



Sounds Wild and Broken

Sonic Marvels, Evolution's Creativity,
and the Crisis of Sensory Extinction



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Author of *The Songs of Trees*

VIKING

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PREFACE

On the sidewalk that runs along the edge of Prospect Park in Brooklyn, katydids and crickets spice the air with their late-summer songs. Sunset was hours ago, but the heat dallies, animating pulsing rasps and trills of insects hidden in tree branches. The pavement's light has its own rhythm, a regular pattern from widely spaced streetlights along the park's wall. The insects are drawn to the lights, gathering in the glowing orbs of leaves around each lamp. As I walk, sound and light rise and fall around me, a subtle swell.

The katydids sing with snappy, buzzing triplets—*ka-ty-did*—repeated in a steady pulse, one per second. A few singers abbreviate the song to doublets and slow the pace. Unlike nights when the performers unite in a park-wide beat, powerful enough that I feel it in my chest, tonight's katydids seem uncoordinated, each finding its own rhythm. These pulsations contrast with drawn-out, single-toned trills of tree crickets that twine their songs into a sweet and almost unvarying drone.

Security lamps behind a building in the park spill light upward into a cluster of oak trees. One hundred or more starlings gather in the branches. No sleep for these roosting birds, though. Stimulated by bright lights, they squeal, chitter, and whistle at one another, fluttering and jostling among twigs.

A large airplane passes low overhead, lined up along the western edge of the park as it completes its descent into LaGuardia Airport. The sound starts as a thread on the southern horizon, fattens to a heavy, rough rope as it smothers the insects' songs, then tapers to a frayed, rumbling tail as it

leaves us. In the daytime, during peak landing hours, these planes pass every two minutes.

Other vehicles join: the whirring complaint of car tires on asphalt, the bark and rumble of accelerating engines, a distant clash of horns at the angry intersections of Grand Army Plaza, and the fizz of speeding e-bikes.

I walked here from a chamber music concert in the basement of the public library. Musicians merged their bodies with wood, nylon, and metal, a chimeric union of animal, oil, tree, and ore that reawakened sound from its slumber on printed sheet music. Afterward, I spoke with friends and our tremulous vocal folds imparted fugitive meaning to breath. In music and speech, nerves enlist the air as a neurotransmitter, erasing the physical distance between communicating bodies.

All these sounds draw their energy from the sun. Algae basked, grew, were entombed, then turned to dark oil. We hear the algae roaring now as their long-buried stores of sunlight are released from jet and car engines. The e-bike is juiced by electricity from a coal power plant, the snared light of old forests. This year's crop of sunlight, held in maple and oak leaves, feeds the katydids and crickets. Wheat and rice do the same for humans. It is night here, but the sun still shines, photons transmuted to sound waves.

An ordinary evening. A few insect sounds and some birds. Cars and planes on their rounds. Human music and voices. I take this for granted. A planet alive with music and speech.

Yet it was not always this way. The wonders of Earth's living voices are of recent origin. And they are fragile.

For more than nine-tenths of its history, Earth lacked any communicative sounds. No creatures sang when the seas first swarmed with animal life or when the oceans' reefs first rose. The land's primeval forests contained no calling insects or vertebrate animals. In those days, animals signaled and connected only by catching the eye of another, or through touch and chemicals. Hundreds of millions of years of animal evolution unfolded in communicative silence.

Once voices evolved, they knit animals into networks that allowed almost instantaneous conversation and connection, sometimes at great distances, as if by telepathy. Sound carries its messages through fog, turbidity, dense thickets, and night's dark. It passes through barriers that block aromas and light. Ears are omnidirectional and always open. Sound not only connects animals, its varied pitches, timbres, rhythms, and amplitudes carry nuanced messages.

When living beings connect, new possibilities appear. Animal voices are catalysts for innovation. This is paradoxical. Sound is ephemeral. Yet in its passage, sound links living beings and wakes the latent powers of biological and cultural evolution. These generative powers, acting over hundreds of millions of years, produced the astonishingly diverse sounds of the living Earth. The words on this page, inked stand-ins for human speech, are but one of the productions of the fruitful union of sound, evolution, and culture. Hundreds of thousands of other wonders ring out across the world. Every vocal species has a distinctive sound. Every place on the globe has an acoustic character made from the unique confluence of this multitude of voices.

The diverse sounds of the world are now in crisis. Our species is both an apogee of sonic creativity and the great destroyer of the world's acoustic riches. Habitat destruction and human noise are erasing sonic diversity worldwide. Never in the history of Earth have sounds been so rich and varied. Never has this diversity been so threatened. We live amid riches and despoliation.

“Environmental” problems are often presented in terms of atmospheric change, chemical pollution, or species extinction. These are essential perspectives and measures. But we also need a complementary frame: Our actions are bequeathing the future an impoverished sensory world. As wild sounds disappear forever and human noise smothers other voices, Earth becomes less vital, blander. This decline is not a mere loss of sensory ornament. Sound is generative, and so the erasure of sonic diversity makes

the world less creative. The crisis exists within our own species too. The burdens of noise—ill health, poor learning, and increased mortality—are unjustly distributed. Racism, sexism, and power asymmetries create dire sonic inequities.

Listening opens us to the wonders of communication and creativity. Listening also teaches us that we live in an age of diminishment. Aesthetics—the appreciation and consideration of the perceptions of the senses—should therefore be central guides amid the convulsions of change and injustice that we live within. Yet we are increasingly disconnected from sensory, storied relationship to life's community. This rupture is part of the sensory crisis. We become estranged from both the beauty and brokenness of much of the living world. This destroys the necessary sensory foundation for human ethics. The crises in which we live, then, are not just “environmental,” of the environs, but perceptual. When the most powerful species on Earth ceases to listen to the voices of others, calamity ensues. The vitality of the world depends, in part, on whether we turn our ears back to the living Earth.

To listen, then, is a delight, a window into life's creativity, and a political and moral act.

Sounds
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PART I

Origins

Primal Sound and the Ancient Roots of Hearing

At first, sound on Earth was only of stone, water, lightning, and wind.

An invitation: listen, and hear this primal Earth today. Wherever life's voices are hushed or absent we hear sounds largely unchanged since Earth cooled from its fiery start more than four billion years ago. Pressing against mountain peaks, wind yields a low and urgent roar, sometimes twisting into itself with a whip crack as it eddies. In deserts and ice fields, air hisses over sand and snow. On the ocean shore, waves slam and suck at pebbles, grit, and unyielding cliffs. Rain rattles and drums against rock and soil, and seethes into water. Rivers gurgle in their beds. Thunderstorms boom and the surface of the Earth echoes its reply. Sporadic tremors and eruptions of the underworld punctuate these voices of air and water, sounding with geologic growls and bellows.

These sounds are powered by the sun, gravity, and the heat of the Earth. Sun-warmed air stirs the wind. Waves rise as gales strafe the water. Solar

rays lift vapor, then gravity tugs rain back to Earth. Rivers, too, flow under gravity's imperative. The ocean tides rise and fall from the pull of the moon. Tectonic plates slide over the hot liquid heart of the planet.

About three and a half billion years ago, sunlight found a new path to sound: life. Today all living voices, save for a few rock-eating bacteria, are animated by the sun. In the murmurs of cells and the voices of animals, we hear solar energy refracted into sound. Human language and music are part of this flow. We are acoustic conduits for plant-snared light as it escapes to air. Even the growl of machines is animated by the burn of long-buried sunlight.

The first living sounds came from bacteria that sent infinitesimally quiet murmurs, sighs, and purrs into their watery surroundings. Bacterial sounds are now discernible to us only with the most sensitive modern equipment. A microphone in a quiet laboratory can pick up sounds from colonies of *Bacillus subtilis*, a species of bacteria commonly found in soils and mammalian guts. Amplified, these vibrations sound like the hiss of steam escaping from a tight valve. When a loudspeaker plays similar sounds back into flasks of bacteria, the cells' growth rate surges, an effect whose biochemical mechanism is as yet unknown. We can also "hear" bacteria by balancing them on the tip of a microscopic arm. This bacteria-coated strut is so small that every shudder from their cell surfaces makes it quiver. A laser beam directed at the arm records and measures these motions. This procedure reveals that bacteria are in constant shimmering motion, producing tremulous sound waves. The crests and troughs of the waves—the extent of the cell's vibratory movement—are only about five nanometers, one-thousandth of the width of the bacterial cell, and half a million times smaller than the deflections in my vocal folds when I speak.

Cells make sound because they are in continuous motion. Their lives are sustained by thousands of inner streams and rhythms, each one tuned and shaped by cascades of chemical reactions and relationships. Given this dynamism, it is not surprising that vibrations emanate from their cell surfaces.

Our inattention to these sounds is puzzling, especially now that technologies allow our human senses to extend into the bacterial realm. Only a couple of dozen scientific papers have so far examined sound in bacteria. Likewise, although we know that bacterial membranes are studded with proteins that detect physical movement—shear, stretch, touch—how these sensors function with sounds is unknown. Perhaps there is a cultural bias at play here. As biologists, we're immersed in visual diagrams. In my own training, not once was I asked to use my ears in a lab experiment. The sounds of cells exist not only on the edge of our perception, but of our imagination, shaped as it is by habits and preconceptions.

Do bacteria speak? Do they use sound to communicate with one another just as they use chemicals to send information from one cell to another? Given that communication among cells is one of the fundamental activities of bacteria, sound would at first seem a likely means of communication. Bacteria are social beings. They live in films and clusters that are so tightly woven that they are often invulnerable to chemical and physical attacks that easily kill solitary cells. Bacterial success depends on networked teamwork and, at the genetic and biochemical levels, bacteria are constantly exchanging molecules. But to date, there are no documented examples of sonic signaling among bacteria, although their increased growth rates when exposed to the sounds of their own kind may be a form of eavesdropping. Sonic communication may be ill-suited to bacterial societies. They live at a scale so tiny that molecules can zip from one cell to another in a fraction of a second. Bacteria use tens of thousands of molecules within their cells, an extensive, complex, and ready-made language. For them, chemical communication may be cheaper, faster, and more nuanced than sound waves.

Bacteria, and their look-alike cousins the Archaea, were the only life on Earth for about two billion years. Larger cells—amoebas, ciliates, and their kin—evolved about 1.5 billion years ago. These larger cells, the eukaryotes, later gave rise to plants, fungi, and animals. Single eukaryote

cells, like bacteria, are full of trembling motion. They, too, are not known to communicate by sound. No yeast cell sings to its mate. No amoeba shouts warnings to its neighbors.

Life's quiet continued with the first animals. These ocean dwellers had bodies shaped like disks and pleated ribbons made of cells held together by strands of protein fiber. If we could hold them now, they'd feel like filmy seaweed, thin and rubbery. Their fossil remains are lodged in rocks about 575 million years old. Collectively, they are known as the Ediacaran fauna, named for the Australian hills where some of their number were unearthed.

The bodily simplicity of the Ediacaran animals obscures their pedigree, leaving no telltale marks to assign them to groups we'd recognize today. No segmented body armor like arthropods. No stiff column down their backs like fish. No mouths, guts, or organs. And almost certainly, no sound-making devices. There is no hint on these animals of any body part that could make a coherent scrape, pop, thump, or twang. Contemporary animals with more complex bodies but superficially similar body shapes—sponges, jellyfish, and sea fans—are also voiceless, suggesting that these first animal communities were quiet places. To the hum of bacteria and other single-celled creatures, evolution added only the sloshes and swirls of water around soft disk- and fanlike animals.

For three billion years, life was nearly silent, its sounds confined to the tremors of cell walls and the eddies around simple animals. But during those long, quiet years, evolution built a structure that would later transform the sounds of Earth. This innovation—a tiny wiggly hair on the cell membrane—helped cells to swim, steer, and gather food. This hair, known as a cilium, protrudes into the fluid around the cell. Many cells deploy multiple cilia, gaining extra swimming power from clusters or pelts of the beating hairs. How cilia evolved is not fully understood, but they may have started as extensions of the protein scaffolding within the cell. Any motion in the water is transmitted into the weave of living proteins in the core of

the cilium and then back into the cell. This transmission became the foundation for life's awareness of sound waves. By changing electrical charges in the cells' membranes and molecules, cilia translated motions exterior to the cell into the chemical language of the cells' interiors. Today all animals use cilia to sense sonic vibrations around them, using either specialized hearing organs or cilia scattered on the skin and in the body.

The rich animal sounds that we live among today, including our own voices, are a twofold legacy of the origin of cilia 1.5 billion years ago. First, evolution created diversity of sensory experience through the many ways that cilia are deployed on cells and on animal bodies. Our human ears are just one way of listening. Second, long after sensitivity to vibrations in water first appeared, some animals discovered how to use sound to communicate with one another. The interplay of these two legacies—sonic sensation and expression—fed evolution's creativity. When we marvel at springtime birdsong, an infant discovering human speech, or the vigor of chorusing insects and frogs on a summer evening, we are immersed in the wondrous legacy of the ciliary hair.

Unity and Diversity

In the moment of our birth, we are dragged across four hundred million years of evolutionary time. We turn from aquatic creatures to dwellers of air and land. We gasp, sucking the alien gas into lungs previously filled with warm, salty ocean. Our eyes are pulled from the dim, reddish glow of the deep into jabbing brightness. The chill of evaporation slaps our drying skin.

No wonder we wail. No wonder we forget, burying the memory in the soil of the subconscious.

Our earliest and only experience of sound before birth was the hum and throb of an aquatic cocoon. Our mother's voice found us, as did the sounds of her surging blood, breath flowing in lungs, and churning digestion. Fainter were the sounds of the world beyond our mother, from places then unimaginable to our mostly unformed brains. High tones were attenuated by the enclosing walls of flesh and fluid, and so our first sonic experiences were low and often rhythmic as her body pulsed and moved.

In the womb, hearing develops gradually. Before twenty weeks, our world is silent. At about twenty-four weeks, hair cells start to signal through nerves running to rudimentary auditory centers in the partly developed brain stem. Cells tuned to low-frequency tones mature first, and so our hearing starts with bass throbs and murmurs. Six weeks later, furious growth and differentiation of tissues result in a frequency range of hearing similar to that of an adult. Sound flows from mother's fluids into ours, directly stimulating the nerve cells in the innermost part of our ears, unmediated by ear canals, drums, or middle ear bones.

All of this gone, in a moment.

Birth removes us from our watery surrounds, but our final aural transition to air happens hours later. The fatty vernix that swaddles us at birth lingers in the ear canal, muffling airborne sound for a few minutes or, for some, days. Soft tissues and fluid likewise recede over hours from the bones of the middle ear. When these vestiges of our fetal selves finally dissolve, our ear canals and middle ears are filled with the dry air that is our inheritance as terrestrial mammals.

Yet even in adulthood the hair cells of our inner ears are bathed with fluid. We keep a memory of the primal ocean and womb inside the coils of our inner ear. The rest of the ear's apparatus—pinnae, middle ear chamber, and bones—delivers sound to this watery core. There, deep inside, we listen as aquatic beings.

I lie belly-down on the wooden dock. The splintery boards toast me with the stored heat of the summertime Georgia sun. In my nose, the sulfurous, ripe aroma of salt marsh. The flowing water under the dock is turbid, a mud soup sweeping past on a falling tide. I'm on Saint Catherines Island, a barrier island whose eastern shores face the Atlantic. Here, on the western side of the island, ten kilometers of salt marsh separate me from the

flood-prone piney woods of the mainland. In the humid air, these woods are mere haze on the horizon. Salt marsh grasses, interrupted by narrow, twisting tidal creeks, cover the intervening distance. These grasses grow knee or waist high on all the mudflats, as thickly packed and as deep green as lush fields of young wheat.

The marshes seem monotone, their uniform verdure spiced only by snowy egrets stalking the creek edges and the pumping wing beats of glossy ibises passing overhead. But these are the most productive habitats known on Earth, capturing and turning into plant material more sunlight per hectare than the lushest of forests. Marsh grasses, algae, and plankton thrive in the happy confluence of fertile mud and strong sun. Such abundance supports a diverse animal community, especially of fish. More than seventy fish species live in these tidal marshes. Ocean-dwelling fish also swim here to spawn. Their larvae grow in the protection and plenty of the marshes, then catch a ride to adulthood on an outbound tide.

For all terrestrial vertebrate animals, rich salt water such as this was our original home, first as single-celled creatures, then as fish. About 90 percent of our ancestry was underwater. I clamp headphones over my ears and drop a hydrophone from the dock. I'm taking my ears back to where they came from.

The heavy capsule, a waterproof rubber and metal ball containing a microphone, sinks quickly, pulling the cable after it. I wedge a cable loop under my knee, holding the hydrophone above the creek bottom's mud and debris, about three meters down in the opaque water.

When I first release the hydrophone, all I hear is the high gurgle of streaming water. As it descends, the swirling sounds fall away. Suddenly I'm plunged into a pan of sizzling bacon fat. Sparkles surround me, a sonic shimmer. Every glistening fragment is a fleck of sunlit copper, warm and flashing. I've arrived in the acoustic domain of snapping shrimp.

This crackling is common in tropical and subtropical salt waters worldwide. Its sources are the hundreds of species of snapping shrimp that live

in seagrass, mud, and reefs. Most of these animals are half the length of my finger or smaller, equipped with one hefty claw for snapping and a lighter one for grasping. I'm hearing a chorus of claws.

As the claw snaps shut, a plunger slams into a socket, shooting forward a jet of water. In the wake of this jet, water pressure drops, causing an air bubble to pop into existence, then collapse. This implosion sends a shock-wave through the water, the snap that I'm hearing. The sound pulse lasts less than a tenth of a millisecond, but it is strong enough to kill any small crustacean, worm, or fish larva within three millimeters of the claw tip. Shrimp use the sound as a territorial signal and jousting weapon. As long as they keep a centimeter away from their neighbors, they can spar unharmed.

The combined racket of snapping shrimp is, in some tropical waters, loud enough to befuddle military sonar. In World War II, US submarines hid among the snapping shrimp beds off Japan. To this day, navy spies deploying hydrophones must work around the sonic haze of shrimp claws.

My first lesson in this sonic immersion is that the underwater world can be a boisterous place. Before I donned the headphones, airborne sound came to me in bursts: squalls of whistles from boat-tailed grackles, pulses of cricket and cicada sound, occasional nasal caws from fish crows, and the melodies of distant songbirds. Underwater, the shrimp innervate their surroundings with unflagging sonic energy. There are no silent spaces between song phrases or cries. Sound travels more than four times faster in salt water than in air, adding to the sense of brightness. This is especially true at close range, between the reflective surfaces of the muddy bottom and the upper water boundaries, where sounds have not been attenuated by the viscosity of water.

Into the cloud of shrimp sound come stammering bursts of knocks. Each batch lasts a second or two, a cluster of ten or more taps. Then a pause of five or so seconds, more regular taps, interrupted by occasional hesitations. The taps sound like an impatient fingernail drumming on a hard-

cover book, sharp and low, with a touch of resonance. The sounds come from silver perch close by. These finger-length fish come to the salt marsh to spawn before returning in late summer to the deeper waters of the estuary and offshore. Alongside these knocks come faster bursts of tapping, almost purrs, the calls of the Atlantic croaker, a bottom-feeding fish that grows as long as my forearm.

Waa! The bleat of a lamb, but quieter. These complaints occasionally poke into the background of shrimp, perch, and croaker, and come from an oyster toadfish, probably hiding in its lair on the bottom of the tidal creek. Like their namesake, toadfish are scaleless and warty, with huge gulping mouths. Their fist-sized heads and tapered bodies are also well endowed with spines. Males call to attract females to shallow burrows. After mating, males stay with the fertilized eggs for weeks, defending them and cleaning the nest. The one I hear now is muffled and soft. He must be at some distance from the hydrophone, perhaps burrowed into debris around the dock's pilings.

All three of the fish that I hear through my hydrophone make sound by vibrating their swim bladders. Each bladder is an air-filled sac running inside the fish, stretching for about one-third of the body length below the spine. Muscles pressed against the thin walls of these bladders shiver, and these motions evoke squeaking or grunting sounds from the air within. The muscles are among the fastest known in any animal, contracting hundreds of times per second. Sound waves from the swim bladder flow into the fish's tissues and then into the water. For these fish, the whole body is an underwater loudspeaker.

The acoustic realm of these shrimp and fish seems alien to me. I'm used to the melodies, timbres, and rhythms of humans, birds, and insects. Here, though, percussive sounds dominate: the sparkle of thousands of hammer blows by shrimp claws, the knocks of perch and croaker, and the unmodulated burr of the toadfish.

But unity undergirds these differences.

The shrimps' stony, articulated exoskeleton bristles with fine sensory hairs. Sound also stimulates clusters of stretch receptors in their joints, where cilia transmit motion to nerves. At the base of antennae, tiny sand grains enclosed within gelatinous balls of sensory cells are stirred into motion by sound. Hearing, for snapping shrimps, is an experience for the whole body. Unlike human ears that detect pressure waves on our eardrums, shrimp and other crustaceans hear by detecting the displacement of water molecules, especially low-frequency motions. Sound, for them, arrives not as the push and shove of a wave, but as the tickle of moving molecules.

Fish, too, hear through sensors spread all over their body surface. Cells capped with jelly-enclosed cilia line both the skin and watery canals just below the skin's surface, a network known as the lateral line system. Unlike the touch receptors deeply buried in our dry, keratinous skin, these fish sensory cells live in intimate contact with the water around them. The lateral line system is especially sensitive to low-frequency sounds and wafts of flowing water. Rudiments of the lateral line system appear on human skin as embryos, but we lose any trace as we mature, shedding this sensory embrace of our surroundings long before we are born.

Fish also hear using inner ears. These are the same structures that our ancestors brought with them when they came onto land. We humans hear with modified fish ears.

Like the lateral line system, the fish's inner ears unite sensation of sound and motion. Three looping semicircular canals detect body motion by sensing the flow of fluids in the canals over hair cells. Connected to these canals are two bulging sacs lined with sound-sensitive hair cells. In many fish species, tiny flat bones in the sacs overlay some of these hair cells. When the fish moves, the bone lags, dragging on the hair cells and magnifying the sense of motion. In many species, the swim bladder also gathers and transmits sound waves to the inner ears.

Among land vertebrates, the fish's flat ear bones and swim bladders are absent. The hearing sacs are elongated into canals, expanding the range of

sound frequencies that the ear can perceive. In mammals, the canal is so long that it coils, forming what we now call the cochlea, from the Latin for “snail shell.” Our language divides sensations of “sound,” “body motion,” and “balance,” but they all emerge from hair cells in interconnected fluid-filled canals in our inner ears. The link in human cultures between music and dance, and between speech and gesture, is deeply rooted in both our bodies and in the evolutionary history of animals.

Ancient kinship among vertebrates is present in sound making too. Although vertebrate animals make sound in very different ways, these processes share an embryological origin. A small segment of nervous tissue at the intersection of the hindbrain and the spinal column develops into the nerve circuit that controls sound making in adult animals. This circuit acts as the pattern generator for vocalization across animals with very different forms of sound making: from the swim bladders of fish, to the larynges of terrestrial animals, to the unique syringes in the chests of birds, along with thousands of sonic variations made by croaking and booming vocal sacs, strumming pectoral fins, and drumming forearms.

The region of the spine that orchestrates vocalization also coordinates the actions of the pectoral region, the muscles of the front fins or limbs. This linkage reveals the need for fine control of timing in both vocalization and movement. All calls and songs have rhythmicity, from the steady hum of the toadfish to the layers of repetition in the song of a bird. The same is true for the coordinated movements of fins, legs, or wings. Just as hearing in vertebrate animals is closely allied with a sense of motion, sound production is linked to body movement. Rhythmicity of sensation and action shares an embryological root.

When we humans talk and gesticulate, or sing and play musical instruments, we evoke ancient connections. When my hands thump out rhythms on piano keys or strum a guitar, I’m enacting the same bodily relationships among voice, limbs, and sound that create the bleats of a toadfish or the melodies of a forest songbird. When Henry Wadsworth Longfellow wrote

that “music is the universal language of mankind,” he stated an embryological and evolutionary truth that far transcends the bounds of “mankind.”

Lowering a hydrophone from the dock was a revelatory moment. The expansion of my awareness came from two intersecting directions. I understood that my unaided human senses utterly failed to convey to me the richness of the marshes. The water surface, especially when obscured by streams of opaque tidal mud, is a formidable barrier to human understanding. When I heard the lively below-water chatter, I pierced, for a moment, a sensory barrier. Now when I’m at the marshes, I imagine and feel their diversity and fecundity, despite the visual uniformity of their above-water plants. Listening below the water surface opened me to the previously hidden life of the marsh.

Alongside this understanding of the nature of a particular place, my sense of self changed. Lying on the dock and, later, reading about animal voices and ears, my thoughts and feelings about identity shifted. Evolution has drastically reworked the mammalian body as it transformed us from fleshy-finned swimmers to four-legged land lumberers. But under these terrestrial bodily accretions is unity with our distant aquatic relatives, unity not just of pedigree but of lived sensory experience. I’m a fish talking in air, strutting and breathing on land, yet experiencing the sea through trembling hair cells in coiled watery tubes in my ears. My hydrophone and headphones created a curious loop. In listening to the subaquatic world, I used tubes of modified seawater buried in my inner ears.

But human ears are only one of the sound sensors present here. Earth’s sonic diversity is not only present in the varied voices of animals. Part of the world’s richness is the diversity of aural *experience*.

As mammals, we inherited triplet ear bones and a long tightly curled cochlea. Birds have a single middle ear bone and a comma-shaped cochlea. Lizards and snakes have a short cochlea whose sound-sensitive hair cells are arranged in patches, not in a single smooth gradient as in our ears.

These are three independently evolved mechanisms within the vertebrate clan for hearing in air, dating back about three hundred million years. Each lineage lives within its own construction of sound. Lab experiments on the behavior of captives give us a crude sense of what these differences might mean for perception. Compared with mammals, birds cannot hear as high. Birds are relatively unconcerned with the sequence of sounds but are highly attuned to rapid-fire acoustic details in each note in a song, picking out subtleties that human ears miss entirely. Birds are also especially adept at hearing how sound energy is layered into different frequencies, the overall “shape” of the sound, rather than attending to the relative pitches that are the particular focus of mammalian ears and brains. Where we discern a melody in bird or human song—shifting frequencies between notes—birds likely experience the rich nuances of the inner qualities of each note.

Fish and shrimp are immersed in sound as the movement of water molecules directly stimulates their surface hairs and as sound waves flow unimpeded into and through their bodies. Bacteria and free-living eukaryotes, too, feel the vibratory signal on their membranes and cilia. On land, insects hear airborne sounds with hairs on their body surface and modified stretch receptor organs in their skeletons, the same organs used by both insects and crustaceans to feel motion and vibration in their legs. Specialized hearing organs independently evolved at least twenty times in different groups of insects. Crickets have drumlike hearing organs in their front legs, but grasshoppers hear through membranes on their abdomens. Many flies hear with a sensor in their antennae. Among moths, hearing organs evolved at least nine different times, resulting in “ears” on wing bases, along the abdomen, or, in the case of the sphinx moths, on the mouthparts. We humans can feel vibrations on our skin and in our flesh as well as in our ears, but these are crude and blurry sensations compared with the nuanced whole-body hearing experience of these other beings.

It is a convenient shorthand to say that the shrimp, fish, bacteria, birds,

insects, and I “hear” the same sound. *To hear* is a verb that reveals the narrowness of our sonic perceptions and imaginations. We have no such limitation when we describe how animals move: They lope, strut, crawl, sidle, wing, creep, sashay, slide, trot, flutter, and bounce. Here is a lexicon that recognizes the diversity of animal motion. But we have an impoverished vocabulary for hearing. Hear. Listen. Attend. These words do little to open our imagination to the multiplicities of sonic experience.

What is the verb for the sensation created by a snapping shrimp’s foreleg joints or the direction-sensitive hairs on its claws? When the bony plate in a croaker’s ears slides over a membrane covered in hair cells, what should we name the resulting experience? The ciliary hairs in the lateral lines of the fish are immersed in the water around them, surely yielding a different experience from the movement of a triplet of bones in our middle ears. We lack any word to convey the mystery of the sphinx moth’s mouth palpus when sensing an approaching bat.

Without a diverse vocabulary for hearing, our minds lapse into inattention and our imagination is limited. Hobbled by weak verbs, language must draw on adjectives, adverbs, and analogies. A shrimp claw listens spikily, perhaps, through narrowly tuned hairs. A fish’s low-frequency lateral line hearing is oozy, deep, and fluid. The birds’ aural attention, fueled by high body temperatures, is fevered and has a narrower range of pitch perception than ours, trimmed off at its top by a stumpy, uncoiled cochlea. Is bacterial hearing like pressing a trembling thumb into jelly, viscous and enveloping?

Yet despite the limitations of language and human sense organs, our experiences of the world are encouragements to imagination. Listening opens our minds to other ways of being. At any place on Earth, thousands of parallel sensory worlds coexist, the diverse productions of evolution’s creative hand. We cannot hear with the ears of others, but we can listen and wonder.

At the dock, in my headphones, a whir cuts into the fish and shrimp sounds. It builds in loudness over five seconds then abruptly ends. Cough.

Another sputter. An outboard engine has been lowered—the whir was its electric motor easing down the blades—and is now cranking. Two more turns of the starter and the engine comes alive.

The engine's voice clouds the water, a chug pitched at about the frequency of human speech. The shrimp keep on crackling and their sound joins the outboard in my ears, two textures, one growly, one sparkly, each holding steady. The outboard idles for a minute, then, in an instant, roars. The propellers are spinning, shredding the water. As the boat pulls away, the intensity of the sound wavers, perhaps as the propeller turns toward and away from my hydrophone. Over the next minute, through the hydrophone, I hear the noise climb in frequency, up three octaves from the start, as the engine's scream fades into the distance. The croaker keeps pulsing its thumping song every ten seconds or so. The silver perch and oyster toadfish fall silent.

Sensory Bargains and Biases

Like a painter applying a delicate brushstroke to a canvas, my audiologist extends her arm and slides a slender foam plug into my right ear. A thin tube runs from the plug to an electronic console and a laptop. A gurgle bursts into my ear. Then the room stills. In the quiet, my senses waken: Winter sun through dusty clinic windows. Odor of floor cleaner and latex. A metal cart clinks far down the hallway.

Suddenly a high-pitched tone darts into the foam-plugged ear. No, I'm wrong, not a single tone but a weird two-note chord. It pulses, repeats, and pulses again, quieter. Then more tones, lower pitched. We're running down a series. Every time a sound hits my ear, two spikes leap from a trembling horizontal line on a graph on the laptop screen.

Unlike the hearing test I took last month, squeezing a trigger whenever I heard a tone, I now sit empty-handed. This test directly probes the cilia-bearing hair cells of my inner ear, with no conscious involvement on my

part. On the screen, I see the graph twitch with every burst of sound. Sometimes the graph kicks up, but I hear nothing.

My audiologist loops the tube and earplug to my left ear. She clicks the machine back on. Another gurgle. Silence. Then come the tones, working their way through the sequence. Now that I've figured out how to read the graph, I stare unblinking at the line, waiting. There it is: my ear answering back! Just to the left of the two big spikes is a third, a miniature, that pokes up whenever sound floods my ear. It is ankle high to its tall companions, but jabs up always in synchrony with them. Nearly always. For some sounds, even ones that I can hear, the junior spike is absent or merely flutters.

The small spike on the graph shows me the hair cells of my inner ear in action. When the incoming double tone hits them, they shoot out a pulse of sound in answer. This reply is too quiet for me to hear, but the microphone picks up its signal. My ears, then, are not passive receivers of sound. They are active participants in the process of hearing, making their own vibrations. This ability comes from the cilia-bearing cells in the inner ear, descendants of the oar-like hairs on the membranes of ancient free-living cells, now lodged in watery coils in my head.

As I sit in the sterile, white-walled examination room, thinking of the motions of these tiny hairs, my imagination turns to pond scum. One of my favorite exercises with students is to scoop up some slimy ditch or lake water and peer into the lively throng through a microscope. The unaided eye sees only slime. Glass lenses directed at microscope slides reveal dozens of species in every drop. Some species, especially the emerald cells of the larger algae, creep like cargo ships maneuvering in port. Others, tethered by slender tails to fragments of vegetation, pump globular heads back and forth, wafting bacteria into cuplike maws. Green globules zip past, leaving eddying wakes. Glassy needles glide. Slipper-shaped cells spiral, halt, reverse, then set off again in new directions.

The motion we see under the microscope is all driven by cilia. Some cells have hundreds, a beating pelt, others have just a single one, elongated into

a millionfold difference in energy levels, from a snowflake falling into a drift in the quiet woods to the clap of thunder echoing in a canyon.

What I see on the audiologist's screen is the activity of my outer hair cells. Normally the cells would pulse with the same frequency as the incoming waves. But the test I'm undergoing throws them into confusion. The two incoming tones are precisely calibrated to hit the membrane very close together and, like two people shaking a rug at slightly different rates, the activated outer hair cells cause the membrane to judder with the weird collision of these two drivers. Part of this judder—a harmless distortion of the waves in my ear—then flowed back out of the cochlea. The third spike on the screen was the squeal of my outer hair cells.

At the end of the test, my audiologist clicks at her laptop and the spiking lines disappear, replaced with a graph that shows how my hair cells performed. At low sound frequencies, the cells did fine in both ears. In my right ear, those tuned to higher frequencies have stopped bouncing or have slowed their motion. In my left ear, it is those focused on the mid-ranges that have quieted. These inactive cells are not resting or asleep, they're defunct. Unlike birds that can regrow damaged hair cells, human inner ear cells get one life only.

The crystal ball, my audiologist calls this test. For someone in their fifties, my results are unexceptional. In future years, more hair cells will bow out, especially in the higher frequencies.

Most of us are born with hale outer hair cells, full of vim all up and down the cochlear membrane. But from then on, it's all downhill, part of the cellular die-off that marks time in our bodies. We can hasten the decline with loud sounds—guns, power tools, amplified music, engine rooms—and with medications poisonous to hair cells, including common drugs like neomycin and high doses of aspirin. But even a life spent drug-free in quiet surrounds would not protect our ears from the erosive power of passing years.

Such is the cost of living in a body richly endowed with sense organs.

Our every sensory experience is mediated by cells. Aging is a cellular process. Over time, cells accumulate defects in their form and DNA, eventually slowing or ceasing their work. And so to experience the passage of time in an animal body is to experience sensory diminishment. This is the deal evolution has bequeathed us: we get to enjoy sensory experience, but in bodies where the scope of perception dwindles as we age. The only animals known to have broken this deal are freshwater-dwelling relatives of jellyfish called *Hydra*. Their body consists of a sac topped by tentacles. Nerves weave through the body in a net, with no brain or complex sense organs. This uncomplicated design, made from a handful of cell types, allows *Hydra* to regularly purge and replace any defective cells. They live without any signs of aging. But these eternally youthful, inverted jellyfish have only rudimentary senses: a hazy grasp of sound and light delivered by single cells buried in their skins. Our bodies are too complex to self-renew as *Hydra* does. But we therefore have more well-developed senses, mediated by complex organs. We can blame advancing deafness and the other diminishments of age on Faustian forebears. They exchanged ageless bodies for richly sensual lives. This evolutionary bargain was forced on them by one of life's seemingly unbreakable rules: all complex cells and bodies must age and die.

I mourn the progressive loss of my hearing. The voices and music of people, birds, and trees give me connection, meaning, and joy. But alongside the sadness, I try to accept and enjoy evolution's bequest. These diverse voices exist only because our bodies are complex and therefore ephemeral.

Our hearing cells and organs not only lock us into a trajectory of aging. They also bias sensory experience. It is not the case that in my youth I had perfect hearing and now I've lost some of this transparent connection to the world. Even before my hair cells started dying off, what I heard was highly mediated. Everything that I hear is an imperfect rendering. The inner and outer worlds converse and entangle in my ears.

My mind protests. Sound is sound, surely? Am I not just hearing what surrounds me, connected to the world by open ears? No. This is an illusion. What we perceive is a translation of the world and every translator has special talents, errors, and opinions. Sitting in the clinic, gazing at spikes on a graph, I'm seeing the chatter of my cochlear hair cells. I'm face-to-face with part of the hidden chain of interpretation. Along every step of the path from external sound to internal perception, our body edits and distorts.

The ear trumpets, pinnae, on either side of our heads, along with the ear canal, amplify sound by fifteen to twenty decibels. This boost is the equivalent to walking across a large room to stand next to someone who is talking. Sound waves also bounce around the cups and folds of the pinnae. This clash of waves cancels out some high frequencies. Push your ear flaps forward. You'll hear a change in brightness. As we move our heads, the sound reflections shift, cutting out slightly different frequencies. From these subtleties, our brain extracts information about where sound is located on the vertical plane. We edit sound even as it enters the ear canal.

The middle ear—the eardrum and three ear bones—has the task of converting sound vibrations in air to vibrations in the fluid inside the cochlea. The air-to-water transition faces a physical challenge. When a wave in air hits water, most of the energy bounces back. This is one reason why we can't hear poolside chatter when we swim underwater. To solve this problem, the tiny bones of the middle ear gather vibrations from the relatively large eardrum and, using the levering action of the longer “hammer” bone pivoting onto the shorter “anvil” and “stirrup” bones, these bones focus vibrations onto a much smaller window leading to the cochlea's watery tubes. This conversion both amplifies, increasing the pressure of sound waves by about twenty times, and puts a slight filter on the sound, trimming extremely high and low frequencies.

Then the cochlea imposes a more severe filter. The upper and lower ends of our hearing are set by the sensitivity of cochlea. The stiffness of the

membrane, the responsiveness of outer hair cells, and the tuning of nerve sensitivities determine not only upper and lower bounds of our perception of pitch but also our ability to discriminate among sound frequencies. In general, we can discriminate among pitches of one-twentieth of a half step on a piano keyboard. Between the notes B and C, for example, we can potentially, if we concentrate, hear twenty additional microtones. But this is only true for quieter sounds. Our ears hear subtle differences in pitch in whispered or spoken words, but for shouts our discrimination of pitch is coarser. Intense sound bucks the cochlear membrane and overwhelms auditory nerves. We have finer discrimination at lower frequencies than high. The shrill sounds of high-pitched insect songs, for example, all sound about the same pitch to us, even for those that, when experienced with the objectivity of a graph of sound frequencies, differ significantly. But for the lower sounds of human speech, we perceive subtle differences among sound frequencies.

Nerve signals and the brain's processing add their own layers of interpretation. Nerves in the cochlea fire when inner hair cells are stimulated. Each of these cells responds to a particular range of sound frequencies corresponding to its place on the high-to-low scale of the cochlear membrane. The width of these ranges and their overlap set another limit on frequency discrimination. The nerve impulses from the cochlea then flow to the auditory nerve through a series of processing centers in the brain stem and then to the cerebral cortex. There, the brain interprets incoming signals in the context of expectations, memories, and beliefs. What passes into conscious perception is an interpretation, not a transcript. This is most vividly illustrated by auditory illusions. By playing different sounds into each ear or by looping sounds to create repetition, pioneering acoustic psychologist Diana Deutsch found that she could trick the brain into hearing phantom words and melodies. These illusions reveal that what we "hear" emerges from the brain's attempts to extract order from incoming signals, even when no such order exists. The words and melodies that we hear are

partly a product of our background, each of us hearing words and music relevant to our culture.

Our brains do not just receive input from the ears, they send out signals to the ears, adjusting the cochlea to local conditions. In noisy environments, the brain suppresses the sensitivity of the outer hair cells, like a hand reaching out to crank down the volume on a loudspeaker. This reduces the masking effect of noise, allowing meaningful sounds to be more clearly distinguished. The hair cells in our ears are less jumpy in a noisy restaurant, for example, than they are in a quiet forest.

These layers of interpretation bias our perceptions of loudness. When we walk on pavement, for example, we perceive the sound as about twice as loud as footsteps on soft grass. This accords with the increase in sound intensity, the amount of energy hitting our eardrums. But in a carpentry workshop, our ears mislead us. The circular saw sounds about twice or three times as loud as the power drill. But the actual sound intensity, the rate at which energy pounds our ears, is about one hundred times higher. The extent of this biased perception depends, too, on sound frequency. For loud low-frequency sounds—the clap of thunder, for example—muscles tug on middle ear bones, dialing back the intensity of the sound that flows to the cochlea. But for loud high-frequency sounds such as power tools, this protective reflex is weaker.

The distorted scaling of subjective experience adapted us to subtle differences in the quiet sounds of the preindustrial world. The meanings in human speech, especially the textures of emotion, are conveyed through tiny changes in sound intensity. The same is true for information gleaned from the sounds of wind, rain, plants, and nonhuman animals. Our ears evolved to pay attention to quiet voices and are out of place in persistently loud environments. In an industrial society—surrounded by engines, power tools, and amplified music—it would be helpful to have a more nuanced experience of the upper end of the loudness scale. We'd better

through specialization, and specialization circumscribes power. Hearing, like other senses, both reveals and distorts. It opens us to the multifarious sonic waves of the world. It also, necessarily, conveys warped and edited perceptions of sound energy.

And so evolution has built hearing organs tuned to the ranges of frequency and loudness most relevant to the success of each species. The human range of hearing therefore reveals the sounds our ancestors found most useful. If our ancestors had been eaters of mice and moths, both of which communicate with ultrasound, we likely would have evolved to hear much higher frequencies, as do many smaller predatory mammals like cats. If these forebears had sung underwater across ocean basins, they would have evolved water-adapted ears tuned to low frequencies, as did the whales.

The richer the sensory experience, the more convincing the perceptual illusion. Before I faced my own attenuation of hearing, I lived within that illusion, giving little thought to the limits of my senses. I had no embodied experience to teach me that my ears convey active interpretations of sound energy. Seeing at the audiology clinic the liveliness of my hair cells taught me otherwise. I understood that the price of sensory experience is to live—always, from birth—in a perceptual box, a space much smaller than the diverse flows of energy of the world. The walls of the box bend and filter incoming sound, manufacturing the shape and texture of my sonic perception.

The stab of sadness that I experienced in seeing the marks of my dead and dying hair cells on the audiologist's graph jolted me into a better appreciation of both the limits and the precious value of my senses. Distortions and narrowing boundaries are the price of nuanced and rich sensation. My hearing connects me to sound, of course, but also to the bargains that evolution struck on its long path from the cilia-covered cells of the primal oceans to the aural wonders of animal inner ears.

PART II

The Flourishing
of Animal Sounds

Predators, Silence, Wings

Grasshoppers clatter away from me as I walk the verge of a country road. Crickets chirp from hiding places in the unkempt thatch of grass. A fritillary butterfly wings past. Every minute or two, I pass through a thin cloud of midges and I wave my hands to sweep away their mote-like bodies. The cicadas, loud and persistent yesterday afternoon, give only sporadic croaks and stuttering whines in the cool morning.

On one side of the road, exposed rock the color of raw liver angles up the valley slope. Entombed within this stone are the ancestors of the insects that fly and sing around me. One of this fossilized swarm bears the earliest known sound-making structure of any animal, a ridge on the wing of an ancient cricket. This fossil is the oldest direct physical evidence of sonic communication.

There should be a shrine here. A monument to honor the first known

earthly voice. But pilgrimages instead lead away from these mountains in southern France to the chapels and cathedrals of the lowlands. The Camino de Santiago passes by; pilgrims tread the road unaware that the deepest known root of all song and speech lies in the stones under their feet.

I am on the southern edge of the Massif Central, a complex of mountains and steep riverine valleys that curves inland along the Mediterranean coast, then stretches north, covering nearly one-sixth of France's land area. Unlike the coastal plain, the geography here is rugged and the human population sparse. Volcanism, collisions with the Alps and Pyrenees, and the push of continental plates have wrought a complex mix of rocks across the Massif. Where I walk, the carmine color of the stone alongside the road was born hundreds of millions of years ago in the hot, dry interior of a continent. Iron, leached and oxidized in wind-blown soils, left its mark. These rocks, the Salagou Formation, named for a local river, are made from sediments laid down in a semiarid basin into which heavy rains sometimes carved lakes and rivulets. Scrubby ferns and conifers grew beside these wet areas, adding patches and corridors of green to an otherwise bare landscape. The formation dates from the Permian, 270 million years ago, a time when all Earth's landmasses were united in one giant continent, Pangaea.

Jean Lapeyrie, a local medical doctor, discovered in the 1990s that the colorful outcrops near his home were, in some places, richly peppered with fossilized insects. He made collections and, through collaborations with researchers across the world, opened a rare window into a time when the earliest members of modern families of insects mingled with now-extinct groups. Mayflies, lacewings, thrips, and dragonflies flew alongside ancient forms, including several relatives of modern crickets and grasshoppers.

Most of the insect fossils are of wings. Insect bodies decompose quickly, but their wings are made of dry, tough protein. Blown or washed into water channels or mud cracks, the wings became entombed in silty ooze. Later, unearthed from their funerary vaults by geologists' hammers, wing

or even a brush of a tiny body against vegetation can deliver information leading to the next meal. For prey, too, vibrations in air or through the ground are useful, serving as warnings of close-at-hand danger. Sonic awareness of the presence of others also helps in the intimate social negotiations of mating. These sounds of insect bodies and movement—whishes, sighs, and crinkles—are quiet and travel only a few centimeters or, for the heavy rustlings of the largest, a meter.

Ancestral crickets possessed well-developed hearing organs in their legs, arrays of cilia-bearing cells that detect minute vibrations in the ground and pressure waves in air. After *Permostridulus*'s time, these capabilities were further expanded when evolution added a thin-membraned eardrum to cricket forelegs. This innovation, dating to about two hundred million years ago, was surely precipitated by the evolution of sound-making wings. Once sonic communication started, natural selection favored refinements in hearing.

We don't know why *Permostridulus* made its sound. Living crickets sing to attract mates and defend territories. It is possible that the wing's sound gave the ancient insect an advantage in the breeding season, perhaps by garnering attention, bluffing away rivals, or revealing location to searching mates, just as the chirping of crickets does today. As long as the breeding advantage was larger than the increased risk of predation, the song would have been favored by natural selection.

Perhaps, though, the wing's sound-making ridge served a defensive purpose. A burst of sound can startle attacking predators, buying time for an escape. This sonic defense would have been especially effective in a world where such calls were rare. Imagine the shock that a pouncing spider experienced on feeling a buzz in its jaws or hearing an unexpected rasp at close quarters. To this day, vibratory startle responses are common. Pluck an arthropod from its home and you'll often get a short blast of sound. Animals as diverse as lobsters, spiders, millipedes, crickets, beetles, and pillbugs all give defensive vibrations. Experiments with predatory

wasps, spiders, and mice show that these vibratory alarms do indeed offer protection, startling attackers enough to allow potential prey to escape.

This uncertainty about the function of sounds highlights a difficulty in human language. In describing the sounds of other species, we project human nouns onto nonhuman beings. *Song* is anything we judge to have an aesthetic root, a sound made to please or persuade. Most often, we reserve the term for sounds whose repetitions have timbres or melodies that are pleasing to our ears. We name shorter sounds *calls*: the chirps of begging nestling birds; the sharp high notes of flocking birds; the bell-like exclamations of frogs in breeding season; or the grunts, cries, and sighs of monkeys discovering and sharing food. Calls can unite a flock, communicate from offspring to parents, signal alarm, or mark territories. But the functions of animal sounds are more diverse than our simple classification allows. Often the division between song and call is arbitrary and usually reveals more about the effect of the sound on human aesthetics than its roles among nonhuman animals. I follow common usage, but where social functions are unknown, as in *Permostridulus*, or only partly known, as in most nonhuman animals, this terminology is a mere sketch.

Whatever its function, the wing ridge in *Permostridulus* presaged further developments in an insect group whose relatives would become some of the world's singing champions. *Permostridulus* is close kin to the taxonomic order named Orthoptera, from "straight wing," which today comprises more than twenty thousand species, most of which sing. Some, the crickets and katydids, make sound by rubbing files and plectra on their wings. Others, grasshoppers and giant flightless crickets called wetas, rasp hind legs onto ridges on their abdomens. Sound-making wings and legs are supplemented in some species by rasping mouthparts, wheezing air tubes, drumming abdomens, and wings shaped to crackle and snap as they fly.

Permostridulus is, for now, the earliest known singer in the fossil record. But it was surely not the first animal to make a communicative sound. The fossil record is incomplete and gives us only very conservative estimates of

the antiquity of evolutionary innovations, especially innovations like tiny ridges on insect wings that do not preserve well in stone. To cast our ears further back in time than the testimony of fossils, we can infer the past indirectly, using evolutionary family trees reconstructed from genetic comparisons among modern species. These trees, when calibrated to the ages of known fossils, give estimates of when groups of species diverged from one another. It seems that the cricket clan appeared around 300 million years ago. Almost all the living descendants of these first crickets sing. It is likely, then, that their common ancestor did too. Other contenders for early singers are the ancestors of treehoppers, cicadas, and other hemipteran bugs. Their common ancestors may have communicated with sound waves transmitted from vibratory organs in their bodies through wood or leaves. Like the crickets, these ancestors date to about 300 million years ago. Stoneflies, common insects in many waterways whose adults breed on stream-side vegetation, communicate by tapping out duets on vegetation, yielding drumming rhythms unique to each species. Their origin dates to nearly 270 million years ago, and so their soft percussion likely was another early animal communicative sound.

Later, other members of the Orthopteran order left spectacular fossils. In the Triassic, the geologic period after the Permian, fossils of cricket-like wings possess stridulatory files and, perhaps, rudimentary “windows.” These windows, flat panes of membranous tissue, have no known function for flight and appear to be smaller versions of the wing windows in living crickets that focus and amplify sound, giving their chirps a clear tonal quality. These Triassic crickets likely sounded sweet, not ragged and raspy as the coarse file of *Permostridulus* surely did. The most well preserved of all Orthopteran fossil sound-making devices are the wings of a katydid from 165-million-year-old Jurassic rocks in Inner Mongolia. The fossil is so exquisitely well preserved that broad dark bands are still visible across the forewings. A sound-making ridge lies across each wing, close to the attachment point to the body, and comprises a row of just over one hundred small teeth. The

spaces between these teeth gradually increase, as they do in many modern katydids. As wings scissor closed, they accelerate. Evenly spaced teeth would produce a sound of increasing pitch, like running an accelerating fingernail across a comb: *brr-eee!* But the increasing spacing between the teeth exactly compensates for this acceleration, yielding a pure-toned sound: *eeee!* It seems likely that teeth in the extinct species did the same.

The team of scientists who described this fossil, led by Jun-Jie Gua and Fernando Montealegre-Z, described the morphology of the wing and made a speculative re-creation of its sound. Comparing the dimensions of the fossil to those of living species with known sounds, they estimated that the katydid made sixteen millisecond pulses of just over six kilohertz. To human ears, these are brief taps of pure tone, with a high, bell-like timbre. Fossil plant remains from the same rocks as the katydid suggest that this singer's home was an open woodland of ancient coniferous trees and giant ferns. The katydid's sound frequency would have traveled especially well in this habitat, and so the song and its ecological context seem well matched. Unlike *Permostridulus*, this katydid was also likely heard by vertebrate animals. By this time, amphibians, dinosaurs, and early mammals could hear higher frequencies. Like many modern katydids, this ancient insect may have sung at night, reducing the risk from predators.

Insect wings first evolved as stubby extensions of the external skeleton. Studies of wing development in modern species suggest that this evolutionary feat was accomplished by a merger of the actions of genes that control body armor with those that build legs. We have no fossils of the first flap-like wings, but evolutionary trees built using the genes of living species strongly suggest that the first wings evolved between 400 million and 350 million years ago. These first wings probably slowed the jumping descent of plant-climbing insects, a behavior still seen today in the bristle-tails, cousins of modern insects. Many insects at the time grazed on plant spores that were held in capsules at the tips of branches. Gliding would have been a useful skill in these forests of fern- and conifer-like plants.

Wings also allow easy access to food, rapid dispersal to new habitats, and more efficient searches for mates. The earliest fossil of a complete wing—veined, shaped with leading and trailing edges, and large enough to support flight—is 324 million years old. By about 300 million years ago, the fossil record contains dozens of winged insect species.

Insect wings also provide materials that readily make sound. Their flat, lightweight surfaces broadcast vibrations, animal versions of the papery interiors of electric loudspeakers. Flight muscles move with fast, repetitive motion and are well supplied with oxygen for sustained action. Any insect that developed a propensity to repeatedly rub wings without flying might make sound. Thickened or corrugated wing veins made the sound louder and more tonal.

Among animals like primitive crickets that lived in thick foliage or the jumble of debris on the ground, sound making was perhaps especially advantageous. Sound allows mates to find one another in the tangle of miniature jungles where sight lines are blocked.

After the long silence of Earth's first 3.5 billion years, insects gave the terrestrial world its first songs. Ancient forests of fern, cycad, club moss, and conifer were brightened with sounds that would be familiar to our ears. When we hear crickets chirping from the mulch in a city park, in a mountain meadow, or along a rural road, we are transported to the first days of song on Earth.

Why did communicative sound take so long to evolve? Bacterial and single-celled life existed for three billion years with no known sonic signals. Although all these cells could sense water motions and vibrations, none reached out to others with sound. The first three hundred million years of animal evolution, too, seem to have lacked any communicative signals. No known fossil from this time has a rasp or other

relatives, and the ancestors of insects. All these creatures could, through sensors in their legs, detect vibratory motions in soil or plants.

The early animal communities in the ocean and on land, then, seem to have been hostile places for sound making. In water, where sound creates fast and far-reaching molecular movements, the danger was especially acute. But even on land, the fact that many of the early colonists were predatory scorpions and spiders likely created a high cost for sound making. If the first animals in the oceans and land had been only vegetarians, the sonic diversity of the world might have bloomed much earlier.

But this is not only a tale from long ago. A survey of living animals lends support to the idea that predation is a powerful silencer. To this day, animals whose lives are sedentary or slow and whose bodies lack weaponry are voiceless. Among worms and snails, for example, only a couple of species are known to make sound. A marine worm that lives enclosed in glass sponges in deep waters off the coast of Japan makes popping sounds when it fights, drawing water into its mouth then expelling the fluid with a snap. The sharp strands of the worms' glassy home protect the fighters from passing predators. A land snail of tropical forests in Brazil makes quiet squeaks as it oozes bright, likely poisonous mucus when attacked by predators, the equivalent, perhaps of the warning buzz of disturbed bees. The other eighty-five thousand species of molluscs and eighteen thousand species of annelid worms are, as far as we know, mute except for the slither and bubble of their body movements. The same is true for nematodes, flatworms, sponges, and jellyfish. This silence is not the result of anatomical deficiency. The plate-like doors to snail shells would make excellent rasps. Soft, muscular flesh can make sound too, as popping worms, fish swim bladders, and our own vocal folds demonstrate.

Only two branches of the animal family tree account for almost all the voices and songs of our contemporary world: the vertebrate animals—fish and their terrestrial descendants, including us—and the arthropods—

crustaceans, insects, and their kin. Both are often swift and weaponized. Sound required a measure of fearless verve from its first animal makers.

The first half a billion years or more of Earth's sonic history comprised the voices of wind, water, and rock. Then came three billion years of hum from bacteria and the slosh, skitter, and chomp of early animals, a time with many incidental sounds of life but no known communicative voices. A long silence from the living world.

Then, a revolution. Terrestrial insects evolved wings. This likely broke the silencing power of predation. Wings on a tiny insect enabled escape. The costs of sound making plunged, allowing sonic communication to gain a foothold.

That sound-making insects evolved after they gained the power of flight does not prove that a release from predation caused the evolution of the first animal calls and songs. Cause and effect are hard to infer across such spans of time. If predation did act as a silencer, we can make a prediction, though. If examples of sound making are found in the fossil record from creatures older than *Permostridulus*, they will be from fierce, fast, or heavily protected animals. Perhaps an early insect with powerful hind legs or wings, an ancient prototype of a grasshopper. In the water, we'd expect sound from predaceous trilobites or crustaceans, and fish well suited to rapid escape or bristling with defensive spines.

As I walk the road verge in southern France, I am struck by the vigor of the insect sound around me. At any one spot on the road, I hear a dozen grasshoppers purring. The air is a haze of blended chirps from uncountable crickets. Jean-Henri Fabre, the great French scientist and poet of insects, wrote of crickets in this region filling the air with their "monotonous symphonies" in the late nineteenth and early twentieth centuries.