



Editorial: Evolution and Function of Acoustic and Visual Signals in Avian Brood Parasitism

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Editorial on the Research Topic

Evolution and Function of Acoustic and Visual Signals in Avian Brood Parasitism

Avian obligate brood parasites lay eggs in other birds' nests, leaving the host to care for the parasitic young (Soler, 2014). To be successful, parasites must have the ability to evade the frontline defenses and deposit their egg in the host nest, the eggs must be accepted by hosts, and once they hatch, their offspring must elicit provisioning from the host to obtain food and survive until their independence (Davies, 2011). During these stages, the parasites may display acoustic and visual signals which may play a key role to trick, manipulate, or circumvent the hosts defenses and, in response, the hosts may discriminate, reject, or deter the parasitism event. There are numerous examples of these signals in the literature, from host vocalizations serving to recruit conspecifics to repel brood parasites *via* enhanced nest defenses; parasitic chicks producing vocal and acoustic signals during the begging display which tap into host parent-offspring communication pathways; and hosts using these clues to reject parasitic eggs or chicks. These events form a classic coevolutionary process (Davies, 2000; Yang et al., 2019). During these coevolutionary events, brood parasites may evolve visual mimicry of host eggs (e.g., Moksnes and Røskft, 1995; Spottiswoode et al., 2011), nestlings (e.g., Langmore et al., 2003; Tanaka and Ueda, 2005), as well as acoustic mimicry of host begging calls (Ursino et al., 2018; Wang et al., 2020; Lama et al., 2022).

Although visual signaling between brood parasites and their hosts has been studied extensively (Davies, 2011; Soler, 2014), less attention has been paid to the coevolution of acoustic signals between brood parasites and their hosts (Wang et al., 2020). As such, this Research Topic fills an important gap in understanding the evolution of adaptations related to visual and acoustic signals between brood parasites and their hosts, which is needed for a complete understanding of how visual and acoustic signals are used in these systems. Here, we provide an overview of this Research Topic and indicate how recent papers on the subject have advanced our understanding of this aspect of brood parasite-host coevolution.

When confronted with a parasitic egg in the nest, egg rejection is the most common host defense and it is generally achieved using visual signals (Spottiswoode and Stevens, 2010; Hanley et al., 2019). The seminal studies on egg rejection behavior demonstrated that hosts utilize the perceivable differences between their own eggs and those of the parasite to recognize the foreign eggs (Rothstein, 1975, 1982). In this section, four of the five papers have focused on the proximate mechanisms of egg rejection. Hanley et al. advocate for using a receptor noise-limited model as a null model for understanding the proximate mechanisms hosts use when deciding to reject foreign eggs in an

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attempt to explain why some hosts appear to make counterintuitive choices. Samaš et al. conducted a meta-analysis of avian egg traits that cue the rejection of brood parasitic eggs and found that hosts rely primarily on eggshell color traits and maculation patterns. Molina-Morales et al. investigated intra-clutch egg variation and egg rejection in the magpie (*Pica pica*), a host of great spotted cuckoo (*Clamator glandarius*), and showed that low intra-clutch variation in the blue-green coloration at the middle region of the eggs was associated with an increased chance of rejection. Weaverbirds are known for their egg variation and Lahti examined the eggs and rejection behavior of the little-known Rüppell's weaver (*Ploceus galbula*), a host of the diderik cuckoo (*Chrysococcyx caprius*; Lahti). He found that weavers used three features to recognize foreign eggs: the brightness of ground color, the brightness of spots, and the spotting pattern at the broad end of eggs. These results suggest this host uses brightness rather than the more distinctive chromatic variation to recognize eggs because of the importance of achromatic contrast in dark enclosed nests. In contrast to studies of common hosts mentioned above, Abernathy et al. examined the red wattlebird (*Anthochaera carunculata*), a host that has been parasitized by the Pacific koel (*Eudynamis orientalis*) in Australia for a relatively short period of time. This host rarely rejected foreign eggs, but populations subjected to higher parasitism rates responded aggressively toward koel mounts indicating the importance of frontline defenses in newly exposed host populations. Collectively, these studies demonstrate that there is no single, universal approach used by all hosts when it comes to the recognition of parasitic eggs, and that different selection pressures can result in the same adaptive behavior by hosts.

Nest desertion is another form of parasitic egg rejection and the only brood parasite host that routinely rejects parasitism by burying parasitic eggs is the yellow warbler (*Setophaga petechia*), a host of the brown-headed cowbird (*Molothrus ater*) (Sealy, 1995). Turcotte-Van De Rydt et al. compared the circulating corticosterone levels in yellow warblers that accepted cowbird eggs to those that deserted clutches and found corticosterone was higher in females who abandoned clutches. Hosts can also defend their nests against parasitism by attacking and mobbing adult parasites (Welbergen and Davies, 2009; Yang et al., 2021), and Tolman et al. showed that a common host like the reed warbler (*Acrocephalus scirpaceus*) does not fine tune its mobbing of cuckoos as the risk of parasitism changes seasonally. In response to these host attacks, some species of cuckoos have evolved to resemble hawks (Davies and Welbergen, 2008) and Go et al. quantified the hawk-like features in four sympatric *Cuculus* cuckoos, finding these traits were widespread in the cuckoos although features varied across species. York reviewed studies to explore the adaptive basis of predator resemblance in avian brood parasites and natural variation in host responses to these stimuli. The author suggested that different modalities of information can have independent effects on hosts and that predator resemblance takes advantage of multiple sensory and cognitive processes (York).

In addition to visual signals, acoustic signals can play an important role in the interaction between brood parasites and

hosts (Wang et al., 2020). For hosts, referential alarm calls may encode information to indicate a variety of threats including brood parasites (Bártol et al., 2002; Yang et al., 2014). The yellow warbler emits a "seet" alarm call that serves as a signal to conspecifics that a cowbird is near the nest (Gill and Sealy, 2004; Kuehn et al., 2015). Lawson et al. found that the red-winged blackbird (*Agelaius phoeniceus*) eavesdropped on warbler seet calls and mediated its nest defense based on these alarms and cowbird chatter calls when the risk of parasitism was lower during the nestling stage. Wang J. et al. compared defenses of the Oriental reed warbler (*A. orientalis*) over the nest cycle and in contrast, found no evidence that the alarm calls provided specific information regarding the threat of brood parasitism. Surprisingly, the behavioral response of hosts was stronger in the nestling stage than in the egg stage, which supports the offspring value hypothesis and suggests that cuckoos may act as nest predators.

Some brood parasites have evolved mimetic acoustic signals. Adult male indigobirds (*Vidua* spp.) mimic songs and other vocalizations of their respective hosts. DaCosta and Sorenson examined variation within and among indigobird species in the non-mimetic components of their vocal behavior and found strong species effects for the non-mimetic vocalizations, which may due to phenotypic plasticity, genetic divergence for speciation, or both. Cuckoos also mimic hawks acoustically by producing "bubbling" calls that distract hosts and reduces the likelihood of egg rejection in some populations (York and Davies, 2017). However, Wang Y. et al. found no evidence that these calls affected host response and was insufficient for suppressing bird activities. Unlike female cuckoo vocalizations, male cuckoo calls do not have any apparent role in countering host defenses and instead are sexually selected (Moskát et al., 2017; Moskát and Hauber, 2022). Esposito et al. analyzed acoustic variables and visual display sequences of male common cuckoos to determine whether these signals are multimodal by nature and complement one another as is known to occur in other brood parasites (O'Loughlen and Rothstein, 2010). They found significant variation among calls, but the vocal displays were not associated with visual displays; males either vocalized and remained motionless or displayed visually without vocalizing (Esposito et al.).

Parasitic nestlings must also tap into the host parent-offspring communication system to receive food (Anderson et al., 2009). Nonetheless, Crudele et al. found that shiny cowbird (*M. bonariensis*) chicks reared by the chalk-browed mockingbird (*Mimus saturninus*) begged more intensively to playbacks of conspecific chatter calls than to host calls, while those reared by the house wren (*Troglodytes aedon*) begged with a similar intensity to the two playbacks. This indicates that the shiny cowbirds exhibited preferential begging responses to the conspecific chatter call. Finally, Rojas-Ripari et al. reviewed how parasitic young are able to manipulate hosts to stimulate parental feeding and escape host discrimination. They focused on host chick mimicry, exaggerated begging, host-attuned begging signals, and sensory exploitation. They stressed the importance of considering these adaptations from the host's perspective using experimental manipulations.

The 16 papers in this Research Topic illustrate the diversity of visual and acoustic signals and how the selection pressures imposed by avian brood parasitism may underlie the evolution of them. Many of the contributed papers explore visual signals and show the major advances in the field over the past several decades ranging from the conceptual development of signals during the first line of defense, to egg rejection and begging displays. There is increasingly more work being done on acoustic signals, such as host alarm or mobbing calls toward parasites, and vocal mimicry by parasite adults and chicks. However, the Research Topic also revealed several gaps in our knowledge, which bring the following questions for further studies. (1) What is the stimuli that brood parasites use to recognize conspecifics once they leave host nests? (2) Do the nestling calls of parasites show specific adaptation to their host species or populations? (3) What additional proximate cues do hosts use to reject foreign eggs (4) What are the proximate cues used in the rare cases where hosts discriminate against parasitic nestlings? (5) Does the recognition threshold varies with parasitism pressure in different host populations? (6) Is there a difference between parasites that used visual or acoustical

signals to mimic hosts? (7) Is there a negative relationship between acoustic and visual signals? (8) How does auditory perception influence acoustic signals in parasite-host systems? These questions provide new directions and challenges for future research. Overall, we hope that this issue will serve to encourage further studies, which in the end will enhance our understanding of the coevolutionary process of the visual and acoustic signals in parasite-host systems.

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CY drafted the manuscript. BP, CU, JY, and JR improved the manuscript. All authors contributed to the article and approved the submitted version.

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