Chapter 4

Darwin's Beaks

What a trifling difference must often determine which shall survive, and which perish!

—Charles Darwin,
letter to Asa Gray

When Darwin was a student there, Christ's College was known as the school of John Milton and the Reverend William Paley. Paley was required reading for a B.A., and Darwin read him over and over, "charmed and convinced by the long line of argumentation." In fact, Paley's *Evidences of Christianity* and *Natural Theology* gave Darwin "as much delight as did Euclid."

Natural Theology: Or Evidences of the Existence and Attributes of the Deity Collected from the Appearances of Nature had been a best seller when it was first published in 1802. The book's first lines are sometimes quoted even today. "In crossing a heath, suppose I pitched my foot against a *stone*, and were asked how the stone came to be there," Paley begins; "I might possibly answer, that, for anything I knew to the contrary, it had lain there forever: nor would it perhaps be very easy to show the absurdity of this answer. But suppose I had found a *watch* upon the ground. . . ."

A watch would require more explanation than a stone. A watch, says Paley, implies a watchmaker. Someone had to invent it; someone had to put it together. And if that is true of a watch, Paley asks, how much more so of the living things we find on the heath? Even the simplest working parts of the smallest plants and animals go so far beyond our mortal powers of artifice that they imply "an artificer of artificers," a creator of creators, a God.

That was the world view of both Darwin and FitzRoy while they were standing on the black lava of the Galápagos, where a live bird looks almost as surreal as a watch on a heath. And afterward, that is how FitzRoy remembered the beaks of the Galápagos finches. "All the small birds that live on these lava-covered islands have short beaks, very thick at the base, like that of a bull-finch," FitzRoy writes in his *Beagle* memoirs (three volumes, with Darwin's memoir tacked on as a fourth). FitzRoy is mistaken, of course; his description fits only one out of the thirteen Galápagos finches, the heavy-duty lineman's pliers of *magnirostris*. But in any case, such a powerful beak—FitzRoy goes on to suggest—must be perfect for hunting and pecking on iron-hard lava and crushing berries for their juice. "This appears to be one of those admirable provisions of Infinite Wisdom by which each created thing is adapted to the place for which it was intended."

Darwinism is often spurned by the devout as a branch or prop of atheism. Yet Paley inspired Darwin at least as much as he inspired FitzRoy, and it was precisely this tradition of natural theology that led Darwin to the most original and unconventional step in his argument, his theory of the importance of variations.

If living things are well made, Darwin argued—if they are admirably adapted to their places in nature, contrivances more elaborate than watches—then even the slightest variations must make a difference to the individual animals and plants that are saddled with them. Some variations must help living things run better, some worse, and some—a very few variations, arising only once in thousands of generations—might help them fit into an entirely new spot in the economy of nature.

The beak of a bird makes a natural test of this step in Darwin's argument, not only because the beak is so easy to measure, but because it is so obviously vital to the life of the bird. Darwin's finches can't put food in their mouths with their wings. They can't use their claws either, any more than we can dine comfortably with our feet. They have to use their beaks. Beaks are to birds what hands are to us. They are the birds' chief tools for handling, managing, and manipulating the things of this world (*manus* meaning hand).

The shape of a bird's beak sets tight limits on what it can eat. Although the bones and the horny sheaths of the mandibles are a little more flexible than they look—a woodcock can poke deep down into the mud, part its beak at the very tip, and grab an earthworm—still, these are not many-jointed and articulate instruments like our hands. Each beak is a hand with a single permanent gesture. It is a general-purpose tool that can serve only a limited number of purposes. Woodpeckers have chisels. Egrets have spears. Darters have swords. Herons and bitterns have tongs. Hawks, falcons, and eagles have hooks. Curlews have pincers.

There are about nine thousand species of birds alive in the world today, and the variety of their beaks helped confirm Paley's belief in an inventive God. Flamingos' beaks have deep troughs and fine filters, through which the birds pump water and mud with their tongues. Kingfishers' beaks have such stout inner braces and struts that a few species can dig tunnels in riverbanks by sailing headlong into the earth, over and over again, like flying jackhammers. Some finch beaks are like carpentry shops. They come equipped with ridges inside the upper mandible, which serve as a sort of built-in vise and help the finch hold a seed in place while sawing it open with the lower mandible.

But plain or fancy, each beak can do only so much. The flamingo's beak is good for filtering pond water. The hawk's is good for ripping up a rabbit, a fox, or another bird. If the flamingo and the hawk ever tried to trade jobs, the hawk would drown in the pond scum, and the flamingo would get its eyes poked out.

Darwin extrapolates from big variations like these to the much smaller variations between individuals. According to his theory, even the slightest idiosyncrasies in the shape of an individual beak can sometimes make a difference in what that particular bird can eat. In this way the variation will matter to the bird its whole life—most of which, when it is not asleep, it spends eating. The shape of its particular beak will either help it live a little longer or cut its life a little shorter, so that, in Darwin's words, "the smallest grain in the balance, in the long run, must tell on which death shall fall, and which shall survive."

None of Darwin's readers doubted that the hooks, swords, spears, and pincers of the world's birds are of adaptive value. That was the pious, conventional, and commonsense view of Paley. But many readers did doubt that individual variations mean as much as Darwin says. He himself never actually saw a slight variation help or hurt the chances of an animal or plant in its struggle to survive.

Darwin does give one passage in the *Origin* the promising heading "*Illustrations of the Action of Natural Selection.*" "In order to make it clear how, as I believe, natural selection acts," this passage begins, "I must beg permission to give one or two imaginary illustrations. Let us take the case of the wolf. . . ." Then he gives a few quick sketches to show that hypothetically, in a hard winter, when there is almost nothing else for a wolf to eat but deer, the fleetest and slimmest wolves would be expected to do best. Darwin makes similar arguments about nectar-bearing flowers and honeybees, all logical and hypothetical. That is the end of the section.

These sketches are so vivid that they enter straight into the minds of Darwin's readers. For years, those who accepted and those who rejected them felt no compelling need to go beyond them—and certainly not Darwin's bulldog, Huxley. "But the question now is:—Does selection take place in nature?" he asks, rhetorically, in one of his defenses of Darwinism. "Is there anything like the operation of man in exercising selective breeding, taking place in nature?" In answer he asks us to imagine what it must be like for a species of animal in nature, surrounded by fifty or one hundred others, with "multitudinous animals which prey upon it, and which are its direct opponents," and others preying on those, and still others indirect helpers, etc. He concludes that "it seems impossible that any variation which may arise in a species in nature should not tend in some way or other, either to be a little better or worse than the previous stock. . . ."

Even after half a century, Darwin's point about variations was still being defended with imaginary illustrations, and attacked for being imaginary. "The whole question [of the struggle for existence] has been discussed very largely from the *a priori* standpoint, throughout the whole period since the appearance of the *Origin of Species*," wrote the geneticist Raymond Pearl in 1911. "The 'rabbit with his legs a little longer,' the 'fox with the little keener sense of smell,' the 'bird of dull colors which harmonized with the background,' *et id genus omne*, have been made to do valiant service."

Darwin himself never tried to produce experimental confirmation of this particular point. It is at once extremely logical and extremely hard work to prove. Certainly he could not prove his case with his finches. He never learned much more about the details of their struggle for existence than he did during that first glimpse on San Cristóbal, when he watched the birds hopping together under the bushes, "scratching in the cindery soil with their powerful beaks and claws." If anything, those mixed flocks argued *against* his case. He saw finches with long thin beaks and short fat parrot-like beaks all hopping on the same lava, eating identical bird food. If beaks with such widely different shapes could handle and crack the same seeds, then what could it possibly matter if, among the parrot-beaked finches, one bird's

beak was a little fatter than another's, or if, among the sharp-beaked finches, one was a little sharper?

On Daphne Major, for instance, the beak of the average *magnirostris* is 14, 15, and 16 millimeters in width, length, and depth. The beak of the average *fuliginosa* on Daphne is only about 7, 8, and 7 millimeters—that is, less than half as big. Yet Darwin saw both species eating the same food. If those two tools can do the same work, then what is the point of the Grants' measurements of two neighboring cactus finches, one with a beak 14.9, 8.8, and 8 millimeters, and the other 15.8, 9.7, and 9 millimeters? Variations that small would seem to mean nothing.

Natural selection is supposed to scrutinize the slightest variations in nature, "daily and hourly." But as far as Darwin could say after his five weeks in the Galápagos, natural selection is blind to the beak of the finch. No wonder he left them out of the *Origin*.

An ornithologist named Osbert Salvin looked over some museum specimens of Galápagos finches in the 1870s, four decades after Darwin collected them. It was Salvin who noticed how variable the finches can be, one from the next, in the length of their legs, in their wingspans and their weights, and especially in their beaks.

Salvin felt the Galápagos was "classic ground" (even in the 1870s). Having discovered that the islands' finches represent an extraordinary range of variations, he must have been disappointed that these variations seemed to have so little influence on the survival of the fittest. "The members of this genus," he wrote, "present a field where natural selection has acted with far less rigidity than is usually observable." Of course, the action of natural selection had never been observed at all.

Like Darwin, most of the series of scientific pilgrims who made their way to Darwin's islands arrived in the wet season, or what passes for a wet season in these desert islands. All of the bushes and trees were in leaf and flower, and there were plenty of seeds on the ground. The scientists watched closely, and they saw exactly what Darwin had seen. Most of the ground finches were hunting and pecking together beneath the half-naked bushes. All those different beaks were cracking the same birdseed.

One after another, this series of careful ornithologists concluded that the shape of the beak of a ground finch makes no detectable difference in the food it eats. "To look at the bills of these birds in the hand, we would conjecture wholly different diets," wrote the biologist and explorer William Beebe, who sailed out to Daphne Major through clouds of yellow butterflies in the wet season of 1923. "The small, delicate mandibles of *fuliginosa* would seem adapted to insect food, or at least small, rather soft seeds," he said. "At the other extreme, the huge beak of *magnirostris*, almost as large as the entire head, would be equal to the hardest of acorns." But both birds were eating identical foods. "What a mad country for birds and butterflies!"

It seems unbelievable now; but the action of natural selection is so easy to miss that Darwin's finches were considered by generations of ornithologists to be an exception, or even a counter-illustration, to Darwinism. In 1935, the hundredth anniversary of Darwin's visit to the islands, the ornithologist Percy R. Lowe gave a commemorative lecture before the British Association on the birds of the Galápagos. Lowe confined his talk to the Galápagos finches. He called them—apparently for the first time—Darwin's finches. But having read the by-now-extensive literature, Lowe declared his belief that the birds are not separate species at all, but "hybrid swarms." He thought their extraordinary variations would prove to be as meaningless as the varieties of coats in the stray mutts and cats in an alley. The beak of the finch offered "no scope for Natural Selection."

("Yes, he really said that, didn't he," Peter Grant says now. " 'No scope for natural selection.' Which was a wonderful way of stimulating people to go out and try to disprove him.")

Three years later, another British ornithologist anchored off San Cristóbal, Darwin's first island. Like Darwin he was a young man in his twenties. Lowe's lecture had piqued his interest, and although the Galápagos Islands had seemed "impossibly remote," he had been encouraged to make the trip by Julian Huxley, a grandson of Darwin's bulldog.

David Lack stayed through almost all of the wet season—one of the wettest wet seasons in the Galápagos in this century. The wet season is the finches' breeding season, and Lack saw a lot of breeding. He saw that the thirteen species of finches in the islands rarely interbreed. He even built aviaries in the long, hot, humid afternoons and tried to get the birds to hybridize inside them, but they would not cooperate. They seemed to be very particular in choosing their mates. So Lowe had been wrong to call them "hybrid swarms."

Still, even though the birds were not breeding together, most of the ground finches were feeding together, eating the same seeds. Lack had to agree with Lowe that the beak of the finch offers "no scope for natural selection." "In fact," Lack concluded, "there is no evidence

whatever, in any of the island forms of Geospizinae [Darwin's ground finches], that their differences have adaptive significance." He wrote up this result in a monograph, but its publication was delayed by the outbreak of World War II.

It was some time after Lack got home to England that, like Darwin before him, he did a double-take. As he looked over his data he noticed that the species of finches whose beaks are most nearly identical do not live together on any of the islands in the archipelago. The cactus finch (*Geospiza scandens*) breeds on Daphne Major, for example, and also on all of the biggest islands in the archipelago except Fernandina; the large cactus finch (*Geospiza conirostris*) breeds on Genovesa and Española. Lack had never seen breeding colonies of both cactus finches on any one island. What is more, if two finch species with rather similar beaks do share an island, their beaks are more divergent in their measurements on that island than they are elsewhere. That is, the longer beak is longer than average, and the shorter beak is shorter than average, almost as if they were consciously trying to get out of each other's niches.

Lack found these patterns in case after case, not only in his own data books, but also in measurements of the thousands of museum specimens that had been collected since Darwin. Like Darwin, he could not see evolution in action, and he assumed it would be too slow to watch; but he could infer, looking back at the Galápagos, that something must be going on.

Lack was influenced in part by other biologists' studies of microcosms smaller than the Galápagos. Place two different species of *Paramecium* in a test tube, and come back in a few days. One species will have conquered the top of the test tube, and the other owns the bottom of the test tube, and the border in the middle is a no-cell's-land. Likewise with barnacles: one species takes the high tide line and another takes the low tide line.

Such experiments seemed to show that no two species eating the identical foods in identical ways can coexist peaceably in the same test tubes, on the same rocks, or on the same islands without one species driving the other to extinction. This is just the sort of competition and conflict that Darwin had imagined might lead to the extinctions of many branches and twigs on the tree of life; the branches in the middle would die off, and the survivors would bend and twist and diverge to either side as if to minimize competition by making themselves as different as possible.

Lack made charts of the beaks and their distributions in the archipelago. On island after island, Darwin's process seemed to him to have exterminated one or the other of two like-beaked species, or else to have pushed the survivors far enough apart to coexist. Whenever species with very similar beaks try to colonize the same island, Lack decided, they are thrown into competition. The struggle grows so bitter that one or the other species of finch is driven to extinction. But occasionally two like-beaked species evolve enough local differences that the intensity of their competition is reduced. Then both species survive.

Lack turned a classic negative case into a classic positive case, and helped to end the eclipse of Darwinism. In 1947 the very title of his monograph, *Darwin's Finches*, had a triumphant ring to it. Darwin's finches really are Darwin's. There is scope for natural selection in the beak of the finch.

The book had a powerful influence on specialists and on the general public, even though Lack had not actually seen natural selection in action any more than Darwin had.

DURING THEIR FIRST FIELD SEASON in 1973, the Grants and the Abbotts measured not only finch beaks but also finch behavior. They staked out eight sites of twenty-three thousand square meters. At each site they marked off a grid of reference points by tying red flagging tape to hundreds of cactus bushes and torchwood trees. Each morning they would crisscross one of the grids with binoculars, notebooks, and stopwatches, and see what the finches ate for breakfast.

The Grant team discovered that the ground finches were concentrating on about two dozen different species of seeds. So the members of the team put each of these two dozen kinds of seeds between the points of a vernier calipers and measured them as carefully as they measured the birds' beaks. They also measured the seeds' hardness with the McGill nutcracker. This is a gadget that Peter Grant designed with the help of an engineer at McGill University, in Montreal, his first teaching post. The McGill nutcracker is a pliers with a scale attached. Squeeze a seed with the pliers, and the scale shows how much force it takes to crack the seed open. Modern physicists measure force in a unit they named for the founding father of their science: the newton. To crack a grass seed, which is a speck about the size of a poppy seed, takes very little force, less than 10 newtons. A big cactus seed,

the size of a peppercorn, takes more than 50 newtons. Cracking the toughest seeds in the Galápagos requires a force of 250 newtons, which is enough force to lift more than a thousand cactus finches into the air.

Peter Grant combined the measurements of seed size and seed hardness and rated each kind of birdseed as the finches might themselves, in a sort of Struggle Index. The small soft ones of *Portulaca* score the lowest on this index, only 0.35. The big hard seeds of *Cordia lutea* score highest, almost 14. Any of the finches can handle *Portulaca* in its beak, but very few are up to *Cordia*.

The Grant team also kept a census of the numbers of each kind of seed on the lava. To do this objectively they used a random-number table to select a single plot of lava, one meter square, somewhere in each grid. Then they counted every single fruit and seed they could find on that square of lava, whether it was dangling from the top of a cactus tree or lying in the middle of a cactus patch. Next they chose a much smaller plot within that square meter, again at random, and they sifted the hot cindery soil, collecting every fruit and every seed they found. Finally they withdrew to their tents and spread out their trophies on white trays to count one by one. And they repeated the whole routine fifty times.

"Most miserable piece of data we did," says Peter Boag, who, with his wife, Laurene Ratcliffe, joined the Grant group early on.

"Sift the dirt!" groans Ratcliffe. "Count every seed, every single seed! That's *Portulaca*. That's *Rynchosia*. That's *Setaria, Acalypha, Mentzelia, Heliotropium* . . . aaargh!"

"People think fieldwork is so romantic," Boag says, "but a lot of it is real slog. This was absolutely the worst."

They got to know the Galápagos birdseed so well that they could recognize the main species at a glance. They could often recognize a seed as it shattered in the tip of a finch's beak. "That's one advantage of the Galápagos," Boag says now. "You know exactly what the birds are getting. *That's* why we all want to work there. Not because it's nice. Because it's simple."

In most parts of the world, one might find two hundred species of plants in a single spadeful of earth. It would be impossible to find out exactly what a flock of birds is getting in its beaks as they move by the hour from lawns to woods to meadows to the banks of a stream. But on Daphne Major the finch watchers could get almost a God's-eye view of their flocks, which never went anywhere and never migrated for the winter. And of course when the watchers unrolled their mist nets, adds Ratcliffe, "every bird you caught was a finch."

"No one anywhere has duplicated the kind of fieldwork we did in the Galápagos—because it was so *simple*," Boag says. "Those ecosystems are stripped to the bare bones."

By the end of their first stay in the islands, the members of the Finch Unit thought they knew the finches' tastes in seeds, fruits, insects, leaves, buds, and flowers. On Daphne Major alone the team had watched and made notes while medium ground finches ate 4,000 meals. They knew exactly what the finches were eating, and they knew the size and shape of the beaks the finches were eating them with. And most of the ground finches were eating the same seeds and fruits, just as Darwin had seen in his first glance on San Cristóbal.

Before Peter Grant left the islands, the acting director of the Charles Darwin Research Station, Tjitte de Vries, gave him some advice. He reminded Peter that in the Galápagos the first half of each year is wet and the second half is dry. The Grant team, like Darwin, Beebe, Lack, and all the rest, had visited the birds in the wet season. But the dry season might be the time to watch life squeeze Darwin's finches.

Darwin's process can be hard for us to spot when nature is flush, when we behold "the contented face of a bright landscape or a tropical forest glowing with life," as Darwin writes in *Natural Selection*, ". . . & at such periods most of the inhabitants are probably living with no great danger hanging over them & often with a superabundance of food. Nevertheless the doctrine that all nature is at war is most true. The struggle very often falls on the egg & seed, or on the seedling, larva & young; but fall it must sometime in the life of each individual, or more commonly at intervals on successive generations & then with extreme severity."

THE GRANTS CAME BACK a few months later. Even from the air they could see the difference as they flew in to the small airport on the island of Baltra (built by the United States Sixth Air Force during World War II and maintained now by the Ecuadoran Air Force). Everywhere the lava was brown, black, red; almost no green below the highlands of Santa Cruz. At the research station, de Vries told them that there had been no rain at all at the station in the months of April, May, June, and July.

The Grant team recaptured many of the birds they had caught during their first trip, and dangled them again in the spring balance. The finches had lost weight, and when the members of the team counted the seeds on the same plots as before, they could see why the birds might be hungry. There was not much bird food on the ground any more. The plants had dropped all their leaves and seeds and had stopped making new ones, and the birds had eaten so many of the old seeds that their platter was almost clean. At the study site on the island of Genovesa, the volume of finch food was down by 84 percent.

Not only was there less food for the finches, there was also less variety. Only about half of their favorite kinds of food were left. And in the wet season most of the seeds on the ground had been so small and soft that the average seed had rated only 0.5 on the Struggle Index. The seeds that remained were mostly big and tough, and the average was higher than 6.

In the wet season every ground finch had the same favorite menu, seven kinds of soft seeds and fruits. Each ground finch had spent about half its foraging time on those seven. But now the ground finches spent only about a thirtieth of their time on them.

Magnirostris has the biggest beak and the most powerful jaw muscles of any of the finches. It is the only finch that is strong enough to break and rip off the Grants' metal bands from its ankles. *Magnirostris* was now concentrating on big, heavy seeds, the seeds that almost none of the other finches can crack.

The long, thin beak of the cactus finch is another of the most distinctive-looking beaks among the ground finches. Cactus finches were now taking advantage of their beaks' special talents and dining almost exclusively on cactus seeds.

It was the same with all six of the ground finches. Now that they were reduced to tough foods, the birds' tool-kit beaks were determining what the birds ate. They had become specialists, and each bird's specialty was set by the shape of its beak.

Smaller, local variations were making a difference too. The Grants can often tell which island a finch comes from just by glancing at it. *Fortis* on Daphne, for instance, is smaller than *fortis* on Santa Cruz, even though the islands are in plain sight of each other and within flying range for the finches. Meanwhile cactus finches on Daphne have narrower, finer beaks than cactus finches on Santa Cruz.

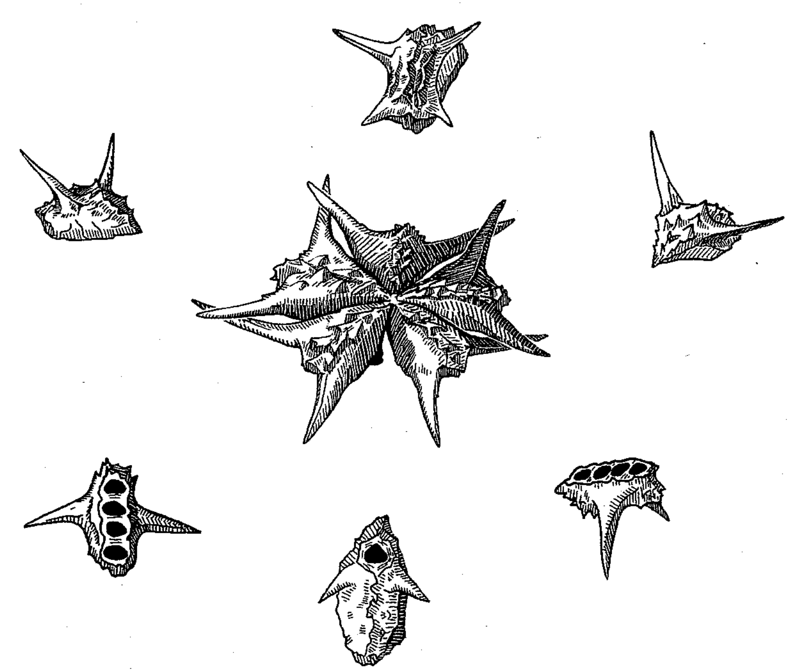
These variations from population to population are often much subtler than the variations between species, a matter of a millimeter or so. But they too make a mortal difference. They help determine what each population can do to get through the dry season. For example, the average length of a *fortis* beak on the island of Pinta is slightly deeper than on Daphne Major. Torchwood stones on the two islands are almost identical in size and hardness. But on Daphne, Grant says he has seen some of the *fortis* take as much as six minutes to crack open a single stone. That is a long time for a bird to struggle, and most of the time the bird just gives up after a while and drops the stone. On the island of Pinta, however, the *fortis*—with their slightly deeper beaks—are much faster with torchwood stones, and four out of five *fortis* can crack them. The difference in their beaks is only a millimeter.

Among finches of the same species on the same island, individuals often vary by smaller amounts than that. Now we are down to the level of variation that Darwin himself argued is the cornerstone of evolution. Not even Lack ever suggested that differences this small can matter in the beak of the finch. But Peter Boag made a clear and simple test of their significance a little later in the watch on Daphne Major, after hundreds of *fortis* had been banded. Boag walked around and around the island. Each time he spotted a *fortis* with a band on its ankle, he watched the bird until he saw it pick up a seed, and he wrote down what kind of seed it was. Boag found that in the dry season the birds with the biggest beaks eat the biggest seeds, the birds with medium-sized beaks eat medium-sized seeds, and the birds with the smallest beaks eat the smallest seeds: another Goldilocks-and-the-Three-Bears result.

ONE OF THE FINCHES' MOST BITTER STRUGGLES for existence is their running battle with a weed called caltrop. The Grants have made a case study of this. It is a classic demonstration of the war of nature, and in fact caltrop's name is rooted in the fields of war. For more than a thousand years, soldiers have sown battlefields with a certain kind of low-tech booby trap: spiky iron balls. Generally each ball has four spikes, so that one spike always sticks up to calk, or cut, a man's foot or a horse's leg. Roman charioteers threw caltrops behind them to prevent pursuit. Yankee pioneers sowed the grass outside their log cabins with smaller caltrops—some called them iron stars—when there were Indians around. Caltrop, the plant, also bears the Latin name of *Tribulus*, from the same Latin root as tribulation: *tribulare*, to afflict or oppress.

Like many other plants, including the star thistle and the water chestnut, caltrop defends its fruit with sharp spines. Each roundish fruit is divided into half a dozen sections, or mericarps, and as long as the fruit is still on the caltrop plant, each section holds the seeds inward, to the center, with the sharp spines facing out. When the fruit dries, these mericarps fall one by one to the ground. There is a single row of seeds nestled inside each mericarp, like peas in a pod. One mericarp holds as many as half a dozen large, nutritious, nutty-flavored kernels, each kernel in its own woody compartment, like chocolates wrapped in wooden foils inside a locked wooden box.

A caltrop's mericarp can be awkward in a finch's beak, almost as awkward as an iron star beneath a human foot or a horse's hoof. In



Caltrop. The large armored object in the center is a caltrop fruit. When it dries, it breaks into pieces called mericarps. The mericarps hold three to six seeds apiece. In this picture, finches have taken one seed from the mericarp at the bottom, and all of the seeds from the mericarps to its left and right, leaving small, black hollow cells where the seeds had been.
Drawing by Thalia Grant

fact, two species of finches on Daphne Major, the cactus finch and the small ground finch, have never been seen to try to open them. The only species that do attack mericarps are the large and the medium ground finches, *magnirostris* and *fortis*, and each species has its own tactics.

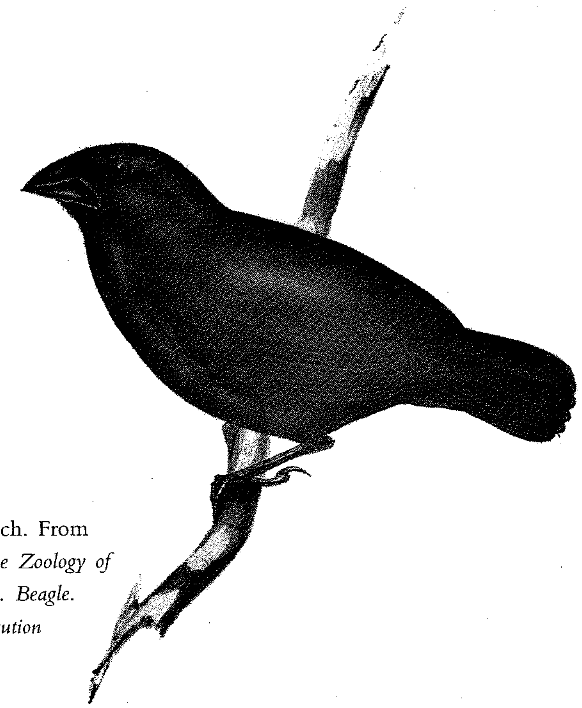
Magnirostris (whose beak is almost twice as wide and twice as deep as the beak of a *fortis*) picks up a mericarp, holds it near the midpoint of its beak, and squeezes its mandibles together. After a while the mericarp shatters into fragments. Then *magnirostris* picks up each fragment, holds it on one side of the beak, and crushes it. "When a *mag* is working on a *Tribulus*," Peter Grant says, "I can hear it cracking."

To crack a whole mericarp like this takes an average force of more than 200 newtons. Apparently that is more force than a *fortis* can muster. Instead it braces the mericarp against the ground and bites and twists the woody sheet that guards the row of seeds, as if peeling off a lid. This operation requires about 54 newtons of force, which seems to be about the best a *fortis* can do.

Neither species has it easy, and Grant has seen birds of both species use a rock to help them. The finch holds the mericarp in its beak, braces the upper mandible against a rock, and squeezes the lower mandible closed on the seed while pressing the upper mandible against the rock.

Now, *magnirostris*, because it crushes the whole mericarp in its powerful beak, can eat every last seed before it moves on to another mericarp. But *fortis*, with its smaller beak and weaker jaw, has to peel off the lid, exposing and eating one seed at a time. Typically it eats only one or two seeds and then moves on. It almost always eats the seeds in the same order too, starting at the narrow, pointed end of the mericarp and working toward the blunt end, as charmingly methodical as a child eating corn on the cob.

Watching these birds combing the dry lava for *Tribulus* seeds is like watching people hunt through a bowl of pistachio shells for the last unopened nuts, the ones that were thrown down before as too tough to crack. Birds of both species will often pick up a mericarp, work at it for a few seconds—sometimes longer—and then drop it and move on, like someone dropping a sealed pistachio nut back in the bowl. The finches prefer mericarps with only two spines, and mericarps with four spines are likely to be dropped. One indication that *magnirostris* has an easier time than *fortis* at eating caltrop, says Grant, is



Medium ground finch. From Charles Darwin, *The Zoology of the Voyage of H.M.S. Beagle.* *The Smithsonian Institution*

that a *magnirostris* cracks many more mericarps than it rejects, while a *fortis* rejects many more than it cracks.

Darwinian competition is not only the clash of stag horns, the gore on the jaws of lions, nature red in tooth and claw. Competition can also be a silent race, side by side, for the last food on a desert island, where the competitors never fight one another, and the only sound of battle is the occasional crack of a *Tribulus* seed. Finches are locked in the most deadly competition even when they feed together in flocks. When times are hard, their lives depend on how efficiently they can forage for food—how little energy they can expend in getting how much energy in return. They are hungry, they are thirsty, and they are trying to keep their budget in balance. And as poor Mr. Micawber used to say, "Annual income twenty pounds, annual expenditure nineteen nineteen six, result happiness. Annual income twenty pounds, annual expenditure twenty pounds ought and six, result misery."

The race is to the swift, and *magnirostris* is clearly the winner. It can eat more than four seeds from two mericarps in less than a minute, while *fortis* gets only three seeds from two mericarps in more than a minute and a half. In fact *magnirostris* gets about two and a half times as much energy per minute, and because it gets more seeds out of each mericarp it has to hop around less too, which also saves energy.

Of course, *magnirostris* is bigger than *fortis*, not only in beak but in body size, so it needs more food. It needs one and a half times as much energy to meet its minimum daily metabolic requirements. But since the big beak of *magnirostris* earns the bird two and a half times as much energy, it still comes out ahead.

A few *fortis* have found a trick that helps them even the score. One of them sometimes trails a *magnirostris* around on the lava. As soon as the *magnirostris* cracks a mericarp, Grant says, the *fortis* rushes up, steals a piece, flies a little way off, and cracks it. Not every *fortis* on Daphne seems to know this trick; the Grant team has spotted only about half a dozen of them doing it. (Likewise on Daphne Major, cactus finches sometimes open cactus buds, and *fortis* has never been seen even trying to open them. But sometimes a *fortis* will wait beside a cactus finch, *scandens*, and after the *scandens* has torn open the bud, the *fortis* joins in.)

So the trials and tribulations of caltrop are not only harder on *fortis* than *magnirostris*; they are harder on some *fortis* than others. *Fortis* with bigger beaks can crack the mericarp and gouge out the seeds faster than those with smaller beaks. Tiny variations are everything. A *fortis* with a beak 11 millimeters long can crack caltrop; a *fortis* with a beak only 10.5 millimeters long will not even try.

"The smallest grain in the balance" can decide who shall live and who shall die. Between a beak big enough to crack caltrop and a beak that can't, the difference is only half a millimeter.

Incidentally, the beak of the finch may be exerting selection pressure on the caltrop itself. The Grants have not made a careful study of this. But out of curiosity Peter once compared the caltrop on the eastern rim of the crater, where there is heavy *fortis* traffic, and the caltrop on the northwest inner wall of the crater, about 20 meters down from the rim, where *fortis* rarely goes. Where there are many finches, each mericarp has fewer seeds, but it has longer and more numerous spines. In the steep, rugged, protected place, the mericarps have more seeds and fewer, shorter spines.

Peter suspects that the caltrop is evolving in response to the finches. Where the struggle for existence is fierce, the caltrop that is likeliest to succeed is the plant that puts more energy into spines and less into seeds; but in the safer, more secluded spot, the fittest plants are the ones that put more energy into making seeds and less energy into protecting them. The finches may be driving the evolution of caltrop while caltrop is driving the evolution of the finches.

According to the greatest authority on plants of the Galápagos, Duncan Porter, this species of caltrop comes from Africa. It may have traveled across the Pacific from island to island on the boots, pantaloons, and hairy legs of sailors, whalers, and buccaneers. If that is how it reached the Galápagos, then the very earliest date for its arrival on Daphne Major is 1535, which is the year the first European saw the Galápagos (it was the unlucky Fray Tomás de Berlanga, the third bishop of Panama, who was so glad to get away from the islands that afterward he did not even bother to name them).

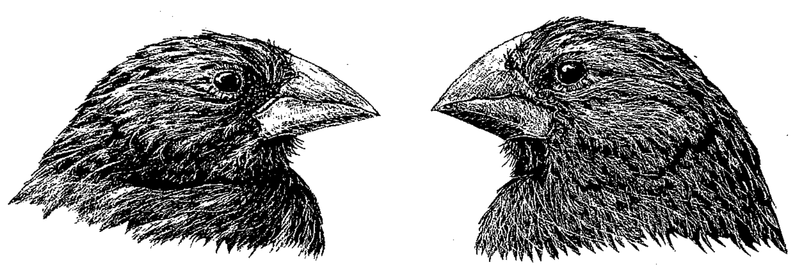
We will never know when the first *Tribulus* seed reached Daphne Major. Probably it was not the year the good bishop collided with the islands, for he is unlikely to have seen Daphne Major, or to have stopped there if he did. So the war of beaks and spines on this islet may very well have evolved in the brief space of a few centuries—since the first seabird landed on the crater floor with a caltrop stuck to its webbed foot, or since the first human being sailed around the island a few times and planted a boot on the welcome mat.

"WHAT A TRIFLING DIFFERENCE must often determine which shall survive, and which perish!" Darwin wrote. To many of his critics this has seemed pure conjecture, but after a good part of a lifetime on Daphne Major, the Grants find it obvious. "I often think of piano playing," Rosemary Grant says. "I know I try to play the piano in spite of small hands, and how much easier it would be if my fingers were only a little longer. Or think of tweezers," she adds. Everyone in *El Grupo Grant* needs tweezers, because they collect cactus spines, especially during a nest census or a seed-and-fruit census, and some of Daphne Major's longest-suffering human inhabitants have come to consider tweezers "the most indispensable item of Daphne equipment." A complete tweezers kit includes a slant tip, a square tip, and a pointed tip. Often you can use any one of them to do the job of another, but that makes clumsy work and takes a long time. "And what a small difference in shape and size there is between the different kinds!" says Rosemary.

The Grants see the importance of variations on display not only on Daphne Major but throughout the archipelago. The second most closely watched island in their study is Genovesa, which the Grants began watching intensively in 1978. The work on Daphne is mostly Peter's, and the work on Genovesa is mostly Rosemary's. When they are alone the Grants call Daphne "Peter's Island" and Genovesa "Rosemary's Island."

On Genovesa, Rosemary has focused on the cactus finch *conirostris* (a finch that Darwin never saw). These cactus finches, like their congeners on Daphne, all eat more or less the same food when the food is cheap, but in times of famine they tend to specialize. Those with significantly longer beaks can hammer open the fruits of the cactus and probe the cactus flowers. Those with longer and deeper beaks can crack the big, tough cactus seeds. Those that have significantly deeper beaks than the others can strip the bark from the trees to get at the bugs beneath. It is one more demonstration that Darwin was right about the importance of slight variations. All this is precisely the kind of illustration that Darwin asks his readers to imagine in the *Origin*.

Once we accept that slight variations can help decide who lives and who dies, Darwin takes his thesis a step further. He argues that favorable variations will be more likely to be passed down. They will spread through the population, from one generation to the next, while



Two medium ground finches on Daphne Major: same species, same age, same island, yet one beak is strikingly deeper than the other.
Drawing by Thalia Grant

variations that hurt individuals in the population will tend to dwindle and die out.

During the eclipse of Darwinism this point seemed as much a matter of faith as the rest of Darwin's theory. Believers accepted it, skeptics rejected it. In the 1930s, for instance, the British evolutionists Robson and Richards analyzed the handful of studies that purported to show evolution in action. Robson and Richards concluded that even where natural selection might just possibly have been detected in action, the case studies did not prove Darwin's point because, in the opinion of Robson and Richards, the variations in question had not been passed down, and variations that are not passed down cannot lead to evolution.

Peter Boag has a background in genetics. After the Grant team had been watching Daphne a few seasons, Boag decided, as part of his thesis project, to try to measure the relation of parent bill size to offspring bill size in Darwin's finches. That is, he would measure how accurately the variations in their beaks are passed down—a factor that matters as much to their evolution as the presence of the variations themselves, or their influence on the lives of the individual birds. Improbable as it sounds, no one had ever actually tried to measure this factor, known in the jargon of genetics as heritability, in the wild. The more accurately the variations are reproduced—the more heritable they are—the faster the work of evolution could proceed among these finches. And without actually making the measurements, Peter Boag explains, "We didn't have any basis to judge."

Boag looked over all of the finch group's data, several years' worth, and he compared the sizes of the offspring and the sizes of their parents. He found that the body size of a finch does indeed depend very strongly on the size of its parents. A finch's size is highly heritable.

Boag also compared the birds' beaks to their parents'. The shape and size of the beak too is highly heritable. The beak of the finch is passed down faithfully from one generation to the next.

There was one loose end that could invalidate Boag's results. Suppose for the sake of argument that on Daphne Major in those years, *fortis* finches with bigger-than-average beaks were able to get more food. And suppose birds that eat better as babies grow up to be bigger-beaked adults. If so, a pair of big-beaked parents would have tended to provide more food for their babies, and their babies would have grown up big-beaked too. Big-beaked parents would have big-beaked offspring, small would have small, and yet the effect would have nothing to do with genetics. Despite the correlations that Boag had found, the size and shape of the beak of the finch might not be passed down from parent to chick.

This was nothing more than the age-old question of nature versus nurture, and Boag knew how to test it. If he took some eggs from a pair of big finches and put them in the nest of a pair of small finches, would the young grow up looking like their true parents or their foster parents?

Boag never did have a chance to perform this experiment during his watch on Daphne. And in retrospect, the finch watchers are glad he didn't, because their study is now so sensitive that the large number of egg switchings that Boag planned would have caused unnatural disruptions from that day to this. In fact, locally, Boag might have changed the course of evolution.

Instead, the egg switch was performed by Jamie Smith, after he left the Galápagos and set up shop among the sparrows on Mandarte Island. Smith switched many eggs from one sparrow nest to another, just as Boag had planned to do on Daphne. He found that the foster birds took after their true parents, not their adoptive parents. Being raised by a larger bird does not make you a larger bird. The young birds resemble their true parents, even though they are not raised by their true parents. This is very strong evidence that it is nature, not nurture, that plays the larger role in deciding the size of the sparrows and the shape of their beaks. As with the finches, the sparrows' beak variations get passed down with remarkable fidelity from one generation to the next.

Recent studies have shown that even the smallest details of bird life, everything from the exact size of the eggs to the number of the eggs and the date they are laid, are heritable too (at least to some degree). They are passed down from generation to generation in species after species of birds. This seems to be the rule rather than the exception in nature, just as Darwin imagined it to be, although not all variations in the living world are passed down as faithfully as the beak of the finch.

ORIGINALLY THE GRANTS HAD PLANNED to study Darwin's finches for a few months and lug home as much data as they could. Then they would try to sort out some of the forces that have made the birds what they are. In other words, the Grants were planning to take a snapshot. And if Darwin had been right about the slow pace of evolution, no one could ever take more than a snapshot. Watching these birds would be like watching the stars for an astronomer, or the mountains for a geologist. Even one hundred years in the Galápagos would be a snapshot.

But as the pieces fell into place, the Grants and their team began to understand that they had something worth watching. They would have to come back. The birds are exceptionally variable in their beaks. They are exceptionally sensitive to these variations. They pass on their variations with exceptional fidelity. Each of the requirements of Darwin's process, each of the prerequisites for evolution by natural selection, is heightened in Darwin's finches to an almost unnatural degree.

"Slow but sure moves the might of the gods," says the chorus in Euripides' *The Bacchae*. Slow but sure moves the power of natural selection, says Darwin. But here on Daphne Major, among Darwin's finches, the action might be swift and sure.

No one had ever stood watch before among Darwin's finches, so the Grants could only wait and see. As things turned out, they did not have long to wait.

Chapter 5

A Special Providence

. . . there's a special providence in the fall of a sparrow.

— William Shakespeare,
Hamlet

And for myself I am fully convinced that there does exist, in Nature, means of Selection, always in action & of which the perfection cannot be exaggerated.

— Charles Darwin,
Natural Selection

Before he leaves Daphne's north rim, Peter Grant stoops and scans the dirt by the path. With his floppy-brimmed sun hat and gray beard he looks both cheerful and grave, reading the dust. He is hunting for a *Tribulus* seed.

"There was a time when you'd just say, 'There's one, there's one, there's one.' Now you've got to search for them," he says.

He kneels beside a *Tribulus* plant, or what is left of it. After almost four years of drought, the plant has withdrawn to the roots. It looks like a black claw hiding from the sun. All around it the lava is coated with layers of old guano, and the glare on this white paint makes Peter squint, even though the morning sky is still overcast. He brushes aside a pebble or two.

"Here's a *Trib*," he says at last, holding it up in his palm. The *Tribulus* plant dropped this mericarp during the last wet season, to wait for the next wet season. Now the plant is a withered stump, and the mericarp, still waiting, has bleached to the color of driftwood.

Though it is guarded by two long sharp spines, this mericarp has been chipped open at one end. Within the broken place, Peter can see

two dark pod holes, side by side, like tiny eye sockets, both empty. "Just two seeds taken out," he says.

At this moment, up and down the volcano, four hundred Darwin's finches are doing what Peter has just done. They are turning over pebbles, inspecting the lava, raking the cindery dust with their claws, sometimes poking their heads down into dark crevices, looking for the last bleached seeds. To open new ground, one of them will sometimes brace its head against a big rock and roll over another rock with its feet. A finch that weighed less than 30 grams was once seen rolling over a rock that weighed almost 400. That is like a man rolling a boulder that weighs one ton. It is the labor of Sisyphus, and unlike Sisyphus, Darwin's finches cannot keep it up forever. They are wearing down the horny sheaths of their beaks. Some of them have scraped their feathered crowns almost bald. Their occasional reward is a treasure like the object in Peter's palm, one more tough vitamin capsule, a husk with a few kernels no one else has eaten.

In the Grants' first four years on this island, they never saw the struggle for existence get this intense. Those were good years for Darwin's finches. By the end of the Grants' first season, for instance, there were about fifteen hundred *fortis* on Daphne Major. Nine out of ten of those *fortis* were still alive in December, just before the next rains came. There were also about three hundred cactus finches on the island that first April, and nineteen out of twenty of them survived the dry season and made it through to December.

Their fourth year, in 1976, was especially wet and green. There were great bouts of rain in January and February, and light showers in April and May, a total of 137 millimeters of rain, which is a good year for Darwin's finches.

The fifth year of the study, 1977, began well too. Rain fell right on schedule in the first week of January. Within days, green leaves unfolded and flower buds opened all over Daphne Major, with here and there a few caterpillars crawling on the buds, fast food for Darwin's finches. There were more than one thousand *fortis* and almost three hundred cactus finches on the island.

By this time the Grants' first pair of colleagues in the islands, Ian and Lynette Abbott, had gone back to Australia, and Jamie Smith had gone back to Canada. The Daphne watch had been taken over by Peter Boag and Laurene Ratcliffe. Boag was eager for the island's *fortis* to start laying eggs, because he needed more parents and offspring for his study. He had also received special permission from the staff of the National Park Service of Ecuador to perform his egg-switching experiment. After the *fortis* eggs hatched, he was planning to band the foster chicks. The next season he would measure their beaks' length, depth, width, and finish his Ph.D. with a bang.

After the first rain, a few pairs of cactus finches mated. (Cactus finches often breed before much rain has fallen, perhaps because they make most of their living from cactus.) The birds laid their eggs in nests they built in the cactus trees, and the eggs hatched fine.

Fortis do not breed until a little more rain has fallen. Peter and Laurene waited for the next good cloudburst, the one that would trigger the *fortis* to mate. But after the first week of January the sky above Daphne Major was like the sky that hangs over the Grants this morning, gray, low, and gloomily quiet. There was one more shower, a very light one, then nothing but clouds and heat.

The small rain that fell in the first week of the year did not settle into the soil. There is no place on Daphne's slopes for water to pool, and there is not much dirt to soak it up. The rain ran down the sides of the volcano as if pouring off a roof, and trickled away into the sea. Whatever was left was baked away by the sun or dried in the sea breezes on the rim and in the eddying winds that circle within the great bowl of the crater, stirred as if by a fire in the crater bowl each morning, as the rising sun begins to heat the lava.

Peter and Laurene checked on the nests when the cactus finch chicks were seven days old. Cactus finches build domed nests deep inside the cactus bushes, where they are well protected from owls. The chicks were peeping away with as much energy as they do every year. Peter and Laurene reached into each cactus bush, lifted the chicks out, set them down in a hat, and measured them one by one. In a normal year, flies and moths would have been flitting around the cactus trees by now, and the chicks' mothers and fathers would have been bringing bugs to the chicks. The air should have been so thick with bugs that three sweeps of a net through the air would come up with hundreds. But at the end of that January the island was still so dry that there were few flowers to bring out the insects. Three sweeps of the net came up with only a couple of bugs.

When Boag and Ratcliffe sampled the contents of the chicks' crops with an eyedropper they saw that most were almost empty. They found a little pollen, a few bits of flowers, or a seed kernel, sometimes a small spider.

All over Daphne, leaves shriveled, flowers wilted. Boag and Ratcliffe had not planned to stay on the island this long. The way things usually went, they would go early in the year and band the fledglings in their nests on the seventh day. Then they would leave the island and come back later on to see how all the young birds were doing. But this year, Peter and Laurene were stuck. They could not leave the island until the *fortis* had their fledglings.

From the upper rim of the crater, Boag watched the horizon. The wind usually comes from the south, and it is blocked by the much larger and taller island of Santa Cruz, which lies 8 kilometers to the windward of Daphne Major. Storms drop most of their rain on the south side of Santa Cruz, so that the north side of the big island, and all of Daphne Major, lies in a rain shadow. Boag could see regular downpours along the coast of Santa Cruz. The island of Santiago, 30 kilometers to the northwest, where Darwin passed a fortnight, got soaked too that spring.

"We panted, drank water, and read books," says Laurene. "I read *The Agony and the Ecstasy.* Peter read every single book on World War II."

"That's the place to read *The Rise and Fall of the Third Reich,*" says Peter.

A few scattered showers fell on a few scattered days, 24 millimeters of rain in all. This was not enough to move the *fortis* to pair off and mate, and it was not enough to fill the air with moths and flies. Two out of three of the cactus finches' chicks died in the nest, and those fledglings that did make it out stayed close to their parents for twice as long as usual, some of them for more than a month. They hopped beside their mothers and fathers and begged with piercing cries and much shaking of their wings.

During the previous June, when the island was wet and green, there had been more than 10 grams of seeds in an average square meter of lava. The finches had already eaten their way through many of those seeds during the dry season of 1976. Even if the rains had fallen as late as March or April of 1977 the seed supply would soon have rebounded, and the *fortis* would have begun to pair off and breed and lay eggs for Boag's experiment. But the weeks went by, and the rains did not come, and the birds did not pair off. Day after day they went on pecking over the same square meters for the same diminishing supply of seeds. By June of that year there were only 6 grams of seeds per square meter. By December there would be only 3 grams.

As they always do in dry times, the birds went on looking for the easiest seeds. But now they were sharing the last of the last of the pistachio nuts. They were down to the bottom of the bowl. In June of the previous year, four out of five seeds that a finch picked up were easy, scoring less than 1 on the Struggle Index. But as the small, soft, easy seeds of *Heliotropium* and other plants disappeared, the rating climbed and climbed, peaking above 6. The birds were forced to struggle with the big, tough seeds of the *Palo Santo,* and the cactus, and *Tribulus,* symbol of the struggle for existence, a seed sheathed in swords.

Back in 1973, it had been quite rare to see a *fortis* try to crack one of the iron stars of the *Tribulus,* and when one of the birds did try, it needed an average of almost fifteen seconds to crack the mericarp. Boag and Ratcliffe got out the stopwatch again. A *fortis* could now get the side of its beak across a corner of a mericarp and twist, twist, until the capsule chipped in less than six seconds. The birds were getting a lot of practice with *Tribulus*—that is, those birds that could handle it at all.

Some of the very smallest *fortis* on the island, the ones whose beaks were too small for caltrop, were poking around the *Chamaesyce* instead. The herb *Chamaesyce* has small soft seeds, but it also has a milky, sticky latex when its leaves are wounded and its stems are broken. These little *fortis,* along with the very smallest birds on the island, the immigrant *fuliginosa,* began hunting for seeds in the *Chamaesyce* in spite of its latex. The feathers on the crowns of their heads got so matted, gummy, and sticky that they rubbed off afterward as the birds raked the cinders and gravel looking for more seeds. Their bare scalps were exposed to the sun all day. Boag and Ratcliffe began to find little bald finches lying dead on the lava.

They kept up the routine of capturing and measuring finches, dangling them in the weighing cup and recording the numbers in their waterproof notebooks (that year they did not need them to be waterproof). By June, many of the birds' weights were down as much as a quarter from the June before. A large number of these finches had failed to molt, although by now they badly needed a new set of feathers. Some of their contour feathers were so worn that the down underneath was exposed, as Boag would report later in his now-famous paper on the drought of 1977. He and Laurene found dead *fortis* lying on the lava with feathers so disheveled they looked as if they had been combed the wrong way. The fraying of feathers was hardest on the smallest species, the *fuliginosa,* which when not eating the small, soft

seeds of *Chamaesyce* were poking about for bugs in the lichen on the torchwood trees, Boag says, or hawking for bugs from a naked branch. They needed all their contour feathers for flight.

Even in good years, finch watchers have to be careful never to leave a bucket of water standing open in camp, or Darwin's finches will jump in and drown. On one island another Galápagos biologist, an iguana watcher, did leave a jerrycan open once, and in the morning it was full of finches. The bucket is like an oasis—it draws thirsty animals from far and wide. Once at the Charles Darwin Research Station a centipede a foot long crawled into an open bucket, and as grasshoppers hopped in, the centipede ate them one by one.

This year the whole camp on Daphne Major became an oasis of sorts. A flock of finches—mostly juveniles, birds born the green year before—hung around the finch watchers' tent and picked up crumbs. Peter and Laurene grew particularly attached to one female finch—"Number 1750 or something like that," Boag says. "She would follow us around the camp. She didn't make it through the drought, unfortunately."

Down on the crater floor the blue-footed boobies shifted their weight from one leg to the other to cool off their webbed feet. Boag stuck a thermometer into the ground, in the tortured shadow of a cactus, and the soil was hotter than 50° C (122° F). Even where there were seeds lying out in the open, the heat was keeping the finches from foraging there between the hours of 11 a.m. and 3 p.m. Meanwhile at night Peter and Laurene would be shivering in their tent if temperatures got down to 75° F, because their bodies were so used to the heat. Boag lay awake and wondered how his flocks were doing, just as biblical shepherds once did in a far-distant desert: "In the day the drought consumed me, and the frost by night."

Now and then a frigatebird harried a blue-footed booby out of its kill of fish. If the fish dropped on the island, as many as ten or twenty finches would flock around it. They also scavenged broken eggs and fresh booby guano. They hung close when the boobies fed their young and fought for the fish scraps, and when owls left something of their kill, finches fought over that too.

In other years the finches had ignored the lava lizards that scuttle about the rocks. But once that year, Peter and Laurene saw a female cactus finch eating a black lizard tail, and nearby they spotted a female lizard with a freshly broken stump. Some days later, they saw the same bird chase after another female lava lizard, pecking at its tail.

She might have started a new entry on the finch menu—but that was the end of the episode. Another time they saw a blue-footed booby wounded by a frigatebird. A *fortis* stood beneath the wounded booby and drank the blood as it dripped on a rock.

"We just sat there, month after month," Boag says. "At the time, we were depressed. We were losing the breeding season, so we wouldn't get a generation. Plus, all these birds were disappearing. We kept up doing the normal checks and censuses. But our feeling was not the thrill of seeing evolution in action, as one might conclude from reading the subsequent papers, but the moderate despair of doing a research project and seeing your birds *dying*."

All of the cactus finch fledglings died before they were three months old. Not a single *fortis* laid an egg or built a nest. Of course, this was the whole design of the study: to watch and see—"on spec," says Boag—if there were going to be any minor selective episodes. But now that a selective episode was definitely in progress, Boag was wretched. The egg switch would have been a wonderful experiment, and he was sure that watching natural selection in action would never make him Dr. Boag. At best, the events that he and Laurene were documenting this year would make a page of someone else's thesis a long way down the road. "We thought it very unlikely that we'd be able to measure it at all," Boag says. "We thought, watch ten years, and then *maybe*. So I didn't recognize what was going on—the magnitude of the effect."

THEY WENT HOME at last and went through their data. There were only five or six months between field excursions, so they had very little time before they had to go back into the field for another round: just enough to get the data out of their notebooks and type them up while they could still interpret their scrawls and scribbles. Peter and Laurene got their data out of the field books and saw who was left alive and who had died. But there wasn't much time.

Boag pondered the shambles of his thesis. To get a large enough statistical sample of family resemblances he had to measure many hundreds of adults and their young. Even in a normal year only a fraction of the adults that he measured would breed. Only a fraction of those that bred would build a nest that he and Laurene would find. He would band all of the nestlings he found, and about half of those would die. He might measure two thousand birds, and he might end

up with only one hundred of their offspring. "They're very precious birds, if you see what I mean," he says now. "Each dead bird is a lost data point. So that was my main concern. I was not thinking of each bird as a data point for *selection*. I was thinking of it as a lost data point for *heritability*."

When he and Laurene went back in January 1978, they watched the bright yellow flowers of the cactus trees open up all over the island, as they do at the turn of each year. All of Darwin's finches converged on the blossoms, gorging themselves on the pollen and drinking the nectar.

Boag and Ratcliffe did the usual census. They found fewer than two hundred finches alive on the island. Just one finch in seven had made it through the drought. They measured these survivors, and they also measured the mummified carcasses of the dead finches they found lying on the lava, banded and unbanded. The island is large enough that the finches that disappear each year usually disappear without a trace. They never found the body of their camp finch or most of the others. But they collected all the numbers they could, and at the end of that season, they went home again and they typed them into the computer for analysis.

Today when they lecture on the selection event of 1977, Peter Grant and Peter Boag plot the effects of the drought in three curves. The curves start in March 1976, when the island of Daphne Major was still green and lush. They end in December 1977, when the cactus flowered and the worst of the drought was over.

All through the drought the total mass of seeds on the island went down, down, down. The average size and hardness of the remaining seeds went up, up, up. The total number of finches on the island fell with the food supply: 1,400 in March 1976, 1,300 in January 1977, fewer than 300 in December.

Next they take the finches species by species. At the start of 1977 there were about 1,200 *fortis* on Daphne. By the end of the year there were 180, a loss of 85 percent.

At the start of the year there were exactly 280 cactus finches on the island. By the end of it there were 110, a loss of 60 percent.

Of the smallest ground finches, *fuliginosa*, there were a dozen on the island at the start of 1977, and only one of them survived the year.

They also plot the age of the survivors. Many of the survivors were the oldest birds on the island, and had been banded by the Grant team in 1973. Not a single *fortis* was born that year on the island, and only a single one of the *fortis* that had been born the year before survived the drought. Only one of the young cactus finches born the year before survived. The drought practically wiped out the cohort that was born the year before that too. That generation became rare, and rarer with each passing year, like steel pennies minted in a war.

At last, Grant and Boag look at the beaks of the survivors. They know how variable the beaks are. They know how much the variations matter. They know how the plants were doing, what the weather was doing, how life on the island was squeezing the finches. They know all these figures with unprecedented precision, as well as the dimensions of the finches that made it through the drought and the finches that did not.

Among *fortis*, they already knew that the biggest birds with the deepest beaks had the best equipment for big tough seeds like *Tribulus*; and when they totted up the statistics, they saw that during the drought, when big tough seeds were all a bird could find, these big-bodied, big-beaked birds had come through the best. The surviving *fortis* were an average of 5 to 6 percent larger than the dead. The average *fortis* beak before the drought was 10.68 millimeters long and 9.42 deep. The average beak of the *fortis* that survived the drought was 11.07 millimeters long and 9.96 deep. Variations too small to see with the naked eye had helped make the difference between life and death. The mills of God grind exceeding small.

Not only had they seen natural selection in action. It was the most intense episode of natural selection ever documented in nature. One result was a bizarre tilt of the sex ratios on the island. At the start of the drought there were about 600 males and 600 females. By the end of the drought more than 150 of the males were still alive, but only a pitiful remnant of the females. Males are typically larger than females by 5 percent, with proportionately bigger beaks, so the males generally had an edge.

In other words, among the males the biggest survived, and among females the biggest survived, but many more males survived than females. And what made the difference between life and death was often "the slightest variation," an imperceptible difference in the size of the beak, just as Darwin's theory predicts.

Many people—even biologists, even today—find the power of slight variations hard to believe. "Once, just as I was beginning a lecture," says Peter Grant, "a biologist in the audience interrupted me:

'How much difference do you claim to see,' he asked me, 'between the beak of a finch that survives and the beak of a finch that dies?'

" 'One half of a millimeter, on average,' I told him.

" 'I don't believe it!' the man said. 'I don't believe a half of a millimeter really matters so much.'

" 'Well, that's the fact,' I said. 'Watch my data and then ask questions.' And he asked no questions."

"*None*," Rosemary agrees. "And he sat there scowling, fidgeting and talking the whole time."

NATURAL SELECTION BY ITSELF is not evolution. It is only a mechanism that, according to Darwin, can lead to evolution. As Peter and Rosemary Grant put it, natural selection takes place within a generation, but evolution takes place across generations.

In the drought of 1977, they had seen and documented natural selection in action. The decimation of the finches by selection had been as ruthless as the aristocratic breeder of bulldogs in Darwin's day who said, "I breed many, and hang many."

But the finch watchers did not yet know if the episode would translate into an evolutionary change. They only knew that, according to theory, it was possible, since the beak variations are heritable: the changes that are wrought upon one generation can be passed on to the next, becoming muffled and compressed or stretched and warped, over the years, as they pass down the line of the generations and onward into the future.

This is a step the founders of Darwinian theory considered logically inevitable, but which many of those who came after Darwin have doubted. Raymond Pearl again: "In the minds of an astonishingly large number of people, which number includes some rather great names in the world of science, it is precisely the same thing to show that something logically must be so, as it is to show that it is so. If the formal rules of logic are satisfied, truth seems to them to be thereby established. No further evidence is demanded. As everyone knows, this attitude led practically to the intellectual bankruptcy of the whole evolution theory. . . ."

On January 9, 1978, the clouds rained at last on Daphne Major. More than 50 millimeters fell that day. The rain fell on nothing green, only rocks and dead-looking trees and withered weeds. The rain streamed down the sides of the mountain.

All over the island, the male finches, the drought's survivors, did what they do each year in the first bout of rain. They flew to the highest points in their territories: to the crown of a tree that rises from a fissure toward the sky, or the crazy steeple of a cactus on the summit of a rockfall. Perched on these wet command posts, looking as skeletal and tattered as they had ever been in their lives, each cock opened his famous beak, like a rooster in a barnyard in the first light of day, and began singing in the rain.

The rain transformed the island. Within a week there were leaves and flowers on the torchwood. Green stems shot up before the finch watchers' eyes. "*Merremia* seedlings were 5 centimeters tall," Peter Boag reported afterward; "*Portulaca* was in complete leaf, and *Amaranthus* was 2 centimeters tall." Soon *Tribulus* and a dozen other plants had green fruits or seed heads, and the buds of the *Portulaca* were crawling with bugs. From the sea the dusty sides of the old volcano turned from its dull predawn shade of brown to a noon-green emerald, a tropical paradise.

Not a single pair of finches on the island had survived intact. The drought had taken the life of at least one member of every couple. But as the rains fell, many of the females' beaks began turning dark brown, and the males' beaks turned black, signs that the birds were ready to mate once again.

The males built nests in the cactus and sang for days on end from the highest cactus top they owned. The females hopped from territory to territory, inspecting the nests and presumably the singers.

Of course the skewed sex ratio put a spin on that breeding season. Among *fortis* there were now six males for every female. Each female could choose among many males, but only one male in every six could win a female.

The males flew after the females that visited their territories in what the finch watchers call the "sex chase." The females hopped around and flew around to visit nest after nest, and took part in chase after chase, before one by one they each settled down with a single male.

Again the finch watchers watched and measured. They found that the males the females had picked were not a random sample, any more than the ones the drought had spared were a random sample. The successful males tended to be the largest of the large. They were the males with the very blackest, most mature plumage and the ones with the deepest beaks.

Because of the crazy sex ratio, most of the males were left out; only a very small subsample of survivors had a chance to mate. But every single one of the eligible females was able to pair off. One female cactus finch set a record for the island, breeding five times and producing thirteen young.

Now it became of great significance that variations of body and beak are passed on from one generation to the next with fidelity. As a result, the males' unequal luck in love helped to perpetuate the effects of the drought. The male and female *fortis* that survived in 1978 were already significantly bigger birds than the average *fortis* had been before the drought. Of this group the males that became fathers were bigger than the rest. And the young birds that hatched and grew up that year turned out to be big too, and their beaks were deep. The average *fortis* beak of the new generation was 4 or 5 percent deeper than the beak of their ancestors before the drought.

In the drought of 1977 the Finch Unit had seen natural selection in action. Now in its aftermath they saw evolution in action, in the dimensions of the birds' beaks and in many other dimensions too.

After that, the watchers on Daphne Major had to keep watching. They had to keep coming back. Not only is Darwin's process in action among Darwin's finches, not only can natural selection lead to evolution among their flocks, but it leads there much more swiftly than Darwin supposed possible. The finch watchers had to find out what would happen next.

But even if they had quit there, what they had seen on Daphne Major from 1973 through 1978 would be enough to fill an old and rather embarrassing lacuna in Darwinism. In 1909, at the centenary of Darwin's birth, during a scientific meeting at Cambridge University, the German biologist Weismann asked whether natural selection can really explain the first small steps of evolutionary change. "To this question even one who, like myself, has been for many years a convinced adherent of the theory of selection, can only reply: '*We must assume so, but we cannot prove it in any case.*' "

Several human generations later, Darwin's descendants no longer have to assume. They can supply what Weismann wanted with case after case and, now, with Darwin's finches.

One of Peter Grant's graduate students, Trevor Price, has reviewed those early years using powerful mathematical tools that did not exist in the 1970s. These tools allow investigators to disentangle which among all the changing features of a bird or a fish or a fern is most strongly selected during a selective episode. That is, they help show investigators which changes in the living form were essential and which were simply following along, which parts of a living form were the targets of selection. This technique (it is known as partial regression analysis) was developed in 1983 by the evolutionary theorists Russ Lande and Steve Arnold. As soon as Lande and Arnold published the technique, Price applied it to Boag's drought. This reanalysis brought the evolutionary event into even sharper focus.

Price knew that the survivors and their offspring were larger in weight, wing length, tarsus length, and also in beak length, depth, and width. However, partial regression analysis shows that not all of those were selected by the drought with equal emphasis. During that terrible drought on Daphne Major, among *fortis*, nature was selecting most powerfully for bigger body size and deeper beaks. Nature was *not* selecting for longer beaks; a *fortis* with a long beak had no special advantage in the drought. And nature was rejecting the birds with wider beaks. So it was big birds with deep but relatively narrow beaks that were favored: perhaps, Peter Grant writes, "because a narrow yet deep bill was the best instrument for performing the difficult task of tearing, twisting, and biting the mericarps of *Tribulus* to expose the seeds."

So the birds were not simply magnified by the drought: they were reformed and revised. They were changed by their dead. Their beaks were carved by their losses.

In most places on this planet, the sight of a dead bird is so rare that it shocks us, even scares us. We recoil as if something has gone wrong in the cosmos, as if a shutter has creaked open that should have been kept closed, exposing a shadow world beyond our world, a place we were not meant to see.

But on the desert island of Daphne Major, dead birds are commonplace. They are everywhere. The lava is always littered with wishbones and beaked skulls. Whole seabirds lie outstretched here and there as if still in flight, odorless and mummified like feathered pharaohs in the dry and desiccating heat. Each generation lies where it falls, and the next generation builds on the ruins of the one before. They hatch in a morgue, breed in a crypt, and lie down with their ancestors, as if here not only life but death too is asking to be watched.

Evolution discloses a meaning in death, although the meaning is like some of the berries that Darwin tasted in the Galápagos, "acid & Austere." There is a special providence in the fall of a sparrow. Even drought bears fruit. Even death is a seed.