

Are egg colors and patterns signs of phylogenetic relatedness in parrotbills?

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Abstract Egg colors and patterns have long been of interest for ornithologists and evolutionary biologists, with several hypotheses proposed to explain them. These include: Wallace's hypothesis, the structure hypothesis, the brood parasitism hypothesis and the post-mating sexual selection signal hypothesis. However, none of these are sufficient to elucidate the evolutionary mechanism involved. In this study, egg polymorphism and phylogenetic relationships within the avian family Paradoxornithidae were investigated. When compared with phylogenetic information, we found that egg color matched two size-related clades within the Paradoxornithidae. The larger parrotbills all lay patterned eggs with pale background colors, whereas the smaller parrotbills lay plain pale blue eggs. To our knowledge, this is the first study to detect such a relationship between egg color and pattern and phylogeny in parrotbills, suggesting that they are under strong phylogenetic constraints and can be treated as an important indicator of phylogenetic relationship.

Key words Egg polymorphism, Parrotbill, Phylogenetic relationship signal hypothesis, Phylogenetic tree

Avian eggs vary greatly in color and pattern among species, ranging from completely plain to complexly patterned (Gill 2007). The mechanism and evolution of this phenomenon has long been of great interest to ornithologists and evolutionary biologists. To date, several hypotheses have been proposed to account for the function of avian egg coloration and patterning (Soler et al. 2005; Kilner 2006).

Firstly, the cryptic hypothesis suggested that egg color acted as camouflage serving to reduce the risk of egg predation (Wallace 1889; Newton et al. 1896; Lack 1958), and has been supported by both laboratory and field experiments (Weidinger 2001; Underwood & Sealy 2002). Egg color can also function as a visual signal for birds nesting in dark environments (Avilés et al. 2006). Secondly, the physical

hypothesis, suggests that the physical properties of egg pigments serve a role in thermoregulation and function in strengthening eggshells. This hypothesis has been verified by laboratory experiment (Montevicchi 1976) and field investigations, including those on ostriches *Struthio camelus* and Egyptian Vulture *Neophron percnopterus*, both of which lay white eggs to avoid overheating (Bertram & Burger 1981). In addition, pigments compensate for eggshell thinning, which is caused by structural variation in the shell and calcium deficiency (Solomon 1997), and egg patterns serve a structural function (Gosler et al. 2005; Gosler et al. 2011). The third hypothesis, the sexual selection hypothesis, suggests that egg coloration functions as a post-mating sexually-selected visual signal to assess the quality of offspring so that male partners adjust parental investment accordingly (Moreno & Osorno 2003). As biliverdin is responsible for blue and green colors and a vital antioxi-

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dant, females make a tradeoff in their allocation for themselves against oxide radicals and in investment in the production of blue-green eggshells (Moreno & Osorno 2003; Soler et al. 2005). The most comprehensive hypothesis relates to avian brood parasitism. Takasu's (2003, 2005) analysis provided a theoretical background for the evolution of egg color polymorphism in species experiencing brood parasitism. Experimental and comparative research supports the argument that brood parasitism is a powerful selective force in the evolution of egg coloration in parasitic birds (Soler & Moller 1996; Soler et al. 2003), such as in the Common Cuckoo *Cuculus canorus* (Davies 2011) and their hosts, such as parrotbills *Paradoxornis* spp. (Yang et al. 2010, 2013, 2014b). The hypothesis, however, has its limits when it comes to predicting variation in egg coloration among species (Stokke et al. 2002). To our knowledge, no single hypothesis effectively explains the variation in avian egg coloration (Kilner 2006).

The explanations for the patterns of egg coloration in parrotbills are ambiguous (Martin 1995, 2004). Parrotbills are native to central, east and southeast Asia, and represent a relatively little known group of old world passerines except for the well-studied Vinous-throated Parrotbill *Paradoxornis webbianus* and Reed Parrotbill *P. heudei* (Kim et al. 1995; Lee & Yoo 2004; Robson 2007; Lee et al. 2010). Nineteen of twenty parrotbill species are found in China, and Three-toed Parrotbill *P. paradoxus*, Spectacled Parrotbill *P. conspicillata*, Rusty-throated Parrotbill *P. przewalskii* and Grey-hooded Parrotbill *P. zappeyi* are endemic to China (Robson 2007; Zheng 2011). Most parrotbill species are relatively widespread, except for the Black-breasted *P. flavirostris*, Grey-hooded and Rusty-throated parrotbills, which are considered globally threatened and classified as Vulnerable by BirdLife International (BirdLife International 2012a, b). Although taxonomists have long debated the phylogenetic relationships of the parrotbills (Harrington 1914; Baker 1922; Oates et al. 1936; Cibois 2003); more recently their grouping into three major phylogenetic clades based on genetic analysis and morphological characteristics has become widely accepted (Dickinson et al. 2004; Alström et al. 2006; Yeung et al. 2006; Robson 2007; Yeung et al. 2011; Alström et al. 2013). These three clades are; 1) large species, 2) small brownish species and 3) small yellowish species (Yeung et al. 2006; Yeung et al. 2011). Independently, Penhallurick and Robson (2009) split two previous genera of parrotbills into eight genera

that fall into two groups based solely on morphology.

For this study, we applied the 'two-group taxonomic system' for parrotbills to avoid confusion, and we reviewed all parrotbill egg color information available in published literature and unpublished data in order to illustrate the pattern of egg coloration associated with phylogenetic relationships.

MATERIALS AND METHODS

We surveyed articles from the peer-reviewed scientific literature, including both articles and book chapters that contained parrotbill information, by using appropriate key words, such as parrotbills, Paradoxornithidae, and key word combinations. No limit was imposed with respect to year of publication or journal title. We also added unpublished data about the breeding information of three parrotbills.

Liu et al. (in press) constructed a multilocus phylogenetic tree for parrotbills. Our methodology in detail involved us in applying a multispecies coalescent algorithm (*BEAST) as implemented in BEAST 1.7.5 (Drummond & Rambaut 2007; Heled & Drummond 2010) based on two mitochondrial genes Cytochrome b (cyt b, 1042 base pairs (bp)), NADH dehydrogenase subunit two (ND2, 1041 bp), two nuclear loci, the nuclear recombination activating gene one (RAG1, 962 bp), the nuclear intron two of archaean (ARCN1, 742 bp), and the Z-linked intron five of ADAM metallopeptidase with thrombospondin type one motif six variant two (ADAMTS6, 550 bp), from 16 of 20 extant species retrieved from Yeung et al. (2011). The specific phylogenetic relationship tree was constructed by Liu et al. (in press), to which we added egg color in order to illustrate the distribution of egg coloration and patterning. Egg colors and patterns, based on color classification by human eye, were assessed according to the information collected from peer-reviewed literature and unpublished data.

RESULTS

After surveying all of the papers retrieved by our search protocol, we pooled the data together and found that parrotbill egg color can be classified into two groups (see Fig. 1); the plain group including blue or white eggs without spots or patterns, and the patterned group including pale eggs with patterns. The plain group consisted of: *P. nipalensis*, *P. verreauxi*, *P. fulvifrons*, *P. atrosuperciliaris*, *P. conspicillatus*, *P. zappeyi*, *P. brunneus*, *P. alphonisianus*, and *P.*

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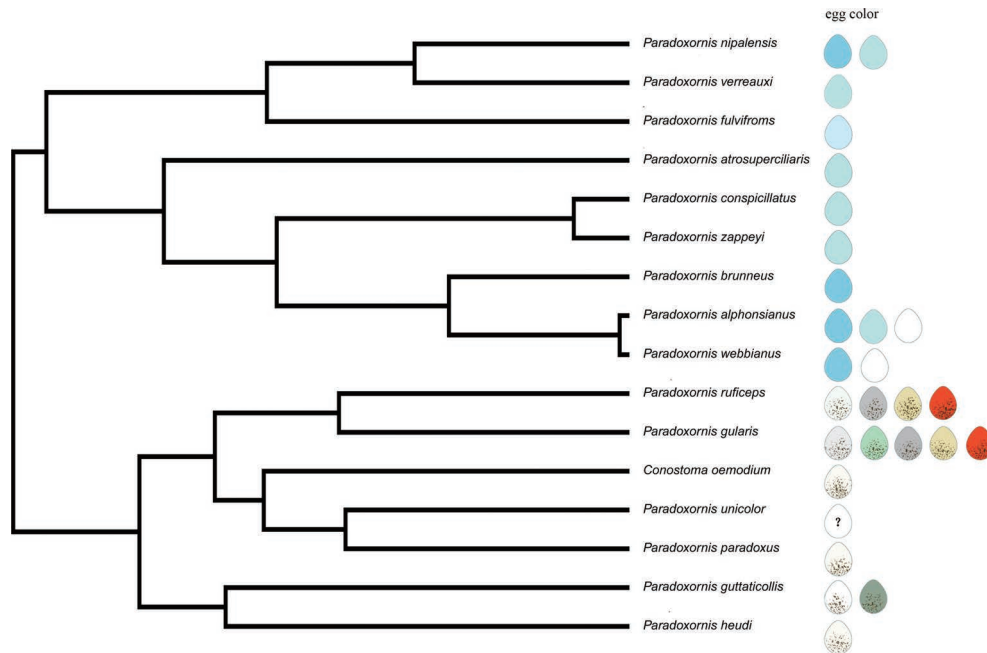


Fig. 1. The multilocus species tree of parrotbills overlaid with egg color for each species. The paintings of egg colors and patterns were based on color classification by human eye, according to the information collected from peer-reviewed literature and unpublished data. No egg information is available for *P. unicolor*. All of the eggs were painted by Xiaonong Yang.

webbianus, while the patterned group consisted of: *P. ruficeps*, *P. gularis*, *Conostoma oemodium*, *P. paradoxus*, *P. guttaticollis*, and *P. heudei*.

The parrotbill phylogenetic tree reveals two clades of species (Fig. 1). One clade consists of small species, while the other consists of large species, which received >0.95 posterior probability support for every node. The tree topology is overall congruent with previous studies by Yeung et al. (2011), with classification of parrotbill egg color exactly matching the two clades based on the phylogenetic tree. Almost all large parrotbill species lay pale eggs with patterns, whereas small parrotbills lay plain blue eggs.

DISCUSSION

It is widely acknowledged that the diversity of egg colors and patterns is associated with evolutionary causes, functional roles and life history traits (Kilner 2006; Cassey et al. 2010; Cherry & Gosler 2010; Cassey et al. 2012). However, no single hypothesis seems to explain adequately the diversity among birds (Reynolds et al. 2009). The present study has shown that the egg colors and patterns of parrotbills are strongly associated with phylogenetic relationships, confirming similar results from a comparative

analysis (Cassey et al. 2012). Cassey et al. (2012) found that average concentrations of protoporphyrin and biliverdin were positively correlated and both strongly co-varied with phylogenetic relatedness in 49 breeding bird species in Britain. Patterned eggs with red spots were contained in certain clades, which also gave an indication of phylogenetic relationship between *Garrulax* and *Trochalopteron* species, based on combined mitochondrial and nuclear gene data (Luo et al. 2009). The differentiation between large and small parrotbills, in terms of egg color, suggests that this may be under strong phylogenetic constraint (Yeung et al. 2011), and can be treated as a signal of phylogenetic relatedness. Moreover, Walters (2006) classified *P. webbianus*, *P. nipalensis* and *P. atrosuperciliaris* within the genus *Suthora* based on eggs color and pattern (Walters 2006), indirectly supporting the phylogenetic relatedness signal hypothesis.

Egg patterns have also been viewed as compensating for eggshell thinning caused by structural variation in the shell and calcium deficiency (Solomon 1997). Gosler et al. (2005, 2011) suggested that the egg pattern of the Great Tit *Parus major* serves the structural function of increasing egg strength. According to the structural-function hypothesis we predicted

that large parrotbills should lay patterned eggs to enhance the strength of relatively larger eggs given the same calcium availability, a prediction that was supported by the data from four sympatric parrotbills in Wawu Plateau, Sichuan Province, China. Large *C. oemodius* (egg mass c. 7.5g) and *P. paradoxus* (egg mass c. 3.0 g) both lay patterned eggs. In contrast, small *P. fulviformes* (egg mass c. 1.3 g) and *P. zappeyi* (egg mass c. 1.2 g) lay plain blue eggs (Zhu 2014). Further work is necessary to assess its generality among all parrotbills.

The present study indicated that polymorphic eggs exist both in large and small parrotbills. As suggested previously, the arms race between brood parasites and their hosts may be one of the driving forces of egg polymorphism (Kilner 2006; Yang et al. 2010; Kilner & Langmore 2011). In the cuckoo-parrotbill parasitic system, the polymorphism of Vinous-throated Parrotbill and Ashy-throated Parrotbill eggs is an outcome of disruptive selection driven by coevolution (Lee & Yoo 2004; Yang et al. 2010; Lee & Jabłoński 2012; Yang et al. 2013). Yang et al. (2014a) proposed that the pale blue eggs of the Ashy-throated Parrotbill may represent an ancestral morph before division into two distinct color morphs. The brood parasite hypothesis supports egg polymorphism among the small parrotbills; however, there is little evidence from the large parrotbills. For example, the eggs of *P. ruficeps*, *P. guttaticollis* and *P. gularis* are also polymorphic with white, dull creamy or blue-grey background colors, blotched with light brown, dark brown or reddish (Walters 2006), although no information has been recorded concerning brood parasitism in these three parrotbill species. The only brood parasitism found among the large group is in the Reed Parrotbill, which is parasitized by the Common Cuckoo, but only at a low rate of 4.6 % (Yang et al. 2014a; Yang et al. 2014b). Such low level parasitism is not adequate to support egg polymorphism among the large parrotbills. More breeding information is necessary to illustrate the cause of egg polymorphism in parrotbills.

Technological and theoretical efforts have revolutionized studies that require modeling the practical aspects of avian vision (Cuthill et al. 2000; Ödeen & Håstad 2003; Hunt et al. 2009). The hosts of brood-parasitic cuckoos can perceive UV differences between their own and parasitic eggs (Cuthill et al. 2000; Cassey et al. 2010; Yang et al. 2010). Future studies of perceptual modeling should focus on the differences in egg colors among diverse species of

birds and other visually oriented animal lineages.

In conclusion, the colors and patterns of parrotbill eggs are under strong phylogenetic constraint and may indicate a major phylogenetic split between species groups. Furthermore, interspecific egg polymorphism among some parrotbill species may be an adaptation to the arm races in cuckoo-parrotbill parasitism.

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egg polymorphism in parrotbills

Table 1. Breeding parameters of small parrotbills.

Species	Size (cm)	Nest height (m)	Egg size (mm)	Clutch size	Egg color and pattern	Resource
<i>Paradoxornis nipalensis</i>	11.5	0.6–1.5	15.7×11.9	2–4	pale blue or blue	Baker 1922; Robson 2007
<i>P. verreauxi</i>	11.5	1.5–1.8	15–16×11.8–12	2–4	pale milky-blue eggs	Hachisuka & Udagawa 1951; Yang et al. 2011
<i>P. fulvifrons</i>	12.0–12.5	0.7–1.9	15.62×12.70	2–5	blue	Hu et al. 2014
<i>P. atrosupercillaris</i>	15	>2	19.5–18.4×15.2–13.6	1–3	pale blue or blue	Baker 1922; Robson 2007
<i>P. conspicillatus</i>	14.0–15.0	0.5–1.5	14.7–16.5×11.8–13.0	3–5	pale blue eggs	This study
<i>P. zappeyi</i>	12.5	0.8–1.2	14.9–16.4×12.2–12.8	2–4	sky-blue	Robson 2007; Jiang et al. 2009
<i>P. brunneus</i>	12.0–13.0	0.6	15.2–17.5×12.7–13.5	2–4	pale or deep blue	Baker 1922; Robson 2007
<i>P. alphonsianus</i>	12.5–13.0	0.5–1.5	14.9–19×12–13	2–6	white or pale blue	Yang & Wang 1984; Li et al. 1993; Guo et al. 2006; Yang et al. 2010
<i>P. webbianus</i>	11.0–12.5	0.4–2.0	14.2–17.8×11.2–14.5	2–6	azure to blue, or white	Zheng et al. 1987; Kim et al. 1995

Table 2. Breeding parameters of large parrotbills.

Species	Size (cm)	Nest height (m)	Egg size (mm)	Clutch size	Egg color and pattern	Resource
<i>Paradoxornis ruficeps</i>	19.0–19.5	0.6–2.4	21.5–22.6×16.7	2–4	glossy white to dull cream marked with yellowish-brown spots	Baker 1922; Robson 2007
<i>P. gularis</i>	15.5–18.5	2.0–3.0	20.3–22.0×15.5–18.0	2–4	white to greenish-white or grey with yellowish or reddish, spots	Robson 2007
<i>Conostomaem odium</i>	27.5–28.5	1.6–2.6	27.8–28.2×20.3–20.8	2–3	dull white, sparsely blotched, with pale yellowish-brown spots	Robson 2007; Zhu 2014
<i>P. unicolor</i>	21.0	–	–	–	–	Robson 2007
<i>P. paradoxus</i>	20.0	2.4	23.69×17.89	3–4	pale milky-white ground with brown spot and large spots around larger end	Zhu 2014
<i>P. guttaticollis</i>	18.0–22.0	0.9–1.0	22.1–23.5×15.8–16.5	2–4	pale green-grey with brown spots	Baker 1922; Robson 2007
<i>P. heudei</i>	18.0–20.0	1.3–1.7	18.0–18.8×14.2–14.5	2–5	medium-glossed greenish-white with large blotches	Zheng 1984; Zheng et al. 1987; Zhao 2001; Robson 2007