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Editorial

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Personality, recognition cues, and nest sanitation in obligate avian brood parasitism: what do we know and what comes next?

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Obligate avian brood parasitism (ABP) refers to a special kind of breeding strategy observed in birds in which some species (parasites) do not invest parental care in their offspring but rather impose this duty on other species (hosts; Soler 2014). Such special breeding behavior has received attention since ancient times. For example, "The Book of Poetry" (11th–6th century B.C.) recorded the parasitic behavior of cuckoos in China. Only ~1% of bird species have evolved to engage in such behavior, and the cost incurred by the hosts has triggered a variety of anti-parasitic defenses in the latter (Yang et al. 2019), leading to textbook coevolution between parasitic and anti-parasitic adaptations between the parasites and hosts (Davies 2011). Both the parasitic and anti-parasitic behaviors vary across species, populations, and individuals (Davies 2000; Yang et al. 2010; 2015a, 2015b, 2015c, 2015d), and they change over time and individual age, experience (Moksnes et al. 1993, 2000; Moskát et al. 2014), and possibly personality (Avilés and Parejo 2011). Although ABP has been the subject of numerous studies since Darwin's time, the personalities of the parasites and hosts have not been taken into account much in previous studies. As to the recognition cues, which are used by the hosts to discriminate parasites, have received more studies, but mostly focused on egg recognition that there is still a dearth of exploration to the nestling recognition (Wang et al. 2020). Furthermore, nest sanitation, a behavior that is similar in pattern to egg rejection, was proposed to be a pre-adaptation of the latter in hosts (Rothstein 1975); however, the conclusions from previous studies were mixed. In this special column of *Current Zoology*, we provide empirical data and theoretical discussion of these research topics. Here I provide a brief introduction of the articles in this special column, and encourage future studies by providing perspective on some research gaps.

Personality in ABP

Personality, which was once defined as existing solely in humans, is a characteristic way of thinking, feeling, and behaving that distinguishes one person from another (Goldberg 1990). In the late 1930s, the concepts of personality were expanded to animals, and studies of the concept became more frequent alongside recent trends in ecology and behavioral and evolutionary biology (Gosling 2001). Animal personality is now defined as inter-individual differences in behavior that are consistent across different contexts within a certain time (Kaiser and Müller 2021). Personality is quite widespread in the animal kingdom, not only in vertebrates (Gosling 2001) but also in invertebrates (Kralj-Fišer and Schuett 2014). Personality has been hypothesized to influence the anti-parasitic defenses in hosts (Avilés and Parejo 2011), but empirical studies have been rare. Trnka and Grim (2014) tested the association between aggressiveness and egg rejection in great reed warblers *Acrocephalus arundinaceus* but found negative results. However, Zhang et al. (2021) showed that fast-exploring and less neophobic individuals of species Daurian redstart *Phoenicurus auroreus* were more likely to reject parasitic eggs. Personality is one of the most significant gaps in research into ABP. In this special column, the study "Personality of hosts and their brood parasites" by Møller and Si (2021) used meta-analyses on all 98 host species of common cuckoo *Cuculus canorus* and found that different aspects of behavior displayed by host birds during escape and subsequent handling as reflected by tonic immobility were related to the rate of rejection of cuckoo eggs. Factors such as individual physiological states such as hormone levels are important mediators of animal behavior, including personality. Another study published in this special column by Ruiz-Raya (2021) pointed out the potential role of oxidative stress, immunological state, and developmental stressors in hosts' rate of egg rejection and proposed new hypotheses that could stimulate future research into behavioral host responses toward brood parasitism. Additionally, Yang et al. (2021) investigated the coevolutionary interaction between Himalayan cuckoos *Cuculus saturatus* and 2 sympatric and closely related potential hosts belongs to the family Pycnonotidae, the brown-breasted bulbul *Pycnonotus xanthorrhous* and the collored finchbill *Spizixos semitorques*. This study illustrated that the

bulbuls selected specific nest sites that were further away from forests than those of finchbills, and they behaved more aggressively toward cuckoos than finchbills. These favor them to escape parasitism from Himalayan cuckoos.

Egg/Nestling Recognition Cues

Whereas many previous studies have investigated the cues for parasite egg recognition by hosts, nestling recognition cues have received much less attention, probably because nestling recognition per se is a rare host defense strategy against brood parasites (Grim et al. 2003). In recent years, studies of revealing nestling recognition in hosts are increasing (Yang et al. 2015a, 2015b, 2015c, 2015d; Huo et al. 2018; Noh et al. 2018). However, the recognition cues of nestlings were unclear for the most part. In previous studies, Colombelli-Negrel et al. (2012) found that superb fairy-wrens *Malurus cyaneus* used vocal signature as a cue to distinguish between Horsfield's bronze-cuckoo *Chalcites basalis* and their own nestlings. However, the largebilled gerygone *Gerygone magnirostris* recognized bronze-cuckoo *Chalcites minutillus* nestlings by the number of hatchling down-feathers as a visual cue (Noh et al. 2018). In this special column, Hanley et al. (2021) analyzed 23 eggshell reflectance data from 84 host species, and demonstrated that the cowbird *Molothrus ater* eggshell phenotypes were better predicted by hosts that rejected (i.e., that select) than hosts that accepted their eggs (i.e., do not select). These findings suggest that diffuse coevolution may select for unique eggshell phenotypes in distinct cowbird populations, and potentially other generic and specialist populations. Furthermore, Attisano et al. (2021) found that the fantailed gerygone *Gerygone flavolateralis*, a host of lacking recognition on cuckoo eggs, frequently rejected nestlings with lacked down feathers. Another study on nestling recognition by Noh et al. (2021) indicated that the large-billed greygone *G. magnirostris*, a primary host of little bronze-cuckoo *C. minutillus*, may use begging call structure as a cue for nestling recognition that selects for age-specific vocal mimicry in cuckoo nestlings.

Nest Sanitation as a Pre-adaptation of Egg Rejection

Nest sanitation refers to the removal of a variety of non-egg objects from nests such as dropping egg shells, vegetation, fecal sacs, invertebrate parasites, occasionally dead nestlings, and unhatched eggs by parents; therefore, its behavioral pattern is similar to that of egg ejection (Guigueno and Sealy 2012; Yang et al. 2015a, 2015b, 2015c, 2015d). Nest sanitation has been hypothesized to constitute the ancestral state of egg rejection behavior because nest sanitation is ubiquitous, whereas egg rejection is not (Rothstein 1975). However, previous studies gave mixed conclusions, with some studies found supporting evidence (Yang et al. 2015a, 2015b, 2015c, 2015d; Feng et al. 2019) whereas the other did not (Luro and Hauber 2017; Peer 2017; Su et al. 2018). In this special column, Stratton and Dearborn (2021) associated the behaviors of nest sanitation with egg rejection in herring gulls *Larus argentatus* but found no support for the nest sanitation hypothesis, whereas Li et al. (2021) conducted meta-analyses of previous studies on the relationship between these 2 behaviors and showed that the rejection frequency of nest sanitation was consistently higher than the frequency of egg rejection across different host species or populations. This result suggests that nest sanitation, which is an ancient behavior, is more fundamental than egg rejection, but the effect of the former on the latter is complex and needs further study.

Perspective

To the best of our knowledge, few studies have investigated the effects of personality in ABP. The nestling recognition cues by hosts also receive insufficient studies whereas the role of nest sanitation in egg rejection is largely unclear. Based on this situation, there are several factors recommended for future studies. (1) Whereas the role of personality on egg rejection behavior of hosts needs further study, there are almost no studies of other anti-parasitic defenses such as nesting preference, nest defense, and chick recognition, and these matters merit attention. Anti-parasitic defenses at different stages may exhibit consistent or contrary responses related to personality, depending on different properties of the defenses themselves and the interaction between them. These factors need to be taken into account. (2) Whereas some attention has been paid to the personalities of the hosts, there have been far fewer studies of the personalities of the parasites. These are challenging to perform because their parasitic behaviors are cryptic and difficult to observe and monitor. However, studying parasites' personalities, as related to parasitic behaviors, would help us understand the coevolution of personality between parasites and hosts. Attention should be paid to the association between parasites' personalities and their behaviors during parasitism, such as perching preference, egg-laying time, destructive behavior against hosts' eggs, and response toward hosts' aggression. (3) These suggestions deal with adults among both hosts and parasites, but the nestlings should also be considered in future studies. For the parasite nestlings, we could investigate the effects of personality on their eviction and killing behaviors toward host nestlings, or competitive behavior such as begging calls. For the host nestlings, we could also survey the effect of personality on begging calls, especially among species that are parasitized by noneviction parasites. The reaction of nestlings to parental alarm is also a valuable factor that may be associated with personality in both parasites and hosts. (4) Animal personality includes a variety of behavioral traits such as activity, aggressiveness, boldness, sociability, neophobia, and exploratory behavior. These behavioral traits of personality may be correlated, and they may interact and act as an integral whole. Studying personality in ABP above should take as many of these traits and their interactions as possible into account for analyses. (5) Animal personality is closely related to such physiological factors like hormones, and thus, the latter should be taken into consideration during future studies of personality in ABP. (6) A combined approach of integrating visual, acounstic, and olfactory signal is needed to better reveal the recognition cues of nestlings in hosts. Elucidating nestling recognition and its cues in hosts would help us better understand the whole picture of coevolution between brood parasites and hosts. (7) Finally, a standardized methodology, such as 3D printing, is suggested to investigate the association between nest sanitation and egg rejection in hosts. This would increase the comparability and reliability for further meta-analyses across different species and populations.

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