

BROOD PARASITISM AND MIMICRY AS A FORM OF COEVOLUTION

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Introduction

Coevolution is a reciprocal genetic change in one species in response to a genetic change in another species. The reciprocal changes seen in avian brood parasite systems make them optimal for studying coevolution. In brood parasitism, the parasite lays eggs in the nest of an unrelated host. If parasitism is successful, the parasite's offspring receives parental care from the host, crucial to its survival. Three general long-term outcomes of host-brood parasite interactions have been identified: lack of rejection by hosts, successful resistance by hosts, and coevolutionary cycles (Soler, 2014). Lack of rejection results when a parasite is able to invade a nest despite lacking any sort of resemblance to the host in either the egg or nestling forms. Here the hosts lack the ability to recognize their own eggs or young. As a result, these hosts cannot develop defenses in response to parasitism and will not reject eggs or young from the nest. Successful resistance results when hosts evolve recognition to a level where they can reject nearly all parasites, successfully preventing exploitation. This outcome is difficult to reach because recognition is typically costly, leading us to the possibility of coevolutionary cycles (Soler, 2014). To understand coevolutionary cycles, first we must understand coevolution between a pair of species.

To be classified as antagonistic coevolution, both parties must demonstrate reciprocal changes in response to fitness costs caused by each other. In response to fitness costs from parasite, hosts may evolve recognition that allows them to distinguish their eggs or youth from parasites. Hosts with the ability can then reject parasites from the nest, creating fitness costs for the parasites. As a result, parasites have evolved mimicry, a method to imitate the host's egg or

young. Rejection ability in hosts requires the parasite to become a more effective mimic in order to remain in its host's nest. These reciprocal changes suggest coevolution is occurring, and many studies provide evidence that changes are actually reciprocal. Because avian parasite-host systems often involve hosts that are parasitized by a single parasite, they are ideal for this study (Rothstein, 1990). Parasites and hosts are in direct interaction, giving us the opportunity to observe direct fitness costs through host rejections and parasite success.

Evolutionary theory by Nuismer and Thompson takes coevolution one step further, suggesting that coevolution occurs not only within pairs of species, but within networks of species as well (2006). When multiple species are involved, Thompson states that natural selection will favor individual parasites that prefer the currently least defended host species. His next idea is that coevolutionary cycles may result where parasites will change from a highly defended host species to a host with poorer defenses, only for defenses to improve in the new host after a period of time. In theory, the old host is predicted to lose defenses when it is no longer parasitized, making it a viable host again in the future once it becomes easier to parasitize (Soler, 2014). Although the theory has support through modeling, it is difficult to prove how these cycles really work and whether they are common in the case of cuckoo brood parasitism. Only a minuscule portion of the cuckoo's vast history on Earth has been observed, leaving many questions open to discussion. Various examples of brood parasite systems at differing life cycle stages exist to provide evidence of coevolution occurring today, however more research is required to fully understand why parasites choose certain hosts and how coevolutionary cycles might play a role.

Brood parasite systems

The common cuckoo, *Cuculus canorus*, is one of the greatest examples of a host-parasite coevolutionary system. Female cuckoos lay colored eggs that match the color of a given host, except in cases where the host is unable to distinguish its own eggs from those of other species. As a species, cuckoos have a number of different hosts, such as in Britain where five hosts are commonly exploited: meadow pipits, reed warblers, dunnocks, robins, and pied wagtails (de L. Brooke & Davies, 1988). Individual females favor one host species and are specialized at mimicking the color of that species' egg. Eggs of certain cuckoos have been observed to be more accurate mimetically than eggs of cuckoos that target different hosts. As de L. Brooke and Davies demonstrate in their experiment, some hosts are more adept at discriminating between their own eggs and mimics. When host species are more discriminating, cuckoos tend to lay more accurate mimetic eggs. In some cases like the dunnock, eggs do not mimic the host at all, likely due to inability of the host to discriminate. To test their hypothesis that mimicry is maintained when hosts reject unlike eggs, they experimentally placed model eggs representing different species into host nests. Indeed, dunnocks were found to not reject unlike eggs from their nest. Great reed warblers (a central European host tested along with the British hosts), meadow pipits, and reed warblers rejected unlike models while accepting models that mimicked their own species (see Figure 1). Selection acts on the host to discriminate mimetic eggs, which then leads to selection on the mimic to lay more accurate eggs capable of fooling the host, setting the stage for a coevolutionary arms race.

Table 2 The proportion of nests at which various types of model cuckoo eggs (Fig. 1) were rejected by hosts

Host	Proportion of nests where model cuckoo egg rejected					Significance of difference	Numbers of rejections by		
	Pied wagtail type	Redstart type	Reed warbler type	Meadow pipit type	Great reed warbler type		Ejection	Desertion	Other
Robin	2/7	1/7	—	2/11	—	NS	2	3	—
Pied wagtail	7/14*	10/13	5/7	12/18	—	NS	12	21	1§
Dunnoek	0/7	0/5*	0/4	1/6	—	NS	—	1	—
Reed warbler	13/16	17/28	0/19*	4/11	—	$P < 0.001$ †	16	7	11
Meadow pipit	9/25	15/18	4/15	6/27*	—	$P < 0.001$ †	5	29	—
Great reed warbler	—	5/5	—	1/2	1/5*	$P = 0.024$ ‡	6	1	—

Experiments were done in Cambridgeshire (reed warbler, robin, dunnoek), mostly on Derbyshire moorland (meadow pipit), all over Britain (pied wagtail) and in Burgenland, eastern Austria (great reed warbler). NS, not significant.

* Model cuckoo eggs mimicking the host eggs. † χ^2 test, 3 d.f. ‡ Fisher-exact test, excluding meadow pipit treatment.

§ Built new nest on top of parasitized clutch ('built over'). || 2 built over, at 9 nests birds were seen pecking at model[§].

Figure 1. Data from de L. Brooke and Davies 1998 experiment

For coevolution to occur, there is typically a fitness cost to the host associated with parasitism by the mimic. Fitness losses are a typically a result of parasites removing or destroying host eggs from nests, removing or killing host young, or outcompeting host young (De Mársico, Gantchoff, & Reboreda, 2012). When parasites engage in this activity, all of the host's offspring are typically targeted, creating large fitness costs for the host (Rothstein, 1990). The large costs result in strong selective pressure on the hosts to evolve adaptations to recognize parasites and reject them (Soler, 2014). As more parasites are rejected, they evolve counter-adaptations to avoid rejection. This is evident through the above study of common cuckoo, where we can see that mimetic accuracy improves when hosts become better discriminators. When hosts have the upper hand, the selective pressure then falls on the mimics to evolve closer imitations that can fool the host. Although the mimicry of eggs is the most commonly studied form of mimicry, studies have also shown that mimicry occurs at different stages of the life cycle.

Recent study by Langmore et al. provides evidence that coevolution may exist beyond the egg stage and into the nestling stage. This was previously thought to be maladaptive due to the mechanism that hosts of *C. canorus* use to recognize their own eggs. Studies have shown that birds recognize eggs through an imprinting process where they remember their own egg type

during the first time they lay eggs, and they will reject different egg types in future breeding attempts (Lotem, 1993). Lotem proposes that this mechanism would be maladaptive if used for nestlings. Once a parasitic cuckoo emerges from an egg as a nestling, it often removes all other eggs and nestlings from the nest. If a host is unfortunate enough to be parasitized during its first breeding attempt, it would then be fatal in terms of fitness for the host to imprint the parasitic cuckoo as its young. This phenomenon is called “misimprinting cost” by Lotem because of the costs that host would suffer by rejecting its own young due to incorrect imprinting. A study on the Australian bronze-cuckoo, *Chalcites*, demonstrates that some hosts are able to discriminate between nestlings (Langmore et al., 2011). As with the common cuckoo, bronze-cuckoos remove all host offspring from the nest. However, bronze-cuckoo hosts lack defenses at the egg stage and are not able to discriminate between their own eggs and mimetic eggs (Langmore, Hunt, & Kilner, 2003). Instead, they appear to have evolved defenses at the nestling stage, and hosts have been observed to reject bronze-cuckoos by physically removing them from the nest (Sato, Tokue, Noske, Mikami, & Ueda, 2010). To show that nestling mimics imitate their hosts accurately, avian visual modelling was used by Langmore et al. to quantify differences between the mimic and the host from a bird’s point of view. Data with % reflectance at different wavelengths shows that colors of cuckoo bodies and gapes are nearly identical to their hosts (see Figure 2). Four closely related species of *Chalcites* were studied, yet we can see clear divergence from each species towards the coloration of their respective hosts. Since hosts have shown ability to reject bronze-cuckoos, mimicry in *Chalcites* is highly likely to be a reciprocal adaptation to counter host discrimination. Rejection acts as a response to brood parasitism, while mimicry acts as a response to rejection, making this case a great example of coevolution at the nestling stage.

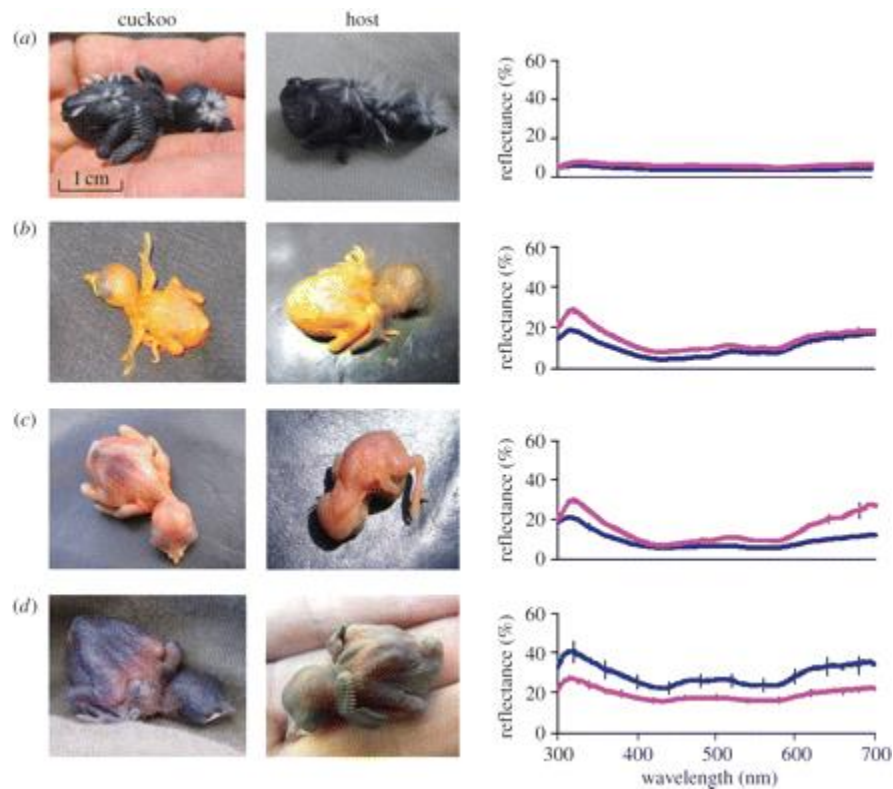


Figure 2. Cuckoo nestlings are highly accurate mimics of their hosts.

De Marsico’s study on the screaming cowbird, *Molothrus rufoaxillaris*, which mimics the baywing, *Agelaioides badius*, shows that adaptations can exist past the nestling stage and during the fledgling stage instead. Baywings rear both screaming cowbirds and another brood parasite, the non-mimetic shiny cowbird *Molothrus bonariensis*, during the nestling stage. However, shiny cowbirds experience high post-fledgling mortality rates of 83% as a result of host rejection while the mimetic screaming cowbird has a rate of 0% (De Marsico et al., 2012). As with the bronze-cuckoo experiment, they used avian visual modelling to confirm that screaming cowbirds were visually similar. It is clear that the screaming cowbird has developed traits to avoid rejection by the baywing, but development of baywing rejection remains unclear. In theory, it would be more cost effective to reject young at the egg or nestling stages as seen in other systems. A possible explanation is that Baywings are constrained from distinguishing eggs or chicks because of dark

and crowded nests (Fraga, 1998). One theory states that hosts evolve discrimination at later stages when parasites have broken down defenses at earlier stages (Langmore et al., 2003). Although the earlier stages have not been broken down in this case, the idea is similar because the host is unable to discriminate at earlier stages if Fraga's explanation is true. The alternate hypothesis is that Baywings are expressing pre-existing preferences for fledglings with visual cues for Baywing traits. In this hypothesis, Baywings would not be responding to fitness costs from parasitism, and this would not be a case of coevolution. More research on this system is required to clearly understand whether Baywing adaptations are reciprocal. Given that the Baywing shows similar rejection criteria than the bronze-cuckoo and experimental methods were similar in the two studies, the Baywing example still appears to be a case for coevolution at the fledgling stage.

An interesting system has been discovered where *C. canorus* mimics a predator, rather than its host, to increase its chances of remaining in the nests of reed warbler hosts. The sparrowhawk, *Accipiter nisus*, is dangerous to the reed warbler *Acrocephalus scirpaceus*, who recognize the hawks from their barred underparts. Amazingly, some common cuckoos have evolved resemblance of these barred underparts. Since reed warblers are reluctant to act aggressively towards hawks, cuckoos with barred underparts are less likely to be mobbed by reed warblers (Welbergen & Davies, 2011). Mobbing has been shown to be an effective defense against parasitism (Welbergen & Davies, 2009), and mobbing behaviors are targeted towards parasites more often than a neutral bird (2011). Despite the different target of mimicry, this system appears to be another example of coevolution. Reed warblers evolved mobbing behavior to reduce parasitism, and cuckoos have reciprocally evolved hawk mimicry to avoid mobbing. Hawk mimicry is currently imperfect, with imitation of barring being the only resemblance,

opening up the opportunity for hosts to respond by evolving discrimination. If discrimination improves, one could predict that these cuckoos will evolve more hawk-like features in other parts of their bodies. Welbergen and Davies suggest observing the hawk-cuckoos *C. varius* and *C. sparveroides* in Asia as systems for further study. High degrees of resemblance have been observed in these hawk-cuckoos, so one would expect that the degree of discrimination is also high if the hawks are in a coevolutionary arms race with the hawk-cuckoos.

History of cuckoos and cuckoo rejection ability

Examples are well documented in contemporary studies, however there is a lack of knowledge regarding the biogeographic history of brood parasites (Soler, 2014). Cuckoos evolved 65-144 million years ago (Nicholas B Davies, 2000), so many questions about origins of coevolutionary interactions are left unanswered because we cannot observe interactions that occurred millions of years ago. One question presented by Soler is “Why are many potentially suitable common cuckoo host species not currently parasitized?” Knowing that brood parasitism and host adaptations have possibly had millions of years to evolve, one possible answer is that there are many species that have evolved highly efficient rejection ability (Rothstein, 1990). Although efficient rejection ability is thought to be costly, a long period of evolutionary time would allow these adaptations to develop. When studies have targeted suitable non-parasitized hosts, results have shown that these hosts reject cuckoo eggs at higher rates than hosts parasitized by the cuckoo today (N. B. Davies & Brooke, 1989). These results suggest that coevolutionary arms races could have occurred in the past, with certain hosts winning the battle and evolving efficient rejection ability. Although we cannot say for sure what has occurred over time, the idea conforms to the logic that hosts could develop nearly 100% rejection rates given a long period of

time and selective pressure. Further research on the recognition mechanisms of suitable hosts could help lead us in a certain direction. For instance, if the recognition mechanisms for potential hosts are not costly, that would explain why rejection is more effective in potential hosts than currently targeted hosts. If the mechanisms are costly, then it may be more likely that host-parasite interactions played an important role and that a long period of time was needed for evolution.

Coevolutionary cycles: how common are they?

The above observations by Davies and Brooke seem to support the idea that parasites prefer the currently least defended host species. Does this lead to coevolutionary cycles? John Thompson's model tackles the idea of coevolutionary cycles by looking at outcomes when there is one parasite and two possible host species (2006). The idea that adding more species in an interaction will create more coevolutionary possibilities was first proposed by Davies and Brooke (1989), and then named as coevolutionary alternation by Thompson. In context of host-parasite interactions, coevolutionary alternation is the process of repeated cycling of evolutionary changes where parasite preference for a host depends on the relative levels of host defense (Nuismer & Thompson, 2006). As discussed earlier, parasites are predicted to change from a highly defended host to a poorly defended one, but could later return to using the first host again when host defenses decrease after a period of not being parasitized. This series of events is predicted based on the idea that host defenses are costly, so when hosts are no longer parasitized, selection will favor regression in these defenses (N. B. Davies & Brooke, 1989; Marchetti, 1992). However, there is a lack of concrete evidence supporting widespread loss of host defenses. While coevolutionary cycles appear to be possible, only a small amount of host species

have demonstrated that outcome compared to lack of rejection, successful resistance, or intermediate rejection without cycles (see Figure 3). These results suggest that hosts do not lose defenses so easily when they are not parasitized. Tying in with the ideas discussed earlier, successful resistance with nearly 100% rejection ability may be the most likely long-term outcome when rejection is possible.

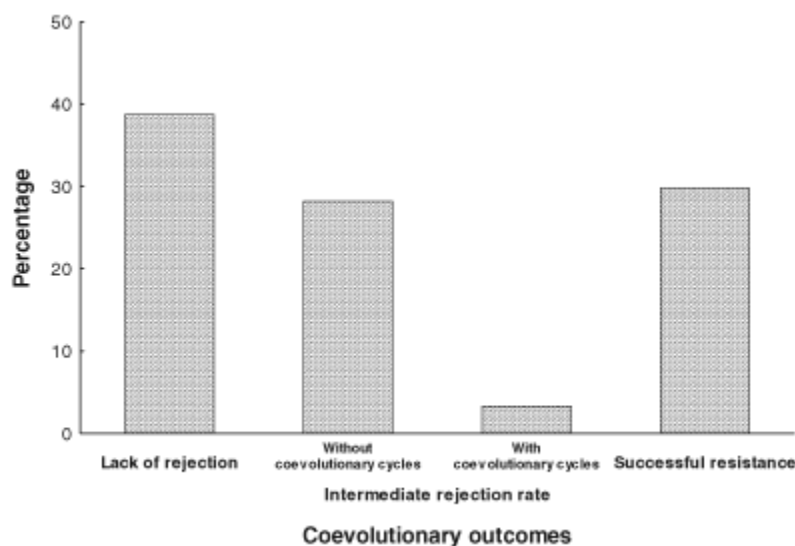


Figure 3. % of hosts (N = 182) with the long-term outcome of coevolutionary cycles

Conclusion

Many examples exist that demonstrate coevolution is an occurring phenomenon. Common cuckoos demonstrate coevolution with their various hosts through differing degrees of egg mimicry. Bronze-cuckoos show accurate mimicry at the nestling stage to a number of hosts, despite post-egg mimicry first being predicted to be too costly. With more evidence, screaming cowbirds can be another great example of post-egg mimicry, this time at the fledgling stage. Lastly, there is the example of common cuckoos using hawk mimicry rather than mimicry of their host, showing that coevolution can occur even with a different system of mimicry. Hawk mimicry also appears to be imperfect, providing some interesting questions for future research as

these cuckoos may be earlier in an evolutionary arms race compared to others. For instance, one could study the more hawk-like hawk cuckoo to learn whether discrimination is better in their hosts, leading to more accurate mimicry.

Cuckoos have had millions of years to evolve, so much is unknown about early origins of brood parasitism and the coevolution involving parasites and hosts. Theories have been divided over what long-term outcomes are most likely to occur through host-parasite interactions. Coevolutionary cycles were proposed to be a likely outcome, however this outcome has only been observed in a small number of host species. Thoughts on rejection ability of hosts have also been divided. Rejection ability is considered costly by many, but studies show that there are suitable hosts out there with highly effective rejection ability. These hosts simply are not being used because parasites choose less defended hosts. For coevolutionary cycles to occur, the next step would be for suitable hosts to decrease defenses to reduce their costs. As this is not observed often, perhaps rejection ability is not as costly as previously thought. An alternate explanation is that we are not noticing some evolutionary changes because they have occurred over thousands or millions of years. Either way, further research would strengthen understanding on host-parasite coevolution and maintenance of host rejection ability.

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