (2017) did not directly address this in their study. To explore this further using their data, we compared the egg shapes of the pallid cuckoo, which has evolved host-races exhibiting excellent egg color and pattern mimicry (Starling et al. 2006), to four of its hosts (Figure 4C). From this preliminary analysis (Figure 4C), we see little support for the hypothesis that pallid cuckoo host-races have evolved egg shapes tailored to match those of their target hosts. Although the pallid cuckoo host-race parasitizing black-headed honeyeaters

produces egg shapes that overlap hosts' considerably (82%), the same is not true for the pallid cuckoo-host races parasitizing the yellow-throated honeyeater (*Lichenostomus flavicollis*), the fuscous honeyeater (*Lichenostomus fuscus*), and the strong-billed honeyeater (*Melithreptus validirostris*) hosts (23%, 4%, and 29% overlap in egg shape space, respectively). This result echoes our finding that the common cuckoo, despite laying eggs that generally match the range of egg shapes laid by its various hosts, has not evolved host-specific egg shape similarity. Therefore, in both the common and pallid cuckoos, there is apparent egg shape similarity between the cuckoo and its various host species—but there appears to be little egg shape differentiation at the host-race level. However, Oriental cuckoo (*Cuculus optatus*) host-races might buck this trend: a recent study showed that different cuckoo host-races lay eggs with variable breadths that resemble those of their hosts, presumably due to selection imposed by host defenses (Meshcheryagina et al. 2018). Moving forward, it will be productive to extend these analyses to diverse brood parasite–host systems and to complement museum-based egg shape analyses with field-based experiments on host rejection of eggs based on size and shape.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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AUTHOR CONTRIBUTIONS

Derya Akkaynak (Conceptualization-Equal, Data curation-Equal, Formal analysis-Equal, Investigation-Equal, Methodology-Equal, Project administration-Equal, Software-Equal, Validation-Equal, Visualization-Equal, Writing – original draft-Equal, Writing – review & editing-Equal), Mary Stoddard (Conceptualization-Equal, Data curation-Equal, Formal analysis-Equal, Funding acquisition-Lead, Investigation-Equal, Methodology-Equal, Project administration-Equal, Software-Equal, Validation-Equal, Visualization-Equal, Writing – original draft-Equal, Writing – review & editing-Equal)

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Akkaynak and Stoddard (2023).

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