

## Competition For Life, And... Parasitism In Birds - Part 2

There are a number of birds that engage in what ornithologists call brood parasitism. This habit has evolved independently seven different times, and brood parasites can be found in both temperate and tropical regions. Brood parasites lay their eggs in the nests of other species, which then raise the parasite's young at the expense of their own offspring. Such parasitism seems particularly odious to most human observers, and even some biologists regard the phenomenon with moral indignation. This is easy to understand. Brood parasites are often larger than their foster parents, and there is something about watching a small foster parent feeding a monstrous, greedy nestling that strikes the same indignant chord in our sensibilities that seeing congressmen voting themselves tax breaks does. And if this weren't bad enough, some brood parasites use reprehensible tactics to ensure their own well-being. The young of the European Cuckoo shove the rightful eggs out of the nest before they hatch, and hatchling African honeyguides stab their nest mates to death with a specially modified tooth.

The brood parasite in the system we will describe is the Giant Cowbird (*Scaphidura oryzivora*), a member of the oriole family. Its breeding habits are similar to those of the Brown-headed Cowbird of temperate North America. The female cowbird first locates the

nest of a host species. Then, when the time is right, usually just after the host female has deposited her eggs, she sneaks in and lays the egg or eggs in the nest. Hatchling cowbirds are well suited for their lives as parasites. They develop rapidly and they are aggressive. Baby Giant Cowbirds hatch a week or so before their legitimate nest mates; they also develop much more quickly. Their eyes open within forty-eight hours of hatching, while those of the host nestlings may not open for six to nine days. Unlike the cuckoos and honeyguides, cowbirds do not dispose of their nest mates, but their rapid development gives them a head start over the nest's rightful inhabitants, and they are able to usurp a major share of the food brought to the nest by the parents.

The parasite clearly gains, as its total reproductive effort consists only of finding a suitable host nest and dropping its eggs. It need never bother with raising young, an activity which normally requires a considerable expenditure of risk and effort. The situation is also obviously an enormous evolutionary disadvantage for the duped foster parents, who raise the cowbirds to the detriment of their own offspring. Or is it?

Neal Smith of the Smithsonian Tropical Research Institute studied the relationship between the Giant Cowbird and its host species in Panama. The title of his study, "On the Advantages of Being Parasitized," immediately suggests that something counterintuitive is about to be revealed.

Unlike the Brown-headed Cowbird of North America, which is nonchalant over whom it entrusts its offspring to, the Giant Cowbird selects a particular type of foster parent. There are four such host species in Panama: the Chestnut-headed Oropendola (*Zarhynchus wagleri*), the Montezuma Oropendola (*Gymnostinops Montezuma*), and the Crested Oropendola (*Psarocolius decumanus*), and the Yellow-rumped Cacique (*Cacicus cela*). These four species nest in colonies, and their large, intricately woven pendant nests are one of the characteristic sights in tropical forests. The nests are usually clustered in the canopy of single tree, often a very tall one with an open, spreading canopy, and the trees are frequently found along clearings and riverbanks.

Smith discovered a complex set of interactions between the cowbirds and oropendolas. In some colonies the parasitic cowbirds were sneaky; they skulked around the oropendola nests and stealthily deposited an egg or two when the host females departed. The eggs they laid resembled the eggs of the oropendolas, an adaptation well known in other brood parasites. This is the type of behavior characteristic of brood parasites, and it is to their advantage to be as sneaky as possible. But not all cowbirds behaved in such a fashion. The cowbirds that hung around some oropendola colonies were nothing short of brazen. These female cowbirds were aggressive and often drove off the nesting oropendolas so they could lay their eggs at their own convenience. Rather than lay just an egg or two like their stealthy sisters, these females laid several eggs at a time, as many as five in a single oropendola nest. And their eggs did not at all resemble those of the hosts.

Smith was intrigued by this audacious behavior on the part of a bird that should be sneaky. And he was even more intrigued by the behavior of the oropendola hosts. In those colonies where the sneaky cowbirds laid their eggs, the oropendolas were picky. If they found an egg in their nest that didn't look right, they shoved it out. This behavior, and the stealthiness of the cowbirds, made it obvious that the cowbirds were unwelcome in those colonies. But in the colonies with the brazen cowbirds, the oropendolas just didn't care about foreign eggs in their nests. Even though the cowbird eggs didn't resemble their own eggs, they let them remain, and they didn't even seem to mind getting chased out of their nests so the cowbirds could lay.

Smith eventually found the reason for this peculiar behavioral dichotomy. Oropendolas and caciques are not the only creatures that live colonial nest sites in these large emergent trees. Such trees are also a favored site for colonies of a number of social wasps in the general *Polybia*, *Stelopolybia*, *Protopolybia*, and *Brachygastra*, as well as for various species of meliponine bees. The colonies of these wasps and bees are large, sometimes running to tens of thousands of adults in each nest. The wasps are equipped with potent barbed stings that deliver a nasty venom, and the meliponine bees bite and rub irritating mandibular secretions into the skin and eyes of any creature foolish enough to venture too close to their nests. Both wasps and bees respond with alacrity to any disturbance, but they seem to be most sensitive to such signals as vigorous shaking of the nests and foreign odors like sweat. Once disturbed, these highly social insects use alarm pheromones to alert their sisters of danger and call them to defend the nest.

The association of oropendola nesting colonies with social insects has some obvious benefits for the birds. As long as they can avoid the wrath of the insects, they are protected from numerous potential predators. There are many animals that roam the canopy who would delight in a meal of bird eggs – mammals like opossums, raccoons, kinkajous, and white-faced monkeys relish both eggs and nestlings, and would no doubt enjoy wasp and bee larvae given the opportunity. By defending themselves against these predators, the wasps and bees also afford protection to their more vulnerable neighbors. In addition, the birds are protected from predators like snakes, which would not be interested in the wasp or bee larvae because they would trigger the insects' response by their movement through the canopy. Oropendolas are not the only Neotropical birds who have stumbled on the benefits of aggressive hymenopteran neighbors; some trogons actually build their nests inside wasp nests.

Smith discovered that proximity to a bee or wasp nest afforded the oropendolas respite from a plague of botflies. Botflies of the genus *Philornis* were common parasites on nestling oropendolas where wasps and bees were absent, and unlike Jerry's relatively benign guest, *Philornis* could devastate their hosts. A single botfly larva could severely debilitate a little bird in the nest, and seven such larvae were enough to kill the nestlings. But in some unknown way the presence of aggressive wasps and bees kept the botflies at bay. If the oropendolas built their nests too far from the wasp or bee nests, botfly larvae

might show up in nestlings; but if the bird nests were close to the wasps and bees, there were no botflies.

The association between oropendola colonies and insect colonies is not perfect. In some trees where oropendola colonies are found, there are few if any aggressive wasps or bees. In these trees the birds build their nests on the periphery of the crown, on thin branches that a predator would have trouble negotiating. Although this may afford the birds protection from nest-robbing mammals and reptiles, the botflies are undeterred, and many of the nestlings succumb to their infestations.

Smith found that some of the oropendolas and caciques who had nests in these beeless and waspless trees were able to raise their young without being plagued by botflies. What made these nests interesting was the presence of parasitic Giant Cowbird nestlings. In nests that lacked the brood parasite and were not located in trees with wasps or bees, the botflies infested the hatchling oropendolas and caciques and few survived to leave the nest. It appeared as though the presence of cowbirds was somehow salutary; in some way these parasitic birds seemed to benefit their hosts.

Smith studied the behavior of the nestling cowbirds for some clues to this puzzle. The precocity and aggressiveness of the hatchling cowbird, which gives these brood parasites a head start on the rightful inhabitants of the nest, actually works to the benefit of the host species in the absence of protective wasps and bees. Whenever a cowbird nestling sees a botfly or botfly larva, it responds with a quick peck and a satisfied swallow. They eat these dangerous parasites before they can infest the helpless oropendolas, and in this way benefit their hosts.

Whether we call a cowbird a parasite or a mutualist with respect to the oropendolas thus depends on the abundance and distribution of wasps, bees, and botflies. A shift in the abundance of these insects can have profound effects on the nature of the cowbird-oropendola relationship.

The wasps that help defend oropendola nests also help protect other organisms. In some cases it seems to be a straightforward Commensalistic relationship. Large decticine katydids roost during the day in foliage net to wasp nests and are protected from the same type of predators that might invade the oropendola nests. There is even a species of social wasp that relies on this strategy, but in this case the advantages may suddenly turn into liabilities.

The Central American wasp *Mischocyttarus immarginatus* is a delicate creature as wasps go. The adults, which are slender and patterned in black and yellow stripes, are rather docile and their colonies rarely contain more than a few dozen individuals in an open platform of exposed brood cells. You can often touch a *Mischocyttarus* colony without eliciting a defensive reaction. A wasp with this placid disposition and fragile nest is obviously

no match for a hungry opossum. Most species of *Mischocyttarus* build their frail nests in a inaccessible cavities under the lip of a stream bank or far out on the tip of a palm frond. But *Mischocyttarus immarginatus* has found an alternative defensive ploy. This species usually builds its nests in the company of another species of social wasp, one with more aggressive adults and with larger colonies. Often it chooses a member of the *Polybia occidentalis* group, who build large, conspicuous, globular or cylindrical paper nests in bushes and on cacti and tree limbs. These aggressive neighbors undoubtedly help protect the timid *Mischocyttarus immarginatus* in much the same way that other polybiine wasps help protect the oropendolas.

This would appear to be a cost-free adaptation by *Mischocyttarus* to the problem of mammalian predation, a clear example of a commensalistic relationship. And so it is during the wet season. But *Mischocyttarus immarginatus* is most abundant in the dry forests of Guanacaste Province in northwestern Costa Rica, where there is a long and pronounced dry season. The forest here drops its leaves during this season, exposing the *Polybia occidentalis* nests, which are very conspicuous because of their size and shape. The thousands of fat larvae in these exposed nests become increasingly desirable as populations of many other insects decline, and a variety of birds, both large and small, soon begin to raid the nests. Red-throated Caracaras and kites will brave the stings of the adult wasps and smash the *Polybia* nests into fragments to devour the grubs.

The onslaught comes quickly; it is not unusual to find half of the *Polybia* nests in a given area destroyed within two weeks. The *Mischocyttarus immarginatus* nests are destroyed along with the *Polybia* nests. There are always a few solitary *Mischocyttarus immarginatus* nests around, and not all of the *Polybia* nests fall prey to birds during the dry season, so the system persists and *Mischocyttarus immarginatus* continues to seek the seasonal advantages of an aggressive neighbor. But the delicacy of this arrangement is easily seen, and a slight lengthening of the dry season might suddenly shift the balance, making it more profitable for *Mischocyttarus immarginatus* to seek sheltered nest sites like most other species of *Mischocyttarus*.

The simple passage from night to day can also alter the ecological relationships between two species. During the day, tropical dung scarab beetles face stiff competition from a variety of flies for a scarce resource. The flies often possess a keen sense of smell that enables them to detect and locate a fresh dung pile rapidly. They are generally the first insects to arrive, and they lay eggs that hatch rapidly into voracious larvae. These eggs contaminate the dung for the beetles that arrive later because the fly maggots grow fast enough to starve out the beetle larvae. But some dung beetles have accepted the aid of another creature to help reduce competition with flies.

If you look closely at the adult dung scarabs, you will sometimes see lumps on the limbs and underside, waxy little globules that are in fact a living, shifting blanket of mites. The abundance of these mites might lead you to believe that the beetles are suffering a

slow, itchy, bleeding death – an impression particularly vivid if you happen to be suffering from an infestation of chiggers at the time. But this is not necessarily the case. Many of these mites are merely hitchhikers; when the beetle arrives at a pile of dung, the mites scamper off to scour the surface of the heap, feeding on whatever eggs and larvae they find. More often than not these eggs turn out to be those of flies. Studies done this same phenomenon in the northern temperate zone demonstrate clearly that mites greatly increase the beetle's ability to compete with flies.

In the temperate zone most dung beetles are diurnal, but in the warm tropics there are many species of nocturnal dung-eating scarabs. These large, relatively clumsy beetles fall easy pretty to birds and large lizards during the day, and perhaps they have become nocturnal to avoid such predation. Also, many tropical mammals are nocturnal, so perhaps availability of food may have pushed these beetles to be active at night. Whatever the cause, these nocturnal scarabs face less competition from dung-eating flies. Without the flies, the hitchhiking mites become a liability rather than an asset, and a relationship that is mutually beneficial during the day suddenly becomes one-sided at night. Nothing is known of the biology of the mites that infest nocturnal dung scarabs, but we doubt that they confer the same advantages to a night-feeding scarab as they do to a day-feeding one, and it is possible that they actually interfere with the beetle's activities. The daytime mutualist may thus become a nighttime parasite.

These interspecific associations reveal something of the complexity of the tropics. There is little doubt that such complexities are more prevalent in the tropics than in the temperate zones, but the dynamic and patchy qualities of the living world are characteristic of all habitats. Such relationships resist textbook labeling and mental pigeonholing, forcing one to consider the particular and the peculiar. An appreciation of the unique is to us the essence of natural history, and although we must call on general principles to explain what we see, we consider the real world, with all of its messiness and confusion, far more interesting than any neat theory or model. William Blake's claim that "to generalize is to be an idiot" does have a ring of truth. Perhaps those souls who seek order in the structure of life can find some solace in the fact that we have deliberately sought out complicated relationships to make our point. Straightforward types of symbioses are common: yet even these simple relationships are changing as natural selection works on all involved. The "endless forms" that Darwin's vision brought forth from a static world are not just the limbs and colors of individuals, but the rich and still dimly understood relationships that thread among them.