EGG DISCRIMINATION BY THE VINOUS-THROATED PARROTBILL, A HOST OF THE COMMON CUCKOO THAT LAYS POLYCHROMATIC EGGS

BY

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A thesis submitted to the Faculty of Graduate Studies in partial fulfillment
of the requirements for the degree of

Master of Science

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THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES
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ABSTRACT

Understanding how hosts discriminate between parasitic eggs and their own eggs is important to our understanding of coevolution between brood parasites and their hosts. This study dealt with the significance of egg colour in the rejection by hosts and the sex-specific strategy in a host species, the Vinous-throated Parrotbill (*Paradoxornis webbianus*), which lays immaculate polychromatic eggs and in which both sexes reject parasitic eggs. In the first chapter, I examined the discriminative ability of parrotbills in relation to colour by experimentally parasitizing, and quantifying the degree of colour mimicry of introduced eggs by scoring from good to medium to poor. Hosts rejected parasitic eggs that differed more substantially in colour from their own eggs, regardless of size.

The second objective was to determine whether females and males have evolved different egg-discrimination mechanisms. I found differences in responses of females and males depending on egg manipulations. Females consistently rejected only foreign egg(s), regardless of whether the foreign egg-type was in the majority or in the minority. On the other hand, males rejected only foreign eggs when the eggs were in the minority; however, they removed their own eggs when the foreign egg-type was in the majority. This sex-specific egg-discrimination mechanism may be an efficient defense strategy against parasitism in a host species that lays polychromatic eggs.

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GENERAL INTRODUCTION

Several hosts of avian brood parasites can discriminate between their own eggs and parasitic eggs, and this ability apparently has evolved as a counter-adaptation against parasitism that imposes extreme fitness costs on hosts (Davies and Brooke 1989b, Øien et al. 1995). Results of previous experiments suggested that the discriminative ability is acquired by observational learning of the characteristics of host's own egg when laying the first clutch (Rothstein 1978; Lotem et al. 1992, 1995; Moksnes 1992; Lahti and Lahti 2002; Moskát et al. 2008). In a theoretical modeling study, Rodriguez-Gironés and Lotem (1999) proposed that host's learning mechanisms rely on conditional factors between obligate brood parasites and hosts. For example, when parasitism frequencies are low and intra-clutch variation is great, hosts may learn their whole clutches and tolerate the range of egg types in the nest (i.e., an extended learning mechanism, Rodriguez-Gironés and Lotem 1999), whereas in cowbird hosts that are not frequently parasitized with non-mimetic eggs, female hosts probably imprint on their first egg before being parasitized to reduce the cost of mis-imprinting (Rodriguez-Gironés and Lotem 1999, Davies 2000). Various discriminative strategies likely have been evolved among host species. The Great Reed Warbler (*Acrocephalus arundinaceus*) and Blackcap (*Sylvia atricapilla*) in Europe reject foreign eggs by memorizing the characteristics of their own eggs, and the hosts' repeated experience and memory would be crucial in decisions to reject a parasitic egg (Hauber et al. 2006, Honza et al. 2007b, Moskát and Hauber 2007). On the other hand, in some rejecter species, experience apparently does not influence the decision for egg rejection. Regardless of their age, some hosts of cuckoos (*Cuculus* spp.) and cowbirds

(*Molothrus* spp.) frequently reject parasitic eggs (e.g., Sealy and Neudorf 1995, Amundsen et al. 2002, Stokke et al. 2004).

According to the coevolutionary arms race between cuckoos and their hosts, as a counter-adaptation against perfect mimicry of cuckoo eggs, hosts may evolve eggs with distinctive characteristics, or greater interclutch variation (Brooke and Davies 1988, Davies 2000). Selection, therefore, may favor evolution of egg polymorphism in hosts (Takasu 2003, Kilner 2006). Indeed, some species of cuckoos and their hosts lay polymorphic eggs within the same population. The Village Weaverbird (*Ploceus cucullatus*), a host of Diederik Cuckoos (*Chrysococcyx caprius*), lays eggs ranging from white to emerald to turquoise, with or without spots (Collias 1993). Another host of the Common Cuckoo (*Cuculus carnorus*), the Vinous-throated Parrotbill (*Paradoxornis webbianus*), lays blue or white eggs (Kim et al. 1995b). The Common Cuckoo also lays eggs of distinctive types that are matched to eggs of each different host; for example, eggs of cuckoos that parasitize Meadow Pipit (*Anthus pratensis*) nests are brown with spots, whereas cuckoos that use the Redstart (*Phoenicurus phoenicurus*) as a host also lay immaculate blue eggs (Moksnes et al. 1995, Davies 2000). Polymorphic cuckoo eggs may be specialized for a particular host species to match that host's eggs (Davies and Brooke 1989a), whereas egg polymorphism of hosts may evolve to outpace egg mimicry by cuckoos (Kilner 2006). The cycle of evolutionary change of better recognition and better trickery likely influences the diversity of egg appearance in hosts and parasites. Egg appearance, therefore, is central to our understanding of coevolution between parasites and their hosts (Øien et al. 1995, Underwood and Sealy 2002).

In species that lay polychromatic eggs and in which both sexes reject foreign eggs, such as the Vinous-throated Parrotbill, females and males may have evolved different mechanisms of egg discrimination because the sexes find themselves in different circumstances while breeding. In Village Weaverbirds and Vinous-throated Parrotbills, egg colour is genetically determined rather than influenced by environmental factors (Collias 1993, Kim et al. 1995b). These authors demonstrated that females always lay eggs of the same type regardless of their breeding partners from one breeding attempt to the next. On the other hand, egg colour in nests of males occasionally changed when the males paired with different females (Kim et al. 1995b). In this case, if the male learns his partner's egg-type through imprinting (see above), he may later reject his partner's egg when paired with a female that lays eggs of a different colour. To minimize the risk of rejecting their own eggs, therefore, males should not depend on experience or memory when they discriminate between parasitic eggs and their own eggs.

In the present study, I tested the importance of egg colour in the interaction between the Common Cuckoo and Vinous-throated Parrotbill and investigated whether there is a sex-specific strategy for egg discrimination. In Chapter 1, to determine whether ground colour provides an important cue on which to discriminate parasitic eggs, I investigated the responses of the Vinous-throated Parrotbill to parasitic eggs (real cuckoo, model cuckoo, and conspecific eggs) in relation to the degree of colour mimicry. As well, I examined the egg-colour patterns of the same individuals from year to year or between clutches within the same breeding season to explore the suggestion of Kim et al. (1995) that parrotbill egg colour is genetically determined. In Chapter 2, I investigated the learning mechanisms of females and males to discriminate between their own eggs and parasitic eggs. To determine especially whether different strategies are adopted by males and females, I examined the responses of males and females, respectively, depending on when the foreign egg type was in the minority and when it was in the majority in their nests by egg manipulations.

BACKGROUND OF STUDY SPECIES

The parrotbills are a small group of three genera and 21 species usually placed within their own family Paradoxornithidae (Clements 1974, Robson 2007), or within the larger babbler tribe Timaliini (Sibley and Monroe 1990). All but two of the parrotbills are placed within the genus *Paradoxornis*. The parrotbills are a predominantly east Asian group with a distribution center in southern China. The only parrotbill distributed outside of Asia is the European species, the Bearded Parrotbill (*Panurus biamarcus*), also known as the Bearded Tit or Bearded Reedling (Robson 2007). Currently six subspecies of the Vinous-throated Parrotbill are known although distribution and subspecific variation are not completely understood (Robson 2007). The range of the Vinous-throated Parrotbill extends from extreme northern Vietnam north along the east coast of China and as far west as eastern Yunnan, Sichuan and Shaanxi provinces, then north to Manchuria and southeastern Siberia (Ussuriland) as well as throughout the Korean Peninsula, where it is the only parrotbill species (Won and Gore 1971). It also occurs on Taiwan and has been introduced to northwest Italy (Robson 2007). Dement'ev and Gladkov (1970) also mention its occurrence in northeastern Burma, however this likely refers to Brown-winged Parrotbill when these species were considered conspecific. In most of its range the Vinous-throated Parrotbill occurs below 1400m in elevation and to approximately 1500m in South Korea (personal observation); however, *C. w. bulomachus* occurs to 3100m on Taiwan (Robson 2007).

The Common Cuckoo breeds throughout the range of the Vinous-throated Parrotbill except for Taiwan and the southernmost portion of the range of the parrotbill in Vietnam (Payne 1997). The Common Cuckoo has been recorded as a brood parasite of over 100 species (Payne 1997) including three parrotbill species, the Bearded Parrotbill (Wyllie 1981), the Black-breasted Parrotbill (*Paradoxornis flavirostris*) (Baker 1942 but see Becking 1981 for criticism) and the Vinous-throated Parrotbill (Kim 1996, Lee 2002). There is no record of the Vinous-throated Parrotbill acting as a brood host for the Common Cuckoo outside of Korea (Lowther 2007).

The Common Cuckoo breeds throughout the Palearctic from northern Scandinavia south to the Mediterranean (including the northern shores of Africa) and Turkey, then east through Siberia to Japan and south to the Himalayas and China (Davies 2000). The breeding biology of the Common Cuckoo in Asia is poorly known except for a few studies conducted in Korea (Kim 1996; Lee 2002, Kim 2006) and Japan (Royama 1963, Nakamura 1990, Nakamura et al. 1998). In Korea, the Common Cuckoo has at least two additional brood hosts, the Daurian Redstart (*Phoenicurus auroreus*) (Yonhap News 2005), also with polychromatic eggs varying from white to pale greenish and pale blue and sometimes with brown spotting (Collar 2005) and the Common Stonechat (*Saxicola torquatus*) (Aves Korea) with predominantly blue or bluish-green eggs, sometimes spotted reddish brown (Collar 2005). Interestingly, the Common Cuckoo has not been recorded parasitizing the Oriental Reed Warbler (*Acrocephalus orientalis*) in Korea, a species which lays pale brownish maculated eggs and which it regularly parasitizes in Japan (Brazil 1991) where Vinous-throated Parrotbill does not occur.

The egg colour of Vinous-throated Parrotbills is described as two colours: blue and white (Park 1993 and Kim et al. 1995b, Lee 2002) and the proportion of egg colour are different among areas or years (Kim et al. 1995b). Lee (2002) suggested that more than two egg-colours may be beneficial to hosts in a coevolutionary interaction with the Common Cuckoo because makes it difficult for cuckoos to match their host clutches and different parasitic eggs are rejected by hosts at a high frequency. However, there is no direct evidence that parasitism by cuckoos exerts evolution of egg-colour polymorphism in the Vinous-throated Parrotbill. A full comparison of the degree of polychromatism in the Vinous-throated Parrotbill where allopatric and sympatric with the Common Cuckoo has not been conducted; however, anecdotal evidence points to the possibility of co-evolutionary processes. For example, parrotbill populations in Taiwan where Common Cuckoos are vagrant have only blue eggs (Yamashina 1933) and the same appears to be true in the extreme southern portion of the Korean peninsula (Busan area) where Common Cuckoo is very uncommon and where no white eggs were found in a sample of approximately 200 parrotbill nests (Woo Young-Tae, unpublished data). Elsewhere on the Korean peninsula, where Common Cuckoos occur more frequently (personal observation) Vinous-throated Parrotbills lays eggs with two or three colours and show high rejection frequencies of non-mimetic parasitic eggs. This suggests that egg polychromatism in parrotbills may have evolved as an anitparasitim defence. Further comparative studies in portions of the range in China and elsewhere would be needed to clarify this. Furthermore, because parasitism by cuckoos leads to a dramatic reduction of host breeding success (Davies 2000), the egg-colour ratio of blue to white parrotbill eggs may be indicative of the extent of historical interaction with Common Cuckoos.

CHAPTER 1. Importance of egg colour in the coevolutionary interaction between the Vinous-throated Parrotbill and Common Cuckoo

INTRODUCTION

Hosts of avian brood parasites have evolved strategies such as egg discrimination and rejection to eliminate the extreme costs to their breeding attempt from parasitism (Davies and Brooke 1989a, Øien et al. 1995). In turn, high-level egg discrimination by hosts and rejection of non-mimetic eggs may lead parasites to reinforce egg mimicry, which renders it difficult for hosts to discriminate the parasite's eggs (Davies 2000). Parasites and hosts, therefore, have evolved variable strategies to increase each other's breeding success, through a coevolutionary arms race (Payne 1977), in which egg appearance may play a major role (Øien et al. 1995, Takasu 2003). Results of several experimental studies have suggested that host species that reject parasitic eggs use the signature information provided by visual differences in ground colour, spot patterns or size to discriminate parasitic eggs (Victoria 1972; Davies and Brooke 1988; Lahti and Lahti 2002; Marchetti 2000; Underwood and Sealy 2002, 2006; Moskát et al. 2008). However, the parameters on which discrimination is based may be used differently among host species.

In many hosts of cuckoos and Brown-headed Cowbirds (*Molothrus ater*), results of previous experiments have suggested that hosts use differences in colour or spot pattern to discriminate between their own eggs and parasitic eggs rather than shape, mass, or size (Victoria 1972, Rothstein 1982, Lawes and Kirkman 1996, Lahti and Lahti 2002, Underwood and Sealy 2006). Moskát et al. (2008) revealed that ground colour is a significantly more important cue for egg discrimination than spot patterns in Great Reed Warblers. On the other hand, Marchetti (2000) determined that egg size is important in the rejection of foreign eggs by Hume's Yellow-browed Leaf Warbler (*Phylloscopus humei*). Although obligate brood parasites, such as the Common Cuckoo, lay eggs that are small relative to their body size to adjust to the usually smaller eggs of hosts (Payne 1974, Moksnes and Røskaft 1995, Krüger and Davies 2004), nevertheless, cuckoo eggs laid in nests of small passerines are generally still larger and, hence, non-mimetic in size (Davies 2000). For example, cuckoo eggs are more than two times larger than those laid by the Vinous-throated Parrotbill in Korea (Table 1.1 of Methods). If hosts discriminate and reject parasitic eggs based on differences in size, such as in Hume's Yellow-browed Leaf Warblers (Marchetti 2000), most large cuckoo eggs would be rejected; eventually, the coevolutionary interaction between cuckoos and their small passerine hosts may cease because mimicry through egg size would be more constrained physically than colour or spotting patterns.

In the present study, I investigated the importance of egg colour in the interaction between the Common Cuckoo and Vinous-throated Parrotbill, a host species that lays immaculate eggs of more than two colours within the population (Kim et al. 1995b). In host species, great interclutch variation in egg appearance has been thought to evolve as a counter-adaptation against perfect mimicry by cuckoos (Øien 1995, Underwood and Sealy 2002); sometimes selection may result in the evolution of egg polymorphism in both hosts and parasites (Takasu 2003, Kilner 2006). This variation in egg appearance is inherited (Collias 1993, Gibbs et al. 2000, Gosler et al. 2000), although egg colour is sometimes affected by environmental conditions (e.g., climate or food) because these factors may influence female condition during egg formation and the laying period (Avilés et al. 2007).

Several cuckoo hosts in Europe and Africa, such as warblers of the genus *Acrocephalus* (Davies and Brooke 1988), the Red Bishop (*Euplectes orix*, Lawes and Kirkman 1996) and Southern Olive Thrush (*Turdus olivaceus*, Honza et al. 2005), frequently reject non-mimetic model cuckoo eggs but accept closely matching models. Meanwhile, Lee and Yoo (2004) reported that Vinous-throated Parrotbills rejected at high frequencies of both non-mimetic and mimetic model cuckoo eggs, suggesting that Vinous-throated Parrotbills are able to discriminate foreign eggs precisely.

Despite egg discrimination ability and considerable rejection by the Vinous-throated Parrotbill, little is known about specific cues that parrotbills use to distinguish differences between their own eggs and parasitic eggs. I hypothesized that in a host species that lays immaculate polychromatic eggs, such as Vinous-throated Parrotbills, ground colour may provide an important basis on which to discriminate parasitic eggs. Accordingly, I investigated the responses of the Vinous-throated Parrotbill to parasitic eggs in relation to the degree of colour mimicry by observing nests naturally parasitized by Common Cuckoos, and experimenting with conspecific and model cuckoo eggs. As well, I collected data on the egg-colour patterns of several same individuals to determine whether parrotbill egg colour is consistent from year to year or is influenced by breeding partners, to confirm the suggestion of Kim et al. (1995b) that egg colour is under genetic control, rather than influenced by environmental factors (see Avilés et al. 2007).

Hypotheses

Hypothesis 1. Egg colour is genetically determined.

Prediction : Each female lays constant egg colour regardless of year and mate.

Hypothesis 2. Egg colour is an important cue for egg rejection.

Prediction : Hosts reject parasitic eggs that differed more substantially in colour from their own eggs, regardless of size, i.e., cuckoo versus conspecific eggs.

METHODS

Study site and species

Fieldwork was conducted at Yangseomyeon, Yangpyeong-gun, Gyonggi-do, South Korea (37°32'N, 127°20'E, Figure 1.1) from early April to late July in 2005–2007. This area consists of farmland with hedges, cultivated fields, woodland with shrubs and bushes, and a stream with reed beds. Vegetation was mainly large trees such as *Quercus variabilis, Q. mongolica, Q. serrata, Prunus serrulatavar. spontanea, Fraxinus rhynchophylla* and *F. mandschurica*, and shrubs *Salix grasilisfyla, Rosa multiflora, Ligusturm obtusitolium, Rubus parvifolius, Strphanandra incise, Corylus heterophylla* and *Phragmites communis* (Park et al. 1993). Vinous-throated Parrotbills and Common Cuckoos are widely distributed from lowlands into mountainous areas. Twenty flocks of the Vinous-throated Parrotbill were found in this area (Figure 1.2).

The Vinous-throated Parrotbill is a small (approximately 11g), sexually monomorphic passerine that builds open-cup nests that are occasionally parasitized by Common Cuckoos in South Korea (Kim 1996, Lee 2002). Vinous-throated Parrotbills are distributed in East Asia, from China to Korea, but not Japan, and they are a common

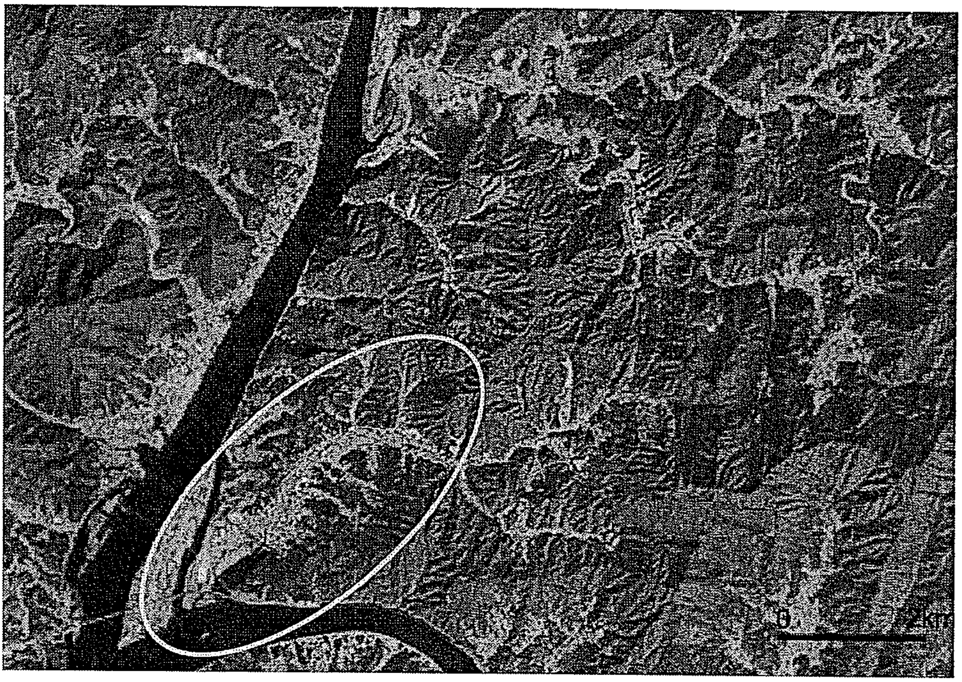


Figure 1.1. The study area, Yangseomyeon, Yangpyeong-gun, Gyeonggi-do, Korea.

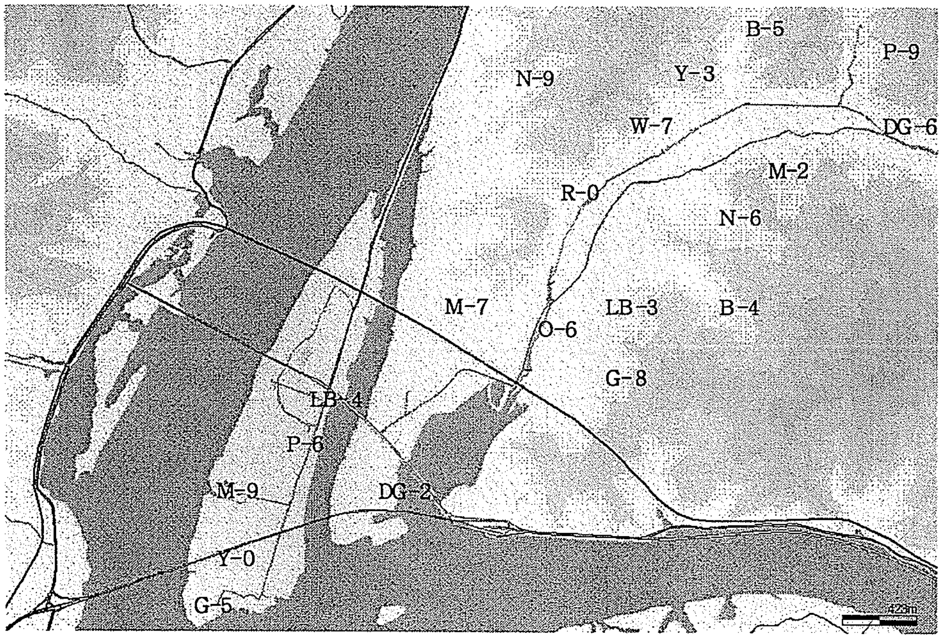


Figure 1.2. Distribution of Vinous-throated Parrotbill flocks in this study area (letters on the map indicate flock name).

residents in Korea (Won and Gore 1971). Nest building and incubation are conducted equally by males and females (Park et al. 1993, Kim et al. 1995a). Of 198 parrotbill nests I examined, most contained 5 eggs (59%) or 6 eggs (35%), although some nests contained 4 eggs (4.5%) or 7 eggs (1.5%) during the study. Eggs have been described as dichromatic- immaculate blue or white (Park et al. 1993, Kim et al. 1995b, Kim 1998, Lee and Yoo 2004, Lee et al. 2005); however, in my study, I identified visually an intermediate colour between blue and white: pale blue, although this colour was not common. A sample of eggs of each colour-type was photographed and collected for specimens from deserted nests or experimental nests in 2005-2007. Eggs were classified into three groups as white, pale blue, or blue; colour differences among categories were distinctive to human observers (Figure 1.3). To determine colour types of experimental nests, all eggs were directly compared to both white and blue eggs collected from other parrotbill nests by at least two observers. The proportion of egg colours depended on area and year (see Kim et al. 1995a), but blue eggs were always more frequent than white eggs (see also Kim et al. 1995b, Lee 2002, Kim 2006).

In Korea, few studies of parasitism by Common Cuckoos have been conducted (Kim 1996, Lee 2002). Common Cuckoos lay single blue eggs in parrotbill nests in the afternoon from late May to early July, and they remove one to three host eggs before parasitism (Lee 2002). Parasitism frequency is approximately 5% in central Korea (Lee 2002). Blue cuckoo eggs were found in white and blue host clutches, and no white cuckoo eggs have been recorded in Korea (Kim 1996, Lee 2002).

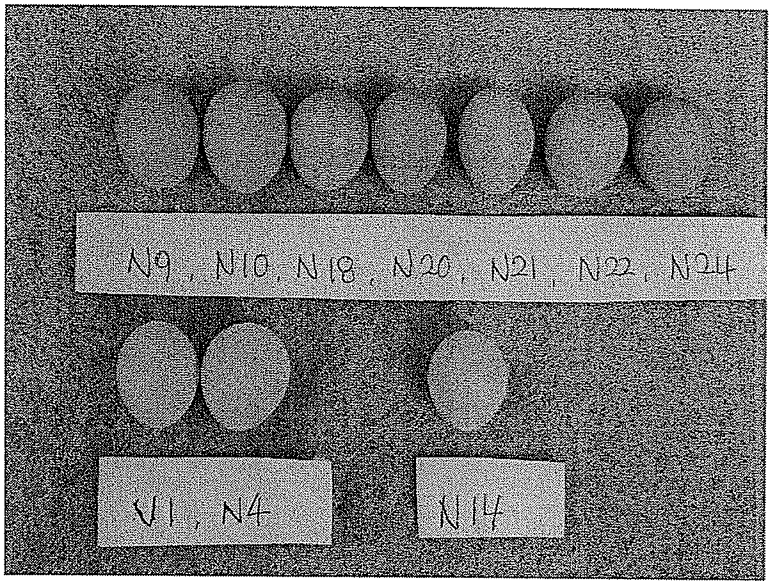


Figure 1.3 Vinous-throated Parrotbill eggs from different nests: blue (top row), pale blue (bottom left), and white (bottom right).

Experimental parasitism

To investigate the discriminative ability of Vinous-throated Parrotbills to parasitic eggs, 115 nests were experimentally parasitized with model cuckoo ($n = 38$) and real conspecific eggs ($n = 77$) at nests during the egg-laying period or early in the incubation stage. To avoid pseudoreplication, experiments were conducted with different parrotbill flocks each year (2005-2007) and at least one adult at each experimental nest was individually marked at 40% of nests in 2005, 77% in 2006, and 89% in 2007. Rejections by the same individuals were excluded from analysis.

Model cuckoo egg. To determine responses of parrotbills towards parasitic eggs, 38 nests were artificially parasitized with model cuckoo eggs in 2005. I switched a host egg with a model egg in nests between 1500 and 1800 hours to mimic the afternoon laying time of cuckoos (see Wyllie 1981). I inspected each experimental nest every afternoon between 1500 and 1800 for six consecutive days to determine the host's response (Lee and Yoo 2004). If model eggs were missing or peck marks were found on them, I considered the model as rejected (Lee 2002). If the model egg remained in the nest without damage, the egg was considered accepted.

Model eggs sometimes lead to an increase in rejection costs to hosts when rejecting parasitic eggs, although many hosts can eject large cuckoo eggs without damaging their own eggs (Marchetti 2000). To minimize the damage that might be incurred because the model eggs were slightly heavier than real parasite eggs, and of a different physical structure, model cuckoo eggs were made of plasticine with a thin membrane of plaster that mimicked real eggshells, following the methods of Lee (2002). The thin membrane of model eggs enabled parrotbills to puncture and grasp the model eggs as if they were real cuckoo eggs when they remove the eggs from nests. To mimic blue eggs of the Common Cuckoo, models were covered with acrylic paint mixed blue, pale blue and grey (Figure 1.4) and varnished to waterproof the models. Model eggs were similar to real cuckoo eggs in size and weight (Table 1.1). The models matched host blue eggs but poorly matched host white eggs (Figure 1.5).

Conspecific eggs. To determine whether egg colour is crucial for egg rejection by Vinous-throated Parrotbills, I introduced single conspecific eggs from another parrotbill clutch between 1500 and 1800 in 77 parrotbill nests (11 in 2005, 40 in 2006, and 26 in 2007), and the degree of colour mimicry of the introduced eggs was scored from good to medium to poor (see Braa et al. 1992, Moksnes 1992). Differences that scored poor mimicry were white versus blue. Differences of medium mimicry were pale blue versus white or pale blue versus blue. Good mimicry was the same colour (i.e., white versus white or blue versus blue). Conspecific eggs from other parrotbill clutches, which ranged from white to pale blue to blue, controlled for egg size. The criteria for rejection and acceptance were the same as for model eggs.

To determine whether egg size is crucial in egg rejection, I compared the rejection frequency between real cuckoo and conspecific eggs. The degree of mimicry in Common Cuckoo eggs was classified as: (1) good (blue cuckoo eggs laid in blue clutches), (2) medium (pale blue cuckoo eggs laid in blue or white clutches), and (3) poor (blue cuckoo eggs laid in white clutches). Although blue eggs of Common Cuckoos match well the colour of the host's blue clutches, the parasitic eggs are approximately 2.6 times larger than those of parrotbills (Table 1.1).

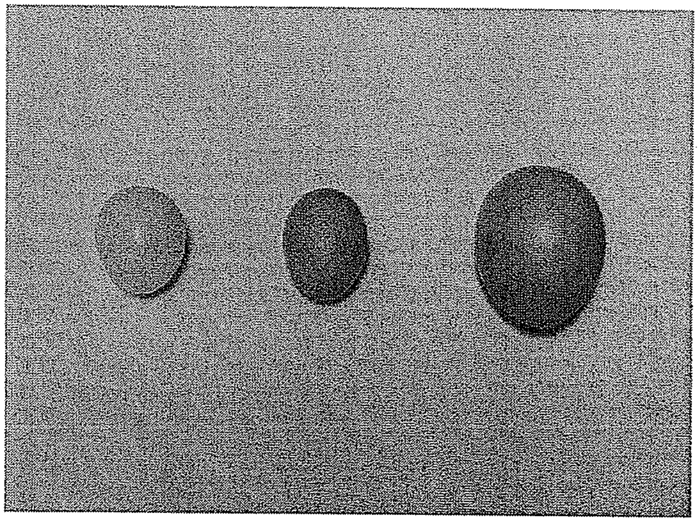


Figure 1.4. White and blue egg of Vinous-throated Parrotbills, and model cuckoo egg on the right.

Table 1.1. Mean size (mm ± SD) and weight (g ± SD) of the Common Cuckoo, cuckoo model, and conspecific eggs.

Egg type	Length x Width (*n*)	Weight (*n*)
Real cuckoo	21.75 x 17.32 ± 0.62 x 0.25 (11)	3.44 ± 0.21 (9)
Model	22.22 x 17.13 ± 0.59 x 0.50 (43)	3.62 ± 0.25 (43)
Conspecific	15.91 x 12.63 ± 0.85 x 0.38 (73)	1.33 ± 0.21 (46)

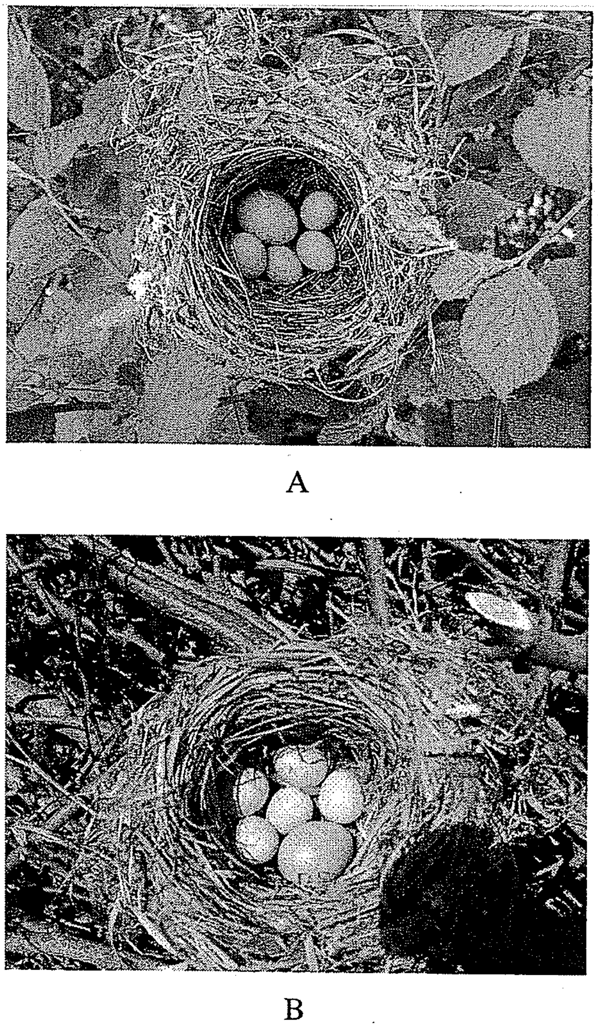


Figure 1.5. Model cuckoo egg in host blue clutch (A) and white clutch (B).

Statistical analyses

I used Chi-square tests and Fisher exact tests, depending on sample sizes, to examine host responses to real cuckoo eggs, model cuckoo eggs, and conspecific eggs when expected values were less than five. I used Chi-square tests to assess differences in the proportion of egg colours within and among years and to compare rejection frequencies in relation to the degree of colour mimicry in conspecific eggs. Fisher exact tests (Zar 1999) were used as follows: (1) to determine whether there were significant differences in rejection of real cuckoo eggs in relation to the degree of mimicry, (2) to test whether there are differences in host responses among years, and (3) to compare responses of hosts to conspecific versus real cuckoo eggs and real cuckoo versus model cuckoo eggs depending on the degree of mimicry because of small sample sizes. Statistical tests were performed using SPSS, version 11.5 (SPSS. Chicago, Illinois). All tests were two-tailed with a level of significance of $p < 0.05$.

RESULTS

Egg colour of the Vinous-throated Parrotbill

A total of 272 parrotbill nests was inspected during three breeding seasons: 88 in 2005, 90 in 2006, and 94 in 2007 (Table 1.2). Egg colours were blue, pale blue, and white (Figure 1.3). Nests with blue eggs were significantly more frequent than white or pale blue eggs in all breeding seasons (Chi-square test, $\chi^2 = 7.682$, df = 1, $p < 0.01$ in 2005; $\chi^2 = 89.867$, df = 2, $p < 0.001$ in 2006; $\chi^2 = 44.191$, df = 2, $p < 0.001$ in 2007). There is no difference in the ratio of egg colour between 2005 and 2007 (Chi-square test, $\chi^2 = 3.215$, df = 2, $p = 0.200$) but the proportion of nests with blue eggs was highest in 2006.

Table 1.2. Number of nests with different egg colour in the Vinous-throated Parrotbill.

Year	White	Pale blue	Blue	Total
2005	31 (35.2%)	0 (0.0%)	57 (64.8%)	88
2006	13 (15.6%)	4 (4.4%)	72 (80.0%)	90
2007	36 (38.3%)	3 (3.2%)	55 (58.5%)	94
Total	81 (29.8%)	7 (2.6%)	184 (67.6%)	272

Pattern of egg colour in relation to breeding partner in females and males

Of 9 cases where breeding attempts of females were detected, all females (LB356, R036, W773, W795, W721, W774, B428, LB416 and Y019) laid eggs of a constant colour regardless of their breeding partners between years or in a subsequent breeding attempt within the same breeding season (Table 1.3). Egg colour of 3 of 8 males (W775, B425 and LB325) changed from white to blue, pale blue to blue, or white to blue from one breeding attempt to the next when they mated with different females (Table 1.4).

Parasitism by Common Cuckoos

Egg-colour dimorphism. Cuckoo eggs were found in 6 parrotbill nests in 2005, 8 nests in 2006, and 5 nests in 2007 (Table 1.5). Common Cuckoo eggs were of two colours: 7 pale blue eggs and 12 blue eggs were found in 19 nests of parrotbills (Figure 1.6).

Pattern of parasitim by Common Cuckoos. Twelve blue eggs were laid in 9 host blue clutches and 3 host white clutches (Table 1.6). Blue cuckoo eggs were well matched with host blue eggs (Figure 1.7), but they were poorly matched with the white eggs. Seven pale blue cuckoo eggs were found in 4 blue clutches and 3 white clutches of parrotbills. Pale blue cuckoo eggs matched host pale blue eggs but neither matched well nor poorly matched blue and white clutches of parrotbills (Figure 1.8); however, no cuckoo eggs were found in pale blue clutches.

Table 1.3. Pattern of egg colour in cases where the female changed mates.

Year	Matings				Egg colour
	Female		Male		
2005	***LB356***	x	LB336	→	Blue
2005	***LB356***	x	LB338	→	Blue
2005	***R036***	x	Y311	→	White
2006	***R036***	x	B523	→	White
2005	***W773***	x	W761	→	White
2006	***W773***	x	W817	→	White
2005	***W795***	x	W744	→	Blue
2006	***W795***	x	W768	→	Blue
2005	***W721***	x	W765	→	Blue
2006	***W721***	x	No band	→	Blue
2005	***W774***	x	W775	→	White
2007	***W774***	x	LB343	→	White
2006	***B438***	x	B425	→	Pale blue
2007	***B438***	x	B404	→	Pale blue
2006	***LB416***	x	P606	→	White
2007	***LB416***	x	No band	→	White
2006	***Y019***	x	P610	→	Blue
2007	***Y019***	x	P623	→	Blue

Table 1.4. Pattern of egg colour in cases where the male changed mates.

Year	Matings				Egg colour
	Female		Male		
2005	W774	x	***W775***	→	***White***
2006	LB305	x	***W775***	→	***Blue***
2007	LB328	x	***W775***	→	Blue
2007	No band	x	***W775***	→	Blue
2005	M 201	x	***B523***	→	White
2006	R036[a]	x	***B523***	→	White
2005	O145	x	***O143***	→	White
2006	O106	x	***O143***	→	White
2006	LB373	x	***LB338***	→	Blue
2006	LB356[b]	x	***LB338***	→	Blue
2006	No band	x	***B403***	→	Blue
2007	O403	x	***B403***	→	Blue
2006	B438	x	***B425***	→	***Pale blue***
2007	B450	x	***B425***	→	***Blue***
2006	LB334	x	***LB325***	→	***White***
2007	No band	x	***LB325***	→	***Blue***
2006	LB358	x	***LB374***	→	Blue
2007	LB323	x	***LB374***	→	Blue

Table 1.4 continued

[a] Female R036 laid white eggs successively in different breeding seasons despite changing her breeding partner.

[b] Female LB356 laid blue eggs successively in different clutches despite changing her breeding partner.

Table 1.5. Number of pale blue and blue Common Cuckoo eggs found in 19 host nests.

Year	Pale blue (%)	Blue (%)	Total
2005	1 (17)	5 (83)	6
2006	4 (50)	4 (50)	8
2007	2 (40)	3 (60)	5
Total	7 (37)	12 (63)	19

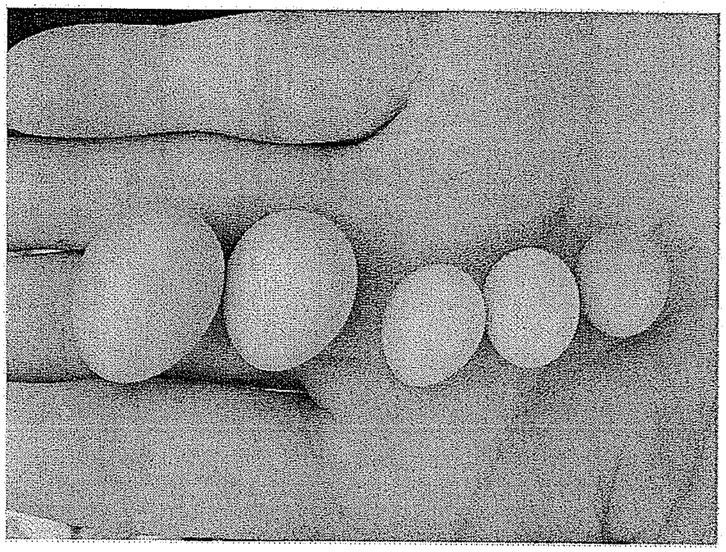


Figure 1.6. Eggs of Common Cuckoos (blue and pale blue) and Vinous-throated Parrotbills (pale blue, white and blue on the right) from different females' nests.

Table 1.6. Number of Common Cuckoo eggs laid in host nests with different egg colour.

Common Cuckoo's egg colour	Host egg colour		Total
	white (%)	blue (%)	
Pale blue	3 (43)	4 (57)	7
Blue	3 (25)	9 (75)	12
Total	6 (32)	13 (68)	19

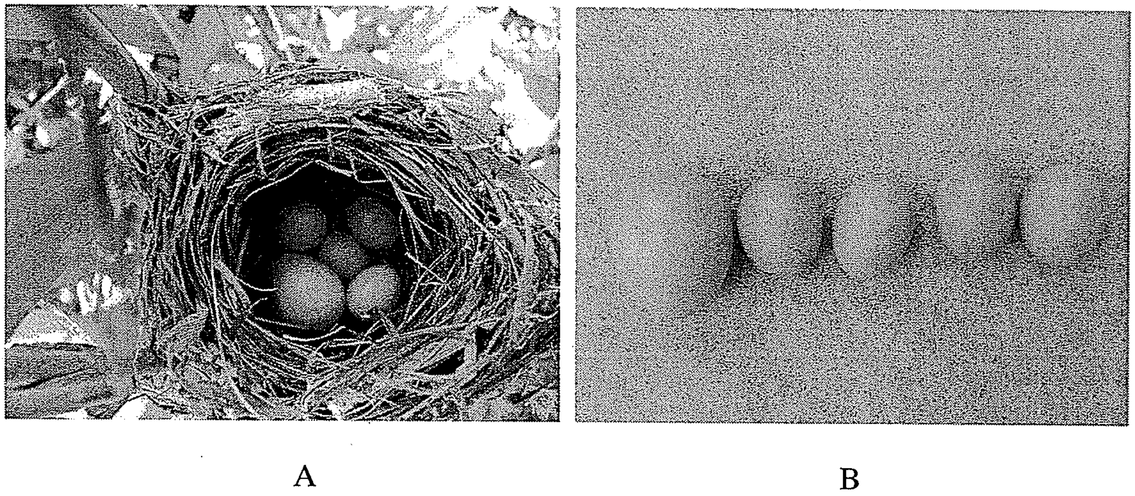
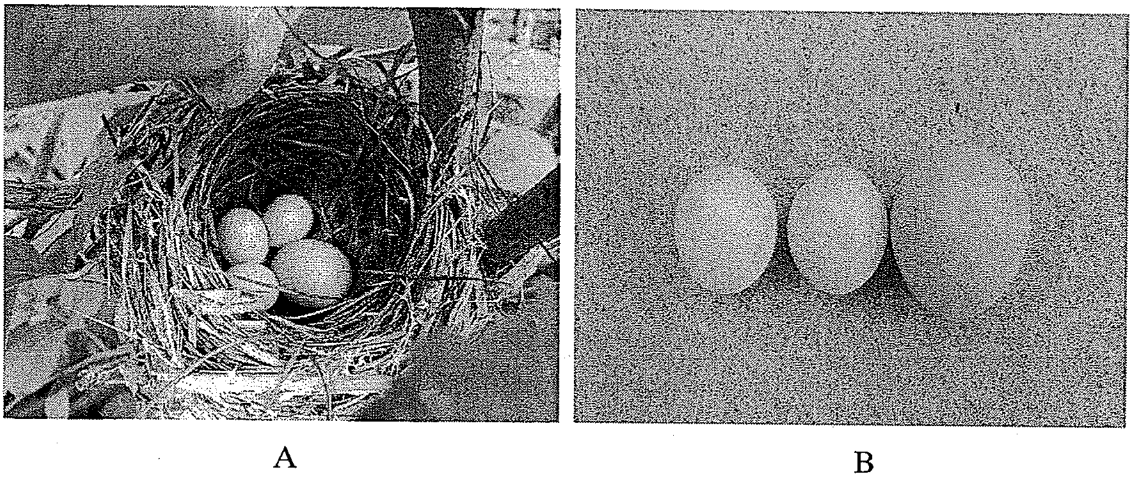


Figure 1.7. A blue egg of the Common Cuckoo in a Vinous-throated Parrotbill nest with blue eggs (A) and eggs from the nest (B).



A

B

Figure 1.8. A pale blue egg of the Common Cuckoo in a Vinous-throated Parrotbill nest with white eggs (A) and eggs from the nest (B).

Responses towards parasitism in relation to the degree of mimicry

Rejection of real and model cuckoo eggs. All real cuckoo eggs that matched host clutches closely (good mimicry) were accepted, all blue cuckoo eggs laid in white clutches (poor mimicry) were rejected, and pale blue cuckoo eggs (medium mimicry) were rejected at a moderate frequency (Table 1.7). There was a significant difference in rejection frequency depending on the degree of mimicry in Common Cuckoo eggs (Fisher's exact test, p = 0.0087).

In the experiment in which model cuckoo eggs were used, parrotbills with blue clutches rejected most blue model eggs (good mimicry), and all model eggs parasitized in white clutches were rejected (Table 1.8). There was no difference in rejection frequency between mimetic model eggs and non-mimetic model eggs (Fisher's exact test, p = 0.295). In colour-mimetic parasitic eggs, there was a significant difference in rejection frequency between real cuckoo and model cuckoo eggs (Fisher's exact test, real cuckoo ($n = 7$) and model cuckoo ($n = 27$), $p = 0.0001$) and all poorly mimetic parasitic eggs were rejected regardless of egg-type.

Table 1.7. Responses of the Vinous-throated Parrotbill towards real Common Cuckoo eggs in relation to degree of mimicry.

Degree of mimicry[1]	Nests parasitized	Acceptance	Rejection	% Rejection
Good	7	7	0	0
Medium	6	3	3	50
Poor	2	0	2	100
Total	15	10	5	33

[1] Good, blue cuckoo eggs laid in blue clutches; medium, pale blue cuckoo eggs laid in blue or white clutches; and poor, blue cuckoo eggs laid in white clutches.

Table 1.8. Responses of the Vinous-throated Parrotbill towards model cuckoo eggs in relation to degree of mimicry.

Degree of mimicry[1]	Nests parasitized	Acceptance	Rejection	% Rejection
Good	27	5	22	82
Poor	11	0	11	100
Total	38	5	33	87

[1] Good, blue model eggs laid in blue clutches of hosts; poor, blue model eggs laid in white clutches.

Responses to foreign conspecific eggs. There was no difference in rejection frequency in relation to degree of colour-mimicry across years (Fisher's exact test, $p = 1.0000$ (good), $p = 0.8728$ (medium), and $p = 0.5153$ (poor)); thus, the data were combined for all breeding seasons. Of 77 introduced conspecific eggs, 18 were mimetic (blue versus blue), 13 were medium-mimetic (blue versus pale blue), and 46 were non-mimetic (blue versus white). Poorly matched conspecific eggs were rejected from 83% (38/46) of nests, whereas most well-matched eggs were accepted and medium-mimetic eggs were rejected at a moderate frequency (Table 1.9). There was a statistically significant difference in rejection frequency among degrees of mimicry in colour (Chi-square test, $\chi^2 = 26.335$, df $= 2$, $n = 77$, $p < 0.001$).

To test whether size influences responses of hosts towards parasitic eggs, rejection of foreign conspecific eggs was compared with that of real cuckoo eggs in relation to degrees of colour mimicry. There is no difference in rejection frequency between real cuckoo eggs and conspecific eggs in relation to degree of mimicry in egg colour (Fisher's exact test: good, $p = 0.5343$; medium, $p = 1.0000$; poor, $p = 1.0000$, Figure 1.9). Vinous-throated Parrotbills rejected parasitic eggs that were more distinctly different in colour from their own eggs regardless of size.

Table 1.9. Responses of the Vinous-throated Parrotbill towards foreign conspecific eggs in relation to degree of colour mimicry between the foreign egg and original clutch.

Degree of mimicry	Nests parsitized	Acceptance	Rejection	% Rejection
Good	18	15	3	17
Medium	13	8	5	39
Poor	46	8	38	83
Total	77	31	46	60

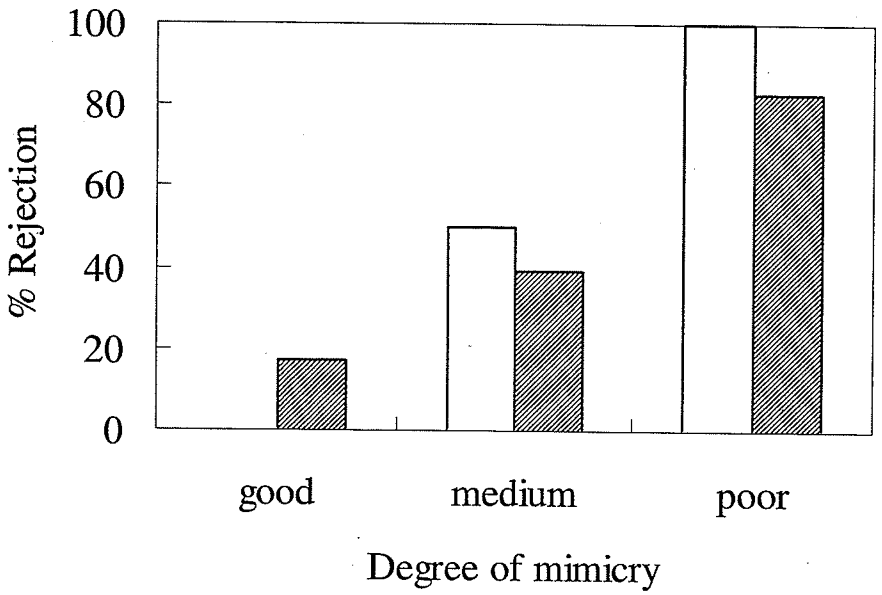


Figure 1.9. Rejection frequencies of real cuckoo eggs (□, $n = 15$) and conspecific eggs (▨, $n = 77$) in relation to the degree of colour mimicry.

DISCUSSION

Variation in egg colour of Vinous-throated Parrotbill and Common Cuckoo

Some avian species lay eggs that vary greatly in appearance (colour or spotting) among clutches, for example, in populations of the Village Weaverbird (Victoria 1972, Collias 1993) and Greater Redheaded Parrotbill (*Paradoxornis ruficeps*) (Ali and Ripley 1971). Egg colour of Vinous-throated Parrotbills was mainly blue and white, sometimes pale blue, although blue clutches were more common than white clutches (blue, 59~80% versus white, 16~36%) in my study area (Table 1.2). Egg colour varies geographically in Vinous-throated Parrotbills, for example, the subspecies in Taiwan (*P. w. bulomachus*) and eastern Manchuria (*P. w. manschurica*) lay only blue eggs (Kim et al. 1995b), whereas, in Korea the subspecies (*P. w. fulvicauda*) lays blue and white eggs, with the proportion of blue clutches varing among areas and years (Kim et al. 1995b). Avilés et al. (2007) suggested that environmental factors influence egg colour because female condition during egg formation and laying may be affected by climatic factors directly (i.e., physiological condition) or indirectly (i.e., food availability). They reported that intensity of egg colouration of females is significantly associated with spring rainfall and temperature in the Common Cuckoo and Reed Warbler (*Acrocephalus scirpaceus*). In species with blue-green eggs, colour and spots depend on female body condition (Moreno et al. 2006, Siefferman et al. 2006, Martínez-de Puente et al. 2007).

Egg colour of Vinous-throated Parrotbills likely is determined genetically rather than by external factors. Female parrotbills always laid eggs of the same colour even when they changed their mates between breeding attempts within the same breeding season or in the next breeding season (Table 1.3). A female that laid pale blue eggs, also laid pale blue eggs in a subsequent nest within the same breeding season, or between years regardless of her breeding partners; this was the same in other females that laid blue or white eggs. On the other hand, egg colour of male parrotbills occasionally changed when they paired with different females (Table 1.4). Collias (1993) and Kim et al. (1995b) demonstrated that in species that lay polymorphic eggs, such as the Village Weaverbird and Vinous-throated Parrotbill, respectively, females laid eggs consistently with the same ground colour or spot pattern throughout their lifetimes. Gosler et al. (2000) found that egg patterns of the Great Tit (*Parus major*) are determined by female sex-linked inheritance rather than female age, size or condition. Although in the present study, I did not determine mechanisms of egg inheritance, i.e., whether maternal, paternal, or both, these data reveal that female parrotbills have an inherent uniform egg colour.

Why do female parrotbills lay eggs of more than one egg colour in this population? Although this question cannot be answered definitively, according to the coevolutionary arms race between cuckoos and their hosts, as a counter-adaptation against perfect mimicry by cuckoos, hosts may evolve eggs with distinctive shape, colour, or marking, or greater interclutch variation, which makes it difficult for female cuckoos to mimic (Brooke and Davies 1988; Davies 2000; Stokke et al. 1999, 2002). Therefore, selection may result in the evolution of egg polymorphism in hosts (Takasu 2003). Although there is no direct evidence that brood parasitism has selected for different egg types in Vinous-throated Parrotbills, this polymorphism partially benefits hosts that are parasitized by Common Cuckoos that lay well-matched eggs. All parrotbills with blue clutches accepted a blue cuckoo egg, but no blue eggs were accepted by hosts that laid white clutches (Table 1.7).

Cuckoo parasitism may influence the proportion of egg colour within this population of Vinous-throated Parrotbills because parasitism reduces the reproductive success of individuals that lay blue eggs (see Takasu 2003), and consequently white clutches may become more common than blue ones. The speed at which white clutches spread in Vinous-throated Parrotbills may depend on the frequencies of parasitism or nest predation (see Takasu 2003). Losey et al. (1997) revealed that the ratio of polymorphic morphs of pea aphids (*Acyrthosiphon pisum*) biased density-dependent parasitism and predation; for example, the proportion of the red-morph increased compared with the green morph when parasitism frequency by the wasp (*Aphidius ervi*) was high, but when predation by ladybird beetles (*Coccinella septempunctata*) was heavy relative to parasitism frequencies, individuals of the green-morph increased. Both parasitism and predation may have a strong effect on proportion of colour polymorphism (Losey et al. 1997). Although frequency of parasitism on parrotbills is low (approximately 5%, Lee 2002), selection pressure by parasitism may be relatively stronger than that by other predators because most hosts re-nest if their nests were depredated; raising a cuckoo chick, however, leads to breeding failure for the whole breeding season (Rothstein 1990; Øien et al. 1995). In addition, Kim et al. (1995b) reported that nest predation, mainly by the Eurasian Jay (*Garrulus glandarius*) and snakes (e.g., *Natrix tigrina*, *Elaphe rufodorsata*), was not related to whether eggs were blue or white in the Vinous-throated Parrotbill, which suggests that both blue and white clutches are under the same predation pressure.

Interestingly, the Common Cuckoo lays eggs of two colours, blue or pale blue, in my study area (Table 1.5, Figure 1.6). Moksnes et al. (1995) noted that of several cuckoo gentes, the frequency of blue cuckoo eggs was only 3.04 % (361/11,870 eggs) in Europe, and the blue eggs were found more frequently in blue clutches of Redstarts, Whinchats (*Saxicola rubetra*), Northern Wheatears (*Oenanthe oenanthe*) and Pied Flycatchers (*Ficedula hypoeuca*) that were matched to cuckoo's own eggs, compared to other species that do not lay blue eggs. High rejection by hosts that lay blue eggs has presumably been a powerful selective agent on the evolution of blue cuckoo eggs (Moksnes et al. 1995). In this context, pale blue eggs may have evolved as an adaptation against considerable rejection by Vinous-throated Parrotbills that lay white clutches. Although blue cuckoo eggs may be more beneficial than pale blue eggs presently when blue host clutches are more common, because all blue cuckoo eggs were accepted at host nests with blue clutches, the high breeding success of the cuckoo may lead to reduction in the proportion of blue clutches, which are matched with cuckoo's own eggs. Eventually, all female parrotbills may lay white eggs and this process may stop when cuckoo females no longer mimic host eggs (see Lovászi and Moskát 2004).

However, pale blue eggs may be a compromise strategy of cuckoos to avoid the final stage in the interaction with parrotbills. Vinous-throated Parrotbills showed a neutral response to pale blue eggs, whereas all blue eggs were accepted or rejected depending on host egg colour (Table 1.7). If white clutches become more common because of the high success of parasitism involving blue eggs, pale blue cuckoo eggs may be more adaptive than blue eggs. Moreover, if female cuckoos selectively parasitize to reinforce egg mimicry, as shown by results from many studies (review in Krüger 2007), the female that lays pale blue eggs may be free to choose parrotbill nests. Over the long-term, the mixed strategy of Common Cuckoo eggs makes it more difficult for the host to evolve a succcessful counter-adaptation. This may explain why blue clutches are more common than white ones in Vinous-throated Parrotbills despite the advantage of white eggs in arms race with cuckoos.

Response of hosts to parasitic eggs

Several experiments have demonstrated that many hosts discriminate foreign eggs from their own eggs and the ability for counter-adaptation may be acquired by observational learning (Victoria 1972, Rothstein 1982, Moksnes 1992, Marchetti 2000, Lahti and Lahti 2002, Underwood and Sealy 2006, Moskát and Hauber 2007, Moskát et al. 2008). Egg appearance, therefore, is important in host responses against parasitism (Øien et al. 1995). Underwood and Sealy (2002) noted that in host species of brood parasites, egg appearance plays a crucial role in the hosts' ability to discriminate between their own eggs and parasitic eggs. Vinous-throated Parrotbills rejected parasitic eggs that differed more distinctly in colour from their own eggs in experiments in which conspecific eggs and real cuckoo eggs were used (Figure 1.9). Colour appears to be more crucial for egg discrimination than size in Vinous-throated Parrotbills.

However, unlike the response towards colour-mimetic real cuckoo eggs (rejection rate, 0%), Vinous-throated Parrotbills rejected most mimetic model eggs (82%, Table 1.8). This high rejection of colour-mimetic model eggs is in accordance with Lee and Yoo's (2004, 77%) and Kim's (2006, 85%) results. The high frequency of rejection of mimetic model eggs may be due to host recognition of model eggs as synthetic objects rather than real cuckoo eggs. However, many studies have successfully used model eggs to quantify host responses towards parasitism (Davies and Brooke 1989a, 1989b; Braa et al. 1992;

Lawes and Kirkman 1996; Marchetti 2000; Lee and Yoo 2004; Honza et al. 2005; Underwood and Sealy 2006). Results from these studies have shown that many host species (e.g., *Acrocephalus* warblers in Europe, Red Bishops in Africa) accepted most mimetic model eggs and rejected non-mimetic models at high frequencies (Davies and Brooke 1989b, Hill and Sealy 1994, Lawes and Kirkman 1996, Lahti and Lahti 2002, Honza et al. 2005). So these results suggest that the host species do not perceive model eggs as synthetic objects.

Another possible explanation is that Vinous-throated Parrotbills can detect subtle differences in blue colouration that humans cannot perceive. Vinous-throated Parrotbills already demonstrated an ability to discriminate different colours (Figure 1.9). Moreover, Cherry and Bennett (2001) demonstrated that most birds are sensitive to near-ultraviolet wavelengths, below 400 nm, to which humans can not access. Avilés and Møller (2003) and Honza et al. (2007a) reported that the green spectrum is important for egg mimcry and recognition in the interaction between obligate brood parasite and hosts, although there is no evidence of differences in egg colour matching in the UV reflection between accpeters and rejecters in some hosts of Brown-headed Cowbird (Underwood and Sealy 2008). In Meadow Pipit (*Anthus pratensis*) populations, Avilés and Møller (2003) found that intraclutch variation in poupulations allopatric with the Common Cuckoo was greater than in sympatric populations in egg appearance of the UV wavelenghths. Also, in Song Thrushes (*Turdus philomelos*) that lay bluish eggs, Honza et al. (2007a) reported that two colours of blue model eggs classified as mimetic eggs by human vision were rejected at a high rate; whereas most Song Thrushes accepted green model eggs that were non-mimetic (Honza et al. 2007a). These authors concluded that egg rejection by Song

Thrushes depended on the degree of mimicy in the UV and green parts of the spectrum. Host and cuckoo eggs, therefore, were not matched despite being classed as similar colours by human observers because birds perceive colouration of objects in different ways (Cuthill et al. 2000). Although model eggs matched blue host eggs closely within the realm of human vision (Figures 1.4 and 1.5 A), blue model eggs covered with acrylic paint may not be a good match when viewed by parrotbills within blue-green wavelengths. Nevertheless, previous experiments by Lee and Yoo (2004) and Kim (2006) were conducted using model eggs; high rejection of mimetic model eggs, thus, may indicate that model eggs did not match parrotbill eggs well at least in birds' vision sometimes in the UV wavelegnths. Therefore, in the present study, responses of hosts to real foreign eggs in relation to the degree of mimicry may account for Vinous-throated Parrotbills being able to discriminate accurately egg-colour differences between their own eggs and parasitic eggs in blue-green wavelengths, compared to other hosts in Europe and Africa. This might constrain female cuckoos that laid eggs in blue clutches of Vinous-throated Parrotbills to match hosts' eggs more precisely compared to hosts that lay eggs that are not blue, such as Great Reed Warblers and Reed Warblers. Blue eggs and polychromatism may contribute to the development of high-level egg discrimination in Vinous-throated Parrotbills.

CONCLUSIONS

Vinous-throated Parrotbills lay polychromatic eggs: blue, pale blue, or white. Egg colour of Common Cuckoo is blue and pale blue. The egg colour of the female parrotbill is inherent and uniform and a female thus lays the same colour eggs throughout her life.

Males on the other hand may change egg colour with each new partner. Both sexes rejected parasitic eggs of different colours from their own egg at a high frequency, suggesting parrotbills have the ability to discriminate their own and parasitic eggs. Hosts likely use differences in ground colour to discriminate between their own and parasistic eggs and ground colour may play a major role in coevolutionary interactions between Common Cuckoos and Vinous-throated Parrotbills.

CHAPTER 2. Egg-discrimination mechanisms in female and male Vinous-throated Parrotbills: a sex-specific strategy of egg recognition in a species that lays polychromatic eggs

INTRODUCTION

Avian brood parasitism imposes extreme fitness costs on many species of hosts (May and Robinson 1985, Lorenzana and Sealy 1999). This has promoted the evolution of defensive behaviours such as aggression towards adult brood parasites (e.g., Sealy et al. 1998, Bártol et al. 2002), chick discrimination (e.g., Langmore et al. 2003), and rejection of parasitic eggs (e.g., Rothstein 1990, Davies 2000). Egg rejection is an efficient anti-parasite strategy used by many hosts (Rothstein 1990, Davies 2000, Soler et al. 2002). Rothstein (1975, 1978) suggested three possible mechanisms of egg discrimination in host species: (1) by discordance, that is, hosts reject only "odd-looking" eggs in their clutches, (2) through learning based on an imprinting-like process on the host female's own eggs, and (3) by repeated episodes of learning during each successive breeding attempt. Results of previous studies have demonstrated that hosts reject parasitic eggs that differ from their own eggs by first learning features of their own eggs rather than those of the particular parasite (Victoria 1972; Rothstein 1974, 1975; Braa et al. 1992; Sealy and Bazin 1995) and the characteristics of hosts' own eggs were learned after laying their first clutches, through an imprinting-like process (Rothstein 1978; Lotem et al. 1992, 1995; Moksnes 1992; Lahti and Lahti 2002). Such imprinting would be costly for host females if their first nest is parasitized during the learning period, because this may lead to mis-imprinting on the parasitic egg-type and the female may accept the parasitic egg throughout her lifetime (Davies and Brooke 1988, Marchetti 2000). This cost will increase if the same individuals are parasitized repeatedly throughout their lifetimes under regimes of heavy parasitism. In a theoretical modeling study, Rodriguez-Gironés and Lotem (1999) suggested that the learning mechanism in hosts likely depends on the interaction between brood parasites and hosts. For example, in cowbird-host systems in which the parasitic eggs are not mimetic and parasitism frequencies are high, females might imprint on their first egg before being parasitized to avoid the cost of mis-imprinting (Davies 2000), whereas hosts should rely on an extended learning period when parasitism frequencies are low, as in many cuckoo-host systems, and intraclutch variation is high (Rodriguez-Gironés and Lotem 1999).

Host species may use various strategies to discriminate parasitic eggs. In recent Hauber et al. (2006) and Moskát and Hauber (2007) suggested a new idea, "phenotype distribution" in which rejection by hosts depends on a different memory template among individuals. Hosts of the Common Cuckoo, for example, the Great Reed Warbler, reject foreign eggs by memorizing the characteristics of their own eggs, therefore, hosts' repeated experience and memory would be crucial in decisions to reject a parasitic egg (Hauber et al. 2006, Honza et al. 2007b, Moskát and Hauber 2007). In other rejecter species, however, experience does not appear to influence the decision for egg rejection. Some hosts of cuckoos and cowbirds frequently reject parasitic eggs regardless of their age (e.g., Sealy and Bazin 1995, Sealy and Neudorf 1995, Amundsen et al. 2002, Stokke et al. 2004). Although the discrimination ability of hosts might be partly inherited (Rothstein 1974, Amundsen et al. 2002), the ability for counter-adaptation may be acquired by observational learning. Therefore, understanding the mechanism of learning in hosts is crucial to solving puzzles in coevolution between brood parasites and their hosts (Marchetti 2000, Moskát and Hauber 2007).

Despite several studies on the mechanisms of egg recognition in host species, egg discrimination by males has been overlooked for the most part. In most host species, only females eject parasitic eggs, perhaps not surprisingly, because females are responsible for incubation in many passerine species (Rothstein 1975, 1978; Davies and Brooke 1988; Lotem et al. 1992, 1995; Soler et al. 2002). If males, however, also incubate, they may be able to reject parasitic eggs given that they have opportunities to see their eggs during laying and incubation (Soler et al. 2002, Honza et al. 2007b). Indeed, males reject foreign eggs in some species where both sexes incubate: Reed Warbler (Davies and Brooke 1988), Blackcap (Soler et al. 2002, Honza et al. 2007b), sub-Alpine Warbler (*Sylvia cantillans*, Soler et al. 2002), Warbling Vireos (*Vireo gilvus*, Sealy 1996, Underwood and Sealy 2006), and Vinous-throated Parrotbill (Lee et al. 2005). Males of Baltimore Orioles (*Icterus galbula*, Sealy and Neudorf 1995) also reject foreign eggs even though they are not responsible for incubation. Defense by both sexes against parasitism is an effective strategy in the conflict between brood parasites and hosts because in such species, the rejecter trait may spread more rapidly than in host species where only females reject parasitic eggs (Rothstein 1975, Sealy and Neudorf 1995, Soler et al. 2002); this is obviously beneficial to hosts in an arms race with parasites.

The Vinous-throated Parrtobill lays immaculate polychromatic eggs with low intraclutch variation and both sexes frequently reject non-mimetic foreign eggs (Lee and Yoo 2004, Lee et al. 2005). In species with polychromatic eggs, females and males may have separately evolved egg-discrimination mechanisms because the sexes find themselves in different circumstances while nesting. Kim et al. (1995b) reported that when male parrotbills mate with different females, eggs tended by males sometimes change from white to blue because one female may have laid white eggs, whereas the male's next female may have laid blue ones. Females, on the other hand, always lay eggs of the same colour regardless of whether they changed their mates (Chapter 1). Males, therefore, may be confronted with differently coloured eggs during successive breeding attempts if they have a new breeding partner, whereas females see the same type of egg at every breeding attempt. Female parrotbills possibly learn their egg-type through imprinting on their first egg or all eggs in their first clutches, and then reject parasitic eggs on the basis of this experience. If, however, the male rejects the egg on the basis of memory or experience, he may later reject his own eggs when paired with a female that lays eggs of a different colour. Males therefore should not depend on previous experience and memory when they make egg-rejection decisions. To minimize the risk of rejecting their partner's eggs, male parrotbills may simply reject an "odd-looking" egg rather than through learning, or they may learn anew their mate's egg-type during every breeding attempt. The goal of this study was to determine whether egg discrimination by parrotbills is based on learning or discordance, and whether different strategies are adopted by males and females.

Hypothesis

Female and male parrotbills have different egg-discrimination mechanisms: (1) females learn their own eggs through an imprinting process, and then reject the foreign egg on the basis of memory, whereas (2) males reject parasitic eggs based on short-term learning of egg-types during every breeding attempt, or alternatively remove an odd-looking egg without the need for learning.

Prediction 1. If birds reject an odd-looking egg (discordance), rather than through learning, their own egg is rejected more frequently when the host's own egg is the odd one.

Prediction 2. Females reject foreign eggs regardless of whether they are in the majority or in the minority and regardless of the time that they are in contact with their own eggs.

Prediction 3. Males respond differently towards the foreign egg depending on whether the egg-type is in the majority or in the minority.

METHODS

Identification of parrotbill sex

Individuals were sexed by mist-netting and banding with numbered aluminum bands and colored plastic bands during breeding seasons (April to July) and wintering seasons (December to January) from 2004 to 2007. Since December 2004, 2,063 parrotbills (1,439 adults and 624 nestlings) have been marked in the study area. The sex of parrotbills captured during breeding seasons (between laying periods and early incubation) was confirmed by cloacal shape. Males have a cloacal protuberance, whereas female cloacae were dilated (Lake 1981): this is a clear and simple method during the breeding season to discriminate sex of parrotbills in this sexually monomorphic species (Lee et al. 2005). During winter, individuals caught were discriminated by molecular sexing from blood samples (Griffith et al. 1998). According to DNA-based sex identification by Griffith et al. (1998), when tested on a gel, males have a single CHD (chromo-helicase-DNA-binding) Z band, whereas there is a second distinctive CHD-W band in females.

Video-recording of colour-marked birds enabled me to determine which sex rejects eggs. Four digital video cameras (JVC GZ-MG70KR and Sony Handycam SR62) were operated continuously for 4 to 8 hours per day during laying and incubation until parrotbills ejected or accepted the experimental eggs. Video-recording took 1 to 5 days per nest depending on the bird's behaviour. With these cameras, I recorded continuously for 8 (high definition) to 30 (low definition) hours, and a battery lasted for 4.5 hours (JVC GZ-MG70) or 8 hours (Sony SR62); thus, I minimized disturbance at the nests. The cameras with tripods were concealed by camouflage covers with acrylic paint and by leaves (Figure 2.1) and were placed 3 to 12 m from the nest.

Experimental manipulation

To determine the mechanisms of egg recognition, I conducted an experiment using conspecific eggs of different colours at two groups of parrotbill nests. In one group, I introduced one foreign conspecific egg into each of 46 nests. In another group, I gradually switched entire host clutches, except for one egg, with foreign eggs throughout laying periods in 24 nests; thus, one host egg became the odd-looking one in the nest. Each nest was selected randomly.

Introduced conspecific eggs do not allow enough time to determine the rejection behaviour of both sexes because their thinner eggshells were punctured easily on the first attempt by the female or male. If the female started pecking the foreign egg, it was

Figure 2.1. Video-camera concealed by camouflage cover and leaves of bushes or shrubs.

removed from the nest before the male had taken his bout of incubation, thus, the male's response could not be determined. These results revealed the first sex, female or male, to reject the foreign egg(s) or host's own egg.

Experiment 1: Introduction of single conspecific egg

To investigate responses of parrotbills towards single foreign conspecific eggs, I switched one host egg with one foreign egg of a different colour during 2005 to 2007. Introduced single foreign eggs, thus, became the odd ones in host nests and hosts were exposed to their own eggs throughout the laying period. Sometimes no host eggs were removed. The number of host eggs does not influence rejection frequency of parasitic eggs (Davies and Brooke 1988, Sealy 1992) and in this study there is also no difference in rejection frequency between two groups irrespective of whether one host egg was removed ($n = 18$) or not ($n = 28$) (Fisher's exact test, $n = 46$, $p = 0.693$). The experimental nests were inspected every day for six days after artificial parasitism to determine host responses. If the foreign egg remained undamaged in the nests for six days, it was considered accepted. I considered the foreign egg rejected if it was removed and the rest of the clutch remained intact and tended by the adults, or the clutch was deserted without nest depredation.

Experiment 2: Switching complete clutches except for one host egg

In these experiments, each of the host's own eggs, except for one egg, was successively exchanged with a foreign conspecific egg throughout the laying period. Each experimental nest mainly consisted of 4 foreign eggs and one host egg, but sometimes 5 foreign eggs and one host egg depending on the hosts' original clutch size. I conducted two experiments (Experiment 2-1 and 2-2) to test the learning mechanism. First, to minimize opportunities that hosts are in contact with their own eggs, I switched each egg soon after it had been laid (between 0600 and 0900) with a foreign egg from the day that the first egg had been laid until the fourth day of egg laying (Experiment 2-1, *n* = 16 nests). Most parrotbills lay 5 eggs or 6 eggs, but sometimes 4 eggs were laid (see study species, Chapter 1). I visited each nest on the sixth day to confirm that the last eggs had been laid. If the host did not lay a fifth egg on the fifth morning (i.e., original clutch size is four), the host's last egg was returned that morning. If a sixth egg was laid the next morning, one host egg was exchanged with one foreign egg. Accordingly, one host egg was left on the day when the clutch was complete, thus becoming the odd one in its own nest. This manipulation allowed me to test whether parrotbills recognize their own egg-type. If they reject all foreign eggs except their own egg, despite minimizing opportunities of exposure to host's own eggs, they likely recognize their own egg-type and reject the eggs on the basis of memory. By contrast, if they reject only their own egg, they could be rejecting the odd-looking egg (i.e., by discordance) or alternatively falsely learning a foreign egg-type as their own throughout the laying period (see Rothstein 1975).

Second, I tested the hypothesis that hosts learn their own egg-type from only the first-laid egg to avoid falsely learning parasitic eggs (see review of Davies 2000). I checked daily host nests found during nest building. Once females laid their first egg, I left the first one in the nests and started switching on the morning the second egg had been laid in 2007 (Experiment 2-2, *n* = 8). All host eggs, except for the first egg, were switched with foreign eggs each morning until clutches were complete; thus, hosts were in contact with their first egg throughout the laying period although hosts were exposed to more foreign eggs. If learning occurred on the first day of egg laying, even if the foreign egg-type was in the majority, I expected that parrotbills would reject most or all foreign eggs and leave only their own egg in the nest in this experiment.

Parrotbill responses were either acceptance or rejection. If birds had not rejected any eggs during the first four days after clutch completion, the responses of hosts were recorded as acceptance. Rejection occurred if hosts ejected the eggs or deserted the nondepredated nest within four days after clutch completion; however, one nest in which rejection occurred after four days was included.

Sometimes the same pair member was found at experimental nests because parrotbills re-nested apart from the first nest if it had been depredated, or attempted a second brood after successful breeding within a breeding season (Kim 1998). Because parrotbills are not territorial, I could not predict owners of the experimental nests until the breeders were captured or video-recorded. To determine whether the same pairs were involved, at least one member of the pair was identified at 40% of 15 nests in 2005, 77% of 39 nests in 2006, and 89% of 46 nests in 2007, by filming and capturing individuals. Most pairs of parrotbills remain mated during the entire breeding season, including re-nesting attempts, but partners changed between breeding seasons (Kim 1998). To reduce the probability that the same breeders were tested twice between years, I changed the main experimental flocks for egg manipulations among years (2005-2007); however, occasionally the same individuals were found and all rejection responses by them were excluded. The data were included if some individuals showed no response for two years but foreign eggs were ejected by their different breeding partners from the previous year.

I occasionally used eggs of the unfertilized White-rumped Munia (*Lonchura striata var. domestica*) instead of white parrotbill eggs when white parrotbill eggs were unavailable during the switches involving conspecific eggs in 2006 and 2007 (frequency of white clutches was lower than blue clutches of parrotbills). White-rumped Munia eggs are similar to white parrotbill eggs in colouration (Figure 2.2) and size (15.84 x 11.94 ± 0.80 x 0.38 mm, $n = 71$ versus 15.91 x 12.85 ± 0.80 x 0.38 mm, $n = 73$ for parrotbills). To determine whether parrotbills that lay white clutches discriminate between munia eggs and their own eggs, munia eggs were introduced into four parrotbill nests with white eggs and all were accepted. Moreover, there were no significant differences in rejection frequency between white parrotbill eggs and munia eggs in experiment 1 (Fisher's exact test, $n = 46$, $p = 0.627$) and experiment 2 (Fisher's exact test, $n = 24$, $p = 0.375$).

Statistical analyses

Statistical tests were performed using SPSS, version 11.5 (SPSS, Chicago, Illinois). I used the binomial test (Zar 1999) to evaluate differences in rejection and acceptance of foreign conspecific eggs each year (2005-2007). To determine whether there are differences in responses of hosts among years, I used Chi-square tests and combined all data from three breeding seasons. Fisher's exact tests were used to compare differences in responses between females and males depending on the number of foreign eggs because of small sample sizes. The Mann-Whitney U test was used to compare the time to reject eggs between females and males. All tests were two-tailed with a level of significance of $p < 0.05$.

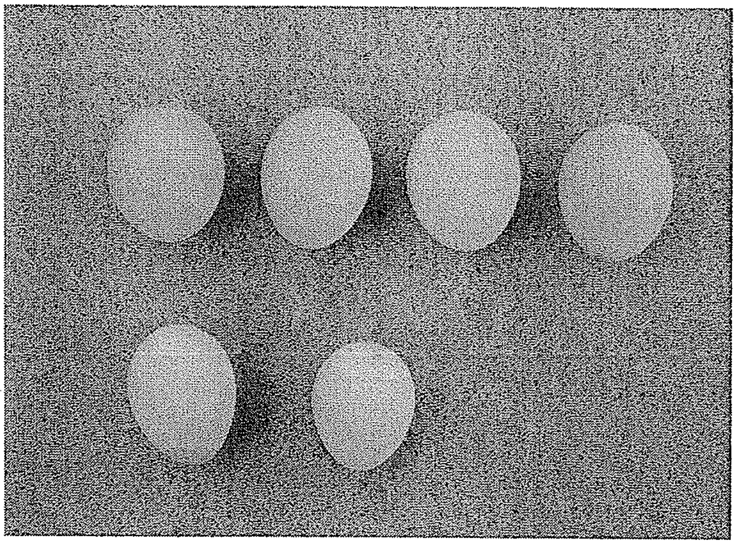


Figure 2.2. Comparison between four white eggs of Vinous-throated Parrotbills (top) from different clutches and two White-rumped Munia eggs (bottom).

RESULTS

Responses of parrotbills to foreign conspecific eggs

Ejection frequencies of single foreign eggs

Parrotbills rejected single foreign eggs in 9 of 10 nests in 2005, 18 of 23 nests in 2006, and 11 of 13 nests in 2007. There was no difference in rejection frequencies among years (Chi-square test, $\chi^2 = 0.719$, df = 2, $p = 0.698$), thus all data (2005-2007) were combined. Introduced conspecific eggs were ejected at a high rate (83%) and were accepted in 8 nests (17%) (Table 2.1).

Rejection frequencies of foreign eggs that are in the majority

There were no differences in responses by hosts whether they were exposed to their own single egg from the first day of laying, or only on the last day of laying (Fisher's exact test, $p = 0.853$). Of 24 nests, acceptance of all eggs was recorded at 13 nests (54%), whereas at 11 nests (46%), Vinous-throated Parrotbills ejected the foreign eggs or their own egg (Table 2.2). At 11 nests in which ejection occurred, in 7 nests parrotbills removed only the majority foreign eggs and then deserted their nests when the nest was left with only one host egg. In 4 nests, individuals rejected only single own eggs and incubated all foreign eggs, thus accepting the foreign eggs (Table 2.2). Rejection of majority foreign eggs occurred in the early stage of the nest cycle in Experiment 2-2, in which hosts were exposed to one egg of their own, but after clutch completion in Experiment 2-1. All own eggs were rejected after clutch completion in both manipulations (Table 2.3).

Table 2.1. Ejection frequencies of single foreign eggs by Vinous-throated Parrotbills.

Year	Nests parasitized	Acceptance	Ejection	% ejection	Binomial test
2005	10	1	9	90	$p < 0.05$
2006	23	5	18	78	$p < 0.05$
2007	13	2	11	85	$p < 0.05$
Total	46	8	38	83	$p < 0.001$

Table 2.2. Responses of the Vinous-throated Parrotbill to majority foreign eggs and to minority own eggs.

Treatment	Nests parasitized	Acceptance of all egg-types (%)	Ejection of	
			all foreign eggs (%)	one host egg (%)
Experiment 2-1[a]	16	9 (56%)	4 (25%)	3 (19%)
Experiment 2-2[b]	8	4 (50%)	3 (38%)	1 (12%)
Total	24	13 (54%)	7 (29%)	4 (17%)

[a] Experiment 2-1: time was minimized in which hosts were in contact with their own eggs before clutch was complete.

[b] Experiment 2-2: hosts were in contact with one of their own eggs from the first day of laying throughout the laying period.

Table 2.3. Timing of ejection of foreign eggs and own eggs in relation to exposure of single host's own eggs during the manipulation period.

Treatment	Egg-type rejection	Timing of rejection	
		During laying	After clutch completion
Experiment 2-1	Own egg	0	3
	Foreign egg	0	4
Experiment 2-2	Own egg	0	1
	Foreign egg	4	0

Sex difference in egg rejection

Responses to single foreign conspecific eggs by females and males: Experiment 1

To determine which sex rejects the foreign egg, egg-ejection by 21 individuals was video-recorded. Single foreign eggs were ejected by 15 females and by 6 males. It took females 2.2 days (SD = 1.05) and males 3.3 days (SD = 2.25) to reject the egg after experimental parasitism, although this difference is not statistically significant (Mann-Whitney U test, $z = -0.881$, $p = 0.378$).

Responses to foreign eggs of majority type by females and males: Experiment 2

Of 11 nests from which ejection occurred, responses of 6 parrotbills (2 females, 4 males) were video-recorded and the sex of 5 rejecters was not determined.

Except for one own-egg, foreign eggs were rejected by 2 females and one male and these rejections occurred during the laying period (Figure 2.3). Single own-eggs were rejected by 3 males (Figure 2.3) after full clutch completion.

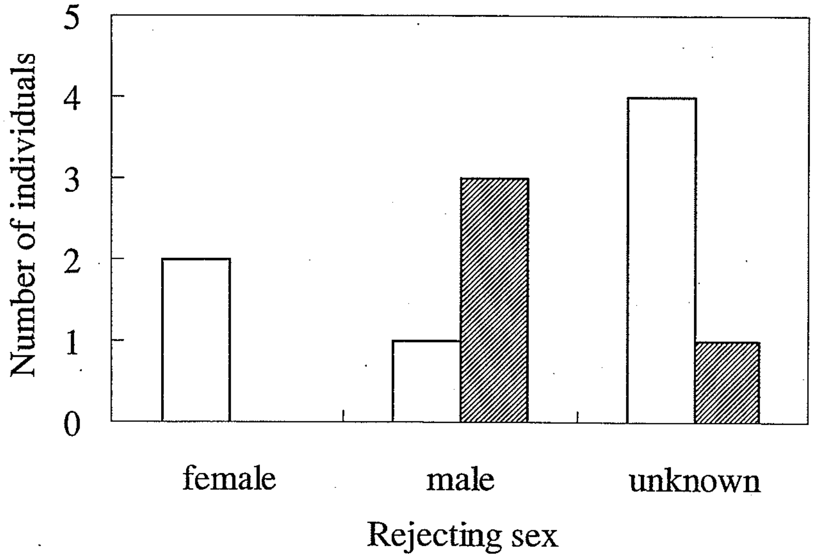


Figure 2.3. Ejection of foreign eggs and single own-eggs in relation to sex in Experiment 2 (□: foreign eggs, ▨: host's own egg).

Egg ejection by females and males in relation to the number of foreign eggs

Females consistently rejected only the foreign egg-type regardless of whether it was in the majority or minority (Table 2.4). By contrast, ejection by males changed depending on the number of foreign eggs (Table 2.4). Males ejected only the foreign egg-type when it was in the minority (Experiment 1); however, they ejected their own eggs more frequently than foreign eggs when the foreign egg-type was in the majority and when experience with their partner's eggs was minimized (Experiment 2). This difference in responses of males towards foreign eggs depending on different egg-manipulations was statistically significant (Fisher's exact test, $p = 0.033$).

Table 2.4. Ejection by female and male parrotbills of foreign conspecific egg(s) depending on whether the foreign egg(s) is in the minority or in the majority.

Sex	No. of foreign egg(s)	Ejection of foreign egg(s)	Ejection of Host's own egg(s)	Fisher's exact test
Female	Minority	15	0	$p = 1.000$
	Majority	2	0	
Male	Minority	6	0	$p = 0.033$
	Majority	1	3	

DISCUSSION

Sex-specific strategy of egg discrimination

Most parrotbills rejected single foreign conspecific eggs (Table 2.1), which suggests that they can detect the difference in colour between their own eggs and parasitic eggs. In Experiment 2, exchanging all host eggs except for one egg with different coloured conspecific eggs (i.e., 4 foreign eggs and 1 host egg), parrotbills behaved as predicted. They rejected foreign eggs that were in the majority but accepted their own egg, rejected only their own single egg, and accepted all foreign and their own eggs (Table 2.2), which indicates that there is more than one strategy of egg recognition within this population.

Which individuals reject only the majority foreign eggs?

Some individuals ejected all foreign eggs that were in the majority, which left the nests with only their own egg; these nests were then deserted, perhaps because the clutch volume had decreased too much (Sealy 1992). This response suggests that the birds already recognized their egg colour before the eggs were removed because experience with their own egg-type was interrupted by removing all their own eggs except for one egg from the nests soon after laying. Rejecters likely ejected the foreign eggs based on memory, which would be the case with experienced females. Although some species of birds rejected eggs at high frequencies apparently irrespective of their experience (Sealy and Bazin 1995, Sealy and Neudorf 1995, Amundsen et al. 2002), hosts' ability to discriminate parasitic eggs may be acquired by learning egg appearances (Moskát and Hauber 2007) and, indeed, results of several experiments have suggested that female hosts learn their own egg-type during laying of their first clutch (Rothstein 1978; Lotem et al. 1992, 1995; Moksnes 1992; Sealy and Bazin 1995; Lahti and Lahti 2002). In Experiment 2, although only a few rejections were filmed, I suggest that most of the foreign eggs were ejected by females because (1) females consistently rejected only the foreign egg(s), regardless of whether the foreign egg-type was in the majority or in the minority (Table 2.4), and (2) most foreign conspecific eggs were removed more frequently by females than males.

Results of other studies have revealed that females lay a constant egg type in Village Weaverbrids (Collias 1993), and Vinous-throated Parrotbills (Table 1.3 in Chapter 1; see also Kim et al. 1995). Such evidence that females experience eggs of the same type at their nests throughout their lifetime leads to the presumption that females do not have to learn their eggs repeatedly during every breeding attempt, although this learning might be reinforced during successive breeding seasons.

In host species with little intra-clutch variation and which are infrequently parasitized, learning through an imprinting-like process might be more beneficial than repeated learning (see Rodriguez-Gironés and Lotem 1999). Hosts laying uniform clutches probably can memorize their own egg-type more clearly and this may improve the host's ability to discriminate and reject parasitic eggs (Kilner 2006). In this context, I suggest that female parrotbills memorize the appearance of their eggs through learning when they lay their first clutch.

Who rejects the host's own egg?

Of 11 nests at which egg rejection occurred, in four nests only single own eggs were rejected and then the foreign eggs were incubated (Table 2.2). This behaviour was exhibited by three males and one individual of unknown sex. Moreover, male parrotbills ejected only the foreign egg-type when it was in the minority (Table 2.4), but ejected their own single egg more frequently than foreign eggs when the foreign eggs were in the majority (Table 2.4 and Figure 2.3). In other experiments, hosts adopt memory-based recognition when they reject the non-mimetic parasitic eggs (Rothstein 1975, 1978; Moksnes 1992; Sealy and Bazin 1995; Hauber et al. 2006; Moskát and Hauber 2007). Memory-based recognition, however, seems likely in females. In a host that lays polychromatic eggs, such as the Vinous-throated Parrotbill, however, males should not rely on memory or experience because the male's egg-type frequently changes depending on who his partner is each in breeding attempt (Table 1.4 in Chapter 1; see also Kim et al 1995). If males reject the egg on the basis of memory, they could err and eject their own eggs. To reduce the likelihood of mistakenly rejecting their new partner's egg, male parrotbills may simply reject only odd-looking eggs (i.e., discordance), or learn anew the egg-type during every breeding attempt. In an egg-manipulation of experiment involving eight species, Rensch (1925) reported that some Garden Warblers (*Sylvia borin*) rejected their own fourth egg that was in the minority and accepted three foreign eggs of Lesser Whitethroat (*Sylivia curruca*). He suggested that hosts may discriminate eggs by discordance in colour. However, Rothstein (1975) pointed out the other species' responses in Rensch's results, when reinterpreted, suggested that most birds recognize their own eggs and reject foreign eggs (i.e., true egg-recognition), rather than by discordance. If rejection is by discordance rather than learning, I expected that most parrotbills would reject their own single eggs when their own egg became the "odd-looking egg" (i.e., 4 foreign eggs and a single own-egg in the nest, Experiment 2). However, in Experiment 2, ejection frequency of an odd-looking egg was low (17%) compared to rejection (83%) in Experiment 1 when the host's own eggs were in the majority (i.e., 4 host's own eggs and one foreign egg in the nest).

In Experiment 1 where males could always see their partner's egg-type throughout the laying period, they "correctly" learned the type that was in the majority. Exchanging gradually all of the host's own eggs except for one egg with foreign eggs of different colour throughout the laying period, however, might lead males to falsely learn the pattern of the foreign eggs that was in the majority, and consequently eject one of their partner's eggs that were in the minority (see Rothstein 1975, 1978). This result suggests that male parrotbills discriminate foreign eggs by learning eggs of the majority type during the laying period and then rejected eggs, rather than by discordance. This mechanism likely enables males to discriminate non-mimetic real cuckoo eggs even though they learn anew their new partner's egg type. Unlike females, males may temporarily learn their partner's eggs to discriminate differences between eggs, and such learning adopted by males is re-established at every breeding attempt. Egg colour polymorphism seems to force a more complicated learning process.

Egg-discrimination mechanisms

In the case of egg recognition, imprinting might sometimes be costly if naïve breeders mis-imprint on the cuckoo egg-type when their nests were parasitized during the learning period, because they may accept cuckoo eggs over the rest of their lifetimes (Davies 2000, Marchetti 2000). To avoid this cost, hosts would imprint on only the first egg of the clutch before they are parasitized; however, if intraclutch variation is great, the female should learn her own eggs based on extensive learning but imprint on only her first egg (see Davies 2000). In the present study, Vinous-throated Parrotbills apparently did not learn only the first-laid egg. If Vinous-throated Parrotbills recognize their own egg-type by imprinting on the first-laid egg, I expected that when own eggs were present in the nest from the first day of egg-laying, rejection of foreign eggs would increase even though these were in the majority. However, host responses in nests where own single eggs were present in the nest from the first day of egg-laying were similar to responses in nests where own single eggs were present only on last day of laying (Table 2.2). This suggests that parrotbills learn to recognize their whole clutches rather than only their first egg, thus prolonging learning (see Lotem et al. 1995), and the laying period becomes very important for Vinous-throated Parrotbills to discriminate parasitic eggs.

Egg discrimination by both sexes and egg polymorphism of parrotbills may evolve as a defense against parasitism. Brood parasitism has been thought to exert strong selection on the appearance of host eggs, leading to great interclutch variation and little intraclutch variation to facilitate discrimination of parasitic eggs (Petrie and Møller 1991, Underwood and Sealy 2002, Kilner 2006). Such pressure may depend on the frequency of parasitism, conspecific or interspecific. Lyon (2003) quantified fitness costs of conspecific brood parasitism in the American Coot (*Fulica americana*), where such parasitism occurs commonly, and suggested that the high cost of parasitism by individuals of the same species promote the high-level discriminative ability of hosts. Collias (1993) proposed that selection pressure by both interspecific and conspecific parasitism influences egg recognition and egg polymorphism of weaverbirds. However, Øien et al. (1995) concluded that selection exerted by interspecific brood parasitism, such as in cuckoos, is considerably stronger than conspecific brood parasitism because parasite offspring in parasitism within a species is raised with host's chicks, whereas cuckoo chicks eject all the host's eggs and chicks, resulting in complete failure of the host's reproductive effort. Although conspecific parasitism reduces the total population production (Lyon 2003), raising chicks of a non-relative may be more costly. In addition, according to studies by Cruz and Wiley (1989) and Lahti (2005), cuckoo parasitism, rather than conspecific parasitism, exerts strong selection pressure on egg polymorphism and rejection of hosts. In the Village Weaverbird population that was introduced from Africa into Hispaniola and that was not parasitized for 200 years, weaverbirds accepted parasitic model or conspecific eggs of different colours, unlike the source populations of Africa (Cruz and Wiley 1989); interclutch variation and consistency in egg appearance within a clutch decreased (Lahti 2005).

Conspecific brood parasitism is present more frequently among precocial species than passerines (Yom-Tov 1980). Peer and Sealy (2000) found no evidence of conspecific brood parasitism in 797 Great-tailed Grackle (*Quiscalus mexicanus*) nests, and concluded that egg rejection has not evolved to counter adaptation against conspecific brood parasitism. In Vinous-throated Parrotbills, conspecific parasitism likely occurs rarely. Lee (2002) recorded intraspecific parasitism in only one of 190 parrotbill nests and in my study area I found conspecific parasitism in one of 272 nests studied in three breeding seasons. Therefore selection pressure by conspecific parasitism may exert little effect on evolution of egg polymorphism in parrotbills.

CONCLUSIONS

Vinous-throated Parrotbills can discriminate between their own and parasitic eggs and the ability may be acquired through learning. Single foreign eggs of different colour were rejected at a high frequency. When a foreign egg-type was in the majority, 54% of parrotbills accepted all egg types, some hosts rejected only foreign eggs (29%), and other hosts rejected only their own single eggs (17%). Host's own eggs were ejected by only males. Females rejected constantly only foreign eggs regardless of whether foreign eggs were in the minority or in the majority. However, males responded differently towards the foreign eggs depending on when the egg type was in the majority, or in the minority. Female parrotbills likely learn their own egg-type when they lay the first clutch and reject parasitic eggs based on previous experience. However, male parrotbills may reject parasitic eggs based on short-term learning of egg-type during every breeding attempt. Egg-colour polymorphism likely lead males to evolve a more complicated learning process.

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