OXFORD

Article

Spatial variation in egg polymorphism among cuckoo hosts across 4 continents

Canchao YANG (ID) [a],*, Xingfeng SI[b,c], Wei LIANG (ID) [a], and
Anders Pape MØLLER (ID) [d]

[a]Ministry of Education Key Laboratory for Tropical Plant and Animal Ecology, College of Life Sciences, Hainan Normal University, Haikou 571158, China, [b]Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China, [c]Institute of Eco-Chongming (IEC), Shanghai 202162, China, and [d]Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France

*Address correspondence to Canchao Yang. E-mail: ccyang@hainnu.edu.cn.

Handling editor: Zhi-Yun Jia

Received on 28 December 2019; accepted on 12 March 2020

Abstract

Although egg color polymorphism has evolved as an effective defensive adaptation to brood parasitism, spatial variations in egg color polymorphism remain poorly characterized. Here, we investigated egg polymorphism in 647 host species (68 families and 231 genera) parasitized by 41 species of Old Word cuckoos (1 family and 11 genera) across Asia, Europe, Africa, and Australia. The diversity of parasitic cuckoos differs among continents, reflecting the continent-specific intensities of parasitic selection pressure on hosts. Therefore, host egg polymorphism is expected to evolve more frequently on continents with higher cuckoo diversity. We identified egg polymorphism in 24.1% of all host species and 47.6% of all host families. The common cuckoo *Cuculus canorus* utilized 184 hosts (28.4% of all host species). Hosts of the common cuckoo and of *Chrysococcyx* species were more likely to have polymorphic eggs than hosts parasitized by other cuckoos. Both the number of host species and the host families targeted by the cuckoo species were positively correlated with the frequency of host egg polymorphism. Most host species and most hosts exhibiting egg color polymorphism were located in Asia and Africa. Host egg polymorphism was observed less frequently in Australia and Europe. Our results also suggested that egg polymorphism tends to occur more frequently in hosts that are utilized by several cuckoo species or by generalist cuckoo species. We suggest that selection pressure on hosts from a given continent increases proportionally to the number of cuckoo species, and that this selection pressure may, in turn, favor the evolution of host egg polymorphism.

Key words: avian brood parasitism, cuckoo diversity, cuckoo host

Although bird eggs display a variety of color morphs among species, the ancestral state is believed to be a simple white shell, without sophisticated pigments (Wallace 1889). A recent study has shown that birds were not the first amniotes to produce colored eggs: egg color pigments have been identified in preserved non-avian theropod dinosaur eggs, but not in ornithischian or sauropod eggs (Wiemann et al. 2018). Bird eggs may be pigmented to increase crypsis and to reduce the risk of predation (Lack 1958). Alternatively, egg coloration may be a thermoregulatory mechanism that prevents the overheating or cooling of the embryo during development (Montevecchi 1976; Bertram and Burger 1981; Wisocki et al. 2019). However, there is no single simple explanation for the variety of bird egg

morphs, as eggs display innumerable colors and patterns, not only among taxa, but also among species with similar nesting habitats and structures, and even among individuals within a single population (i.e., polymorphism) (Swynnerton 1916). One possible and persuasive explanation for egg color polymorphisms is that the evolution of nest site selection and nest structure effectively reduced egg predation risk, and secondary adaptations have resulted in increased egg color diversity (Kilner 2006).

Avian brood parasitism may drive such secondary evolution events, because egg morphs determine the success of parasitism or of anti-parasite defences (Kilner 2006; Yang et al. 2010). That is, the extent to which a parasite egg mimics host egg coloration determines brood parasitism success (Davies 2011) in that the choice to reject an egg, and the precision of that rejection, depends on host recognition of egg coloration, and the differences between the morphs of the parasite and host eggs (Soler 2014). This coevolutionary arms race favors highly divergent parasite egg morphs, allowing the parasite to mimic the eggs of a variety of host species (Davies 2000; Yang et al. 2015a). Correspondingly, the arms race also favors the evolution of diverse egg morphs in hosts, because differences in egg morphs between parasite and host facilitate the correct recognition and rejection of parasite eggs (Yang et al. 2010; but see Hanley et al. 2017, 2019; Abolins-Abols et al. 2019).

Polymorphism is defined as the occurrence of 2 or more clearly distinct phenotypes within a single population (Leimar 2005). Interestingly, 3.5% of all birds species have polymorphic plumage patterns that may have been generated due to selective pressure from prey, predators, and/or competitors, and these patterns may be maintained by disruptive selection (Galeotti et al. 2003). In birds, egg coloration, as well as plumage, may be polymorphic. As biological variations among taxa are obvious (Darwin 1859), egg polymorphism is likely to be less common than egg morph diversity among taxa. However, the former (egg polymorphism) appears to be more well-characterized in the literature (Yang et al. 2010; Vikan et al. 2011). This may be because egg polymorphism is a more recent secondary adaptation, and, as such, the factors driving these variations are easier to deduce (Swynnerton 1916). Avian brood parasitism is regarded as an important factor driving the evolution of egg polymorphism in hosts (Kilner 2006; Spottiswoode and Stevens 2012). Indeed, host populations that have been under pressure from parasitic cuckoos over evolutionary time are more likely to have evolved more egg polymorphism than populations not under pressure from cuckoo parasitism (Yang et al. 2015b). Therefore, host egg polymorphism is associated with coevolutionary temporal interactions with brood parasites such as cuckoos.

Although egg color polymorphism in avian brood parasites has received significant attention (Kilner 2006; Liang et al. 2012; Yang et al. 2016b, 2018), few studies have investigated spatial variations in color polymorphism at geographic scales. Furthermore, parasite diversity that varies among different geographic areas may have a significant impact on the occurrence of egg polymorphism in hosts. Generally, host anti-parasite defences specifically target brood parasites due to coevolution (Langmore et al. 2009; Yang et al. 2014; Noh et al. 2018). In geographic areas with higher parasite diversity, parasitism pressure on hosts is generally high, because hosts encounter a variety of parasites that may pose distinct threats (Yang et al. 2014). Therefore, we predicted that hosts from geographic areas with high parasite diversity would more frequently evolve egg polymorphism as an effective defence against brood parasites (Yang et al. 2018). To test this prediction, we investigated host egg

polymorphism in 647 Old World cuckoo hosts across 4 continents (Asia, Europe, Africa, and Australia). The objective of this study was to characterize the factors that have contributed to the evolution of egg polymorphism in cuckoo hosts. Specifically, we aimed to test (1) whether the number of cuckoo species targeting each host species would predict the frequency of egg color polymorphism in the hosts and (2) whether the frequency of color polymorphism differed among continents with different levels of cuckoo diversity, as would be expected if a higher diversity of brood parasites increased the selection pressure on host defences.

Materials and Methods

Data extraction

A complete list of the host species of Old World cuckoos was obtained from Lowther (2014). We excluded some obviously unsuitable host species from this list (e.g., precocial birds). The validities of 4 *Hierococcyx* species (the northern hawk cuckoo, *Hierococcyx hyperythrus*; the Philippine hawk cuckoo, *Hierococcyx pectoralis*; the Malaysian hawk cuckoo, *Hierococcyx fugax*; and Hodgson's hawk cuckoo, *Hierococcyx nisicolor*) are controversial, and the parasitism records for these taxa are poor. Following Lowther (2014), we therefore considered these taxa an *H. fugax* species complex (hereafter referred to as "Cuckoo complex" in the text, table, and figures). Host eggs data were obtained from the electronic version of the Handbook of the Birds of the World (http://www.hbw.com; del Hoyo et al. 2013) and Web of Science (http://isiknowledge.com, Clarivate Analytics).

Our classification of egg morphs as monomorphic or polymorphic was based on the principle that polymorphic eggs have 2 or more clearly different morphs; all of the other eggs were considered monomorphic (Leimar 2005). Ambiguously described differences among egg morphs were not considered sufficient evidence of egg polymorphism. For example, eggs described as "blue or greenish-blue" or as "white or greyish-white" were not regarded as descriptions of distinct egg phenotypes. Furthermore, eggs with 1 type of continuous macular variation (e.g., the eggs of the great reed warbler *Acrocephalus arundinaceus*) were not considered polymorphic. However, eggs with different types of maculation (e.g., dots vs. lines) were considered phenotypically different. To eliminate the subjective expectations of human observers that might bias the extracted data (Yang and Liang 2016), we used a blinded method to classify host egg morphs: classifications were performed without knowledge of other host data (i.e., species, size, distribution, and habitat). Furthermore, 3 observers independently classified all of the eggs without communicating with each other. Egg morph classification was highly consistent among observers (intraclass correlation coefficient=0.989, $F_{649,1298}$=260.928, $P < 0.001$).

The phylogenetic trees of hosts and cuckoos were pruned from the global bird phylogeny (http://birdtree.org) using the option "Hackett All Species: a set of 10,000 trees with 9993 OTUs each" (Jetz et al. 2012). We sampled 5,000 pseudo-posterior distributions and constructed a Maximum Clade Credibility tree with mean node heights using TreeAnnonator v1.8.2 in the BEAST package (Drummond and Rambaut 2007; Ricklefs and Jonsson 2014). We used the resulting host and cuckoo phylogenetic trees (Supplementary Figure S1) for the following phylogenetic regressions.

Statistical analyses

We used MCMCglmm (generalized linear mixed models using Markov chain Monte Carlo techniques) (Hadfield 2010) to estimate the effect of continent (i.e., Asia, Europe, Africa, or Australia) on the incidence of host egg polymorphism. MCMCglmm is a phylogenetic regression within a Bayesian framework that supports binary dependent variables (Ives and Garland 2010), such as the monomorphic and polymorphic egg coloration patterns in this study. To adjust for the phylogenetic dependence of host species in the MCMCglmm analysis, we set the continent as the fixed effect and considered the order, family, and genus of each host species as random effects. We ran the MCMCglmm in 4 parallel Markov chains for 23,000 iterations each, discarding the first 3,000 iterations as burn-in, and using a thinning rate of 20. We assessed model convergence using the Gelman–Rubin statistic with diagnostic values <1.1 (Gelman and Rubin 1992). We considered the effect of continent on host egg polymorphism "significant" when the 95% Bayesian credible intervals of the parameter estimates overlapped zero (Kéry and Royle 2016). Phylogenetic analyses were performed with R (http://r-project.org), using the MCMCglmm (Hadfield 2010), coda (Plummer et al. 2016), and picante packages (Kembel et al. 2010).

Pearson or Spearman correlations were used to test the relationships between values in pairs of categories, depending on whether a 1-sample Kolmogorov–Smirnov test indicated that the data were normally distributed. Two-way ANOVAs were used to test whether hosts producing polymorphic eggs were parasitized by more cuckoo species than hosts producing monomorphic eggs. In this analysis, the number of cuckoo species targeting each host (i.e., cuckoo diversity) was considered the dependent variable, while the host egg morph (i.e., monomorphic or polymorphic) and the continent were considered fixed effects; the interaction between the 2 dependent effects was also tested. All of the statistical analyses were performed using IBM SPSS 20.0 for Windows (IBM Inc., USA).

Results

General information about cuckoos and hosts

Our analyses included 647 host species parasitized by 41 Old World cuckoo species; the host species fell into 68 families and 231 genera, while the cuckoo species fell into 1 family and 11 genera (Table 1). We identified egg polymorphism in 24.1% of the 647 host species and in 47.6% of the 68 host families. Most cuckoo hosts (97.8%) belonged to the order Passeriformes (Supplementary Table S1).

Egg polymorphism across host families

The common cuckoo had the greatest number of hosts: 184 species (28.4% of all host species). Egg polymorphism was common in these host species (37.5% of all species). Hosts of Chrysococcyx cuckoos also had a higher frequency of egg polymorphism than hosts parasitized by other cuckoos. Eight cuckoo species parasitized hosts with egg polymorphism frequencies >30%. The numbers of host species and the numbers of host families targeted by each cuckoo species were positively correlated with the number of hosts laying polymorphic eggs (host species: $r = 0.84$, $n = 41$, $P < 0.001$, Pearson correlation; host family: $r = 0.77$, $n = 41$, $P < 0.001$, Spearman correlation). However, although the frequency of host egg polymorphism (i.e., the proportion of hosts laying polymorphic eggs) was significantly positively correlated with the number of host species targeted by each cuckoo species, the number of host families targeted by each cuckoo species was not (host species: $r = 0.42$, $n = 41$,

Table 1. The number of cuckoo species known from different continents, according to the definitions of this study

	Europe	Africa	Australia	Asia	Occurrence[a]
Cacomantis castaneiventris			√	√	2
Cacomantis flabelliformis			√	√	2
Cacomantis merulinus			√	√	2
Cacomantis pallidus			√	√	2
Cacomantis passerinus			√	√	2
Cacomantis sonneratii			√	√	2
Cacomantis variolosus			√		1
Cercococcyx mechowi		√			1
Cercococcyx montanus		√			1
Chrysococcyx basalis			√		1
Chrysococcyx caprius		√			1
Chrysococcyx cupreus		√			1
Chrysococcyx klaas		√			1
Chrysococcyx lucidus			√	√	2
Chrysococcyx maculatus			√	√	2
Chrysococcyx minutillus			√	√	2
Chrysococcyx osculans			√	√	2
Chrysococcyx xanthorhynchus			√	√	2
Clamator coromandus				√	1
Clamator glandarius	√	√			2
Clamator jacobinus		√		√	2
Clamator levaillantii		√			1
Cuckoo complex[b]				√	1
Cuculus canorus	√			√	2
Cuculus clamosus		√			1
Cuculus gularis		√			1
Cuculus Lepidus				√	1
Cuculus micropterus				√	1
Cuculus poliocephalus		√		√	2
Cuculus rochii		√			1
Cuculus solitarius		√			1
Eudynamys cyanocephalus			√		1
Eudynamys scolopaceus				√	1
Hierococcyx sparverioides				√	1
Hierococcyx vagans				√	1
Hierococcyx varius				√	1
Pachycoccyx audeberti		√			1
Scythrops novaehollandiae			√	√	2
Surniculus dicruroides				√	1
Surniculus lugubris				√	1
Urodynamis taitensis			√		1
Sum	2	14	16	25	

[a] The number of continents for the occurrence of each cuckoo., [b] "Cuckoo complex" refers to 4 species in the genus *Hierococcyx* (see the text for further explanations).

$P = 0.006$; host family: $r = 0.16$, $n = 41$, $P = 0.324$, Spearman correlation; Figure 1).

Host egg polymorphism in the families most commonly parasitized by cuckoos

All of the cuckoo species parasitized species in the Passeriformes and 19.5% of the cuckoo species also parasitized other bird orders (Supplementary Table S1). All instances of host egg polymorphism identified in this study were recorded in the passerines, with the exception of 1 phoeniculid species in the Bucerotiformes. Within the Passeriformes, most hosts were in the family Muscicapidae (76 species), followed by the Leiothrichidae (48 species) and the
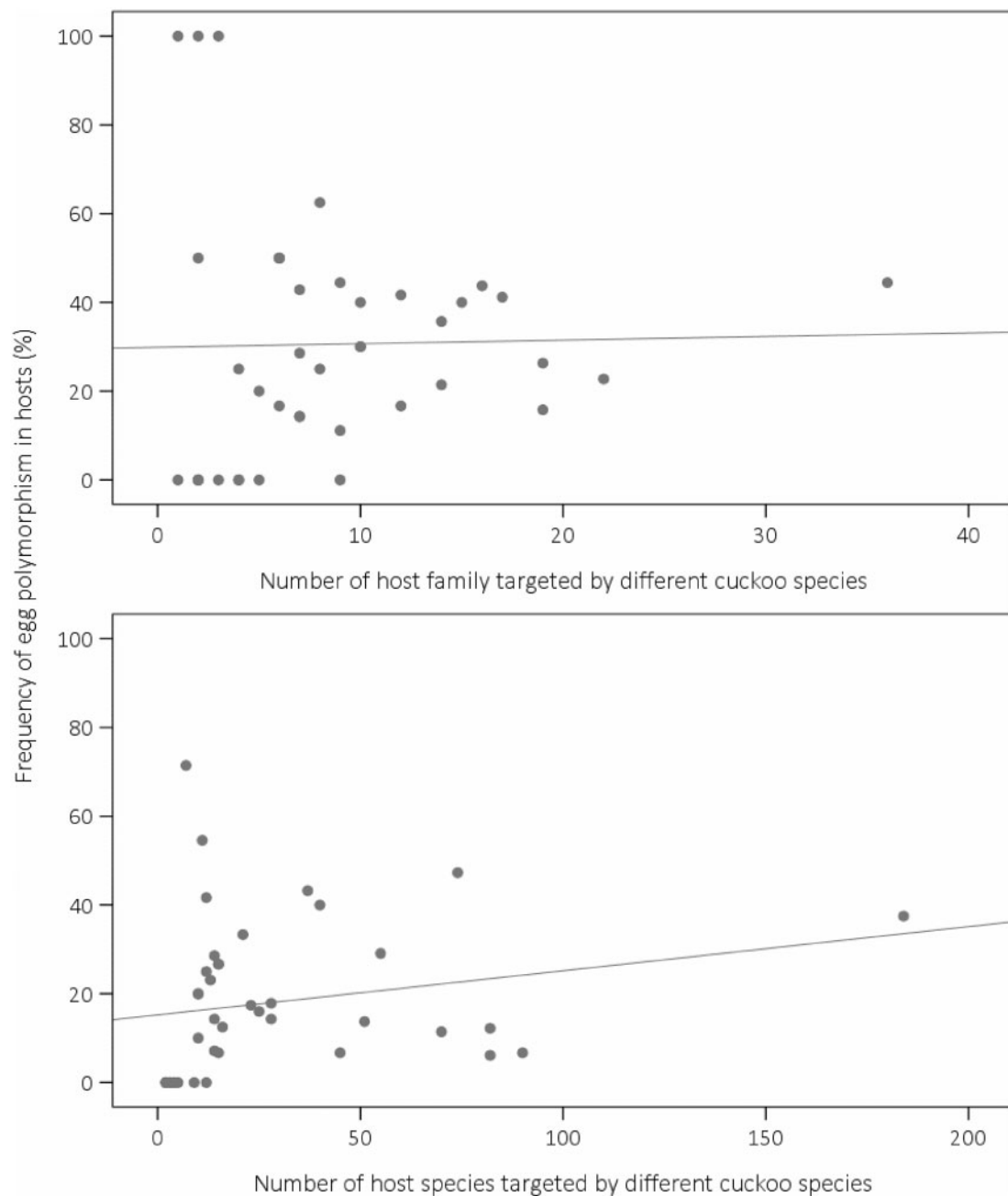
Figure 1. The relationship between the frequency of host egg polymorphism and the number of host family/species targeted by various cuckoo species.

Acanthizidae (48 species). The pattern of host utilization by cuckoos differed from the distribution of hosts among families. However, Pearson correlations showed that the number of host species in a family was positively correlated with the number of cuckoo parasites ($r = 0.70$, $n = 68$, $P < 0.001$, Pearson correlation). Furthermore, the number of host species in a family was also positively correlated with the frequency of egg polymorphism in that family ($r = 0.86$, $n = 68$, $P < 0.001$, Pearson correlation).

Host egg polymorphism among continents

The greatest proportions of host species and families with polymorphic eggs were located in Asia (26.8% of all species and 42.2%

of all families). The proportions of host species and families with polymorphic eggs in Africa were only slightly lower, but Australia and Europe had relatively few instances of host egg polymorphism. The estimated effect of continent on the occurrence of host egg polymorphism excluded zero, indicating that continent was a significant predictor of host egg polymorphism (Figure 2). The hosts producing polymorphic eggs were parasitized by more cuckoo species that the hosts producing monomorphic eggs ($F = 4.447$, $df = 1$, $P = 0.035$, ANOVA; Figure 3). The number of cuckoo species targeting each host species also differed across continents ($F = 21.704$, $df = 3$, $P < 0.001$, ANOVA; Figure 3). However, no interaction effects between continents and egg morphs were found ($F = 0.342$, $df = 3$, $P = 0.795$, ANOVA).

Discussion

In this study, we identified egg polymorphism in 24.1% of 647 host species and in 47.6% of 68 host families. In addition, both the numbers of host species and the numbers of host families targeted by the cuckoo species were positively correlated with the frequency of host egg polymorphism. In cuckoo hosts, polymorphic eggs have most likely evolved as a specific adaptation to parasitism (Kilner 2006; Yang et al. 2010). When targeting hosts with polymorphic eggs, cuckoos are at a distinct disadvantage, because polymorphic host eggs considerably reduce the rate of parasitism success (Yang et al. 2016a, 2018). In a cuckoo-host system where the cuckoo lays mimetic eggs and the host rejects dissimilar eggs, the appearance of an additional host egg morph that is laid at a similar rate to the original morph halves the probability that the cuckoo egg morph will match that of the host. The rate of successful parasitism will further decline if the host evolves 3 egg morphs (Yang et al. 2010). Thus, the

Figure 2. The posterior estimates of the effect of continent on the occurrence of host egg polymorphism. The black dots indicate the posterior means and the bars indicate the 95% Bayesian credible intervals of the parameter estimates.

probability that the cuckoo egg will match the host egg is negatively correlated with the number of host egg morphs. However, it should be noted that this hypothesis assumes that cuckoos do not actively target nests where the host egg matches the cuckoo egg (Yang et al. 2016c). Obviously, if cuckoos only parasitized host nests containing eggs that match the cuckoo eggs, polymorphic host eggs cannot have evolved as a specific adaptation to cuckoo parasitism, because cuckoos would always choose host nests containing the eggs most similar to those of the cuckoo in order to maximise the egg acceptance rate (Honza et al. 2014). However, recent experimental studies have provided unambiguous evidence that cuckoos do not select specific host eggs when parasitizing host nests (Yang et al. 2016c, 2017). Therefore, egg polymorphism is an effective defence against cuckoo parasitism and it occurs more frequently in hosts that are parasitized by multiple families and species of cuckoos.

Cuckoos reduce host rejection risk by laying eggs in host nests containing eggs with matching phenotypes (Table 1). Many hosts have evolved egg polymorphism to counter cuckoo parasitism, but only rarely have cuckoos evolved correspondingly polymorphic eggs. Yang et al. (2010) identified this type of egg polymorphism between the common cuckoo and its parrotbill *Paradoxornis alphonsianus* host, while Vikan et al. (2011) described a similar situation between the common cuckoo and 2 host species: the brambling *Fringilla montifringilla* and the chaffinch *Fringilla coelebs* (Vikan et al. 2011). Recently, polymorphic parasite eggs were also identified in the plaintive cuckoo *Cacomantis merulinus*, which parasitizes the common tailorbird *Orthotomus sutorius* (Yang et al. 2016a). In such cases, polymorphism arises in both species as a result of frequency-dependent selection (Majerus 1998; Yang et al. 2010). Therefore, although egg polymorphism has been identified in cuckoos, it remains much more common in hosts than in cuckoos because cuckoo egg polymorphism cannot increase the overall rate of successful parasitism on hosts that lay polymorphic eggs (Yang et al. 2018).

Our results indicate that the frequency of host egg polymorphism not only varies in time, as has been shown previously (Lahti 2005;
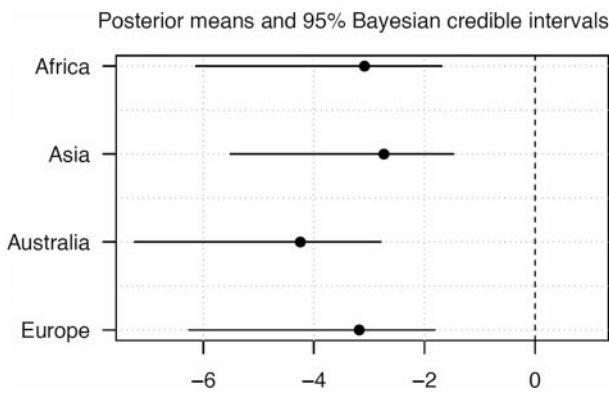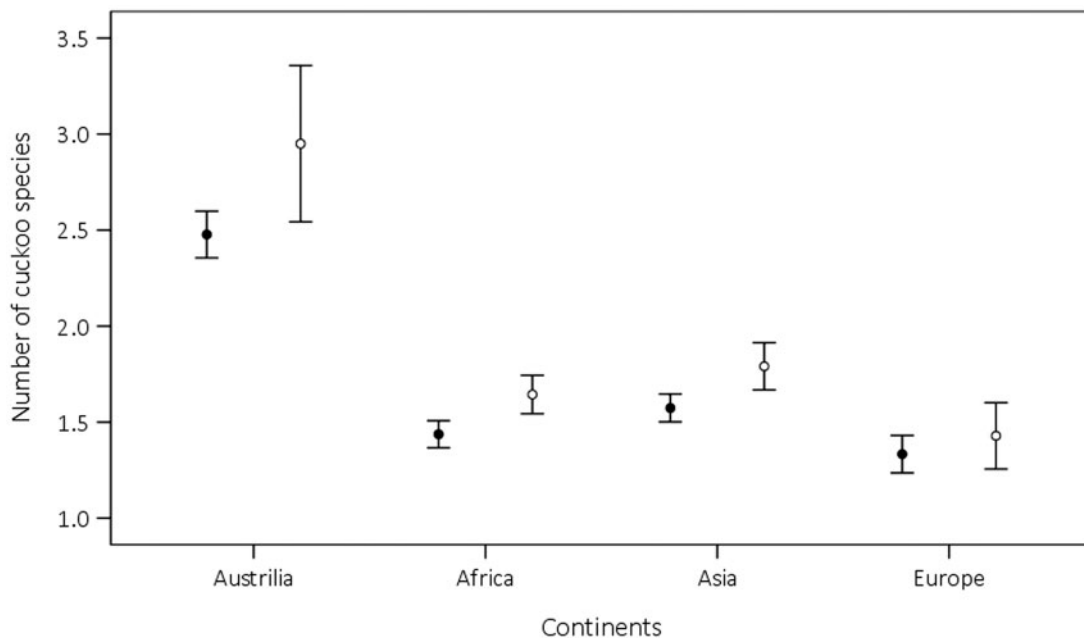

Figure 3. The number of cuckoo species (mean±SE) targeting each host species among continents and the number of cuckoo species targeting hosts producing monomorphic (black circles) and polymorphic (white circles) eggs.

Yang et al. 2015b; Wang et al. 2016), but also in space. Host egg polymorphism occurs more frequently in Asia and Africa than in Australia and Europe, possibly due to the variation in cuckoo diversity among continents: 25 cuckoo species are known from Asia, 14 from Africa, 11 from Australia, and 2 from Europe. Consistent with our prediction that higher cuckoo diversity would lead to a higher frequency of egg polymorphism in hosts, this study found that Asia has the highest diversity of Old World cuckoos (Payne 2005), and, correspondingly, the highest frequency of host egg polymorphism. Although there are substantially fewer cuckoo species in Africa than in Asia, the frequency of host egg polymorphism in Africa was similar to that in Asia. However, this does not necessarily contradict our hypothesis, as there are many avian brood parasites in Africa besides cuckoos (e.g., honeyguides and finches) (Davies 2000; Payne 2005). Therefore, the selection pressure associated with brood parasite diversity in Africa may resemble that in Asia. Furthermore, as we predicted, hosts producing polymorphic eggs were utilized by more cuckoo species than hosts producing monomorphic eggs, and this tendency was consistent across continents. That is, egg polymorphism tends to occur in hosts that are parasitized by multiple cuckoo species. Finally, the number of host species targeted by each cuckoo species was positively correlated with the frequency of host egg polymorphism. Because the number of host species targeted by each cuckoo species might reflect the degree of cuckoo generalization or specialization (i.e., cuckoo species are more generalized when they parasitize multiple host species and vice versa), this result implied that parasitism by generalist cuckoos tends to increase the frequency of egg polymorphism in hosts. In summary, our results suggested that the evolution of egg polymorphism is linked to brood parasitism and higher brood parasite diversity promotes the frequent evolution of host egg polymorphism due to the increase in parasitic selection pressure.

Author Contributions

C.Y. and W.L. initiated the data collection. C.Y. and X.S. analyzed the data and wrote the manuscript. All authors took part in data collection and improving the manuscript.

Acknowledgments

Funding

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest Statement

The authors declare that they have no competing interests.

References

Abolins-Abols M, Hanley D, Moskat C, Grim T, Hauber ME, 2019. Anti-parasitic egg rejection by great reed warblers *Acrocephalus arundinaceus* tracks differences along an eggshell color gradient. *Behav Processes* **166**: 103902.

Bertram BCR, Burger AE, 1981. Are ostrich *Struthio camelus* eggs the wrong colour?. *Ibis* **123**: 207–210.

Darwin C, 1859. *On the Origin of Species*. London: John Murray.

Davies NB, 2000. *Cuckoos, Cowbirds and Other Cheats*. London: T & AD Poyser.

Davies NB, 2011. Cuckoo adaptations: trickery and tuning. *J Zool* **284**: 1–14.

del Hoyo J, Elliott A, Sargatal J, Christie DA, 2013. *Handbook of the Birds of the World*. Spain: Lynx Edicions.

Drummond AJ, Rambaut A, 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol* **7**: 214.

Galeotti P, Rubolini D, Dunn PO, Fasola M, 2003. Colour polymorphism in birds: causes and functions. *J Evol Biol* **16**: 635–646.

Gelman A, Rubin DB, 1992. Inference from iterative simulation using multiple sequences. *Stat Sci* **7**: 457–472.

Hadfield J, 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw* **33**: 1–22.

Hanley D, Grim T, Igic B, Samaš P, López AV et al., 2017. Egg discrimination along a gradient of natural variation in eggshell coloration. *Proc R Soc B* **284**: 20162592.

Hanley D, López AV, Fiorini VD, Reboreda JC, Grim T et al., 2019. Variation in multicomponent recognition cues alters egg rejection decisions: a test of the optimal acceptance threshold hypothesis. *Phil Trans R Soc B Biol Sci* **374**: 20180195.

Honza M, Sulc M, Jelinek V, Pozgayova M, Prochazka P, 2014. Brood parasites lay eggs matching the appearance of host clutches. *Proc Biol Sci* **281**: 20132665.

Ives AR, Garland T Jr., 2010. Phylogenetic logistic regression for binary dependent variables. *Syst Biol* **59**: 9–26.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO, 2012. The global diversity of birds in space and time. *Nature* **491**: 444–448.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H et al., 2010. Picante: r tools for integrating phylogenies and ecology. *Bioinformatics* **26**: 1463–1464.

Kéry M, Royle JA, 2016. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*. London: Academic Press.

Kilner RM, 2006. The evolution of egg colour and patterning in birds. *Biol Rev Camb Philos Soc* **81**: 383–406.

Lack D, 1958. The significance of the colour of turdine eggs. *Ibis* **100**: 145–166.

Lahti DC, 2005. Evolution of bird eggs in the absence of cuckoo parasitism. *Proc Natl Acad Sci U S A* **102**: 18057–18062.

Langmore NE, Cockburn A, Russell AF, Kilner RM, 2009. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behav Ecol* **20**: 978–984.

Leimar O, 2005. The evolution of phenotypic polymorphism: randomized strategies versus evolutionary branching. *Am Nat* **165**: 669–681.

Liang W, Yang C, Stokke BG, Antonov A, Fossoy F et al., 2012. Modelling the maintenance of egg polymorphism in avian brood parasites and their hosts. *J Evol Biol* **25**: 916–929.

Lowther PE, 2014. Host List of Avian Brood Parasites—2 Cuculiformes–Old World Cuckoos. Chicago (IL): Field Museum.

Majerus MEN, 1998. *Melanism: Evolution in Action*. Oxford: Oxford University Press.

Montevecchi WA, 1976. Field experiments on the adaptive significance of avian eggshell pigmentation. *Behaviour* **58**: 26–39.

Noh H-J, Gloag R, Langmore NE, 2018. True recognition of nestlings by hosts selects for mimetic cuckoo chicks. *Proc R Soc B* **285**: 20180726.

Payne RB, 2005. *The Cuckoos*. Oxford: Oxford University Press.

Plummer M, Best N, Cowels K, Vines K, 2016. CODA: convergence diagnosis and output analysis for MCMC. *R News* **6**: 7–11.

Ricklefs RE, Jonsson KA, 2014. Clade extinction appears to balance species diversification in sister lineages of Afro-Oriental passerine birds. *Proc Natl Acad Sci U S A* **111**: 11756–117561.

Soler M, 2014. Long-term coevolution between avian brood parasites and their hosts. *Biol Rev* **89**: 688–704.

Spottiswoode CN, Stevens M, 2012. Host–parasite arms races and rapid changes in bird egg appearance. *Am Nat* **179**: 633–648.

Swynnerton CFM, 1916. On the coloration of the mouths and eggs of birds. II On the coloration of eggs. *Ibis* **4**: 529–606.

Vikan JR, Fossøy F, Huhta E, Moksnes A, Røskaft E et al., 2011. Outcomes of brood parasite–host interactions mediated by egg matching: common cuckoos *Cuculus canorus* versus *Fringilla* finches. *PLoS ONE* **6**: e19288–e19288.

Wallace AR, 1889. *Darwinism: An Exposition of the Theory of Natural Selection with Some Its Applications*. London: Macmillan.

Wang L, Liang W, Yang C, Cheng S-J, Hsu Y-C et al., 2016. Egg rejection and clutch phenotype variation in the plain prinia *Prinia inornata*. *J Avian Biol* **47**: 788–794.

Wiemann J, Yang TR, Norell MA, 2018. Dinosaur egg colour had a single evolutionary origin. *Nature* **563**: 555–558.

Wisocki PA, Kennelly P, Rojas Rivera I, Cassey P, Burkey ML et al., 2019. The global distribution of avian eggshell colours suggest a thermoregulatory benefit of darker pigmentation. *Nat Ecol Evol* **4**: 148–155.

Yang C, Liang W, 2016. The role of blinded methods in the studies of animal behavior. *Chin J Zool* **51**: 663–667.

Yang C, Huang Q, Wang L, Jiang A, Stokke BG et al., 2016a. Plaintive cuckoos do not select tailorbird hosts that match the phenotypes of their own eggs. *Behav Ecol* **27**: 835–841.

Yang C, Li Z, Zhang Y, Wang H, Liang W et al., 2016b. Egg polymorphism and egg discrimination in the Daurian Redstart *Phoenicurus auroreus*, a host of the common cuckoo *Cuculus canorus*. *Ornithol Sci* **15**: 127–132.

Yang C, Liang W, Cai Y, Shi S, Takasu F et al., 2010. Coevolution in action: disruptive selection on egg colour in an avian brood parasite and its host. *PLoS ONE* **5**: e10816.

Yang C, Liang W, Møller AP, 2018. Why do hosts with obvious egg polymorphism suffer low parasitism rates under avian brood parasitism? A theoretical consideration. *Behav Ecol Sociobiol* **71**: 30.

Yang C, Su T, Liang W, Møller AP, 2015a. Coevolution between the large hawk-cuckoo *Cuculus sparverioides* and its two sympatric Leiothrichidae hosts: evidence for recent expansion and switch in host use?. *Biol J Linn Soc Lond* **115**: 919–926.

Yang C, Wang L, Cheng S-J, Hsu Y-C, Liang W et al., 2014. Nest defenses and egg recognition of yellow-bellied prinia against cuckoo parasitism. *Naturwissenschaften* **101**: 727–734.

Yang C, Wang L, Cheng S-J, Hsu Y-C, Stokke BG et al., 2015b. Deficiency in egg rejection in a host species as a response to the absence of brood parasitism. *Behav Ecol* **26**: 406–415.

Yang C, Wang L, Liang W, Møller AP, 2016c. Egg recognition as antiparasitism defence in hosts does not select for laying of matching eggs in parasitic cuckoos. *Anim Behav* **122**: 177–181.

Yang C, Wang L, Liang W, Møller AP, 2017. How cuckoos ind and choose host nests for parasitism. *Behav Ecol* **28**: 859–865.