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Egg Rejection by Both Male and Female Vinous-throated Parrotbills *Paradoxornis webbianus*

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Abstract: In bird species that suffer brood parasitism, the question about which sex is responsible for egg rejection has important implications for determining the coevolutionary relationship between brood parasites and their hosts. In order to determine which sex rejects a parasitic egg in vinous-throated parrotbills (*Paradoxornis webbianus*) which have egg color dimorphism, we conducted model egg experiments and video-recorded the behavior of the focal pair. Both sexes showed rejection behavior to the parasitic eggs. It indicates that the vinous-throated parrotbill may have a high rejection rate and faster spread of any rejection alleles through out populations. However, further studies are still needed to confirm the egg recognition mechanism in this species, which will expand our knowledge of the evolutionary relationship between host and parasite.

Key wards: Egg color dimorphism, egg recognition mechanism, model egg experiments, *Paradoxornis webbianus*, vinous-throated parrotbill

In a study of host defense against brood parasitism, which sex practices rejection behavior and the nature of the egg recognition mechanism play key roles in understanding the population genetics of the rejection trait and determining rejection rate of host populations (Rothstein 1975a; Sealy & Neudorf 1995). Several authors have suggested that only host females reject parasitic eggs (Rothstein 1975a; Lotem et al., 1992, Palomino et al., 1998). Some studies, however, provide instances of males showing rejection behavior to parasitic eggs in the same manner as females (Davies & Brooke 1988; Pinxten et al., 1991; Sealy & Neudorf 1995). Nonetheless, most hypotheses that explain egg recognition of the host species have been formulated based on female behavior only (Rothstein 1975a; Lotem et al., 1992). This might be because in most host species studied, the female alone carries out incubation, and the role of males has been overlooked.

The vinous-throated parrotbill (*Paradoxornis webbianus*), a common resident and general host of the cuckoo (*Cuculus canorus*) in Korea, shows egg color dimorphism: immaculate blue or white. So far, however, only blue cuckoo eggs mimicking the blue morph of the parrotbill have been recorded in the vinous-throated parrotbill gen. In addition, the cuckoo seems likely not to discriminate between the host egg colors when she parasitizes since the blue cuckoo eggs were found occasionally in nests with white parrotbill eggs. As a result, the discordance of egg colors between the cuckoo and the host would make it easier for the host to discriminate and reject the cuckoo eggs, which would lead to a high rejection rate in the host population (Lee & Yoo 2004).

The egg color trait is likely to be determined by the female only (Kim et al., 1995; Kim 1996). The female, therefore, has the same egg-color throughout life but the male has a possibility of exposure to eggs of different colors in each breeding attempt because he could mate with a female who lays different colored eggs in previous breeding seasons (Kim et al., 1995). Thus the male may have difficulty in recognizing the color of his own eggs. On the other hand, as the mating system of the vinous-throated parrotbill is monogamy, the male plays a role similar to the female throughout the breeding periods, from nest building and incubation to fledging (Kim 1998). So, these breeding behaviors are likely to give the male a chance to recognize and reject parasitic eggs. In this context, we carried out model egg experiments to reveal whether the male shows any rejection behaviors to parasitic eggs in the vinous-throated parrotbill, and suggested some considerations regarding the rejection behavior of the male.

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METHODS

The study was conducted during the breeding season of 2001 and 2005 at the man-made wetland in Sa-dong, Ansan-city, Gyonggi-province, Korea. Model eggs were placed in 132 nests for observation of rejection behavior to parasitic eggs in vinous-throated parrotbills (Lee & Yoo 2004; Kim, unpublished data). Ten out of the 132 nests, in which the sex of the individual ejecting the model egg was determined, were used for observation of which sex responds to the model egg. However, we excluded one nest from the results because the male of the nest responded sensitively to the video camera and didn't visit the nest during recording time. We used non-mimetic model eggs in the experiments in order to increase the rejection rate by the host (e.g. blue model egg for white egg nests of hosts and *vice versa*). The model eggs were made so that puncturing by the host was possible during ejection: models were made of plasticine, with a thin layer of plaster, covered with acrylic paint and coated with varnish to make them waterproof and have a glossy surface similar to that of natural eggs. Thus, the model eggs were similar to real cuckoo eggs in shape, size (22 mm × 17 mm) and weight (3.3 g). In order to observe host behavior, we conducted video recordings (Sony MC-1 video camera, Sony DSR-11 VTR and Sony DV 270 ME videotape). The camera was camouflaged, and the VTR was placed about 5 m away from the nest in order to minimize disturbance when we changed the videocassette tapes (usually every 4 h). The nests were recorded for at least 9 to 36 h until the model egg was ejected or damaged by the pairs. We could only identify the pairs at experimental nests after the onset of incubation; we could then catch, color-ring and sex the pair according to cloacal shape so that most experimental parasitism was carried out during the early incubation period. The experiments also occurred early in the morning so as to secure successive recording time even though brood parasitism in natural situations usually occurs in the late afternoon.

RESULTS AND DISCUSSION

Both males and females participated in egg rejection (Table 1) at 9 nests where the sex of rejecters was determined. Rejection by both sexes in this species implies that the probability of rejecting parasitic eggs is higher compared to species in which only females show rejection behavior (see Lee & Yoo 2004). Furthermore, one might assume that if rejection behavior is under genetic control, the velocity with which any rejection alleles spreads into populations would be faster in species in which both sexes have the ability to discriminate and reject parasitic eggs. The rejection behavior of the males in this species seems to be primarily related to species-specific ecological and life-history variables. For example, the male vinous-throated parrotbills, like females, participate in every breeding stage (Kim, 1998). The males frequently visited their nests during the laying period as well as the incubation period. During the laying period, both males and females visited their nest in turn; the duration of their visits usually lasted from about 5 min to more than 2 h per visit (personal observation). These situations will give males more chances to recognize their own eggs and to detect foreign eggs and the cuckoos themselves.

The ejection trials were onset after one or more incubation shifts even though most ejections (6/9) were confirmed on day 1. Below we describe the video recordings at one of those nests for the ejection behavior of the male.

We replaced a host egg with a model one at 09:30 on 17 May 2001 (Incubation onset day) at a nest that contained six host eggs. At 09:50 the male entered the nest. He initiated incubation after inspecting the nest contents, clinging to the nest edge, but he did not show any responses to the model, egg. At 11:27 the female took her turn in

Table 1. Experiments on rejection behavior against model eggs at 9 vinous-throated parrotbill nests where the sex of the rejecters was determined

Nests	Host egg color	Model egg color	Rejecter sex	Breeding stage[1]	Rejected within[2]	Year
A	Blue	White	Male	Incubation	1 day	2001
B	Blue	White	Male	Incubation	1 day	2001
C	White	Blue	Female	Laying	3 days	2001
D	Blue	White	Both	Incubation	1 day	2001
E	Blue	White	Male	Incubation	1 day	2001
F	Blue	White	Female	Incubation	1 day	2005
G	White	Blue	Both	Incubation	2 days	2005
H	White	Blue	Male	Incubation	2 days	2005
I	White	Blue	Both	Incubation	1 day	2005

[1]Breeding stage when experiments were conducted. [2]Day/s showing ejection behavior after model eggs were placed in the host nests.

incubating, but did not react to the model either. At 12:41 the male started incubation again. Nineteen min later, the male cautiously looked at the nest contents for approximately 2 min, but continued to incubate without further responses. At 15:30, after two incubation changes, the male returned to the nest; he began to peck the model. He pecked the model vigorously for 2-3 min and paused to take a rest for approximately 5 min. He then pecked the model again for 2-3 min. He repeated this behavior until the female took charge of incubation. At 17:00 the female entered the nest and incubated the clutch, but still did not respond to the model. At 18:01 incubation was taken over by the male again. As soon as the male entered the nest, he vigorously pecked the model, clinging to the nest edge and repeated the behavior described above. How the male vinous-throated parrotbills discriminate parasitic eggs is still open to question. The most well-known hypothesis about the mechanism for egg recognition is that the host species uses true egg recognition based on an imprinting-like (learning) process during the first breeding attempt (Rothstein 1974, 1975b, 1978; Lotem et al., 1992, 1995). These studies, however, did not include the case of the male in generalizing the hypothesis, though males of some species discriminate and reject parasitic eggs (Davies & Brooke 1988; Pinxten et al., 1991; Sealy & Neudorf 1995). If this mechanism occurs in male vinous-throated parrotbills, a male parrotbill that first mates with a female laying blue eggs will recognize blue eggs as his own through an imprinting-like learning process; however, if in the following breeding attempt he breeds with a female that lays white eggs, then he may be thrown into confusion because the two egg colors are so remarkably different that he is less likely to accept white eggs as his own. Therefore, it seems unlikely that the male vinous-throated parrotbills discriminated and rejected model eggs based on true egg recognition as described above. Furthermore, there are no records of males ejecting their own eggs through recognition error. This suggests that the male parrotbills recognize both colors as their own egg colors. Therefore, we should consider other mechanisms for rejection behavior in male vinous-throated parrotbills, such as successive learning processes or rejection via discordant, rather than true egg recognition during their first breeding attempts. Egg recognition mechanisms could be one of the main factors explaining variation of rejection rate among species and populations within the same species (e.g. evolutionary equilibrium hypothesis; Lotem et al., 1992). Therefore, determining the egg recognition mechanism of males is crucial to broadening our understanding of coevolutionary relationships between hosts and parasites. For that reason, more detailed experiments are needed in order to understand the egg recognition mechanism of male passerine birds such as vinous-throated parrotbill.

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