EVOLUTIONARY LAG IN COWBIRD NESTLING RECOGNITION BY OVENBIRDS

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The phenomenon of brood parasitism was well known to Aristotle centuries ago (Davies and Brooke 1988), and it is even mentioned by the king's jester in William Shakespeare's *King Lear* (I, iv): "For, you know, nuncle,/ The hedge-sparrow fed the cuckoo so long,/ That it had it[s] head bit off by it[s] young." The basic description of this unusual reproductive strategy is quite simple. Parasitic birds lay their eggs in the nests of other species. The host species will incubate the eggs and raise the young of the parasite. While Europe has its parasitic cuckoos, in Massachusetts the Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite that is known to parasitize a wide range of passerine species. The Ovenbird (*Seiurus aurocapillus*) is one of the species commonly parasitized by cowbirds in Massachusetts and throughout the Ovenbird's North American range (Friedmann et al. 1977).

Ornithologists are intrigued by the evolutionary "arms race" between the brood parasite and the host, and have devised a vernacular to describe the adaptations and counteradaptations. In the case of brood parasitism, it seems obvious that spending time and energy to raise the young of another species is maladaptive. Therefore, when counteradaptations have not evolved in the host, researchers wonder why. One proposed theory is the "evolutionary-lag" hypothesis, which suggests that there has been insufficient time for counteradaptations to evolve (Rothstein 1975b). An alternative explanation for the lack of counteradaptations is the "evolutionary-equilibrium" hypothesis, which suggests that the costs of rejection are greater than the costs of acceptance of parasitism, and, therefore, acceptance is more adaptive than rejection (Rohwer and Spaw 1988, Lotem et al. 1992). This paper will review some of the current research investigating the evolutionary "arms race" between parasite and host, describe the relationship between the cowbird and Ovenbird, and present data collected in 1996 and 1997 that suggest Ovenbirds are acting in a manner that lends support to the evolutionary-lag hypothesis, at least where Ovenbirds and cowbird nestlings are concerned.

Rejecters versus Acceptors

Experiments introducing foreign eggs into the nests of potential hosts have been carried out for over 200 years (Payne 1977), but Rothstein (1975a, b, 1976, 1982a, b, 1986) pioneered the technique of parasitizing host nests with model cowbird eggs. Since cowbirds usually deposit one egg per nest and remove one host egg, this is the approach Rothstein (1975 a, b) used. Rothstein (1975, 1976,

1982) found that North American passerines separate into two groups, rejecters or acceptors. Most species are acceptor species, and in these species nearly all the individuals accept cowbird eggs. In the remaining species, almost all the individuals reject the cowbird eggs. There is very little in-between. For example, Rothstein (1976) found that in six rejecter species, 88 - 100 percent of the individuals reject model or real cowbird eggs, and in twelve acceptor species about 90 percent of the individuals accept the eggs. Since there is a tremendous selective advantage for individuals that recognize and reject a parasitic egg, a genetic basis for the behavior will quickly spread throughout the population.

Only about a dozen species are known to reject cowbird eggs (Rothstein 1975a, Rohwer and Spaw 1988, Lowther 1993, Regosin 1994, Sealy and Neudorf 1995; Table 1). This seems like a small number of species considering that cowbirds are known to lay their eggs in nests of over 210 species, with at least 139 of these species successfully rearing cowbirds (Friedmann et al. 1977). Some larger rejecter species grasp cowbird eggs in their bills and carry the eggs away from the nest (Rohwer and Spaw 1988). This technique is known as "grasp-ejection." Smaller hosts, including the three smallest of the rejecter species — Warbling Vireo (*Vireo gilvus*), Cedar Waxwing (*Bombycilla cedrorum*), and Baltimore Oriole (*Icterus galbula*) (Rothstein 1976, Rohwer et al. 1989, Sealy 1996) — can puncture or break eggs (the "puncture-ejection" method), but may be too small to use grasp-ejection. After puncturing the eggs, birds carry them away, either with the bill spiked in the egg ("spike-removal"), or piecemeal.

Table 1. Species that reject Cowbird eggs.

Common Name	Scientific Name
Yellow Warbler	*Dendroica petechia*
Californial Gnatcatcher	*Polioptila californica*
American Robin	*Turdus migratorius*
Gray Catbird	*Dumetella carolinensis*
Western Kingbird	*Tyrannus verticalis*
Blue Jay	*Cyanocitta cristata*
Brown Thrasher	*Toxostoma dorsale*
Cedar Waxwing	*Bombycilla cedrorum*
Baltimore Oriole	*Icterus galbula*
Marsh Wren	*Cistothorus palustris*
Scissor-tailed Flycatcher	*Tyrannus forficata*
Eastern Kingbird	*Tyrannus tyrannus*
Warbling Vireo	*Vireo gilvus*
Loggerhead Shrike	*Tyrannus tyrannus*

There are potential costs to hosts that use the puncture-ejection method. There could be accidental breakage of host eggs, or contamination of their eggs by the contents of broken cowbird eggs. Cowbird eggshells are especially thick (Spaw and Rohwer 1987), and presumably resistant to puncture, so smaller hosts may suffer a greater cost by trying to puncture-eject cowbird eggs than by accepting them. If the costs of rejection are higher than the costs of raising the parasite chicks, we have the possibility of "evolutionary equilibrium," with the adaptive response being the acceptance of cowbird eggs by the host. This equilibrium hypothesis is known as the "puncture-resistance" hypothesis (Spaw and Rohwer 1987, Rohwer and Spaw 1988). When he tested this hypothesis, however, Sealy (1996) did not find support for it. He artificially parasitized nests of the Warbling Vireo, a species that uses the puncture-ejection method, and did not see an increase in breakage or spoilage of host eggs due to puncture-ejection of cowbird eggs.

Other responses to parasitism include nest desertion or covering the parasitized clutch with new nest material and starting a new clutch. For example, Yellow Warblers (*Dendroica petechia*) will bury cowbird eggs under new nest linings. Host species may also behave aggressively toward cowbirds and guard the nest when it is most vulnerable. Unfortunately for the host, aggressive responses may be an indication to the parasite that a nest is nearby and vulnerable to parasitism (Hobson and Sealy 1989). Scientists have been able to test aggressive responses toward cowbirds by presenting hosts with cowbird models near the nest before, during, and after egg-laying (Payne 1977). Most species, including Ovenbirds, do not perceive cowbirds as a threat.

The evolutionary-lag hypothesis assumes that the evolution of egg recognition is in the realm of possible responses of birds to parasitism. While phylogenetic constraints (i.e., constraints on a group of organisms due to their evolutionary history) could preclude certain behaviors from evolving, Rothstein (1982) has pointed out that in the case of cowbird brood parasitism, phylogenetic constraints most likely do not restrict the evolution of recognition. He notes that acceptor species are capable of various levels of recognition. For example, when clutch size is drastically reduced, birds often desert the nest and attempt renesting. It is also not unusual for individuals to remove broken eggs from their nests, an indication of the recognition of problems with their eggs. Finally, there are examples of species in the same taxa, one of which is an acceptor and the other a rejecter. So there are different types of recognition even in acceptor species, and there may be an evolutionary-lag before rejection techniques evolve in more species. The bottom line is that recognition of brood-parasite eggs is possible, and there may just not have been sufficient time for recognition to evolve in species for which exposure to parasitism is relatively recent.

Parasite Counteradaptations

The host-parasite interaction is an evolutionary "arms race," and if the host evolves techniques to avoid parasitism, natural selection will also be acting on the parasite to overcome the host's actions. Since hosts can reproduce, even if parasitized, the selective pressure on the parasite may actually be even stronger than that on the host. If counteradaptations do not evolve in the parasite, it will be unable to reproduce. Some counteradaptations that have evolved in brood parasites include (1) reducing the time needed for egg laying, in some instances to 30 seconds or less; (2) removing a host egg to reduce the chance of detection or to decrease competition for the parasitic nestling; (3) the evolution of mimetic eggs or nestlings; (4) laying eggs with thick shells, making puncture-ejection difficult, (5) evolving adult plumage that reduces conspicuousness, or in the case of some cuckoos, evolving plumage that mimics that of hawks (Payne 1977); and (6) laying large eggs that contain ample nutrients, allowing parasitic nestlings to hatch at a large size, giving them an advantage over the hosts nestlings.

The Relationship Between Ovenbirds and Cowbirds

The detailed observations of Hann (1937) form the foundation of what we know about the relationship between Ovenbirds and cowbirds. The following account of this relationship is based upon his work and our own observations.

It is expected that cowbird laying coincides with the egg-laying period of the host. Parasitizing nests after incubation begins would not be beneficial to cowbird nestlings because the typical parasite strategy is to hatch earlier and develop more quickly than the host. Laying eggs early is particularly important for the cowbird when it chooses an Ovenbird as a host because even though the time for incubation is about the same for cowbirds and Ovenbirds, the typical nestling stage for Ovenbirds is only eight days while the cowbird nestling stage is 10 - 12 days (Hann 1937, Lowther 1993; personal observation). Conceivably it would be maladaptive to lay an egg in a host's nest before any of the hosts eggs are laid because there is the risk of the host abandoning the nest. Apparently, Ovenbirds have not yet evolved this level of recognition, since cowbirds have been known to lay eggs in Ovenbird nests even before Ovenbirds lay their own (Hann 1937)

In our study in Weston, Massachusetts, we often observed female cowbirds moving throughout our study sites, apparently searching for nests. Hann (1937) discusses two instances where he observed a cowbird quietly watching an Ovenbird building a nest. In one case the cowbird was "spying on a nest" for twenty-two minutes and approached within 4.5 meters before flying off. In both cases the Ovenbird appeared not to recognize the cowbird as a threat. Hann believes that the cowbirds generally find Ovenbird nests during nest-building.

As a group of researchers that seems to be constantly searching for Ovenbird nests, we marvel at how adept cowbirds are at finding them!

On two occasions Hann (1937) actually observed a female cowbird depositing an egg in an Ovenbird nest. Both observations occurred about thirty minutes before sunrise. The first of these nests had one Ovenbird egg when a cowbird egg was laid. Later on the same day that the first cowbird egg appeared, the Ovenbird egg disappeared, apparently removed by the cowbird. The next day Hann set up a blind and witnessed a second cowbird egg being laid in the nest. The cowbird took less than a minute to lay its egg. Within six minutes of the cowbird's departure, the Ovenbird was back on the nest. She proceeded to take one hour to lay one of her own eggs. The second time Hann witnessed a Cowbird parasitizing an Ovenbird nest, the cowbird approached the nest while the Ovenbird was on it. The Ovenbird left the nest with a "screech" and remained agitated while the cowbird entered her nest and took about thirty seconds to lay an egg. At this point the nest contained two cowbird eggs but no Ovenbird eggs. Two days later the Ovenbird laid its first egg in the nest.

Hann (1937) found that on numerous occasions eggs would disappear from Ovenbird nests on the day a cowbird egg appeared in a nest, or on the day before it appeared. In 23 instances of egg removal, 10 eggs were removed on the day before a cowbird egg was laid, 10 were removed on the same day, and 3 on the day following parasitism. Over the course of his study about 30 Ovenbird eggs and 4 cowbird eggs disappeared from nests during the egg-laying period. Only one of these eggs disappeared from an Ovenbird nest that was not parasitized. Therefore, it seems that a common cowbird strategy is to remove an Ovenbird egg and replace it with one of its own. At one nest, Hann observed a cowbird approach the nest on the day on which a cowbird egg had appeared early in the morning. The cowbird removed an egg and flew off with it; Hann noted that the cowbird's bill was "sunk deeply into the shell." On a second occasion he observed a cowbird remove an egg from a nest and carry it to about fifteen meters from the nest, where it then ate the egg. He also reports two deserted nests that had the remains of broken eggs in the nest.

We videotaped 22 Ovenbird nests during the 1996 and 1997 breeding seasons. Ten of 22 (45 percent) Ovenbird nests were parasitized with an average of 1.5 cowbird eggs per parasitized nest. In Hann's (1937) study, 22 of 42 nests (52 percent) were parasitized, with parasitized nests containing an average of 1.8 cowbird eggs. The data are comparable even though Hann worked primarily in Michigan and we conducted our research in Weston, Massachusetts. In 6 of the 10 parasitized nests we videotaped, we discovered that baby cowbirds remained in the nest for at least 24 hours after the Ovenbird nestlings had fledged. These cowbird nestlings continued to be fed in the nest by the Ovenbird adults even while the Ovenbird adults were feeding their own Ovenbird fledglings. The other four parasitized Ovenbird nests were subjected to predation, so we do not know whether the cowbirds would have remained in the nest for a period of time after the Ovenbirds fledged.

There are many cues that could be used by Ovenbird parents to distinguish one of their own eggs or offspring from a parasite. Ovenbird eggs are smaller than cowbird eggs, and they are differently colored (personal observation; Hann 1937). Cowbird nestlings are considerably larger than Ovenbird nestlings. Their down and beak feathers are substantially different, as are the color and shape of their beak. Cowbirds beg more vigorously and call more loudly than Ovenbird nestlings and fledglings (personal observation; Hann 1937). At first, cowbird nestlings reach for food from above rather than to the front of the dome-shaped Ovenbird nest, and when they defecate they do not turn to the front as do Ovenbird nestlings (Hann 1937). Finally, cowbirds remain in the nest for at least one day after the Ovenbirds have fledged. In three instances in which we observed fledging on videotape, all Ovenbird nestlings fledged within minutes of each other. Two of these nests had only Ovenbirds, and the third had three Ovenbirds and two cowbirds. In the nest with both Ovenbirds and cowbirds, the Ovenbirds bolted from the nest within seconds of each other, and the cowbirds remained unaffected and stayed in the nest. The Ovenbird parents continued to return to the nest to feed the cowbirds while also feeding the Ovenbird fledglings. This represents unusual behavior for Ovenbirds: because Ovenbird nestlings apparently fledge within minutes of each other, adult Ovenbirds would not normally have to return to the nest to feed a partial brood.

What could be more maladaptive than the relationship between Ovenbirds and cowbirds (at least from the standpoint of the Ovenbirds)? Here we have members of one species, Ovenbirds, returning to feed nestlings of another species for up to two days after their own young have fledged. The nestling cowbirds look and behave distinctly differently from Ovenbird nestlings, yet Ovenbird hosts continue to care for them. Evolutionary lag? Possibly. The problem with suggesting that a behavior doesn't exist because there has not been sufficient time for its evolution, is that such an hypothesis cannot be tested. That is, no one can predict when or whether such recognition will ever evolve — it depends upon random genetic change. Evolutionary equilibrium? We don't think so. To us the feeding of cowbird nestlings after their own young have fledged seems clearly maladaptive, and there is no need to invoke an evolutionary-equilibrium hypothesis to explain the behavior.

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