Butterflies and Bad Taste

Rethinking a classic tale of mimicry

By TIM WALKER

Picture a bird searching for a mid-afternoon snack – perhaps a butterfly. After all, butterflies fluttering from flower to flower make easy targets for a swooping bird.

Suddenly, the bird spies a bright orange butterfly. But instead of attacking, the bird ignores it. Why? Because the bird remembers what happened the last time it ate a bright orange butterfly: It vomited.

So the butterfly survives and continues on its way, courtesy of the bright orange warning that nature painted on its wings.

But was this a false warning? Did the butterfly's color trick the bird into passing up what would have actually made a tasty hors d'oeuvre? If the orange butterfly was a viceroy, *Limenitis archippus*, most biologists would have answered yes. For more than a century, the conventional wisdom has held that this winged insect cloaks a very appetizing body behind the colors of a toxic monarch butterfly, *Danaus plexippus*.

Ritland

The only major visual feature distinguishing a monarch (left) from a viceroy (right) is the black semicircular line bisecting each of the viceroy's lower wings.

New research indicates, however, that the viceroy has successfully deceived scientists, not birds. Entomologists have long labored under the assumption that the viceroy's orange warning colors were just a bluff. Now, two zoologists have demonstrated that to discerning birds, the viceroy can taste just as foul as the noxious monarch.

Nineteenth-century English naturalist Henry Walter Bates first put forth the idea that a species of tasty butterfly could protect itself by evolving to mimic a toxic species. He based this hypothesis on his observations of butterflies in the Amazon river basin during the mid-1800s. One species' exploitation of another's protection system has been called Batesian mimicry ever since.

And for most of this century, biology textbooks have touted the viceroy-monarch relationship as the classic example of Batesian mimicry – a truism that must now be reconsidered.

David B. Ritland and Lincoln P. Brower of the University of Florida in Gainesville have conducted an avian taste test, serving up the abdomens of seven different butterfly species, including viceroys and monarchs, to local red-winged blackbirds. The test aimed to determine which butterfly species, if any, were noxious to the birds. Because these snacks lacked wings, the birds had to base their selections on the taste of the butterflies' bodies alone.

The birds found the viceroy just as unappetizing as the monarch, the zoologists report in the April 11 NATURE. In fact, the birds rejected more than one-third of the viceroy bodies after pecking them just once. These results "clearly refute the traditional hypothesis that viceroys are palatable Batesian mimics," Ritland and Brower say.

Butterfly mimicry is more than a curious biological sideshow. Deciphering mimicry relationships helps biologists understand some of the complicated and dynamic forces that affect the evolution of a species, Brower says.

Why had no one challenged the viceroy's avian palatability before?

One reason, says entomologist Austin P. Platt of the University of Maryland-Baltimore County in Catonsville, is that the viceroy evolved from a group of tasty admiral butterflies. "So it was just widely held that the viceroy itself was also palatable," he explains.

During the last several years, however, a few experiments began to cast doubt on the viceroy's supposed tastiness, according to Richard I. Vane-Wright of the Natural History Museum in London, England. But those experiments used whole butterflies, Ritland says, which meant that the taste-testing birds could have rejected the viceroys because of their orange wings and not because of any noxious taste.

Moreover, Vane-Wright says, many biologists believed butterflies couldn't manufacture their own toxic chemicals to defend themselves from predators; instead, the insects had to absorb the toxins of poisonous plants during their caterpillar stage. And viceroy larvae don't feed on toxic plants.

The adult monarch's chemical defense, however, does depend on toxins in the milkweed plants on which its caterpillars feed, Brower notes. Because monarch caterpillars incorporate the heart toxins, called cardiac glycosides, that milkweeds rely on for their own defense against herbivores, eating a monarch can "really set a bird's heart jumping," he observes.

But the toxicity of an individual monarch depends on the variety of milkweed it ate as a caterpillar, Brower says. A bird that eats a monarch butterfly that dined as a caterpillar on a mildly toxic variety of milkweed will not be poisoned. But a monarch caterpillar feeding on a strongly toxic milkweed variety will become a truly toxic butterfly, potentially deadly to any bird that eats one and doesn't vomit it back up.

Viceroy caterpillars, in contrast, feed on nontoxic willows, and this suggests that viceroy butterflies somehow manufacture their own chemical defense, Vane-Wright says. The observation supports a new view among some lepidopter-

ists that not all butterflies depend on plant poisons for their defenses, but instead develop as "masters of their own evolutionary fate," he says.

For example, Ritland and Brower's results suggest that the viceroy may actually be a "Mullerian" mimic of the monarch. This kind of mutually advantageous mimicry is named for the 19th-century German-born Brazilian zoologist, Fritz Muller, who first described how two or more equally distasteful butterfly species gain greater protection from predators by evolving the same general appearance.

Brower explains the advantage: If each of two chemically protected species has a different wing-color pattern, then a bird will have to eat many individuals of each species before it learns to avoid both. But if both species evolve the same color pattern, then only half as many of each species need succumb before a bird learns to avoid snacking on winged tidbits bearing their colors.

Batesian mimics, as "sheep in wolves' clothing," are very vulnerable to birds that learn to see through their bluff, Vane-Wright says. Ironically, Batesian mimicry becomes riskier as the mimics begin to outnumber their toxic models. Birds soon learn to attack butterflies and taste them to determine whether they are toxic before deciding whether to swallow them, Brower explains.

Because the monarch varies so much in its toxicity, it may not be such a good model for an unprotected species to mimic, Ritland says. He speculates that the viceroy butterfly's own chemical defense evolved because birds learned that not all orange-colored butterflies would cause them to vomit.

Because all of the viceroy's ancestors are dark-colored, many biologists suspect the viceroy spent most of its evolutionary history evolving as a mimic of the monarch, Ritland says. However, Brower suspects the viceroy began evolving its chemical defense and becoming a Mullerian mimic rather recently—perhaps as little as 10,000 years ago—in a move that "changed the rules of the game between the viceroy and the monarch."

Some monarchs migrating south to Florida in the fall may actually represent Batesian mimics of the viceroy, Brower says. Because monarch caterpillars in the northeastern United States feed mostly on mildly toxic varieties of milkweed, as butterflies they possess few cardiac glycosides — and therefore are only mildly noxious to their predators.

Indeed, Brower speculates, birds in Florida may discover that these migrating monarchs are safe to eat, thereby thwarting the mutually beneficial Mullerian mimicry between the viceroy and the monarch. Because birds are particularly adept at learning about changes in their food supply, it's quite likely that some do discover that the monarch migrants are tasty, Ritland explains.

And if nontoxic monarchs become too abundant, the viceroy may actually begin to evolve away from the bright orange wing pattern it adopted many years ago, Ritland suspects.

These possibilities lead Ritland to describe his circle of biologists—those who are trying to decipher the complicated relationships among butterfly mimics—as "players in a great big detective game."

Although Ritland and Brower showed that the viceroy isn't bluffing when it flashes its orange warning, the species isn't above a bit of trickery to repulse a hungry bird. After its first molting, the viceroy caterpillar wears a brown coat with a patch of white — a suit that looks surprisingly like a bird's fecal droppings. □