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Animal chatters

TINBERGEN'S FOUR QUESTIONS

Calanques National Park, near Marseille. It is noontime under the sun of Provence. The heat is intense, the light bright. The garigue smells of thyme, rosemary, and lavender. The background music ("tchik-tchik-tchik") is provided by the cicadas, pressing against the bark of the pine trees, their rostra stuck into the trunk to pump out the beneficial sap. In the deep blue sky, swifts glide like arrows: "Weer!! . . . Weer!!!" A large locust spreads its colorful wings and flies in front of me, then lands a few meters away. Its long hind legs oscillate rapidly as they rub against its wings, producing a strange chirping sound, like rustling sheets of paper. When the legs freeze, the sound stops. On its branch, a subalpine warbler emits its cheerful ritornello, briskly playing sometimes fluted, sometimes squeaky notes. Suddenly, the warbler falls silent and dives into a bush. It soon comes out to sing again. In the background, far away, some sheep bleat. A dog barks. Later, when the sun has waned and it is getting cooler, the cicadas will stop their relentless concert. Others will take their place, and the entire night will rustle with the song of locusts, grasshoppers, toads, and other nocturnal creatures, in an apparent cacophony. Just before daybreak, the dawn chorus of birds will come alive. The cicadas will remain silent, waiting for the heat to start vibrating their cymbals, those small membranes hidden under their wings, which rattle several hundred times a second. "Tchik-tchik-tchik . . . tchik-tchik-tchik . . . tchik-tchik-tchik. . . ." This is the great concert of life!

The soundscape of the Mediterranean scrubland is unique. There is this multitude of sounds produced by animals, to which are sometimes added the breath of wind in the trees and the sound of waves crashing on the shore. For me, they are associated with all the times I've spent in this region of France. Have you ever wondered why animals make these sounds? Not simply to charm our senses, of course: They are not intended for us. In fact, their purpose is to communicate. To *communicate*—that's a big word! And yet . . . these songs, cries, and other shrill sounds are *signals* that, like our human words, allow them to converse with other animals. What do they say to each other, you may ask? This is what I propose to discover in this book. You are about to enter worlds of sound, some of which are familiar but most of which are completely unknown to you and which you never even knew existed. How could you, since some of them are not even accessible to our ears?

Many animals exploit the sound-transmitting properties of water or air to communicate: to find a partner, to defend a territory, to signal the presence of a predator or food source, to collaborate in hunting, to recognize and interact with members of the group. These communications are essential for many species, including our own. We know this well—we whose articulated language demonstrates an incredible complexity, commensurate with that of our social interactions; we whose simple cries, from the moment we are born, signal our emotions and needs to other humans. The fact that animals are comparable to humans has been demonstrated by a great deal of scientific work over the last forty years. We can no longer set our species apart from other animals: each species has its own biological, ecological, social, and sometimes cultural characteristics that define its own world. Acoustic communication systems are therefore diverse, but all are worthy of interest. They are evidence of the diversity of life.[1]

How are animal vocalizations produced? What information do they contain? Can we understand animal languages? For a long time, the diversity of these sound worlds was difficult to access, but technical advances—such as the tape recorder and then the computer—have changed this. In recent decades, scientists have begun to read the scores of animal concerts and decipher their meaning.

I'm involved in the science that studies animal acoustic communications, called *bioacoustics*. Bioacousticians are working to decipher how animals make and hear sounds, what information is encoded in their sound signals, what this information is used for in their daily lives, and also how their acoustic communication systems have developed over the history of life. We will see that studying the richness and complexity of animal acoustic communication can help us understand how our own communication system works—our words, our laughter, our cries. Bioacousticians are a bit like Champollion, the French historian who deciphered Egyptian hieroglyphics using the Rosetta Stone, a fragment of a stele where the same text is written in several languages. To decode animal languages, many other methods must be used, but the goal remains the same: to decipher their meaning. The sounds produced by animals are signals carrying information whose meaning we are trying to decipher.

Bioacoustics is a discipline rooted in ethology, the science of animal and human behavior. The development of this branch of biology is relatively recent, dating back to the 1960s. In 1973, the Nobel Prize in Physiology and Medicine was awarded to three ethologists. The first was Konrad Lorenz. You may have already heard of this Austrian researcher, who became famous for his experiments on imprinting, in which memory of certain events or individuals is built up very quickly and very early in life. Lorenz discovered imprinting in his observations of geese. If goslings hatch in the presence of a human being, they consider that person to be their mother and follow him wherever he goes.[2] The second Nobel laureate was Karl von Frisch. He discovered the dance of the bees, this unique communication system through which the worker bee, on her return to the hive, can inform her sisters of the whereabouts of new flowers.[3] It is impressively precise: the angle formed between the axis of the bee's walk along one of the honeycombs and the vertical axis corresponds to the angle formed between the direction of the sun and the direction of the flowers when exiting the hive. Simply incredible! But there is more: the frequency of the vibrations of the insect's body and wings contains information about the amount of food provided by the flowers. It is by vibrating that the bee signals it is worthwhile to go on a shopping spree. The third researcher was Nikolaas Tinbergen. Of the three, he is my favorite. Tinbergen spent most of his career studying animal behavior using the experimental method.[4] He invented ways of questioning animals in order to understand the causes and consequences of their behavior. For example, in order to test whether it was the red spot on the herring gull's beak that caused the chicks to beg for food, he offered them various objects (sometimes simple sticks) more or less faithfully reproducing an adult's head and bearing a bigger or smaller spot, and in different colors. He then measured the intensity of the chick's behavioral response—its speed in beating the lure with its beak. Tinbergen thus highlighted the importance of the "red spot" signal in the parent-chick relationship in this seabird species. In addition to being a remarkable experimenter, he sought to formalize scientific research in ethology. He explained that in order to fully understand animal behavior, four questions had to be answered. This method is still valid today,[5] and every bioacoustician keeps Tinbergen's four questions in mind when studying sound communication:

(1) What are the *mechanisms* of the behavior I observe?
(2) What are the *evolutionary causes* that explain the existence of this behavior?
(3) How did this behavior *develop over the course of the individual's life*?
(4) What has the *evolutionary history* of this behavior been over geological time?

Let's look at these four fundamental points in more detail. Let's imagine, for example, that you want to understand why American robins, *Turdus migratorius*, sing in the spring and what the drivers of this communication are.

You first need to understand the *mechanisms* of both the production and reception of signals, i.e., the processes that lead an animal to produce a sound and those that explain a behavioral response to what it perceives—for example, to understand why, when a male robin hears another male robin singing, it responds by singing in turn and sometimes by attacking the intruder. What is it about the song that causes this reaction? First and foremost, there must be particular acoustic characteristics identifying the American robin, which ensure that its song is not confused with that of another animal species, especially another bird species. Second, why is the reaction aggressive? Is it, for example, because the robin is ready to reproduce, and the high level of sex hormones circulating in its blood increases its reactivity? If we want to study these proximal causes of the behavior, we need to describe the properties of the stimuli that provoke the robin's reaction, both external (the intruder's song) and internal (hormonal balances). We also want to understand all the physiological processes, from the reception of the stimulus (How does hearing work?) to the expression of the behavioral response (Why all this agitation? To defend one's territory?). To explore these questions, you can set up experiments in acoustic playback with a loudspeaker placed near where the robin sings, and question it directly: "Is this song a territorial signal for you?"

Once you have addressed the first of Tinbergen's questions, you can turn your interest to the second question: the *evolutionary causes* of the communication. Why has this singing behavior rather than another been favored during the evolution of the species? In other words, how does singing confer advantages that might explain why, once it appeared, it has been retained over time? Does singing increase a male robin's likelihood of being noticed by a female? Will an aggressive individual, singing louder, more often, and for longer than others, be more effective in defending its territory and food resources? These two aspects would increase his reproductive success, i.e., the number of young he fathers and who survives into adulthood. Singing behavior would then be favored by the two facets of sexual selection: intersexual selection—females prefer some singers to others—and intrasexual selection—males drive off insufficiently aggressive colleagues more easily. But beware of the other side of the coin: Doesn't singing like a madman increase the probability of being spotted and captured by a predator such as a hawk or any other bird of prey? You could hypothesize that natural selection may have limited this behavior and favored individuals inclined to sing less loudly. Thus, sexual selection, like natural selection—the two major evolutionary mechanisms identified by Charles Darwin—probably participates in the evolution of communication behavior. You can see that things are complicated and that establishing the evolutionary causes of sound communication is not easy: all behavior is the result of a balance between constraints that sometimes have the opposite effect. You should not forget that evolution is also very much subject to chance (so-called stochastic processes). Your task as an evolutionary biologist will certainly be very difficult.

Let's see if it's easier to answer the third question formulated by Tinbergen: How was this communication behavior *acquired during the life* of our American robin? At birth, the robin chick cannot sing. It simply makes short calls to beg its parents for food. In the weeks following hatching, its brain develops and the chick gradually acquires the ability to produce more complex vocalizations. It is then essential that the young chick be able to hear adult songs, which it will learn by imitating. How are the two types of processes articulated? There are the innate processes (a robin will never sing like a wren; it has a genetic predisposition to sing "American robin") and the acquired processes (the young robin learns to sing by imitating an adult). This is a vast field of investigation. We discuss it in detail in chapter 12.

The fourth question remains, which is by far the most difficult to address: What is the *evolutionary history* of the communication that you are studying? To put it plainly, what are the stages that gradually led from the ancestor of birds—a kind of dinosaur, perhaps emitting dinosaur vocalizations[6]—to a robin singing a song? Quite a story, isn't it? All animal species, including humans, are rooted in the depths of time and share common ancestors. While we are beginning to understand the evolutionary mechanisms of diversification of living species rather well, particularly with regard to their genetic heritage, anatomy, physiology, and morphology, reconstructing the evolution of behavior remains a challenge. How and when did birdsong emerge over the course of evolution? Why in some species is it only the males that sing, whereas in many other species females also vocalize? Is song an ancestral trait in both sexes? Were dinosaurs, the ancestors of today's birds, capable of producing sounds? Did they use them to communicate? Can we imagine a tyrannosaurus "singing" to call his or her partner? Did young tyrannosauruses learn their vocalizations by imitating an adult? When and how did this learning happen? Answering all these questions is difficult, if not impossible, because behavior leaves few fossil traces.[7] My great frustration as a bioacoustician is not being able to listen to and record extinct species. I dream of being able to record baby tyrannosauruses and then have their parents listen to these vocalizations. And to see their reactions! It's obviously unlikely that we'll ever be able to achieve this kind of thing—but who knows? Maybe one day we'll be able to reconstruct "real" dinosaurs from fossil genomes, like in *Jurassic Park*. A Japanese team is trying to revive the woolly mammoth in this way. However, there are scientific methods that make it possible to establish solid hypotheses about the evolution of communications. We'll talk about that too.

Most bioacousticians focus their research on only one of Tinbergen's four questions and therefore do not aim to understand all aspects of the sound communication being studied. But keeping all of these questions in mind provides a fertile framework for thinking. Even when one is interested in relatively simple mechanisms, such as how a sound stimulates the robin's eardrum and is then transformed into nerve potentials that can be interpreted by the bird's brain, it is useful to consider that these mechanisms have a history.

Therefore, to conduct research in bioacoustics, a solid knowledge of biology is required. Most of my PhD students and postdocs have years of study in zoology, anatomy, physiology, neurobiology, ecology, ethology, and evolution. But bioacoustics requires, like many other disciplines in the life sciences, proficiency in scientific fields other than biology. In bioacoustics, there is certainly the prefix *bio* (living), but there is above all the root *acoustic*. Studying animal sound communications requires an understanding of what a sound is. Follow me and hang on tight: we're going on a detour through the physics of acoustic waves. Don't worry; it's not that complicated, and it's important for our journey into the world of animal sound. If, however, physics gives you a serious headache, and after trying to read the following chapter (science does require some effort, after all) you have trouble understanding what I have written, I'll take you straight to chapter 3. There, we start our journey by venturing into the Brazilian rainforest. For now, let's try bravely—a little courage! I first explain what a sound is, how it propagates, and how it can be described.

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