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Effect of Host Egg Color Dimorphism on Interactions Between the Vinous-throated Parrotbill (*Paradoxornis webbianus*) and Common Cuckoo (*Cuculus canorus*)

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To investigate the effect of host egg color dimorphism on the vinous-throated parrotbill (*Paradoxornis webbianus*) – common cuckoo (*Cuculus canorus*) interactions, we monitored breeding nests of vinous-throated parrotbills, and conducted model egg experiments, using two colors: white and blue. Of the 190 nests examined in this study, cuckoo parasitism occurred at 10 nests (8 blue and 2 white egg clutches, respectively), and only blue cuckoo eggs were found. This frequency was similar to the egg-color ratio of all host nests found (151 blue and 39 white egg clutches). Vinous-throated parrotbills showed high rejection rate towards both cuckoo eggs and model ones. There was a significant difference in rejection rates towards mimetic (blue) and non-mimetic (white) eggs in blue egg clutches. Mimetic eggs put in nests took significantly longer to be rejected than non-mimetic ones. The most common rejection method used by the hosts was egg ejection (puncture-ejection). The costs of ejecting non-mimetic eggs tended to be lower than those of ejecting mimetic eggs. These results indicate that egg-color dimorphism in this species favors the individuals having white egg clutches in terms of higher rejection rate and lower ejection costs of the parasitic eggs. This study also suggests that egg-color dimorphism of the vinous-throated parrotbill decreases the effect of cuckoo parasitism on host populations.

Brood parasitism is a breeding strategy, in which the parasites receive parental care from unrelated individuals, the hosts (Rothstein, 1990). Brood parasites like common cuckoos (*Cuculus canorus*) are usually detrimental to the reproductive efforts of their hosts; therefore, natural selection should favor host behaviors that deter brood parasitism (Rothstein, 1975, 1990; Rohwer and Spaw, 1988). Such behaviors or defense mechanisms include: (1) aggressive behavior to adult parasites, (2) nest desertion, (3) egg burial, and (4) egg ejection (Rothstein, 1975, 1990; Rohwer and Spaw, 1988). This, in turn, will select for improved trickery by the cuckoo, such as fast egg laying, host egg removing, and egg mimicry (Davies and Brooke, 1988).

Rothstein (1974) suggested a probability of egg-related defense mechanism by hosts, that is to say, if hosts suffer from perfect egg mimicry by parasites, then they will develop egg polymorphism or evolve a single new egg type. Collias (1993) proposed that both interspecific and conspecific brood parasitism could have been involved in the evolution of the high degree of egg-shell-color polymorphism seen today in some bird species such as the village weaver (*Ploceus cucullatus*).

Vinous-throated parrotbills (*Paradoxornis webbianus*), one of the main hosts of common cuckoos, are common residents in Korea (Won and Gore, 1971). Vinous-throated parrotbills have eggs of two colors: immaculate blue and white. An individual female is likely to lay eggs of a characteristic color throughout her life (Kim et al., 1995b). A few studies have been carried out to look at social organization and breeding biology of the vinous-throated parrotbill (e.g. Park et al., 1993; Kim et al., 1995a, 1995b; Lee, 1996; Kim, 1998; Jang, 1999). However, little is known about the recognition and rejection behavior of vinous-throated parrotbills to the parasitic eggs, and there are few empirical data on the effect of egg-color dimorphism of the host on interactions with the parasite. In this study we examined some aspects of the relationships between the common cuckoo and vinous-throated parrotbill.

This study asked three questions: (1) do common cuckoos discriminate colors of host eggs while parasitizing host nests?; (2) is there any difference in host responses to brood parasitism in relation to the host egg colors?; (3) how does the egg-color dimorphism of the host affect the

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relationship between the vinous-throated parrotbill and common cuckoo?

Study Area and Methods

This study was carried out during the breeding seasons of 2000-2001 in and around man-made wetlands at the Institute of Rural Research in Sa-dong, Ansan-si, Kyonggi-do, Korea (37°16′34″ N, 126°50′04″ E). Vinous-throated parrotbills breed from late April to July and have incubation period for 13-15 days. Nests were found by searching suitable habitats and by observing paired birds. Nests were visited every day or every other day during laying period to detect cuckoo parasitism.

During the breeding season of 2001, we conducted experimental parasitism (N=38) by replacing one of the host eggs with a model cuckoo egg in the afternoon during laying or early incubation. The model eggs were made of plasticine, with a thin layer of plaster, covered with acrylic paint and coated with varnish to make them waterproof and to obtain a glossy surface similar to that of natural eggs. Shape, size (22 mm×17 mm) and weight (3.3 g) of the model eggs were the same as natural cuckoo eggs, and the colors were immaculate blue and white. In the experiments, we made experimentally mimetic and non-mimetic conditions at the host nests, depending on the combination of between the color of host eggs and model ones (i.e. mimetic: blue model / blue host eggs, white model / white host eggs, non-mimetic: blue model / white host eggs, white model / blue host eggs). The responses of vinous-throated parrotbills were classified as (1) acceptance, (2) ejection, or (3) desertion. Ejection attempts in which host egg loss led to nest desertion were included in desertion. For the analysis of host response behavior, we used data from natural parasitism and experimental parasitism (N=38) with model cuckoo eggs. We used 6-day acceptance criterion similar to that of Rothstein's (1982) 'full acceptance criterion'. Naturally or experimentally parasitized nests were visited on the first, third and sixth day after parasitism to monitor responses to parasitic eggs. Parasitic eggs remained in the nest over 6 days were considered to have been accepted by hosts.

Table 1. Number of vinous-throated parrotbill nests in relation to egg colors and nests parasitized by common cuckoos

Year	Number of nests (parasitized nests)	
	Blue	White
2000	75 (3)	18 (0)
2001	76 (5)	21 (2)
Total	151 (8)	39 (2)

Results

Egg-color ratio and brood parasitism

In this study, 190 vinous-throated parrotbill nests were examined during the two consecutive breeding seasons (Table 1). Blue egg clutches were observed more frequently than white ones in both years (Binomial test, $P<0.001$). There was no significant difference in egg-color ratio between the two years ($\chi^2=0.153$, df=1, ns).

Brood parasitism by cuckoos was found at 10 out of 190 host nests, which included both blue and white egg clutches (Table 1). The cuckoo eggs are larger than the eggs of vinous-throated parrotbills, but the color of cuckoo eggs is similar to the blue eggs of vinous-throated parrotbill. Frequency of the cuckoo parasitism in blue or white egg clutches paralleled the egg-color ratio of the host population.

Host response to the parasitic eggs

Vinous-throated parrotbills in the study area showed a high rejection rate towards cuckoo eggs and model ones (Table 2). There was a significant difference in rejection rates in relation to colors of parasitic eggs in blue (Fisher's exact test, $P<0.05$), but not in white, egg clutches. This is probably due to the small sample size in white egg clutches. Time to rejection was significantly different in relation to experimental procedures (Table 3). The metic eggs put in nests took significantly longer to be rejected than the non-mimetic ones (Mann-Whitney *U*-test: two-tailed $P<0.05$). Vinous-throated parrotbills used two rejection methods: egg ejection and nest desertion.

Table 2. Responses of vinous-throated parrotbills to real and model cuckoo eggs in relation to egg colors

Clutch types	Egg types	Egg colors	Number of eggs			Rejections/total	% Rejections
			Accepted	Rejected			
				By ejection	By desertion		
Blue egg clutch	Cuckoo egg	Blue	2	2	1	3/5	60
	Model egg	Blue	3	4	6	10/13	77
		White	-	11	4	15/15	100
White egg clutch	Cuckoo egg	Blue	-	2	-	2/2	100
	Model egg	Blue	-	3	1	4/4	100
		White	-	6	1	6/6	100

Table 3. Time span for vinous-throated parrotbills to reject parasitic eggs

Type of parasitic eggs put in host nests	Number of eggs rejected on		
	1st day	3rd day	6th day
Mimetic[a]	4	7	8
Non-mimetic[b]	10	9	2
Total	14	16	10

[a]blue (white) clutches / blue (white) parasitic eggs
[b]blue (white) clutches / white (blue) parasitic eggs

However, the most common rejection method of the vinous-throated parrotbill was egg ejection because most nest desertions (12/13) resulted from clutch reduction due to egg loss during ejection of parasitic eggs. Ejection cost in terms of loss or damage of host eggs during ejection of the parasitic eggs occurred more often in nests replaced with mimetic eggs than non-mimetic ones (χ^2=6.776, df=1, P<0.001; Table 4).

Discussion

Development of egg polymorphism in the hosts would make it difficult for parasites to match their eggs to those of the hosts and thus reduce the effect of brood parasitism on the host populations (Victoria, 1972; Rothstein, 1974; Collias, 1993; Lahti and Lahti, 2002). It can be also assumed that egg-color dimorphism of the vinous-throated parrotbill would make it difficult for the common cuckoo to mimic the host eggs. Egg-color ratio in the study population of the vinous-throated parrotbill was skewed toward the blue morphs. Considering other studies in which egg-color ratio of the vinous-throated parrotbill was studied, the blue egg clutches were still found more frequently than white ones, though there are some differences in egg-color ratio among local populations (Kim et al., 1995b; Jang, 1999). The common cuckoo laid eggs mimicking blue morphs of vinous-throated parrotbills. These findings support the idea that the parasites possibly evolve egg mimicry to the most common egg morph in host species with egg-color polymorphism (Cruz and Wiley, 1989).

Cuckoo eggs mimicking blue morph of the host were found in both white and blue egg clutches. This indicates that the cuckoos did not discriminate host egg colors while parasitizing vinous-throated parrotbill nests. The present study does not support Kim's suggestion (1996) that the cuckoos selectively lay eggs at the host nests with blue egg clutches in order to maximize breeding success. One possible explanation for the lack of discriminating host egg colors in the common cuckoo is that selective pressure for egg-color discrimination is not strong enough to be evolved because the host gets no reproductive success in the year unless it discriminates and rejects parasitic eggs, but the cuckoos lose only the egg that does not match host eggs. Furthermore, it might be difficult that the genes for the egg discrimination behavior spread out among cuckoo populations, though this behavior may arise in some female cuckoos, because this behavior are not needed by male cuckoos and females of other cuckoo gentes parasitizing host species with egg-color monomorphism. Another possibility is that the female cuckoo is likely not to know her own egg color because usually she quickly flies away from host nests after laying her egg, without taking any notice (N.B. Davies, personal communication).

This study suggests that vinous-throated parrotbills possess finely tuned discrimination ability in colors, and egg color is likely to be the first cue in making a decision on whether to accept or reject parasitic eggs in this species. Individuals having white egg clutches would be less damaged by cuckoo parasitism than those which lay blue eggs in terms of higher rejection rate and lower ejection cost to the parasitic eggs. At the population level, egg-color dimorphism of the vinous-throated parrotbill decreases the effect of cuckoo parasitism because the hosts with white egg clutches show perfect rejection to the parasitic eggs and thus overall rejection rate of the host population would possibly be wigher than that of the species with a single egg morph.

One possible idea for the effect of egg-color dimorphism on host-parasite interactions is that a kind of intermittent arms race (cyclic change of brood parasitism rate by parasites and rejection rate of host population) proposed by Soler et al. (1998) can occur in the vinous-throated parrotbill – common cuckoo interactions. Egg-color ratio observed in this study was sharply skewed toward the blue egg clutches. If the brood parasitism, however, occurs at a high level (above 20%) and is maintained

Table 4. Egg loss of vinous-throated parrotbills during rejection of parasitic eggs

Type of parasitic eggs put in host nests	Number of nests at which the parasitic eggs were rejected	Number of host eggs in the parasitized nests	Number of host egg loss	Host egg loss/ Parasitic egg
Mimetic[a]	19	75	23	1.21
Non-mimetic[b]	20	76	10	0.50
Total	39[c]	151	33	0.85

[a]blue (white) clutches / blue (white) parasitic eggs
[b]blue (white) clutches / white (blue) parasitic eggs
[c]1 deserted nest without ejection attempt by host was excluded.

throughout evolution, then the egg-color ratio in the host population is likely to be changed. This is because breeding success of the vinous-throated parrotbill was not affected by egg colors as reported by some studies (Park et al., 1993; Kim et al., 1995b; Jang, 1999) while the rejection rate and ejection cost to the parasitic eggs were affected. Next, if the white egg clutches occur more frequently than blue ones in the host population, the cuckoos will suffer from higher rate of rejection by the host. Consequently, the cuckoo gen being sympatric with the host population would probably become extinct or emigrates from the area. If so, egg-color ratio in the population would be reversed again, that is to say, the blue egg clutches would occur more frequently than the white egg clutches among the host population as in the previous circumstance. This is because the blue eggs seem likely to be more typical of egg morph and more common than white eggs in the open nest passerine birds like the vinous-throated parrotbill, as shown from the cuckoos' mimetic blue eggs, though it is not clearly verified (Lack, 1968; Major and Kendal, 1996; Weidinger, 2001). These lines of predictions would also provide an explanation for the dissimilar egg-color ratio among the local host populations. Further studies, however, are necessary to clarify this.

Although the effect of brood parasitism is decreased by egg-color dimorphism of the host, this study does not support the prediction that egg-color dimorphism of vinous-throated parrotbills would evolve in response to brood parasitism by the cuckoos. Many species in genus *Paradoxornis* have eggs with various background colors and spotting patterns (Robson, 2000). Therefore, further studies on the host-parasite interaction and comparative studies on species belonging to the genus *Paradoxornis* are needed to reveal the origin of egg-color dimorphism of the vinous-throated parrotbill.

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