A Double-billed Dilemma

A West African finch with an evolutionary puzzle in its beak

by Thomas Bates Smith

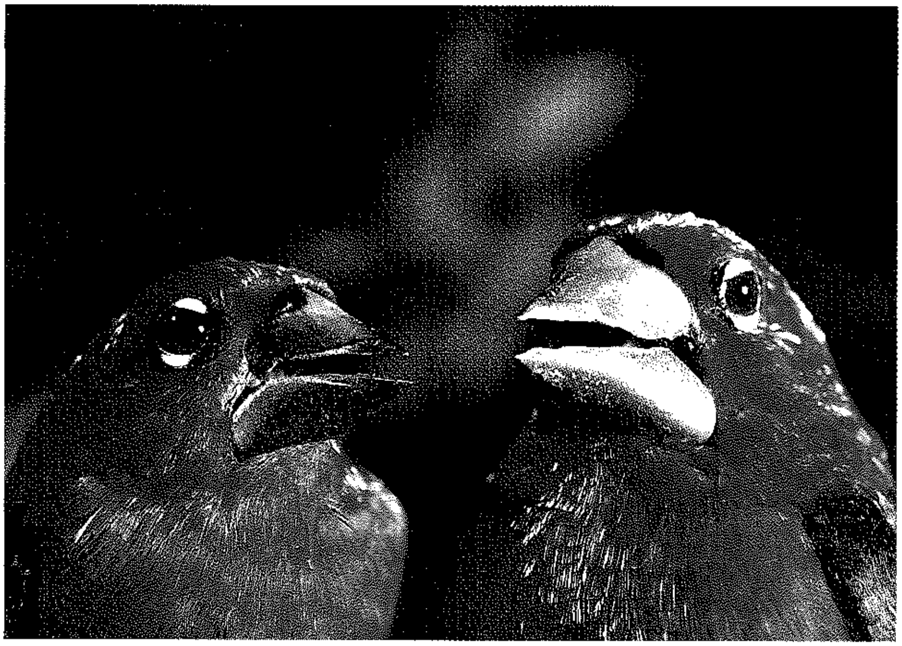
Night sounds fade and light begins to descend through the dense canopy as we paddle our dugout through the narrow channel. Piercing the dense mist, enormous tree trunks rise abruptly at our sides. Overhead, the dawn silence is broken by the defensive "coughs" of talapoin monkeys as they jet across the canopy. It is morning on the Nyong River.

After a forty-minute trip, we reach the place where we have tied our first line of mist nets, thirty-six-foot lengths of fine mesh used for capturing birds. When open, they form a curtain twenty feet high, nearly invisible in the dawn light. After unfurling the nets, we move to the next line. We will return in half an hour to collect, measure, band, and release the birds we catch in them.

In 1985 my wife, Paige, and I left the comforts of Berkeley, California, and established a primitive camp in the remote rain forests of Cameroon, West Africa. Here we lived for two years with little contact with the outside world other than a radio. Our closest neighbors lived half a mile away in the small mud-hut village of Ndibi. Here all long-distance calls are free; they are pounded out on a drum.

We came to study a small finch called the black-bellied seedcracker, one of more than 850 species of birds found in Cameroon. We chose this particular species after reading the account of one of the earliest zoological expeditions to Africa, led by two zoologists from the American Museum of Natural History, Herbert Lang and James P. Chapin. They arrived in Leopoldville, Belgian Congo (now Kinshasa, Zaire), in 1909 on the the first major expedition to the legendary "heart of darkness" region since Stanley had found Dr. Livingstone in 1871. Lang and Chapin's mission was simple: spend two years collecting specimens and studying the natural history of tropical West Africa. However, six years after setting sail for the so-called Dark Continent, they were still there, collecting and studying animals and plants unknown to science. At the end of the expedition, they cataloged an immense amount of material—25,000 skins and skeletons and 100,000 insects—and documented the region's natural history and culture with more than 10,000 photographs. Chapin, only twenty-five years old when he returned to New York in 1915, spent much of the remainder of his career writing what is still considered one of the most authoritative works in African ornithology, the four-volume *Birds of the Belgian Congo.*

Photographs by Thomas Bates Smith



Two male black-bellied seedcrackers exhibit the two bill sizes that characterize the species. The stouter bill of the bird on the right gives it greater crushing power.

On September 3, 1924, nearly nine years to the day after he sailed into New York Harbor, Chapin published a short paper entitled "Bill Size Variation in *Pyrenestes,* a Genus of Weaver Finch," in which he described an unusual phenomenon. He had found that within each of the three species that made up the genus there existed large-billed (about 1.6 cm) and small-billed (1.25 cm) variants but no individuals with intermediate-sized bills. What was unusual was that the size difference had nothing to do with gender or with region: both males and females had bills of either size, and far more perplexing to Chapin, both bill forms were found together across Africa. A comparable phenomenon in humans would be if a continent were inhabited by adults four to five feet tall and six to seven feet tall, with no

A male seedcracker with a large bill feeds on a hard-seeded species of sedge.

one between five and six feet. Given such evidence, taxonomists of the day would have assumed that the bill variants were simply separate species (they could not be "races," or subspecies, since they occurred together geographically). However, Chapin clearly wasn't satisfied. Thirty years after the publication of his 1924 paper, he wrote, "that birds of differing bill size may interbreed may not be doubted.... Yet there must be some reluctance toward mating with a bird of markedly different size, otherwise each population would quickly approach a mean."

If not separate species, then what did these bill variants represent? Chapin wasn't sure. The most interesting possibility, however—and one that Chapin did not consider—was what drew us to Africa.

This was the idea that the two bill sizes represented distinct variants within a single population of interbreeding birds—a phenomenon known as polymorphism. Polymorphisms in color, called phases or morphs, are quite common in natural populations. Black bears are not always black but also show a cinnamon and blue phase. Similarly, snow geese come in a blue phase and a white phase. Although common in nature, the evolutionary mechanisms that give rise to color polymorphisms are poorly understood. (One recent review paper listed a dozen different evolutionary forces that may be working alone or in concert to maintain color polymorphism in European land snails.)

Unlike color polymorphisms, the causes of which can be very hard to pin down, a polymorphism in a trait such as bill size offers biologists an excellent opportunity to study how natural selection might be functioning, because the size of a bird's bill is more directly associated with its ability to survive. These types of polymorphisms—often called trophic polymorphisms because they are involved in processing food—are scarce and occur in only a few species of vertebrates: several species of tropical fishes, two species of larval amphibians, and the hook-billed kite, a bizarre species of tropical hawk that preys exclusively on tree snails.

Despite their scarcity, trophic polymorphisms are thought to play important ecological and evolutionary roles. Some theorists believe they allow a broader use of resources, with each form specializing in a different type of food, thereby minimizing competition within the species. For example, in many birds of prey, females are larger than males, and the sexes have distinct diets—larger bodies being better at subduing larger prey, smaller bodies more agile at catching smaller, swifter prey. Evolutionarily, trophic polymorphisms may be steppingstones in speciation, in which populations first diverge ecologically through a polymorphism and later reproductively, resulting in discrete species. This idea has been advanced to explain the huge explosion of cichlid fish species in the Rift Valley lakes of East Africa, where single lakes sometimes contain several hundred species of fish. There, distinct morphs may have first developed ecologically, by feeding on different foods, and later reproductively, by breeding in the region where they forage.

Our hope was to determine if the different bill variants were distinct morphs and to uncover the possible ecological mechanisms that may have produced them. Our study area in Cameroon, just two degrees north of the equator, experiences drastic seasonal change over the year. During the major wet season, from September through November, the Nyong River rises twenty-five feet, flooding adjacent swamp forests, marshes, and, not infrequently, our camp. Getting around comfortably requires a canoe and plenty of insect repellent. From January to June, however, the waters recede and fires burn along the river, occasionally entering the dry swamp forest and reducing it to ashes.

This annual cycle of fires and floods produces an unusual flora. The upland rain forest, which never burns, contains a great diversity of plants and animals, including primates such as chimpanzees and lowland gorillas. The swamp forest contains various species of medium-sized trees and shrubs, many of which drop their fruit during the rainy season. Here, water currents and fish, in addition to birds, wind, and other common agents, help disperse the seeds. But the plants that dominate the understory of the swamp forest and are the principal food of seedcrackers are grasslike plants called sedges.

By mist netting and measuring many of the seedcrackers, we confirmed Chapin's earlier findings that two distinct bill sizes are found in both sexes and that none of the birds have intermediate-sized bills. Oddly, the bill is the only characteristic that varies. Large- and small-billed seedcrackers differ little in other body characteristics, such as overall size. This is unusual in birds, in which bill and body size tend to vary to a similar degree. Were the bill forms different species or not? The answer could only come from identifying breeding pairs and measuring their bills.

Finding seedcracker nests is like looking for a contact lens on a sandy beach. Male seedcrackers, unlike many male birds, do not defend territories around the nest, so we were unable to find nests by locating singing males. We had to search painstakingly for them, not an easy task in dense forest. Seedcrackers breed during the wet season when sedge seeds are most abundant. Nests are usually built in small trees, often in the swamp forest a few feet above water. Typical of the estrildid subfamily of finches, nests are dome shaped, about the size of a football, and have a side entrance. Over the course of two breeding seasons we found sixty nests. When we were able to measure both parents, we found they did not choose their mates on the basis of bill size. This was the first solid evidence that bill types were morphs of a single species. Since then, we have corroborated these findings using biochemical techniques performed on tissues at the

University of California's Museum of Vertebrate Zoology in Berkeley.

Did the bill variants differ genetically? What were the ecological correlates of bill size? How did the difference arise? Capturing and remeasuring marked individuals over time indicated that the variation was not due to differential wear of the bill. This had to be ruled out, since wear and tear on bills can alter their shape. The bills of European oystercatchers vary, depending on the way in which the individual birds feed on intertidal mollusks. The alternative was that age determined the bill types. This was easily rejected, however, since the bill size of birds we repeatedly caught did not change.

Despite this evidence, we wanted to be sure that the polymorphism truly had a genetic basis and was not induced by environmental factors. Perhaps the type of food parents fed nestlings caused them to have bills of different size. If that was the case, attempts to understand how the polymorphism evolved would be superfluous, since for a trait to evolve, it must have a genetic basis. The solution was to examine the bills of offspring from parents of known bill size under controlled conditions. Easier said than done in the wild. Like many tropical species, seedcracker nestlings suffer a high rate of mortality from predation. Only 15 percent of the nests succeed in fledging offspring. Nest predators abound; the most prominent are arboreal snakes, coucals (large cuckoos), and driver ants, which frequently move through the understory in large swarms, devouring everything in sight, including baby birds. For these and other reasons, controlled breeding experiments were necessary. In a collaborative effort with the Riverbanks Zoo in Columbia, South Carolina, we have successfully exported eighty-five finches from Cameroon since 1985. The breeding experiments at Riverbanks Zoo (the first institution to breed seedcrackers in captivity) are still under way, but preliminary results suggest that bill forms do have a genetic basis. So far, mated pairs have produced offspring that have large or small bills but none with intermediate-sized bills.

So what good is it to have two bill sizes? And why aren't there finches with intermediate-sized beaks? Sometimes asking the question "why" in biology is misleading. Not all traits have functions. Some may be present because they occurred in an ancestor and have been carried along as excess baggage. In birds, however, a close relationship exists between bill size, food habits, and survival. Seedcrackers are no exception. These finches specialize in feeding on two species of sedge seeds that differ enormously in hardness, comparable to the difference in hardness between a walnut and a peanut. The hard-seeded sedge requires as much as sixty pounds of force to crack, while the soft-seeded sedge takes less than one. Both kinds of seeds are most abundant during the wet season, when finches breed. To see if finches differ in the times required to crack the two seeds, we conducted feeding trials using captive birds. Not surprisingly, large- and small-billed morphs differed in their cracking times. Large-billed morphs cracked the hard-seeded sedges more efficiently than small-billed morphs, with the reverse true on the soft-seeded sedge. Yet, both bill types fed more efficiently on the soft than on the hard sedge.

However, during the dry season, when there are no soft sedge seeds available, diets differ greatly. Large morphs become specialists on hard-seeded sedges, which they obtain by foraging on loose seeds in the leaf litter, while small morphs become food generalists, feeding on a wide variety of soft-seeded grasses. Small-billed morphs apparently switch to soft grass seeds because of their inability to feed easily on the hard-seeded sedge even though these seeds are still available. Large morphs fail to switch to soft foods, apparently because of their inability to compete with the soft-seed specialists.

In this way, the feeding ecology of large- and small-billed birds functions as though they were two distinct species. Studies of species that feed on similar foods have shown that diets overlap most when food is abundant and least when food is scarce. Competition for food during times of scarcity is widely thought to cause similar species to diverge in diet. This is exactly the pattern found in seedcrackers and may well be due to competition between morphs.

Closely allied species of seedcrackers have bills more similar in size and shape to the small-billed morph, suggesting that the ancestor of seedcrackers also had a small bill. If for some reason the small-billed ancestor began feeding on the soft sedge, it would have had very little competition from other species, because few birds eat sedges. Under these conditions, ecological theory predicts that competition within species would lead to greater variation in bill size. As a result, any individual that became large enough to take advantage of the hard sedge seeds so far not used for food would have had an advantage. Large morphs may therefore have arisen as a result of specializing on the hard sedge seeds.

The existence of two bill types within one species raises many intriguing evolutionary questions. Might, for instance, one of the types become isolated enough in its habits to stop interbreeding with the other, resulting in a large- and a small-billed species? Sympatric speciation—speciation that takes place in one geographical region—is a very controversial topic in evolutionary biology. Most biologists believe speciation rarely, if ever, takes place this way, but requires that a population first be separated geographically. Nonetheless, sympatric speciation would seem possible if the fruiting of different sedges occurred at different times of the season. Under these circumstances, morphs might prefer to pair with mates of similar bill size in order to match the availability of seeds on which they are most efficient, thereby maximizing the number of offspring that could be successfully fed.

This brings us to Djohong, in the remote northeastern corner of Cameroon. Djohong is a small village bordering the Central African Republic and lies in a transition zone between the forest to the south and the savanna to the north. In the early 1960s, a Belgian ornithologist visited Djohong and collected a single seedcracker, which I happened upon while visiting museums in Europe. This remarkable individual had a bill far greater in size than the largest-billed birds in my study area, but similar in size to birds Chapin had collected in northeastern Zaire. What produced this enormous bill? Although I had my suspicions, I had to wait a year for the answer. It was a three-day trip by four-wheel drive to Djohong, across some of the roughest roads imaginable. Several times during the journey we found troops of baboons camped out on the road, often refusing to move. The Catholic nun who greeted us at the mission still remembered the Belgian ornithologist and directed us to the exact spot where he had collected the finch twenty-five years earlier. There, growing along a small stream, was the reason for the bird's large bill: another species of sedge, with seeds twice as hard as those of the hard-seeded sedge growing in our study area. Did the larger-billed variant represent a new species of seedcracker or yet another bill morph? Future work will tell. But now I understand how Lang and Chapin's two-year expedition ended up lasting six.

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