The evolution of brood parasitism in birds

Alexius W. T. Folk[1]

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Department of Biological Sciences, University of Bergen, Norway

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Alexius T. W. Folk, born 1990, is a PhD fellow at the Department of Biological Sciences (BIO), University of Bergen, Norway. He has spent the past few years studying parasite evolution using experiments on salmon lice and has previously worked with cowbirds. In his spare time, he paints and makes science art.

About 1% of all bird species are obligate brood parasites and reproduce exclusively by laying their eggs in the nests of other birds. In recent years, knowledge has expanded to include a much larger variety of these species from around the world, leading to new insights. In this article I discuss how brood parasites evolve and their coevolutionary relationship with host birds.

Brood parasitism is a kind of parasitism that exploits the parental care of a host to raise the parasite's offspring. The most well-known example is the common cuckoo (*Cuculus canorus*), which always lays its egg in the nest of another bird. Their biology is not as bizarre as some parasitic microorganisms, but brood parasites are unique because they combine some of the characteristics of predators with those of parasites. Brood parasitism can occur whenever there is parental care to exploit and a reliable way to introduce the parasite's offspring, such as social insects and even fish, but it is best known in birds.

Figure 1. A common cuckoo in Nepal. It resembles a bird-eating hawk with its banded plumage and yellow feet and eyes. © Prasan Shrestha / via Wikimedia Commons / CC-BY-SA-4.0

Scientific research on the common cuckoo began in the eighteenth century, but there are written records speculating about its reproductive behavior dating back to the sixth century BCE. Despite this long history, most published research was on just a few brood parasite species until recently. These were the cuckoo species in Europe and the cowbirds in the Americas. Most papers are still on either the common cuckoo (Figure 1) or the brown-headed cowbird (*Molothrus ater*, Figure 2).

There are two general ways that birds can express brood parasitism as a reproductive strategy. *Obligate* brood parasites never raise their own young. By contrast, *facultative* brood parasitism is found in species that typically provide parental care, but where females occasionally lay some or all of their eggs in another bird's nest. Facultative brood parasitism is difficult to detect. This is because it tends to occur between birds of the same or closely-related species, so the eggs and chicks of parasite and host often look identical and only genetic tests can tell them apart. As a result, the true prevalence of facultative brood parasitism is unknown. Based on the available data, waterfowl (Anatidae) are the only bird family where it is described as common, although it occurs in a wide variety of species. This includes backyard birds, and especially the thrush family (Turdidae).

Obligate brood parasitism has evolved independently seven times across five families of today's birds (three times in cuckoos). Working with local experts, scientists now have more detailed information about a much wider variety of these species. This includes the honeyguides and Viduidae finches of Africa and more parasitic cuckoos from Africa, Asia, and Australia. This makes it easier to pick out the common trends and to start answering some of the broader evolutionary questions in avian brood parasitism.

Table 1. Overview of the seven obligate brood parasite lineages in birds, where they are found, their typical level of host specialization, and whether they kill their nestmates as young (nest-eviction). These details are not known for all species, so the last column briefly summarizes the state of knowledge for each lineage.

Lineage (# species)	Example species	Region	Level of host specialization	Nest-eviction	Knowledge base
Family Cuculidae (Cuckoos)					
Tribe Cuculini (57 species)	Common cuckoo (*Cuculus canorus*)	Eurasia, Africa, Australia	Some species have a very high host count, but often specialized individually or as a species	Both	Several species are well-described, some still poorly-described
Tapera & *Dromococcyx* spp. (3 species)	Striped cuckoo (*Tapera naevia*)	Central & South America	At least one generalist species, others are possibly specialists	Yes	Less is known about this lineage
Clamator spp. (4 species)	Great spotted cuckoo (*Clamator glandarius*)	Eurasia, Africa	More generalist, by host variety if not by count	No	Regional gaps in knowledge about hosts
Family Indicatoridae (Honeyguides)					
Honeyguides (17 species)	Greater honeyguide (*Indicator indicator*)	Africa	Both generalists and specialists, as a species or individually	Yes	Only a few species are well-described
Family Viduidae (Indigobirds and whydahs)					
Vidua spp. & cuckoo-finch (20 species)	Cuckoo-finch (*Anomalospiza imberbis*)	Africa	Most are highly specialized as a species or individually, almost all on Estrildid finches	No	Some species are well-described, some still poorly-described
Family Icteridae (New World blackbirds)					
Cowbirds (6 species)	Brown-headed cowbird (*Molothrus ater*)	North & South America	Half are generalists with high host counts, half are specialists	No	The more widespread species are well-described
Family Anatidae (Waterfowl)					
Black-headed duck (1 species)	(*Heteronetta atricapilla*)	South America	Generalist, uses hosts in multiple families, but not dependent on parents for food	No	Often excluded from comparisons because of its uniqueness

How did brood parasitism evolve?

How did facultative brood parasitism evolve? In other words, what might the reproductive benefits be for one female letting another one care for her own eggs? The odds of survival for an egg laid in another female's nest are usually low. A clutch of eggs laid together by the same female (that is, a *brood*) should hatch at the right time, while an egg laid into another nest that already has eggs is more likely to hatch too late, or not at all. If, on the other hand, the egg would be unlikely to survive in the bird's own nest, then spreading eggs over more than one nest can help make the "best of a bad situation" by improving the chance that at least some of them survive. Examples of this include females that have a bad nest location or even no nest, and more generally any extra eggs laid by a female in good enough condition to produce more eggs than she can effectively keep warm.

It is widely believed that obligate brood parasitism evolved from facultative brood parasitism independently in multiple lineages. There is no evidence of any species having become an obligate brood parasite and later regained nesting behavior, but this should be interpreted with caution because some brood parasitic lineages involve recently-diverged species for which evolutionary relationships are not fully resolved. To understand the transition to obligate brood parasitism one would need to measure its reproductive benefits, but there are no examples of a nest-building species where some females are exclusive parasites, which would allow direct comparisons with non-parasitic females. This leaves the option of comparing parasitic lineages to their non-parasitic relatives for shared traits.

A trait that improves the survival of a facultative brood parasite's egg in the nest of another bird could make it more likely for obligate brood parasitism to evolve. The cuckoo family is a good illustration of this. There is no evidence that nest-building cuckoos are more likely to lay parasitic eggs than other birds, and yet cuckoos have evolved obligate brood parasitism three times. However, both parasitic cuckoos and their non-parasitic relatives do share an important trait: they lay one egg every two days. This differs from most other birds, which lay one egg per day. Cuckoo females incubate their egg internally during that extra day, shortening incubation by the host and improving chances for the parasitic chick of being the first one to hatch.

The two-day interval of honeyguides is not shared with their non-parasitic relatives, so it might have evolved after, or concomitantly with, parasitism. This two-day egg-laying interval is, however, not a trait shared by all obligate brood parasites, and on its own it is not enough to lead to brood parasitism. The other parasitic lineages, cowbirds and indigobirds (*Vidua* spp.), lay one egg per day and tend to parasitize their close non-parasitic relatives. There are counterexamples too: domestic pigeons (*Columba livia*) also use internal incubation without being obligate brood parasites.

Generalists and specialists

From this point, the focus will be on the obligate brood parasites. A parasitic species can range from extremely specialist to highly generalist in terms of which hosts it can successfully parasitize – that is, where an egg laid in that host's nest has a chance of surviving to adulthood. A *specialist* brood parasite species has a limited selection of hosts that it can use. This could be a few similar host species, or even just a fraction of the population of one species. For example, each species of indigobird has only one host species, and always a finch in the family Estrildidae. A *generalist* brood parasite species can successfully parasitize a wide variety of hosts and is characterized by its greater flexibility.

Choosing the best example of a generalist species is more complicated, however, because how host specialization should be measured is a matter for discussion. This is often quantified by the total number of host species reported for a brood parasite, but this number does not distinguish frequently-used host species from species that are only occasional hosts. Neither does it inform on how closely related, or physically similar, host species are to each other. In reality host species differ widely, both in their evolutionary relatedness and in the frequency with which they are used as hosts. In addition, the more widespread a given brood parasite, the greater the total number of host species within its geographical range, which can be misleading because at the local scale parasites have access to only a fraction of those potential hosts. Finally, the count of host species increases with the number of papers published on a brood parasite. The two most extensively studied species, the brown-headed cowbird and the common cuckoo, have been recorded laying eggs in the nests of roughly 280 species each, including unsuccessful attempts. When only counting the typical hosts, the cowbird uses around fifty species across its North-American range. The cuckoo, whose range extends over almost the whole Palearctic, uses around thirty frequent hosts in regions where this is documented. By comparison, the greater honeyguide (*Indicator indicator*) has a modest host count, but being one of the only brood parasites (of those with helpless young) that uses hosts from two taxonomic orders, it too appears to be quite flexible in its host use.

What makes a species evolve to be a generalist or specialist? When the environment is relatively stable, specialization pays off by increasing the reliability of the brood parasite's success with its preferred host. When the environment is more unpredictable, using a wider variety of host species spreads the brood parasite's risk of failure among different hosts. The reproductive success of a generalist is less tied to the availability of any one host species. Brood parasites tend to be generalists if they live in colder climates with more variable temperatures, which is important for egg development. In addition, shorter breeding periods increase the chance of missing the time when any single host species is nesting, particularly if the parasite migrates. Being more flexible in their host choice allows them to be more flexible in their timing.

Specialization becomes more likely when more of the available hosts show intermediate levels of parental care and nest density, thereby providing a good balance between nest reliability against host defenses. On the one hand, nests that are closer together are easier to find for the parasite, and reproduction less likely to fail when there are more adults helping to raise the young. One the other hand, an increasing number of host adults near the nest makes it harder for a brood parasite to lay their egg undetected.

Do generalists evolve into specialists over time, or the other way around? The answer is not straightforward, and from what is currently known, generalist brood parasite species seem to become highly diverse without diverging into different species. Individual females from the same generalist species can be specialized on different hosts or habitats, preferring to visit the same type of habitat or nest as the one they were raised in, or preferring to mate with males raised by the same host species. This results in genetic differentiation among lineages within the same parasitic species. At the most extreme, females can inherit specialized traits from genes that pass exclusively from mother to daughter. These maternal lineages are referred to as *gentes* (singular *gens*), of which the cuckoo-finch (*Anomalospiza imberbis*) is the clearest example. It is the most generalist species in the Viduidae lineage, but cuckoo-finch females can be specialized not just on one host species, but on one egg color morph of one host species. Other brood parasites that have gentes-like lineages include the common cuckoo and greater honeyguide, even though the inheritance of specialized traits in those species is not exclusively through maternal genes.

Nest subterfuge

Detecting a brood parasite and preventing it from laying an egg in the nest is the first line of defense for host birds. Should this fail, their reproduction is likely compromised. Most brood parasites will indeed remove at least one egg and may damage others while laying their own, an adaptation that both disguises the presence of an additional egg in the host nest and reduces later competition with the host's offspring.

The traits of hosts that prevent brood parasites from laying eggs resemble, and often overlap with antipredator defenses. Some elaborate nest designs are effective against both predators and brood parasites and probably evolved under selection from both. For example, hosts can build hidden pockets to hide the eggs, or narrow entrances to prevent larger birds from entering. Other behaviors seem more specific, with some hosts moving to block the nest cup with their bodies if they see a brood parasite. Aggressive displays of nest defense can help against both brood parasites and predators, but for brood parasites the cost of being detected might be greater. A brood parasite is not as dangerous to adult birds as a nest predator, so host birds will readily attack them. Brood parasites caught at the wrong time can even be killed by host birds. Even if the brood parasite is unhurt, hosts will be more likely to evict a suspicious egg after seeing a brood parasite nearby.

Female brood parasites have evolved elaborate subterfuges to avoid being seen near a nest. They often time egg-laying for when the host is not at the nest. Brown-headed cowbirds, for example, memorize nest locations and their contents from a safe distance during the day. They return to lay an egg at night, before the host starts sitting on the eggs. Most brood parasites can lay their egg very quickly, even forcefully, and without taking the time to fully crouch down. Host eggs are sometimes damaged when the egg drops onto them. This may have played a role in the repeated evolution of thick eggshells across brood parasite lineages.

Another way to avoid recognition is mimicry. Cuckoo species have evolved banded plumage patterns that resemble those of local hawk species (Figure 1), which is more dangerous to harass. Eventually hosts will counter-evolve to tell the difference, which is probably why a red color morph has evolved in female common cuckoos in addition to the grey morph shared with male cuckoos. The less common color morph in an area is less likely to be recognized. In cuckoo-finches, females instead evolved to resemble a harmless, non-parasitic weaver. Due to the continual process of evolution, however, nothing is static – hosts of the cuckoo-finch have started harassing females from both the harmless and parasitic species.

Coevolution of eggs

The evolution of egg rejection behavior comes at the risk for the host of making mistakes and rejecting their own offspring. This might explain why hosts from an egg-rejecting species will sometimes accept a parasitic egg after a long inspection and even a few pecks. Reliable rejection, on the contrary, has clear benefits and can spread through a population. It selects for counter-defenses in brood parasites, which in turn selects for more sophisticated detection and rejection mechanisms in hosts.

A clear example of such ongoing coevolution between brood parasites and their hosts is found in the tawny-flanked prinia (*Prinia subflava*), the main host of the cuckoo-finch. Each host female lays eggs with a unique color and pattern and

Figure 2. A yellow warbler nest in Michigan with three of that species' eggs (top, smaller), and one parasitic brown-headed cowbird egg (bottom, larger with more spots). © Stylurus / via Flickr / CC-BY-NC-SA 2.0 / *cropped from original*

she learns her signature appearance. Unlike their hosts, the parasites do not appear to know what their own eggs look like. Cuckoo-finches lay their eggs in prinia nests at random and many, but not all, of their eggs are rejected. Over just forty years the diversity of both host and parasite eggs increased measurably, and some prinia females now lay eggs with an olive-green color that the cuckoo-finch has not yet replicated (Figure 3). Prinia females with this trait have an advantage, so it is likely to become more common; in other words, the new olive-green egg color is currently being selected. Eventually some individual cuckoo-finches may be able to produce similar-looking eggs, which will allow them to reproduce successfully, and this trait will be passed on to their daughters. This kind of arms race, maintained over evolutionary timescales, can explain much of the variation and complexity of host and parasite egg color patterns.

The most stunning cases of egg mimicry occur in the species that have gentes, like the common cuckoo and cuckoo-finch, where a large variety of host eggs are closely mimicked by different parasitic females. In many host species only the female parent rejects eggs, while in species where both sexes incubate the eggs the males may also reject eggs, but sometimes less successfully. Egg rejection by hosts probably involves learning the appearance of their own eggs. In one method, host females use the first egg they lay as a reference and then reject any egg that does not match. This method is used by the gray catbird (*Dumetella carolinensis*), which almost always rejects cowbird eggs. Very rarely, a female catbird can learn to reject her own blue eggs if her first egg is replaced quickly enough.

More generally than matching colors, egg mimicry is about the parasitic egg staying undetected within a nest, and this can be achieved in various ways. Brood parasites like bronze-cuckoos (*Chalcites* spp.) that exclusively use host species with dark, enclosed nests lay eggs with very dark shells, making them hard to see. The greater honeyguide, a generalist brood parasite, mimics the size and shape of eggs from different host species that nest in tree cavities and burrows. This can also be self-reinforcing if female honeyguides grow larger when raised by a larger host that can provide more food, or because a large adult female cannot enter the nest of a smaller host to lay her egg.

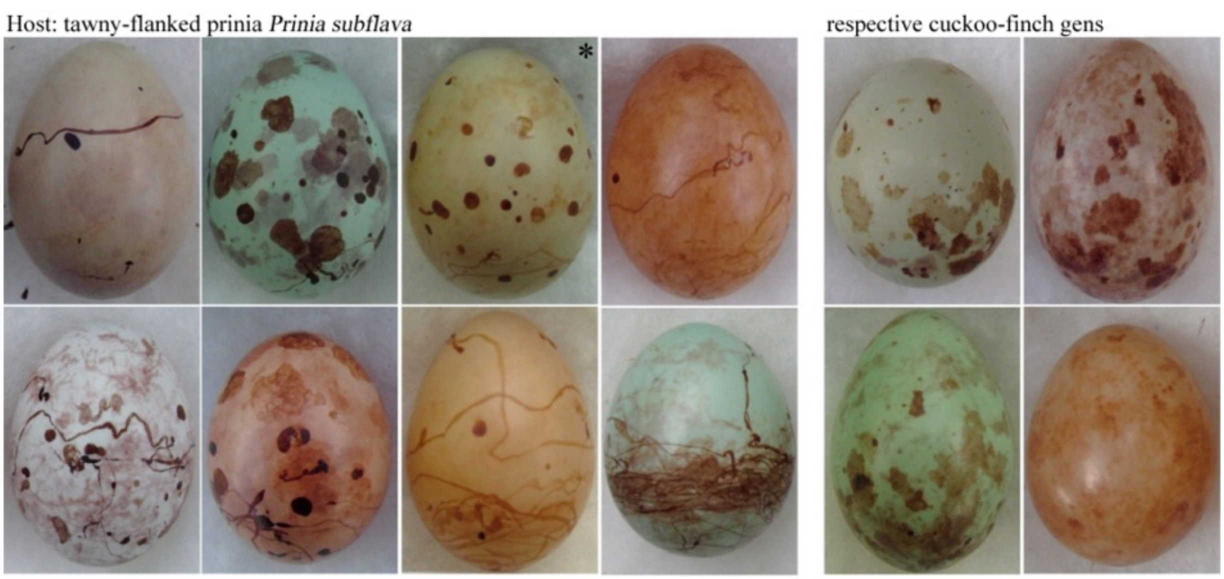

Figure 3. Highly variable egg appearance in the tawny-flanked prinia (left), the main host species used by the cuckoo-finch, compared to the respective parasite gentes (right). The star (*) indicates the prinia's olive-green egg color with no matching cuckoo-finch variant. NB: not to scale.

In the past hosts were often described as "unwitting" victims, but the current understanding is that it is more complicated than that, partly because birds perceive colors differently from humans. Unlike us, many birds can see ultraviolet light, and this is known to have some effect on the rejection of eggs. It is also not clear whether some egg colors are more appealing than others. Less is known about how birds might use their other senses, such as smell and touch, in this context. Hidden costs may also be another obstacle to egg rejection: removing an egg from the nest can be a physical challenge, particularly for smaller birds. Some hosts are unable to do so without damaging their own eggs. A bird could instead abandon the nest and start over, but birds often have a limited time window for breeding. Nest abandonment becomes less likely with repeated parasitism as the season progresses. This is the case for the yellow warbler (*Setophaga petechia*), a host of cowbirds that builds a new nest on top of a parasitized clutch. This unique behavior can result in very tall nests, but yellow warblers also become more likely to accept the next cowbird egg as the season advances (Figure 2).

Nestling mimicry

The idea that once hatched, some brood parasites might mimic the young of their host was previously met with skepticism. Host birds were not known to evict parasitic chicks and therefore selection was thought to be mostly acting on egg rejection. However, as a larger variety of brood parasite species have been described, there is no longer any doubt that some brood parasites use nestling mimicry. Particularly among bronze-cuckoos, nestlings can be a close match to the host's offspring in the color of their skin, mouth, and down feathers. If a shining bronze-cuckoo (*Chalcites lucidus*) does not correctly match one of the two nestling color varieties of the fan-tailed gerygone (*Gerygone flavolateralis*), it gets kicked out.

An intriguing case is that of brood parasites in the *Vidua* genus in Africa and their hosts in Estrildidae. The chicks of both the specialized brood parasites and their hosts have truly bizarre, matching color patterns inside their mouths (Figure 4). This feature is thought to originally have evolved in hosts as it facilitates easier feeding of the young by their parents. The fact that such distinctive mouth patterns are also found in Estrildid finches outside of the geographical range of brood parasites, for example in the Gouldian finch (*Chloebia gouldiae*) in Australia, tends to support this interpretation. Secondarily, this trait would have been mimicked by brood parasites, which in turn reinforced selection also in hosts. Not every lookalike between host and parasite nestlings necessarily reflects evolved mimicry, but young *Vidua* finches also match the sound and posture of their specific host when begging. This recent discovery gives additional support to the mimicry hypothesis. Nestling pin-tailed whydahs (*V. macroura*) are not an exact mimic of the host common waxbills (*Estrilda astrild*), but present a more intense display that might increase their appeal to the host parents over the young waxbills.

Last but not least, mimicry can even occur at a much later stage, after the chicks have left the nest. The screaming cowbird (*Molothrus rufoaxillaris*) almost exclusively parasitizes the greyish baywing (*Agelaioides badius*). The adult cowbirds are entirely black, but the feathers they wear at the time of fledging are an exact match for the brown body and rusty red wings of a young baywing. The resemblance is so striking that the baywing was originally assumed to be a sister species and classified under *Molothrus*, but they are in fact more distantly related. Baywings stop feeding fledglings of another, non-mimetic brood parasite, the shiny cowbird (*M. bonariensis*), but keep feeding the mimetic screaming cowbirds.

Figure 4. A variety of mouth patterns in (non-parasitic) Estrildid finch nestlings from different species. Many of these are hosts to parasitic *Vidua* finches that show specialized mimicry. The star (*) indicates the common waxbill. The top two rows of photos were taken through a triangular prism. Source: in Jamie et al. (2020)

Virulence

Parasites, by definition, reduce the chances for their hosts to reproduce. In other words, they exert selection on their hosts, to an extent that can vary from temporary physical weakness to rapid death. The degree with which parasitic infection reduces the host's reproduction is referred to as *virulence*.

This applies to brood parasites, since they clearly inflict reproductive costs to host birds. The most immediate costs are eggs and young broken or evicted by the parasite, or nest desertion by the parents. Some costs are also paid later by the parents, as raising the parasitic young can reduce their subsequent breeding success. In practice, the virulence of a brood parasite is sometimes simplified by comparing the numbers of host young that survive to fledge from parasitized nests than from unparasitized nests. However, few host species have been studied in enough detail for a reliable estimate. Instead, brood parasites are split into two categories for broad comparison: the *nest-evictors* and the *nest-sharers* (Table 1).

A *nest-evictor* brood parasite directly kills any other eggs or nestlings in the nest soon after it hatches, typically within a few days. Cuckoos in the Cuculini tribe are infamous for shoving their nestmates out of the nest, while honeyguides and parasitic ground cuckoos (*Tapera* and *Dromococcyx* spp.) use their sharp beaks to bite and stab nestmates. The host usually has no surviving young, so they are considered highly virulent.

There is a common misconception that all brood parasites are nest-evictors, but the *nest-sharing* brood parasites compete against the host young in the nest. This term is slightly misleading, however. They can have lower virulence than a nest-evictor, but it is not uncommon for there to be no surviving host young eventually. Very little is known about what happens to host young if they do live long enough to leave a parasitized nest, but the evidence suggests that their mortality is higher. All cowbirds, Viduidae finches, and the *Clamator* cuckoo lineage are nest-sharers. Only one lineage, the Cuculini cuckoos, has both nest-evictor and nest-sharing species.

Figure 5. A nestling brown-headed cowbird begging for food lifts its head higher than the three smaller host nestlings. Illustration: Alexius Folk

The origin of nest-eviction behavior is poorly understood, although it has arisen at least three times. It was recently discovered that both nest-evicting cuckoos and honeyguides share a trait in their egg development. Unlike their hosts and the non-evicting brood parasites, their eggs go through a period of heightened metabolic activity about halfway through incubation. This resembles the egg development of birds whose nestlings can walk after hatching and is believed to be important for the physical task of killing their nestmates.

Differences in virulence of brood parasites should be seen in relation to their degree of specialization, and to current knowledge on how virulence evolves in parasites generally. Briefly, for many parasites virulence is tightly linked with how well a parasite reproduces in the host. The greater the reproductive success of a parasite, the greater its virulence, because the parasite diverts resources from its host, and by doing so decreases the host's reproductive output. Generalist parasites cannot reproduce equally well in all hosts, so their virulence will be lower overall than that of a highly specialized parasite having adapted to a single host type. The same pattern is found for brood parasites: nest-evictors are more likely to be specialists, either as a species or individually, and nest-sharers are more often generalists. In addition, nest-sharers are more likely to lay multiple eggs in the same nest (so-called multiple "infections" are more frequent for nest-sharers), while nest-evictors will kill all younger birds in the nest including parasites.

Nest-sharing brood parasites do not kill the host's young directly, but have adaptations that help them take a greater share of the host parents' effort away from the host young. Like all brood parasites, they tend to be larger and hatch earlier than their hosts. Begging calls from the parasitic young can be more intense than that of its adoptive siblings, triggering greater feeding effort from the adoptive parents. This is the case in the brown-headed cowbird, which has louder begging calls than most of its hosts. In this species' hosts, food is more often given to the larger parasitic nestling, whose open mouth sticks out above others (Figure 5).

Bird parents can be reluctant to invest time and effort on feeding a single chick, instead of re-nesting and producing a full new clutch. Nest-evictor brood parasites show adaptations that help them get food from their host parents. Many cuckoo species, for example, have begging displays that are extremely appealing to their host parents, such as large, brightly colored mouths and rapid begging calls that sound like multiple smaller chicks. The Hodgson's hawk-cuckoo (*Hierococcyx nisicolor*) has a large yellow mouth, but also has a patch of bare yellow skin on its wing. When begging for food it opens its mouth, but also raises its wing, mimicking another open mouth and thus receiving an extra food ration from parents (Figure 6).

Figure 6. A young Hodgson's hawk-cuckoo raising its wing while begging. This increases the amount of open yellow "mouth" the host parent sees when bringing food. Illustration: Alexius Folk

The generalist Horsfield's bronze-cuckoo (*Chalcites basalis*) learns to mimic the sound of host chicks through trial and error. Unsurprisingly with such high stakes, their superb fairy wren (*Malurus cyaneus*) hosts have evolved a fascinating counter-adaptation: they teach their own young a vocal "password" while still in the egg. The cuckoo chick, unable to learn this call, is recognized and abandoned.

Future prospects for brood parasites

To the extent that people are aware of them, attitudes toward obligate brood parasites vary. Cuckoos and honeyguides are culturally important birds, and whydahs are sought after in aviaries for the male's extremely long tail. By contrast, the brown-headed cowbird is widely hated and actively exterminated in parts of North America. Cowbirds are frequently referred to as "lazy," and worse terms. Like all living organisms, evolution alone has shaped the way they behave and reproduce, and they have no malicious motivations. Being a brood parasite is quite a tough life: female brown-headed cowbirds can lay dozens of eggs in a season, but by doing so they compromise their resistance to disease and risk attack while visiting host nests. As a result, the mortality rate of adult female cowbirds is much higher than for males.

Cowbirds are unfairly blamed for the decline of several species of rare birds. This is probably due in part to an inaccurate perception of the continent's forest ecology prior to European colonization. Extensive habitat loss is a much greater threat, but harder to address. The evidence suggests that rare bird populations recover when their breeding habitat is restored, not when cowbirds are removed. Besides, despite thriving in disturbed habitat, brown-headed cowbird populations are likewise declining steadily.

Ultimately, obligate brood parasites are dependent on their hosts to survive. When the populations of almost all birds are decreasing in number, their brood parasites will follow. They can in some cases be even more sensitive to change. They experience most of the same impacts as nesting birds, but their success is also linked to those species. Although not all brood parasites are regarded fondly, their coevolution increases the biodiversity of non-parasitic birds, just like how the more classical parasites have been a major driver of biodiversity as we know it today.

Many of the examples mentioned here are recent discoveries, in species that were poorly described. Such developments are due to increased scientific collaboration with local people living alongside these species, improvements in technology and the affordability of molecular methods, and shifts in thought that challenge old assumptions. There are many more avian brood parasite species still undescribed globally. If the scientific community continues to become more connected, we can expect exciting developments in the study of avian brood parasitism.

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