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AN IMMENSE WORLD

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Introduction

The Only True Voyage

Imagine an elephant in a room. This elephant is not the proverbial weighty issue but an actual weighty mammal. Imagine the room is spacious enough to accommodate it; make it a school gym. Now imagine a mouse has scurried in, too. A robin hops alongside it. An owl perches on an overhead beam. A bat hangs upside down from the ceiling. A rattlesnake slithers along the floor. A spider has spun a web in a corner. A mosquito buzzes through the air. A bumblebee sits upon a potted sunflower. Finally, in the midst of this increasingly crowded hypothetical space, add a human. Let's call her Rebecca. She's sighted, curious, and (thankfully) fond of animals. Don't worry about how she got herself into this mess. Never mind what all these animals are doing in a gym. Consider, instead, how Rebecca and the rest of this imaginary menagerie might perceive one another.

The elephant raises its trunk like a periscope, the rattlesnake flicks out its tongue, and the mosquito cuts through the air with its antennae. All three are smelling the space around them, taking in the floating scents. The elephant sniffs nothing of note. The rattlesnake detects the trail of the mouse, and coils its body in ambush. The mosquito smells the alluring carbon dioxide on Rebecca's breath and the aroma of her skin. It lands on her arm, ready for a meal, but before it can bite, she swats it away—and her slap disturbs the mouse. It squeaks in alarm, at a pitch that is audible to the bat but too high for the elephant to hear. The elephant, meanwhile, unleashes a deep, thunderous rumble too

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low-pitched for the mouse's ears or the bat's but felt by the vibration-sensitive belly of the rattlesnake. Rebecca, who is oblivious to both the ultrasonic mouse squeaks and the infrasonic elephant rumbles, listens instead to the robin, which is singing at frequencies better suited to her ears. But her hearing is too slow to pick out all the complexities that the bird encodes within its tune.

The robin's chest looks red to Rebecca but not to the elephant, whose eyes are limited to shades of blue and yellow. The bumblebee can't see red, either, but it *is* sensitive to the ultraviolet hues that lie beyond the opposite end of the rainbow. The sunflower it sits upon has at its center an ultraviolet bullseye, which grabs the attention of both the bird and the bee. The bullseye is invisible to Rebecca, who thinks the flower is only yellow. Her eyes are the sharpest in the room; unlike the elephant or the bee, she can spot the small spider sitting upon its web. But she stops seeing much of anything when the lights in the room go out.

Plunged into darkness, Rebecca walks slowly forward, arms outstretched, hoping to feel obstacles in her way. The mouse does the same but with the whiskers on its face, which it sweeps back and forth several times a second to map its surroundings. As it skitters between Rebecca's feet, its footsteps are too faint for her to hear, but they are easily audible to the owl perched overhead. The disc of stiff feathers on the owl's face funnels sounds toward its sensitive ears, one of which is slightly higher than the other. Thanks to this asymmetry, the owl can pinpoint the source of the mouse's skittering in both the vertical and horizontal planes. It swoops in, just as the mouse blunders within range of the waiting rattlesnake. Using two pits on its snout, the snake can sense the infrared radiation that emanates from warm objects. It effectively sees in heat, and the mouse's body blazes like a beacon. The snake strikes . . . and collides with the swooping owl.

All of this commotion goes unnoticed by the spider, which barely hears or sees the participants. Its world is almost entirely defined by the vibrations coursing through its web—a self-made trap that acts as an extension of its senses. When the mosquito strays into the silken strands, the spider detects the telltale vibrations of struggling prey and

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moves in for the kill. But as it attacks, it is unaware of the high-frequency sound waves that are hitting its body and bouncing back to the creature that sent them—the bat. The bat's sonar is so acute that it not only finds the spider in the dark but pinpoints it precisely enough to pluck it from its web.

As the bat feeds, the robin feels a familiar attraction that most of the other animals cannot sense. The days are getting colder, and it is time to migrate to warmer southern climes. Even within the enclosed gym, the robin can feel Earth's magnetic field, and, guided by its internal compass, it points due south and escapes through a window. It leaves behind one elephant, one bat, one bumblebee, one rattlesnake, one slightly ruffled owl, one extremely fortunate mouse, and one Rebecca. These seven creatures share the same physical space but experience it in wildly and wondrously different ways. The same is true for the billions of other animal species on the planet and the countless individuals within those species.* Earth teems with sights and textures, sounds and vibrations, smells and tastes, electric and magnetic fields. But every animal can only tap into a small fraction of reality's fullness. Each is enclosed within its own unique sensory bubble, perceiving but a tiny sliver of an immense world.

THERE IS A WONDERFUL word for this sensory bubble—*Umwelt*. It was defined and popularized by the Baltic-German zoologist Jakob von Uexküll in 1909. Umwelt comes from the German word for "environment," but Uexküll didn't use it simply to refer to an animal's surroundings. Instead, an Umwelt is specifically the part of those surroundings that an animal can sense and experience—its *perceptual* world. Like the occupants of our imaginary room, a multitude of creatures could be standing in the same physical space and have completely different Umwelten. A tick, questing for mammalian blood, cares about body heat, the touch of hair, and the odor of butyric acid that

* To understand how varied senses can be in a single species, just look at humans. For some people, red and green look identical. For others, body odor smells like vanilla. For yet others, coriander (cilantro) tastes of soap.

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emanates from skin. These three things constitute its Umwelt. Trees of green, red roses too, skies of blue, and clouds of white—these are not part of its wonderful world. The tick doesn't willfully ignore them. It simply cannot sense them and doesn't know they exist.

Uexküll compared an animal's body to a house. "Each house has a number of windows," he wrote, "which open onto a garden: a light window, a sound window, an olfactory window, a taste window, and a great number of tactile windows. Depending on the manner in which these windows are built, the garden changes as it is seen from the house. By no means does it appear as a section of a larger world. Rather, it is the only world that belongs to the house—its [Umwelt]. The garden that appears to our eye is fundamentally different from that which presents itself to the inhabitants of the house."

This was a radical notion at the time—and in some circles, it might still be. Unlike many of his contemporaries, Uexküll saw animals not as mere machines but as sentient entities, whose inner worlds not only existed but were worth contemplating. Uexküll didn't exalt the inner worlds of humans over those of other species. Rather, he treated the Umwelt concept as a unifying and leveling force. The human's house might be bigger than the tick's, with more windows overlooking a wider garden, but we are still stuck inside one, looking out. Our Umwelt is still limited; it just doesn't *feel* that way. To us, it feels all-encompassing. It is all that we know, and so we easily mistake it for all there is *to* know. This is an illusion, and one that every animal shares.

We cannot sense the faint electric fields that sharks and platypuses can. We are not privy to the magnetic fields that robins and sea turtles detect. We can't trace the invisible trail of a swimming fish the way a seal can. We can't feel the air currents created by a buzzing fly the way a wandering spider does. Our ears cannot hear the ultrasonic calls of rodents and hummingbirds or the infrasonic calls of elephants and whales. Our eyes cannot see the infrared radiation that rattlesnakes detect or the ultraviolet light that the birds and the bees can sense.

Even when animals share the same senses with us, their Umwelten can be very different. There are animals that can hear sounds in what seems to us like perfect silence, see colors in what looks to us like total

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darkness, and sense vibrations in what feels to us like complete stillness. There are animals with eyes on their genitals, ears on their knees, noses on their limbs, and tongues all over their skin. Starfish see with the tips of their arms, and sea urchins with their entire bodies. The star-nosed mole feels around with its nose, while the manatee uses its lips. We are no sensory slouches, either. Our hearing is decent, and certainly better than that of the millions of insects that have no ears at all. Our eyes are unusually sharp, and can discern patterns on animal bodies that the animals themselves cannot see. Each species is constrained in some ways and liberated in others. For that reason, this is not a book of lists, in which we childishly rank animals according to the sharpness of their senses and value them only when their abilities surpass our own. This is a book not about superiority but about diversity.

This is also a book about animals as animals. Some scientists study the senses of other animals to better understand ourselves, using exceptional creatures like electric fish, bats, and owls as "model organisms" for exploring how our own sensory systems work. Others reverse-engineer animal senses to create new technologies: Lobster eyes have inspired space telescopes, the ears of a parasitic fly have influenced hearing aids, and military sonar has been honed by work on dolphin sonar. These are both reasonable motivations. I'm not interested in either. Animals are not just stand-ins for humans or fodder for brainstorming sessions. They have worth in themselves. We'll explore their senses to better understand *their* lives. "They move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear," wrote the American naturalist Henry Beston. "They are not brethren, they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth."

A FEW TERMS WILL act as guideposts on our journey. To sense the world, animals detect *stimuli*—quantities like light, sound, or chemicals—and convert them into electrical signals, which travel along neurons toward the brain. The cells that are responsible for de-

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tecting stimuli are called *receptors:* Photoreceptors detect light, chemoreceptors detect molecules, and mechanoreceptors detect pressure or movement. These receptor cells are often concentrated in *sense organs,* like eyes, noses, and ears. And sense organs, together with the neurons that transmit their signals and the parts of the brain that process those signals, are collectively called *sensory systems*. The visual system, for example, includes the eyes, the photoreceptors inside them, the optic nerve, and the visual cortex of the brain. Together, these structures give most of us the sense of sight.

The preceding paragraph could have been pulled from a high school textbook. But take a moment to consider the miracle of what it describes. Light is just electromagnetic radiation. Sound is just waves of pressure. Smells are just small molecules. It's not obvious that we should be able to detect *any* of those things, let alone convert them into electrical signals or derive from those signals the spectacle of a sunrise, or the sound of a voice, or the scent of baking bread. The senses transform the coursing chaos of the world into perceptions and experiences—things we can react to and act upon. They allow biology to tame physics. They turn stimuli into *information*. They pull relevance from randomness, and weave meaning from miscellany. They connect animals to their surroundings. And they connect animals to each other via expressions, displays, gestures, calls, and currents.

The senses constrain an animal's life, restricting what it can detect and do. But they also define a species' future, and the evolutionary possibilities ahead of it. For example, around 400 million years ago, some fish began leaving the water and adapting to life on land. In open air, these pioneers—our ancestors—could see over much longer distances than they could in water. The neuroscientist Malcolm MacIver thinks that this change spurred the evolution of advanced mental abilities, like planning and strategic thinking. Instead of simply reacting to whatever was directly in front of them, they could be proactive. By seeing farther, they could think ahead. As their Umwelten expanded, so did their minds.

An Umwelt cannot expand indefinitely, though. Senses always come at a cost. Animals have to keep the neurons of their sensory sys-

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tems in a perpetual state of readiness so that they can fire when necessary. This is tiring work, like drawing a bow and holding it in place so that when the moment comes, an arrow can be shot. Even when your eyelids are closed, your visual system is a monumental drain on your reserves. For that reason, no animal can sense everything well.

Nor would any animal want to. It would be overwhelmed by the flood of stimuli, most of which would be irrelevant. Evolving according to their owner's needs, the senses sort through an infinity of stimuli, filtering out what's irrelevant and capturing signals for food, shelter, threats, allies, or mates. They are like discerning personal assistants who come to the brain with only the most important information.* Writing about the tick, Uexküll noted that the rich world around it is "constricted and transformed into an impoverished structure" of just three stimuli. "However, the poverty of this environment is needful for the certainty of action, and certainty is more important than riches." Nothing can sense everything, and nothing needs to. That is why Umwelten exist at all. It is also why the act of contemplating the Umwelt of another creature is so deeply human and so utterly profound. Our senses filter in what we need. We must choose to learn about the rest.

THE SENSES OF ANIMALS have fascinated people for millennia, but mysteries still abound. Many of the animals whose Umwelten are most different from ours live in habitats that are inaccessible or impenetrable—murky rivers, dark caves, open oceans, abyssal depths, and subterranean realms. Their natural behavior is hard to observe, let alone to interpret. Many scientists are limited to studying creatures that can be kept in captivity, with all the strangeness that entails. Even in labs, animals are challenging to work with. Experiments that might reveal how they use their senses are hard to design, especially when those senses are drastically different from ours.

Amazing new details—and, sometimes, entirely new senses—are

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* In 1987, German scientist Rüdiger Wehner described these as "matched filters"—aspects of an animal's sensory systems that are tuned to the sensory stimuli that it most needs to detect.

being discovered regularly. Giant whales have a volleyball-sized sensor at the tip of their lower jaw, which was only discovered in 2012 and whose function is still unclear. Some of the stories in these pages are decades or centuries old; others emerged as I was writing. And there's still so much we can't explain. "My dad, who is an atomic physicist, once asked me a bunch of questions," Sonke Johnsen, a sensory biologist, tells me. "After a few *I don't know*s, he said: *You guys really don't know anything*." Inspired by that conversation, Johnsen published a paper in 2017 entitled "We Don't Really Know Anything, Do We? Open Questions in Sensory Biology."

Consider the seemingly simple question *How many senses are there?* Around 2,370 years ago, Aristotle wrote that there are five, in both humans and other animals—sight, hearing, smell, taste, and touch. This tally persists today. But according to the philosopher Fiona Macpherson, there are reasons to doubt it. For a start, Aristotle missed a few in humans: proprioception, the awareness of your own body, which is distinct from touch; and equilibrioception, the sense of balance, which has links to both touch and vision.

Other animals have senses that are even harder to categorize. Many vertebrates (animals with backbones) have a second sensory system for detecting odors, governed by a structure called the vomeronasal organ; is this part of their main sense of smell, or something separate? Rattlesnakes can detect the body heat of their prey, but their heat sensors are wired to their brain's visual center; is their heat sense simply part of vision, or something distinct? The platypus's bill is loaded with sensors that detect electric fields and sensors that are sensitive to pressure; does the platypus's brain treat these streams of information differently, or does it wield a single sense of electrotouch?

These examples tell us that "senses cannot be clearly divided into a limited number of discrete kinds," Macpherson wrote in *The Senses*. Instead of trying to shove animal senses into Aristotelian buckets, we should instead study them for what they are.* Though I have orga-

* If you were being maximally reductive, you could reasonably argue that there are really only two senses—chemical and mechanical. Chemical senses include smell, taste, and vision. Mechanical senses include touch, hearing, and electrical senses. The magnetic sense might be-

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nized this book into chapters that revolve around specific stimuli, like light or sound, that's largely for convenience. Each chapter is a gateway into the varied things that animals do with each stimulus. We will not concern ourselves with counting senses, nor talk nonsensically about a "sixth sense." We will instead ask how animals use their senses, and attempt to step inside their Umwelten.

It won't be easy. In his classic 1974 essay, "What Is It Like to Be a Bat?," the American philosopher Thomas Nagel argued that other animals have conscious experiences that are inherently subjective and hard to describe. Bats, for example, perceive the world through sonar, and since this is a sense that the majority of humans lack, "there is no reason to suppose that it is subjectively like anything we can experience or imagine," Nagel wrote. You could envision yourself with webbing on your arms or insects in your mouth, but you'd still be creating a mental caricature of *you* as a bat. "I want to know what it is like for a *bat* to be a bat," Nagel wrote. "Yet if I try to imagine this, I am restricted to the resources of my own mind, and those resources are inadequate to the task."

In thinking about other animals, we are biased by our own senses and by vision in particular. Our species and our culture are so driven by sight that even people who are blind from birth will describe the world using visual words and metaphors.* You agree with people if you *see* their point, or share their *view*. You are oblivious to things in your *blind spots*. Hopeful futures are *bright* and *gleaming;* dystopias are *dark* and *shadowy*. Even when scientists describe senses that humans lack altogether, like the ability to detect electric fields, they talk about *images* and *shadows*. Language, for us, is both blessing and curse. It gives us the tools for describing another animal's Umwelt even as it insinuates our own sensory world into those descriptions.

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long to either category or both. This framework will probably make absolutely no sense right now, but should become clearer as you continue in the book. I'm not especially wedded to it, but it is one possible way of thinking about the senses—and one that might appeal to the lumpers among you.

* Let me just say that avoiding visual metaphors when describing other senses is extremely difficult over the length of an entire book. I have tried to do so, or at least to be judicious and explicit whenever I have to resort to visual terms.

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Scholars of animal behavior often discuss the perils of anthropomorphism—the tendency to inappropriately attribute human emotions or mental abilities to other animals. But perhaps the most common, and least recognized, manifestation of anthropomorphism is the tendency to forget about other Umwelten—to frame animals' lives in terms of *our* senses rather than *theirs*. This bias has consequences. We harm animals by filling the world with stimuli that overwhelm or befuddle their senses, including coastal lights that lure newly hatched turtles away from the oceans, underwater noises that drown out the calls of whales, and glass panes that seem like bodies of water to bat sonar. We misinterpret the needs of animals closest to us, stopping smell-oriented dogs from sniffing their environments and imposing the visual world of humans upon them. And we underestimate what animals are capable of to our own detriment, missing out on the chance to understand how expansive and wondrous nature truly is—the delights that, as William Blake wrote, are "clos'd by your senses five."

Throughout this book, we'll encounter animal abilities that others had long thought impossible or absurd. Zoologist Donald Griffin, who co-discovered the sonar of bats, once wrote that biologists have been overly swayed by what he called "simplicity filters." That is, they seemed reluctant to even consider that the senses they were studying might be more complex and refined than whatever data they had collected could suggest. This lament contradicts Occam's razor, the principle that states that the simplest explanation is usually the best. But this principle is only true *if you have all the necessary information to hand*. And Griffin's point was that you might not. A scientist's explanations about other animals are dictated by the data she collects, which are influenced by the questions she asks, which are steered by her imagination, which is delimited by her senses. The boundaries of the human Umwelt often make the Umwelten of others opaque to us.

Griffin's words are not carte blanche to put forward convoluted or paranormal explanations for animal behavior. I see them, and Nagel's essay, as a call for humility. They remind us that other animals are sophisticated, and that, for all our vaunted intelligence, it is very hard for us to understand other creatures, or to resist the tendency to view their

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senses through our own. We can study the physics of an animal's environment, look at what they respond to or ignore, and trace the web of neurons that connects their sense organs to their brains. But the ultimate feats of understanding—working out what it's like to be a bat, or an elephant, or a spider—always require what psychologist Alexandra Horowitz calls "an informed imaginative leap."

Many sensory biologists have backgrounds in the arts, which may enable them to see past the perceptual worlds that our brains automatically create. Sonke Johnsen, for example, studied painting, sculpture, and modern dance well before he studied animal vision. To represent the world around us, he says, artists already have to push against the limits of their Umwelt and "look under the hood." That capacity helps him "think about animals having different perceptual worlds." He also notes that many sensory biologists are perceptually divergent. Sarah Zylinski studies the vision of cuttlefish and other cephalopods; she has prosopagnosia and can't recognize even familiar faces, including her mother's. Kentaro Arikawa studies color vision in butterflies; he is red-green color-blind. Suzanne Amador Kane studies the visual and vibrational signals of peacocks; she has slight differences in her color vision in each eye, so that one gives her a slightly reddish tint. Johnsen suspects that these differences, which some might bill as "disorders," actually predispose people to step outside their Umwelten and embrace those of other creatures. Perhaps people who experience the world in ways that are considered atypical have an intuitive feeling for the limits of typicality.

We can all do this. I began this book by asking you to conjure a room full of hypothetical animals, and I'm asking you to perform similar feats of imagination over the next 13 chapters. The task will be hard, as Nagel predicted. But there is value and glory in the striving. On this journey through nature's Umwelten, our intuitions will be our biggest liabilities, and our imaginations will be our greatest assets.

ONE LATE MORNING IN June 1998, Mike Ryan hiked into the Panamanian rainforest to search for animals with his former student Rex

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Cocroft. Usually, Ryan would have looked for frogs. But Cocroft had taken a liking to sap-sucking insects called treehoppers, and he had something cool to show his friend. Heading out from their research station, the duo pulled off a road and walked along a river. Once Cocroft spotted the right kind of shrub, he turned over a few leaves and quickly found a family of tiny treehoppers of the species *Calloconophora pinguis*. Cocroft had found a mother surrounded by babies, their black backs capped with forward-pointing domes that looked like Elvis's hair.

Treehoppers communicate by sending vibrations through the plants on which they stand. These vibrations are not audible but can be easily converted into sounds. Cocroft clipped a simple microphone to the plant, handed Ryan some headphones, and told him to listen. Then he flicked the leaf. Immediately the baby treehoppers ran away, while producing vibrations by contracting muscles in their abdomens. "I figured it was probably going to be some kind of scurrying noise," Ryan recalls. "And what I heard instead was like cows mooing." The sound was deep, resonant, and unlike anything you'd expect from an insect. As the babies settled down and returned to their mother, their cacophony of vibrational moos turned into a synchronized chorus.

Still watching them, Ryan took the headphones off. All around him, he heard birds singing, howler monkeys roaring, and insects chirping. The treehoppers were quiet. Ryan put the headphones back on, "and I was transported into a totally different world," he tells me. Once more, the jungle noises dropped out of his Umwelt, and the mooing treehoppers returned. "It was the coolest experience," he says. "It was sensory travel. I was in the same place, but stepping between these two really cool environments. It was such a stark demonstration of Uexküll's idea."

The Umwelt concept can feel constrictive because it implies that every creature is trapped within the house of its senses. But to me, the idea is wonderfully expansive. It tells us that all is not as it seems and that everything we experience is but a filtered version of everything that we *could* experience. It reminds us that there is light in darkness, noise in silence, richness in nothingness. It hints at flickers of the unfa-

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miliar in the familiar, of the extraordinary in the everyday, of magnificence in mundanity. It shows us that clipping a microphone onto a plant can be an intrepid act of exploration. Stepping between Umwelten, or at least trying to, is like setting foot upon an alien planet. Uexküll even billed his work as a "travelogue."

When we pay attention to other animals, our own world expands and deepens. Listen to treehoppers, and you realize that plants are thrumming with silent vibrational songs. Watch a dog on a walk, and you see that cities are crisscrossed with skeins of scent that carry the biographies and histories of their residents. Watch a swimming seal, and you understand that water is full of tracks and trails. "When you look at an animal's behavior through the lens of that animal, suddenly all of this salient information becomes available that you would otherwise miss," Colleen Reichmuth, a sensory biologist who works with seals and sea lions, tells me. "It's like a magic magnifying glass, to have that knowledge."

Malcolm MacIver argues that when animals moved onto land, the greater range of their vision spurred the evolution of planning and advanced cognition: Their Umwelten expanded, and so did their minds. Similarly, the act of delving into other Umwelten allows us to see further and think more deeply. I'm reminded of Hamlet's plea to Horatio that "there are more things in heaven and Earth . . . than are dreamt of in your philosophy." The quote is often taken as an appeal to embrace the supernatural. I see it rather as a call to better understand the natural. Senses that seem paranormal to us only appear this way because we are so limited and so painfully unaware of our limitations. Philosophers have long pitied the goldfish in its bowl, unaware of what lies beyond, but our senses create a bowl around us too—one that we generally fail to penetrate.

But we can try. Science-fiction authors like to conjure up parallel universes and alternate realities, where things are similar to this one but slightly different. Those exist! We will visit them one at a time, beginning with the most ancient and universal of senses—the chemical ones, like smell and taste. From there, via an unexpected route, we'll visit the realm of vision, the sense that dominates the Umwelt of most

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people but that still holds surprises galore. We'll stop to savor the delightful world of color before heading into the harsher territories of pain and heat. We'll sail smoothly through the various mechanical senses that respond to pressure and movement—touch, vibration, hearing, and the most impressive use of hearing, echolocation. Then, as experienced sensory travelers whose imaginations have been fully primed, we'll make our most difficult imaginative leaps yet, through the strange senses that animals use to detect the electric and magnetic fields that we cannot. Finally, at journey's end, we'll see how animals unify the information from their senses, how humans are polluting and distorting that information, and where our responsibilities to nature now lie.

As the writer Marcel Proust once said, "The only true voyage . . . would be not to visit strange lands but to possess other eyes . . . to see the hundred universes that each of them sees." Let us begin.

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1.

Leaking Sacks of Chemicals

Smells and Tastes

"I DON'T THINK HE'S BEEN IN HERE BEFORE," ALEXANDRA Horowitz tells me. "So it should be very smelly."

By "he," she means Finnegan—her ink-black Labrador mix, who also goes by Finn. By "here," she means the small, windowless room in New York City in which she runs psychological experiments on dogs. By "smelly," she means that the room should be bursting with unfamiliar aromas, and thus should prove interesting to Finn's inquisitive nose. And so it does. As I look around, Finn smells around. He explores nostrils-first, intently sniffing the foam mats on the floor, the keyboard and mouse on the desk, the curtain draped over a corner, and the space beneath my chair. Compared to humans, who can explore new scenes by subtly moving our heads and eyes, a dog's nasal explorations are so meandering that it's easy to see them as random and thus aimless. Horowitz thinks of them differently. Finn, she notes, is interested in objects that people have touched and interacted with. He follows trails and checks out spots where other dogs have been. He examines vents, door cracks, and other places where moving air imports new odorants—scented molecules.* He sniffs different parts of the same object, and he'll sniff them at different distances, "like he's

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* In the official parlance, an odorant is the molecule itself, and an odor is the sensation that said molecule produces; isoamyl acetate, an odorant, has the odor of bananas.

approaching the Van Gogh and seeing what the brushstrokes look like up close," says Horowitz. "They're in that state of olfactory exploration all the time."

Horowitz is an expert on dog olfaction—their sense of smell—and I'm here to talk with her about all things sniffy and nasal. And yet, I'm so relentlessly visual that when Finn finishes nosing around and approaches me, I'm instantly drawn to his eyes, which are captivating and brown like the darkest chocolate.* It takes concerted effort to refocus on what's right in front of them—his nose, prominent and moist, with two apostrophe-shaped nostrils curving to the side. This is Finn's main interface with the world. Here's how it works.

Take a deep breath, both as demonstration and to gird yourself for some necessary terminology. When you inhale, you create a single airstream that allows you to both smell and breathe. But when a dog sniffs, structures within its nose split that airstream in two. Most of the air heads down into the lungs, but a smaller tributary, which is for smell and smell alone, zooms to the back of the snout. There it enters a labyrinth of thin, bony walls that are plastered with a sticky sheet called the olfactory epithelium. This is where smells are first detected. The epithelium is full of long neurons. One end of each neuron is exposed to the incoming airstream and snags passing odorants using specially shaped proteins called odorant receptors. The other end is plugged directly into a part of the brain called the olfactory bulb. When the odorant receptors successfully grab their targets, the neurons notify the brain, and the dog perceives a smell. You can breathe out now.

Humans share the same basic machinery, but dogs just have more of everything: a more extensive olfactory epithelium, dozens of times more neurons in that epithelium, almost twice as many kinds of olfactory receptors, and a relatively larger olfactory bulb.† And their

* It's no coincidence that I'm drawn to Finn's eyes. Dogs have a facial muscle that can raise their inner eyebrows, giving them a soulful, plaintive expression. This muscle doesn't exist in wolves. It's the result of centuries of domestication, in which dog faces were inadvertently reshaped to look a bit more like ours. Those faces are now easier to read, and better at triggering a nurturing response.

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† I've deliberately avoided putting hard numbers on the scale of these differences. It is easy to find estimates, and very hard to find primary sources for them; after an hours-long search

hardware is packed off into a separate compartment, while ours is exposed to the main flow of air through our noses. This difference is crucial. It means that whenever we exhale, we purge the odorants from our noses, causing our experience of smell to strobe and flicker. Dogs, by contrast, get a smoother experience, because odorants that enter their noses tend to stay there, and are merely replenished by every sniff.

The shape of their nostrils adds to this effect. If a dog is sniffing a patch of ground, you might imagine that every exhalation would blow odorants on the surface *away* from the nose. But that's not what happens. The next time you look at a dog's nose, notice that the front-facing holes taper off into side-facing slits. When the animal exhales while sniffing, air exits through those slits and creates rotating vortices that waft fresh odors *into* the nose. Even when breathing out, a dog is *still* sucking air in. In one experiment, an English pointer (who was curiously named Sir Satan) created an uninterrupted inward airstream for 40 seconds, despite exhaling 30 times during that period.

With such hardware, it's no wonder that dog noses are incredibly sensitive. But how sensitive? Scientists have tried to find the thresholds at which dogs can no longer smell certain chemicals, but their answers are all over the place, varying by factors of 10,000 from one experiment to another.* Rather than focusing on these dubious statistics, it's more instructive to look at what dogs can actually do. In past experiments, they have been able to tell identical twins apart by smell. They could detect a single fingerprint that had been dabbed onto a microscope slide, then left on a rooftop and exposed to the elements for a week. They could work out which direction a person had walked in after smelling just five footsteps. They've been trained to detect bombs, drugs, landmines, missing people, bodies, smuggled cash, truffles, in-

that included a scientific paper that sourced a factoid to a book in the For Dummies series, I fell into an existential void and questioned the very nature of knowledge. Regardless, the differences are there, and they're substantial; it's only a question of exactly how substantial they are.

* In one study, two dogs could detect amyl acetate—think bananas—at just 1 or 2 parts per trillion, which would make them 10,000 to 100,000 times better than humans. But it also makes them 30 to 20,000 times better than six beagles that were tested on the same chemical 26 years earlier, using different methods.

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vasive weeds, agricultural diseases, low blood sugar, bedbugs, oil pipeline leaks, and tumors.

Migaloo can find buried bones at archeological sites. Pepper uncovers lingering oil pollution on beaches. Captain Ron detects turtle nests so that the eggs can be collected and protected. Bear can pinpoint hidden electronics, while Elvis specializes in pregnant polar bears. Train, who flunked out of drug detection school for being too energetic, now uses his nose to track the scat of jaguars and mountain lions. Tucker used to hang off the bow of boats and sniff for orca poop; he has since retired, and his duties now fall to Eba. If it has a scent, a dog can be trained to detect it. We redirect their Umwelten in service of our needs, to compensate for our olfactory shortcomings. These feats of detection are worth marveling at, but they are also parlor tricks. They allow us to abstractly appreciate that dogs have a great sense of smell, without truly appreciating what that means for their inner lives or how their olfactory world differs from a visual one.

Unlike light, which always moves in a straight line, smells diffuse and seep, flood and swirl. When Horowitz observes Finn sniffing a new space, she tries to ignore the clear edges that her vision affords, and instead pictures "a shimmering environment, where nothing has a hard boundary," she says. "There are focal areas, but everything is sort of seeping together." Smells travel through darkness, around corners, and in other conditions that vex vision. Horowitz can't see into the bag slung over the back of my chair, but Finn can *smell* into it, picking up molecules drifting from the sandwich within. Smells linger in a way that light does not, revealing history.* The past occupants of Horowitz's room have left no ghostly visual traces, but their chemical imprint is there for Finn to detect. Smells can arrive before their sources, foretelling what's to come. The scents unleashed by distant rain can clue people in to advancing storms; the odorants emitted by humans arriving home can send their dogs running to a door. These skills are sometimes billed as extrasensory, but they are simply sensory. It's just

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* I can think of one exception: Some marine worms release glowing "bombs" full of luminescent chemicals, whose persistent light distracts predators from the escaping worms.

that things often become apparent to the nose before they appear to the eyes. When Finn sniffs, he is not merely assessing the present but also reading the past and divining the future. And he is reading biographies. Animals are leaking sacks of chemicals, filling the air with great clouds of odorants.* While some species deliberately send messages by releasing smells, all of us inadvertently do so, giving away our presence, position, identity, health, and recent meals to creatures with the right noses.†

"I never thought much about the nose at all," says Horowitz. "It didn't occur to me."‡ When she started studying dogs, she focused on things like their attitudes to unfairness—the kind of topic that's interesting to psychologists. But after reading Uexküll and thinking about the Umwelt concept, she shifted her attention to smell—the kind of topic that's interesting to *dogs*.

She notes, for example, that many dog owners deny their animals the joys of sniffing. To a dog, a simple walk is an odyssey of olfactory exploration. But if an owner doesn't understand that and instead sees a walk as simply a means of exercise or a route to a destination, then every sniffy act becomes an annoyance. When the dog pauses to examine some invisible trace, it must be hurried along. When the dog sniffs at poop, a carcass, or something the owner's senses find displeasing, it must be pulled away. When the dog sticks its nose in the crotch of an-

* Leopard urine smells of popcorn. Yellow ants smell of lemons. Depending on the species, stressed frogs can smell of peanut butter, curry, or cashew nuts, according to scientists who painstakingly sniffed 131 species and won an Ig Nobel Prize for their efforts. Crested auklets—comical seabirds that have tufted heads—roost in massive colonies that, quite delightfully, smell of tangerines.

† One possible exception is the puff adder, a venomous African snake. It sits in ambush for weeks at a time, and protects itself by visually blending into its environment. But somehow, it seems to blend in chemically, too. In 2015, Ashadee Kay Miller found that keen-nosed animals, including dogs, mongooses, and meerkats, can't detect a puff adder, even when they walk over one. Dogs can detect the scent of shed skin, but for reasons that no one understands, the living snakes are undetectable to their noses.

‡ Scientists fall prey to this, too. When Horowitz tallied every study of dog behavior published in the last decade, she found that only 4 percent focused on smell. Just 17 percent described the odor environment in which experiments were done—including airflow, temperature, humidity, or the previous presence of people or food. It's as if vision researchers hadn't thought to mention if their laboratory lights were on or not.

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other dog, it's being indecorous: Bad dog! After all, in Western cultures at least, humans don't smell each other.* "You could give someone a hug, but if you actually sniffed them, that would be very weird," says Horowitz. "I could say that your hair smells great, but I can't say that *you* smell great, unless we're intimate." Time and again, people impose their values—and their Umwelt—onto their dogs, forcing them to look instead of sniff, dimming their olfactory worlds and suppressing an essential part of their caninehood. That was never clearer to Horowitz than when she took Finn to a nosework class.

Oddly billed as a sport, these classes simply train dogs to find hidden scents, under increasingly difficult conditions. That should come naturally, but it didn't to many of the animals in Finn's class. Several seemed to lack any agency: They had to be pulled from box to box by their owners, or were completely unsure what to do. Others became agitated in the presence of other dogs and barked at them. But after a summer of sniffing, those behavioral quirks diminished. The reticent dogs regained their volition. The reactive dogs became tolerant. All seemed more easygoing. Fascinated, Horowitz and her colleague Charlotte Duranton ran their own experiment with 20 dogs. In front of each animal, Duranton placed a bowl in one of three locations: one where the bowl always contained food, a second where it was always empty, and a third where the outcome was ambiguous. The dogs quickly learned to approach the food-filled bowl and ignore the empty one. What about the ambiguous one? A dog's willingness to approach *that* bowl indicates what a cognitive psychologist might call *positive judgment bias* and what everyone else might call *optimism*. Horowitz found that dogs became more optimistic after just two weeks of nosework. As their sense of smell brightened, so did their outlook. (By contrast, dogs didn't change after two weeks of heelwork—an owner-led obedience activity that involves neither olfaction nor autonomy.)

For Horowitz, the implications are clear: Let dogs be dogs. Appreciate that their Umwelt is different, and lean into that difference. She

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* At the Oscars ceremony in 2021, a journalist asked South Korean actor Yuh-Jung Youn what Brad Pitt smells like. Youn replied, "I didn't smell him! I'm not a dog!"

does this by taking Finn on dedicated smell walks, when he's allowed to sniff to his olfactory bulb's content. If he stops, she stops. His nose sets the pace. The walks are slower, but she has no destination in mind. We go on such a walk together, heading a few blocks west of her office and into Manhattan's Riverside Park. It's a hot summer's day, and the air is redolent with garbage, urine, and exhaust—and that's only what I can smell. Finn detects more. He runs his nose along the cracks in the pavement. He investigates a traffic sign. He pauses to sniff a hydrant "because it's been visited by all the other dogs of Columbia University," Horowitz says. Sometimes she'll see Finn sniff a fresh patch of urine, raise his head, look around (or smell around), and find the dog that just left it. The smell isn't just an object unto itself but a reference point, and the walk isn't just an intermediate state between points A and B but a tour of Manhattan's layered, unseen stories.

Once we're inside the park, the air fills with greenery, cut grass, mulch, and barbecues. Another dog walks past and Finn turns to breathe in an odor sample, puffing his cheeks out like a cigar smoker. Two large poodles approach, but before they can get close, their owner pulls them away and body-checks them against a fence. Horowitz looks sad. She's happier when a female Australian shepherd arrives and circles Finn, both enthusiastically sniffing each other's genitals, while we make small talk with the owner. We glean the other dog's sex through pronouns; Finn worked it out through smell. We ask about her age; Finn can guess. We don't ask about her health or readiness to mate; Finn doesn't need to ask. "There was a time when I would try to smell what he's smelling, but I do that less often simply because I know I'm not getting what he's getting," Horowitz says. But there's room for improvement. Though the human nose lacks the anatomical complexity of a dog's and is unhelpfully farther from the ground, it is also underused. By taking more sniffs herself, and paying closer attention to odors, Horowitz says that she has become a better smeller (and a more socially awkward one). "We have perfectly good noses. We just don't use them as well as the dog."

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A FUNNY THING HAPPENS when you mention dogs to neuroscientists who study olfaction in humans, as Horowitz learned while writing her book *Being a Dog*. They get a little territorial, a little . . . well . . . sniffy. Some dislike that dogs get treated like special olfactory paragons when many other mammals are excellent smellers, including rats (which can also detect landmines), pigs (whose olfactory epithelium can be twice as large as a German shepherd's), and elephants (which we'll get to later). Others point to massive discrepancies in studies that test dogs' ability to detect specific odors. These have variously claimed that dogs are a billion times more sensitive than humans, or a million times, or just ten thousand times. In some cases, humans do *better:* Of 15 odorants where both species have been tested, humans outperformed our canine companions on five, including beta-ionone (cedar wood) and amyl acetate (bananas). People also excel at discriminating between smells. While it's easy to find two colors that humans can't tell apart, it's very hard to find indistinguishable pairs of odors. Neuroscientist John McGann has tried, and tells me, "We tried odors that *mice* can't tell apart and humans were like: No, we've got this."

Yet textbooks still claim our sense of smell is terrible. McGann traced the origin of this pernicious myth to the nineteenth century. In 1879, neuroscientist Paul Broca noted that our olfactory bulbs are relatively puny compared to those of other mammals. He reasoned that smell is a base and animalistic sense, and the loss of it was necessary for us to have higher thought and free will. He then classified us (along with other primates and whales) as non-smellers. The label stuck, even though Broca never actually measured how well animals smell, relying instead on sketchy inferences based on the dimensions of their brains. Compared to a mouse, a human has an olfactory bulb smaller relative to other parts of the brain, but also physically bigger, with roughly as many neurons. It's not clear what any one of these metrics says about an animal's experience of smell.*

The textbook perspective is also a Western one, based on cultures

* The olfactory bulb might not even be necessary for smell. In 2019, Tali Weiss identified several women who seem to lack this structure altogether and could smell just fine. How they do it is anyone's guess.

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where smell has long been undervalued. Plato and Aristotle argued that olfaction was too vague and ill-formed to produce anything other than emotional impressions. Darwin deemed it to be "of extremely slight service." Kant said that "smell does not allow itself to be described, but only compared through similarity with another sense." The English language confirms his view with just three dedicated smell words: *stinky, fragrant,* and *musty*. Everything else is a synonym (*aromatic, foul*), a very loose metaphor (*decadent, unctuous*), a loan from another sense (*sweet, spicy*), or the name of a source (*rose, lemon*). Of the five Aristotelian senses, four have vast and specific lexicons. Smell, as Diane Ackerman wrote, "is the one without words."

The Jahai people of Malaysia would disagree, as would the Semaq Beri, the Maniq, and the many other hunter-gatherer groups who have dedicated smell vocabularies. The Jahai use a dozen words for smells and smell alone. One describes the scent in gasoline, bat droppings, and millipedes. Another is for some quality shared by shrimp paste, rubber tree sap, tigers, and rotten meat. Yet another refers to soap, the pungent durian fruit, and the popcorn-like twang of the binturong.* They "have this ease of talking about smells," says psychologist Asifa Majid, who found that the Jahai can name smells as easily as English-speakers can name colors. Just as tomatoes are red, the binturong is *ltpit*. Smell is also a fundamental part of their culture. Once, Majid was told off by Jahai friends for sitting too close to her research partner and allowing their smells to mingle. Another time, she tried to name the smell of a wild ginger plant; children mocked her not only for failing but also for treating the whole plant as a single object, when the stem and flowers *obviously* had distinct smells. The myth of poor human olfaction "might have been overridden much earlier if the humans under consideration had been Jahai instead of Brits and Americans," Majid tells me.

Even Westerners can pull off surprising olfactory feats when given the chance. In 2006, neuroscientist Jess Porter took blindfolded stu-

* The binturong is a black, shaggy, 2-meter-long creature that looks like a cross between a cat, weasel, and bear. It's also known as a bearcat, and makes a cameo appearance in my first book, *I Contain Multitudes*.

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dents to a park in Berkeley and asked them to follow a 10-meter trail of chocolate oil that she had drizzled on the grass. The students got down on all fours, snuffled about like dogs, and looked ridiculous. But they succeeded, and got better with practice.

When I visit Alexandra Horowitz, she challenges me to the same test and lays some chocolate-scented string on the floor. Eyes closed and nostrils open, I kneel down and sniff away. I quickly pick up the smell of chocolate and follow it. When I lose the scent, I cast my head from side to side, exactly like a dog would. But there end the similarities. A dog can sniff six times a second, wafting a steady conveyor of air over its olfactory receptors. I start to hyperventilate after several consecutive sniffs, and when I pause to exhale, I lose the trail. I succeed in tracking the string, but it takes me a minute to do what Finn manages in half a second. Even if I practiced regularly, I couldn't come close; I don't have the hardware. And crucially, Horowitz adds after whipping away the string, a dog can still follow a trail once the odor source is gone. We both try, bending down to sniff. "I don't smell anything left," she says. We humans underestimate our sense of smell, but it's also clear that we simply don't live in the same olfactory world as a dog. And that world is so complicated that it's a wonder we can make sense of it at all.

MANY LIVING THINGS CAN sense light. Some can respond to sound. A select few can detect electric and magnetic fields. But every thing, perhaps without exception, can detect chemicals. Even a bacterium, which consists of just one cell, can find food and avoid danger by picking up on molecular clues from the outside world. Bacteria can also release their own chemical signals to communicate with each other, launching infections and performing other coordinated actions only when their numbers are large enough. Their signals can then be detected and exploited by bacteria-killing viruses, which have a chemical sense even though they are such simple entities that scientists disagree about whether they're even alive. Chemicals, then, are the most ancient and universal source of sensory information. They've been part

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of Umwelten for as long as Umwelten have existed. They're also among the hardest parts of it to understand.

Scientists who work on vision and hearing have it comparatively easy. Light and sound waves can be defined by clear and measurable properties like brightness and wavelength, or loudness and frequency. Shine wavelengths of 480 nanometers into my eyes, and I'll see blue. Sing a note with a frequency of 261 hertz (Hz), and I'll hear middle C. Such predictability simply doesn't exist in the realm of smells. The variation among possible odorants is so wide that it might as well be infinite. To classify them, scientists use subjective concepts like intensity and pleasantness, which can only be measured by asking people. Even worse, there are no good ways of predicting what a molecule smells like—or even if it smells at all—from its chemical structure.* And yet, many animals naturally grapple with the intricacy of olfaction, without any training in chemistry or neuroscience. Their noses are kings of infinite space. How do they work?

The basics became clearer after Linda Buck and Richard Axel made a pivotal discovery in 1991. In work that would earn them a Nobel Prize, the duo identified a large group of genes that produce odorant receptors—the proteins that initially recognize smelly molecules.† We

* Unless you actually stuck your nose over some benzaldehyde, you couldn't guess that it smells like almonds. If you saw dimethyl sulfide drawn on a page, you couldn't foresee that it carries the scent of the sea. Even similar molecules can produce immensely different smells. Heptanol, with a backbone of seven carbon atoms, smells green and leafy. Add another carbon atom to the chain and you get octanol, which smells more like citrus. Carvone exists in two forms that contain exactly the same atoms but are mirror images of each other: One smells of caraway seeds and the other of spearmint. Mixtures are even more confusing. When mixed, some pairs of odors still smell distinct, while others produce a third smell that's unlike the two parents. Meanwhile, perfumes that contain hundreds of chemicals don't smell any more complex than individual odorants, and people typically struggle to name more than three ingredients in a blend. Noam Sobel, a neurobiologist who studies olfaction, has come closer than anyone else to wrangling this complexity. While I was writing this book, he and his team developed a measure that analyzes 21 features of odorant molecules and collapses these into a single number. The closer this smell metric is for any two molecules, the more similar their odors. This isn't quite the same as predicting scent from structure, but it's the next best thing—predicting scent from similarity to other scents.

† The terminology is confusing. In sensory biology, the word *receptor* is usually used to describe a sensory cell, like a photoreceptor or a chemoreceptor. In this case, the odorant receptors are proteins on the surface of those cells. Don't blame me; I didn't make the rules.

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encountered them earlier in this chapter while discussing dogs, but they underlie the sense of smell throughout the animal kingdom. The odorant receptors probably recognize their target molecules, like electric sockets accepting certain cables.* When this happens, the neurons that harbor these receptors send signals to the smell centers of the brain, and the animal perceives a scent. But the details of this process are still murky. There aren't enough receptors to account for the huge range of possible odorants, so the perception of scent must depend on the combination of olfactory neurons that are firing. If one group goes off, you delight at the scent of a rose. If another group activates, you wince at the whiff of vomit. Such a code must exist, but its nature is still mostly mysterious.

Odorant receptors can also vary from one individual to another in dramatic ways. For example, the OR7D4 gene creates a receptor that responds to androstenone, the chemical behind the stench of sweaty socks and body odor. To most people, it's repulsive. But to a lucky few who inherit a slightly different version of OR7D4, androstenone smells like *vanilla*. That's just one receptor out of hundreds, and all exist in varied forms, bestowing every individual with their own subtly personalized Umwelt. Everyone likely smells the world in a slightly different way. And if it's that hard to appreciate the olfactory Umwelt of another human, imagine how hard the task becomes for another species.

We should be skeptical of any claim that pits one animal's sense of smell against another's. I have repeatedly read that an elephant's sense of smell is five times more sensitive than a bloodhound's, but that's an utterly meaningless statement. Does that mean the elephant detects five times more chemicals? Does it sense certain chemicals at a fifth the concentration, or from five times the distance? Does it remember smells for five times as long? Such comparisons will always be flawed because smell is diverse and often unquantifiable. We need to stop asking "How good is an animal's sense of smell?" Better questions would

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* One widely popularized theory, which says that smells are encoded in the vibrations of different molecules, has been thoroughly debunked.

be "How important is smell to that animal?" and "What does it use its sense of smell for?"

Male moths, for example, are tuned to sexual chemicals released by females. They pick up these odorants from miles away using feathery antennae, and slowly flutter over to the source. Smell is so important to them that when scientists transplanted the antennae of female sphinx moths onto males, the recipients behaved like females, seeking out the scent of egg-laying sites instead of mates. Their sense of smell is clearly amazing, as evidenced by the continued existence of moths. But they only put this amazing sense toward a few specific tasks. Moths have been described as "odor-guided drones," and that's not an exaggeration. Many males don't even have mouthparts when they reach adulthood. Freed from the need to feed, their short lives are devoted to flying, finding, and . . . mating. Their behaviors are simple enough that they can be easily diverted. By mimicking female moth odors, bolas spiders can lure male moths into fatal ambushes, while farmers can lure them into traps. Other insects, however, process smells in more sophisticated ways.

IN A LAB IN New York City, Leonora Olivos Cisneros pulls out a large Tupperware container and lifts the lid to reveal a writhing sea of dark-red dots. They're ants. Specifically, they're clonal raiders—an obscure species that's stockier than most ants and, unusually, has neither queens nor males. Every individual is female and every one can reproduce by cloning herself. About 10,000 of them are scurrying around the container. Most have formed a makeshift nest from their own bodies and are tending to their young grubs. The rest are wandering around in search of food. Olivos Cisneros feeds them on other ants, including escamoles—the larvae of a much larger species that she brings over from Mexico.

The clonal raiders are so small that it's hard to focus on any one of them. Under the microscope, they're much easier to see, not just because they've been magnified but also because Olivos Cisneros has painted them. With practiced hands, she uses insect pins to dab

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splotches of yellow, orange, magenta, blue, and green onto the insects' backs, giving each individual a unique color code that can be tracked by an automated camera system. The colors also make them easier to observe by eye. Every now and then, I notice one of them tapping at another with the tips of its clubby antennae. This action, delightfully known as antennating, is the ant equivalent of a sniff. It's the means through which they inspect the chemicals on each other's bodies and discern colony-mates from interlopers. These ants normally live underground and are completely blind. "There's nothing visual going on," Daniel Kronauer, who leads the lab, tells me. "In terms of their communication, everything is chemical."

The chemicals they use are pheromones—an important term that is frequently misunderstood. It refers to chemical signals that carry messages between members of *the same species*. Bombykol, which female moths use to attract males, is a pheromone; the carbon dioxide that draws mosquitoes to my body is not. Pheromones are also *standardized messages,* whose use and meaning do not vary between individuals of a given species. All female silk moths use bombykol and all males are attracted to it; by contrast, the smells that distinguish one person's scent from another's are *not* pheromones. Indeed, despite the existence of pheromone parties where singletons sniff each other's clothes, or pheromone sprays that are marketed as aphrodisiacs, it's still unclear if human pheromones even exist. Despite decades of searching, none have been identified.*

Ant pheromones are another story. There are many, and ants put them to different uses depending on their properties. Lightweight chemicals that easily rise into the air are used to summon mobs of workers that can rapidly overwhelm prey, or to raise fast-spreading alarms. Crush the head of an ant, and within seconds, nearby colony-

* Human pheromones likely exist, but finding them is a chore. In animals, researchers typically look for stereotyped behaviors or physiological reactions that reveal the reaction to a pheromone—a flaring of the lips, a fluttering of antennae, or a rise in testosterone. Humans are so annoyingly varied and complex that few of our actions fit the bill. Some researchers once suspected that women synchronize their menstrual cycles because of some unidentified pheromone, but such synchronicity is itself a myth. Others now think that breasts might release a pheromone that prompts babies to suckle, but again, no chemical has been isolated.

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mates will sense the aerosolized pheromones and charge into battle. Medium-weight chemicals that become airborne more slowly are used to mark trails. Workers lay these down when they find food, leading other colony-mates to foraging hotspots. As more workers arrive, the trail is strengthened. As the food runs out, the trail decays. Leafcutter ants are so sensitive to their trail pheromone that a milligram is enough to lay a path around the planet three times over. Finally, the heaviest chemicals, which barely aerosolize, are found on the surface of the ants' bodies. Known as cuticular hydrocarbons, they act as identity badges. Ants use them to discern their own species from other kinds of ants, nestmates from other colonies, and queens from workers. Queens also use these substances to stop workers from breeding or to mark unruly subjects for punishment.

Pheromones hold such sway over ants that they can force the insects to behave in bizarre and detrimental ways, in disregard of other pertinent sensory cues. Red ants will look after the caterpillars of blue butterflies, which look nothing like ant grubs but *smell* exactly like them. Army ants are so committed to following their pheromone trails that if those paths should accidentally loop back onto themselves, hundreds of workers will walk in an endless "death spiral" until they die from exhaustion.* Many ants use pheromones to discern dead individuals: When the biologist E. O. Wilson daubed oleic acid onto the bodies of living ants, their sisters treated them as corpses and carried them to the colony's garbage piles. It didn't matter that the ant was alive and visibly kicking. What mattered was that it *smelled* dead.

"The ant world is a tumult, a noisy world of pheromones being passed back and forth," Wilson said. "We don't see it, of course. We don't see anything more than these little ruddy creatures scurrying around on the ground, but there's a huge amount of activity, of coordination and communication going on." That's all based on pheromones. These smelly substances allow ants to transcend the limits of

* In September 2020, I noted that the army ant death spiral was the perfect metaphor for the United States' response to the COVID-19 pandemic: "The ants can sense no picture bigger than what's immediately ahead. They have no coordinating force to guide them to safety. They are imprisoned by a wall of their own instincts."

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individuality and act as a superorganism, producing complex and transcendent behaviors from the unknowing actions of simple individuals. They allow army ants to act as unstoppable predators, Argentine ants to create supercolonies that extend for miles, and leafcutter ants to develop their own agriculture by gardening fungi. Ant civilizations are among the most impressive on Earth, and as ant researcher Patrizia d'Ettorre once wrote, their "genius is definitely in their antennae."

Kronauer's research with the clonal raider ant shows how that genius might have evolved. Ants are essentially a group of highly specialized wasps that evolved between 140 and 168 million years ago and rapidly transitioned from a solitary existence to an extremely social one. Along the way, their repertoire of odorant receptor genes—the ones that allow them to sense smelly chemicals—ballooned in size. While fruit flies have 60 of these genes and honeybees have 140, most ants have between 300 and 400, and the clonal raider has a record-breaking 500.* Why? Here are three clues. First, a third of the clonal raiders' odorant receptors are only produced on the underside of their antennae—the parts that they pat each other with during antennation. Second, these receptors specifically detect the heavyweight pheromones that ants wear as identity badges. Third, these 180 or so receptors all arose from just one gene, which was repeatedly duplicated at roughly the time that ancestral ants went from living alone to living in colonies. Putting these clues together, Kronauer reasons that all that extra olfactory hardware might have helped ants to better recognize their nestmates. After all, they are not only looking for the presence or absence of *one* pheromone but weighing up the relative proportions of a few dozen of them. That's a challenging computation, but one that undergirds everything else that ants do. By expanding their powers of smell, they gained the means of regulating their sophisticated societies.

It becomes especially obvious how much ants rely on smell when they are disconnected from that sense. When Kronauer deprived his clonal raiders of a gene called *orco,* which odorant receptors need to

* A word of caution: It is dangerous to assess an animal's sensory abilities by counting its genes. Dogs have twice the number of working odorant receptor genes as humans, but that doesn't mean that their sense of smell is twice as good.

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detect their target molecules, the mutant ants behaved in entirely un-ant-like ways. "Right from the beginning, there was something wrong with those ants," Olivos Cisneros tells me. "It was super-easy to spot." They wouldn't follow pheromone trails. They ignored barriers whose intense smells would ward off normal ants, like lines drawn by Sharpies. They ignored the grubs that they're normally duty-bound to care for. They ignored their colonies altogether, and went walkabout on their own for days at a time. If they accidentally found themselves within a colony, their presence was disruptive. Sometimes they'd release alarm pheromones without provocation, sending their nestmates into an unnecessary panic. "They can't tell that there are other ants there," Kronauer says. "They just can't sense them at all." It's hard not to feel sorry for them. An ant without olfaction is an ant without a colony, and an ant without a colony is barely an ant at all.*

Ants are perhaps the most dramatic example of the power of pheromones, but they're hardly the only ones. Female lobsters urinate into the faces of males to tempt them with a sex pheromone. Male mice produce a pheromone in their urine that makes females especially attracted to other components in their odor; this substance is called darcin, after *Pride and Prejudice*'s male hero. The early spider-orchid deceives male bees into carrying its pollen by mimicking their sexual pheromones. "We live, all the time, especially in nature, in great clouds of pheromones," E. O. Wilson once said. "They're coming out in spumes in millionths of a gram that can travel for maybe a kilometer." These tailored messages drive the entire animal kingdom, from the smallest of creatures to the very biggest.

IN 2005, LUCY BATES arrived in Kenya's Amboseli National Park to study its elephants. On her first day out, her experienced field assistants told her that these animals, which had been observed by scientists since the 1970s, would almost certainly realize that a fresh face had

* There's precedent for this. Back in 1874, the Swiss scientist Auguste Forel showed that an ant's antennae are its main organs of smell. When he removed those antennae, ants wouldn't build their nests, care for their young, or attack interlopers from other colonies.

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joined the research group. Bates was skeptical. How would they know? Why would they care? But as soon as the team found one of the herds and switched off their vehicle's engine, the elephants immediately turned toward them. "One of them came up, stuck her trunk in my window, and had a good sniff," Bates tells me. "They knew someone new was inside."

Over the next few years, Bates came to realize what anyone who spends time with elephants knows: Their lives are dominated by smell. You don't need to know about an elephant's record-breaking catalog of 2,000 olfactory receptor genes, or the size of its olfactory bulb. Just watch the trunk. No other animal has a nose so mobile and conspicuous, and so no other animal is as easy to watch in the act of smelling. Whether an elephant is walking or feeding, alarmed or relaxed, its trunk is constantly in motion, swinging, coiling, twisting, scanning, sensing. Sometimes the entire 6-foot organ periscopes dramatically to inspect an object. Sometimes its movements are subtle. "You can approach a feeding elephant who's heard you coming, and without turning its head, it'll flick just the tip of its trunk toward you," says Bates.

African elephants can use their trunks to detect their favorite plants, even when obscured in lidded boxes, and even when hidden among a messy botanical buffet. They can learn unfamiliar smells: After being briefly taught to detect TNT, which is supposedly odorless to humans, three African elephants could identify the substance more skillfully than highly trained detection dogs. Two of those same elephants, Chishuru and Mussina, could sniff a human and identify the matching scent from a row of nine jars laced with the odors of different people. Asian elephants are no slouches, either. In one study, they could correctly identify which of two covered buckets contained more food through smell alone—a feat that humans can't duplicate and that (in one of Alexandra Horowitz's experiments) even dogs struggled with.* "We could tell the difference if we looked, but if we were just smelling it, there's no way," says Bates. "The level of information they can get is just so far beyond what we can comprehend."

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* Horowitz thinks that the dogs might just not have been motivated to do it.

Elephants can also smell danger. Some time after Bates arrived in Amboseli, one of her colleagues gave a ride to a couple of Maasai men in a jeep that the team had used for decades. The next day, when the team drove out, the elephants were unexpectedly cautious around the familiar vehicle. Young Maasai men will sometimes spear elephants, and Bates reasoned that the creatures were disconcerted by the lingering scents in the jeep—some combination of the cows that the Maasai raise, the dairy products they eat, and the ochre they daub on their bodies. To test this idea, she hid various bundles of clothes in elephant country. When the animals approached washed garments or those worn by the Kamba, who pose no threat to them, they were curious but unconcerned. But every time they got wind of clothes worn by the Maasai, their reactions were unmistakable. "Once the first trunk went up, the whole group *ran* away as fast as they could, and almost always into long grass," Bates tells me. "It was incredibly stark—every group, every time."

Food and foes aside, few sources of odor are as pertinent to an elephant as other elephants. They'll regularly inspect each other with their trunks, probing away at glands, genitals, and mouths. When African elephants reunite after a prolonged separation, they go through intense greeting rituals. Human observers can see their flapping ears and hear their throaty rumbles, but for the elephants themselves, the experience must also be olfactory pandemonium. They vigorously urinate and defecate, while aromatic liquid pours forth from glands behind their eyes, filling the air around them with scents.

Few people have done more to study elephant odors than Bets Rasmussen,* a biochemist who was once crowned "the queen of elephant secretions, excretions and exhalations." If an elephant produced it, Rasmussen likely sniffed it and possibly tasted it. Those secretions, she realized, are full of pheromones, and thus full of meaning. In 1996, after 15 years of work, she isolated a chemical called Z-7-dodecen-1-yl

* Given that elephants live in matriarchal societies that are led by females, it's fitting that the study of elephant senses has been led by women: Bets Rasmussen for olfaction; Katy Payne, Joyce Poole, and Cynthia Moss for hearing; and Caitlin O'Connell for seismic senses. We'll meet the others in later chapters.

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