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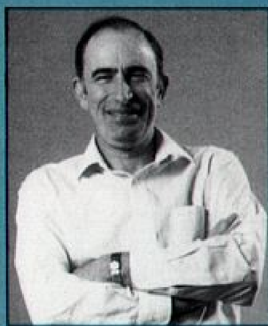
BIRDING FOR FUN



Avian Coevolution

Illustrations by Darryl Wheye

Not only are plants and herbivores coevolving, but so are plants and pollinators, plants and seed dispersers, predators and prey, hosts and parasites, and so on.

IT STARTED FOR ME in 1965, during the hiatus between my early interest in birds and becoming a born-again birder. I had run across what seemed to me a peculiar choice of food plants by caterpillars of the checkerspot butterflies that our group had been doing research on since 1960 (and is still studying). I questioned my botanical colleague Peter Raven about it and, to make a long story short, we began a detailed investigation of the eating habits of caterpillars. Our conclusion was that plants are engaged in a "coevolutionary race" with butterflies and other organisms that attack them. To be anthropomorphic about it, the plants (which can't run away) try to fend off their enemies by evolving an array of poisons, sticky fluids, thorns, and other static defenses. The butterflies and other plant-eaters counterattack by evolving ways to detoxify the poisons or avoid the gums or spines. Each species, of course, is simply changing genetically in response to selection pressures created by its opponent.

It was soon clear to Peter and me that this phenomenon of reciprocal evolution, which we named coevolution, was widespread in nature, occurring wherever organisms of different species were ecologically intimate. Not only are plants and herbivores coevolving, but so are plants and pollinators, plants and seed dispersers, predators and prey, hosts and parasites, and so on. Sometimes a coevolutionary race is involved, as one species "tries" to take advantage of another. Sometimes coevolution is mutually beneficial, as is usually the case with pollination and seed dispersal. In recent decades, coevolution has become a major subdiscipline of evolutionary ecology.

Coevolution enters the lives of birds and birders in many different ways. Nocturnal owls have evolved the ability to combine acute hearing, silent flight, and intimate knowledge of terrain to swoop successfully on rodent prey. The prey, in turn, have evolved agility, keen senses, and a tendency to stay near cover that helps them avoid their nighttime hunters. People have long coevolved with their own predators and prey in similar ways. Our upright posture is thought to be related both to looking out for dangerous animals in tall grass and to carrying weapons. While most of us no longer need fear being devoured by a lion and do not stalk our own dinners, we are still engaged in coevolutionary races with organisms as diverse as the AIDS virus, streptococcus bacterium, malaria protozoan, and corn earworm. Fortunately our own coevolutionary races needn't divert us from enjoying signs of the coevolutionary interactions in which birds are involved.

It's hard to watch owls hunt and observe the present state of their coevolutionary race with rodents and rabbits, but it's relatively easy to recognize the results of coevolution by watching Clark's Nutcrackers. This western species has coevolved a mutually advantageous relationship with pinyon and other pines. The nutcracker evolved a long, sharp bill specialized for prying pine seeds from their cones and a pouch under the tongue for transporting the seeds. In times of abundance, the nutcrackers do not eat all seeds immediately, but store them for consumption later. One nutcracker may cache 30,000 or more pinyon pine seeds in a single season. That pine species has evolved cones, seeds, and fruiting times that increase the chances their seeds will be cached by the birds. The nutcrackers (unlike other seed storers) bury the seeds at the proper depth in areas suitable to the trees' development. Best of all from the pines' point of view, the birds don't remember the locations of all of their caches. Both players in the nutcracker-pine coevolutionary interaction benefit. Nutcrackers get plenty of food, and the reproduction of the pines and the ability of pine populations to migrate in response to climatic change are also enhanced.

More spectacular, but still only partially understood, is coevolution between avian brood parasites and their hosts. European Cuckoos and their victims are the best-studied system. The parasites have evolved eggs with an uncanny resemblance to those of the hosts, presumably in response to the evolution of ever-better discriminatory powers on the part of hosts that often respond to alien eggs by walling them off, tossing them out, or abandoning their nests entirely. Since outreproducing your buddies is the name of the game in evolution, there is obviously a very strong selection pressure to avoid raising someone else's offspring. The current enormous negative impacts of populations of cowbirds expanding into new areas of a variety of North American passerines, such as Kirtland's Warbler and Black-capped Vireo, can be thought of as the beginnings of coevolutionary races that the host species may lose.

The European Cuckoo lays eggs that resemble the eggs of its host, here a Reed Warbler.

One of many unanswered questions about the coevolution of brood parasites and their hosts is whether the present degree of rejection of parasitic eggs by hosts can be traced to the recency of contact of host and parasite. Experimental evidence indicates that, in areas where the parasites do not naturally occur, potential hosts are less likely to reject parasitic eggs than are hosts from places where hosts and parasites occur together. But definitive field data showing that rejection rates are higher where cuckoos or cowbirds have long been in contact with their hosts remain elusive. The question is important to North American birds and birders, since Shiny Cowbirds are now invading the southern United States.

The story is even more complicated because ornithologists do not fully understand the process by which different hosts learn to recognize their own eggs (whose patterns often vary somewhat among themselves). Members of some species may learn the pattern on laying the first egg, and thus become able to recognize an alien egg placed in the nest thereafter. Those of other species may learn the range of variation in their own eggs by observing the characteristics of the entire first clutch. Such birds are less likely to reject one of their own eggs if it differs from the first one laid, but are more vulnerable to being parasitized before the learning period is over. The better strategy depends, among other things, on the parasitism rates and the mimetic capabilities of the parasites. Cowbird hosts, for instance, may risk learning only the general character of their own eggs at first laying, since

Pitohui species may benefit from two types of mimicry. From top, Hooded, Variable, and Rusty pitohuis.

cowbird eggs generally are not mimetic and a fine-tuned ability to discriminate is not so necessary.

Birds also are involved in the textbook example of mimetic coevolution—that of mimicry in butterflies. For example, some butterflies (like the monarch) are distasteful to birds; often after eating one the bird vomits. Such distateful "models" normally are brightly colored, announcing their toxicity to potential diners and making it easier for predators to learn and remember that pattern. Others (such as the viceroy) are tasty, but have evolved prominent color patterns that mimic unrelated distasteful models. The monarch (model) and viceroy (mimic) are the most famous mimetic pair of this sort in North America, but in the tropics there are many examples of groups of unrelated species in which coevolution has produced resemblances that are even more striking. In some tropical cases, the similarity between model and mimic is so strong that one must have a butterfly in the hand and look for structural characteristics of the wing veins or legs to be sure which butterfly *family* it is in.

It is likely that birds are the selective agents primarily responsible for the evolution of these close resemblances between distasteful models and tasty mimics, examples of Batesian mimicry. Birds have excellent vision, and the closer the model mimic resemblance, the more likely the birds will be fooled into mistaking a tasty mimic for the poisonous model. Over millennia, the individuals that are less perfect mimics have been devoured more often than those with a closer likeness to the models, leading to an ever-increasing average resemblance. In some cases, though, all members of a group of closely similar, brightly colored butterfly species are distasteful. The putative reason selection has favored their convergent appearances is that birds need only learn one butterfly color pattern to avoid. Fewer individuals of each butterfly species need die of being tasted in order to educate the birds. This latter type of all distasteful-model mimicry is called Müllerian (both kinds of mimicry were named after their discoverers).

It is also likely that, in addition to being promoters of butterfly-butterfly coevolution, birds are directly involved in the same coevolutionary complexes. They should be evolving better ability both to distinguish between models and mimics, and to tolerate the poisons that the models store in their bodies as defensive mechanisms. But mimicry remains an imperfectly understood area of coevolution, full of fascinating unanswered questions, such as to what extent do the models "flee" from the mimics, continuously evolving new color patterns so the birds would have an easier time distinguishing them from good food and leave them unmolested?

Some years ago I was lucky enough to bird in New Guinea with my friend Jared Diamond, doyen of avian ecologists working in the southwest Pacific (and outstanding digestive physiologist to boot). On our first excursion into the forest, Jared ticked off thirty or so species by ear—before I finally tracked one down for a look and learned that his identifications were accurate. That first bird was a Variable Pitohui, a *pachycephaline* flycatcher related to Australian whistlers. Little did I know then that I was observing a species involved in one of the most interesting examples of coevolution in birds that has just been uncovered—in the area of predator-prey coevolution where, this time, birds, not butterflies, were the prey!

New Guinea hunters refer to several pitohui species as "rubbish birds," which should not be consumed unless their skin is removed and other precautions taken. Recently, scientists noted a numbness, a burning in their mouths, and a pungent odor after netting and handling a pitohui. Subsequently, extracts of the skin and (in some cases) feathers and breast muscles of three pitohui species, when injected into laboratory mice, caused convulsions and death. Chemical analyses revealed the presence of homobatrachotoxin, a deadly poison previously thought unique to dart-poison frogs from South America. The frogs are so named because Amerindian hunters use the frog skins to poison the darts they launch from blowguns at their quarry. The presence of the toxin in two such geographically and taxonomically distinct groups of organisms is a superb example of convergent evolution: natural selection twice solving the same problem in precisely the same way. That problem, of course, is how to keep ahead in the coevolutionary race with predators.

It seems evident that the toxin helps to protect both pitohuis and frogs from being eaten. This notion is supported by the striking colors of the pitohuis, which like those of the frogs and model butterflies are almost certainly announcements of their bitter taste and numbing toxin. As Diamond has pointed out, the possibility of both types of mimicry is present here. The pitohuis often resemble one another and may represent a case of Müllerian mimicry. Five pitohui species (including the three tested) are nuclear species of "brown and black" mixed-species foraging flocks that include some 35 presumably tasty species of other groups whose plumage, like that of the pitohuis, contains substantial areas of brown and black or both. These could be examples of Batesian mimicry.

Coevolutionary interactions seem especially intense in tropical forests. There, hummingbirds with spectacularly sickled beaks pollinate similarly shaped flowers. Other plants produce large-seeded fruits especially designed to attract birds. The birds, in turn, have evolved bills with wide gapes and specialized guts that dissolve the flesh from the impervious seed, which is subsequently regurgitated. And poisonous pitohuis and distasteful butterflies roam. If you can possibly afford a trip to one of these birding paradises, go quickly. They are among the most imperiled habitats on our planet.

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