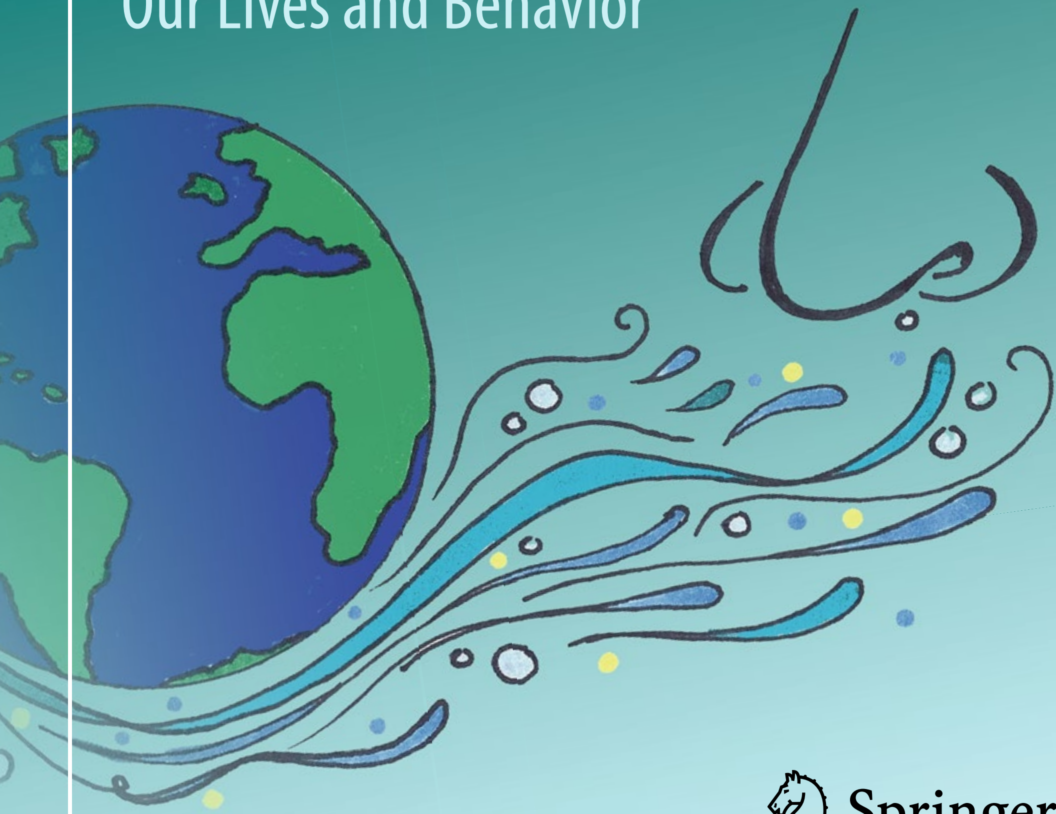
Paul A. Moore

# The Hidden Power of Smell

## How Chemicals Influence Our Lives and Behavior



Springer

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## How Chemicals Influence Our Lives and Behavior

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*To Jen for showing me love,*
*To Meghan for showing me empathy,*
*To Connor for showing me humor,*
*and*
*To Nobody, because even Nobodies*
*are somebodies.*

# Preface

This book provides a mere glimpse into the world that has dominated my career for more than three decades. In studying the minds of animals and attempting to elucidate the role that chemical signals play in decision making, one gets quite close to the subject matter and the organisms involved. At times, this myopic view of nature and its organisms hinders the ability of someone to see the bigger picture of how everything fits together into a coherent picture. Given the structure of science today and the need to become an expert in one area, we are forced to focus and specialize. Writing this book has forced me to read outside of my focal point (aquatic chemical ecology) and engage my mind with researchers and animals far afield from my crayfish. In doing this mental expansion, I found myself amazed and excited about all of the ways that evolutionary processes have developed adaptations that involve the use of the chemical world. Plants that communicate fear signals and animals that cross-dress using special perfumes are just a couple of other worldly adaptations that are often overlooked. I hope that this renewed excitement found its way into this book and I capture the imagination of the reader.

One of the most common questions asked of me is how I got to this point in time. How did I make the decision to study marine and aquatic life? Why lobsters and crayfish? Why chemical signals? I enjoy these questions because they provide me an opportunity to pause and think about seminal events that caused me to choose one path over another. In retrospect, many of these paths look quite linear, but in reality, they are most likely a life-sized game of pinball. Sometimes, we think we know where we are headed and out of the blue a bumper comes along and redirects our life.

As a youth, I would spend my Saturdays watching one of three programs: Saturday morning cartoons, B-grade monster movies like Godzilla or Mothra, or *The Undersea World of Jacques Cousteau*. More than likely, this latter show is the one which captured my imagination about the aquatic world that started me down a path that has taken me to my career. The images shown by the weekly adventures of Cousteau and his team could have been of an alien world. Deep sea corals, sea cucumbers, and large cephalopods were shown in such detail that I imagined that I was really underwater. Because this was before the internet allowed one to find an image and description of some deep sea creature instantly, I really felt that I was privileged to be a part of the discovery of new and fascinating organisms. Cousteau would focus on the diversity of life instead of running a popular culture-driven theme week that merely centered on the charismatic megafauna of sharks and dolphins.

Looking backward on one's life can produce a false sense of predestined steps that ultimately lead to a singular consequence and that consequence is where we are in the present. Probably in reality, a series of innocuous or random events have led us to where we end up. The TV show on the marine environment was a constant narrative of my youth that played against summer vacations spent really exploring the natural world. Every summer, at least for a week if not longer, we would pack up the family in a camper and explore the less charted areas of the United States. This first started in my home state of Michigan with yearly trips to the Upper Peninsula and its many bodies of water and rivers. I fondly remember playing in rivers, looking for crayfish (which would be foreshadowing if our lives were movies), and using rocks, twigs, and branches to redirect the water. I was becoming fascinated with the movement of water through, around, and over the many different obstacles in the northern Michigan streams and rivers. These two factors, Jacque Cousteau and the aquatic life of Michigan, interacted to create inside of me a draw to water in some form.

Maybe the final event that turned into destiny was a simple little job report written around the age of 10 while I was in fourth grade. Through some chance or guided by the unconscious images of undersea life, I selected to do a report on Biological Oceanography. Probably not the most typical job report for most kids in the fourth grade, but the details that I wrote about cemented in my mind that this was the greatest job in the world. Thus, every academic decision I made from that point forward was aimed at achieving that singular goal. I was going to become a biological oceanographer.

These series of events began my love affair with the aquatic life and on a pathway that went from undergraduate work, to graduate work, and on to academic work in the field of science. Being somewhat adventurous, the academic training has allowed me to travel to and explore different aquatic habitats. Working in submersibles, walking on salt flats, diving on crystal clear reefs, slogging through muddy bogs, to some of the most beautiful streams and rivers on the plant, I found one commonality across all of these disparate habitats. Aquatic life is literally awash with chemicals, and organisms have evolved an incredible ability to harness these signals to carry out the basic functions of life. The more that I (and all of the other scientists working in these fields) answered one set of questions, a dozen more popped up. Rather than being frustrated with this increasing level of planned ignorance, I become more and more excited. Science is one of those endeavors where the more you know, the more you recognize that is left to know.

The aquatic realm, in particular, is a habitat that is often devoid of light, so visual signals are not very functional. So, organisms have evolved elaborate mechanisms to use chemical signals to carry out all of the functions that terrestrial life uses visual and auditory cues. The chemical sense has been termed the primal sense because it is the first sensory system to evolve and as such, is deeply connected to evolutionary history that all organisms share. A description of any environment, especially aquatic ones, would be incomplete without highlighting odors.

So, this book is born out of the love affair between aquatic life, chemical signals, and the need to share what I know about this fabulous field. I have covered only a small fraction of the stories and science of chemical ecology. As touched on at the end of each chapter and expounded on in the last chapter, human chemical ecology is still poorly undeveloped compared to our understanding of other animal's use of chemical signals, and that understanding is sadly decades behind the fields of vision and hearing. I am by no means an expert on human chemical ecology, but I offer up these stories in order to enlighten our collective understanding on this hidden sense.

Bowling Green, OH, USA Paul A. Moore

# Acknowledgements

To stand on the shoulders of giants is a paraphrase of Sir Issac Newton's famous quote. If we are honest as scientists, we all stand on the shoulders of greater giants and lesser giants. Our thinking and work would not be possible if there were no researchers that opened the doors of knowledge in front of us and gladly shared their work. This book, although my words, is a synthesis of countless numbers of students, faculty, researchers, and artists that have laid the foundation of knowledge on which I stand. Some of those researchers are named in this book whereas others are hidden just like the chemical signals that they study. I want to recognize all of those individuals (both named and unnamed) for their hard work in trying to bring to light nature's secrets. Nature often guards those secrets well from the prying eyes, ears, and noses of scientists.

The ideas in this book have arisen from countless conversations over dinner or alcohol with friends and colleagues. These include dear friends like Rainer Voigt and Carl Merrill and advisor Jelle Atema who were there at the beginning of my scientific career. These individuals play an instrumental role in launching my early career path. I have been privileged to have spent considerable periods of intellectual growth in some of the most groundbreaking environments that a young scientist could every want. I grew up scientifically in Woods Hole Massachusetts at the Marine Biological Laboratory which itself is surrounded by three other scientific institutions (Woods Hole Oceanographic Institute, National Marine Fisheries, and the United States Geological Survey). I interacted with undergraduates, graduate students, scientists, and Nobel Laureates. If one wants to do Marine Biology, there are few better environments. As a postdoctoral researcher, I spent 2 years at the Monell Chemical Senses Center surrounded by leading researchers all focused on the smell, taste, and trigeminal senses. My office mates, particularly Paul Breslin, my advisor, Bruce Bryant, and two rouge scientists, Larry Clark and Russ Mason, played an important role in cementing my knowledge of the chemical senses. Today, I am lucky enough to spend my summers at the University of Michigan Biological Station where some of the leading ecological researchers gather each summer to teach and perform research. These researchers including Rex Lowe, Steve

Pruett-Jones, Pat Kociolek, Mark Hunter, and others have included me in dinner conversations about ecology and ecological interactions.

From one perspective, I am a scientific mutt. I was trained as a marine biologist working in biomechanics and animal behavior, have done addition training on the neurochemistry of mental disorders and drug addiction, dabbled in neurophysiology of the rat trigeminal system, and now am becoming an ecologist. Each of the groups above has been gracious enough to allow a scientist with a different background to be a part of their conversations. To all of them, I am grateful for their gracious time and expertise. All their thoughts and conversations form the giants whose shoulders I am standing on.

Central to the final product of the words on these pages is the Laboratory for Sensory Ecology. This is a group of individuals who have attached themselves to me as graduate students. They aren't giants (yet), but are outstanding sounding boards. They endure my excited pronouncements about a new study and questions about whether this analogy or that thought works. They are brave enough to tell me when the train has left the tracks and smart enough to read this book as both intellectuals in the discipline and as outsiders looking in. They have read every word in this book and have guided my thinking, writing, and editing. Without their input, there is no book. Unfortunately, I have to just list them alphabetically, but each has provided a perspective that is different from every other member. I hope they can see their thoughts in the book and recognize the depth of contribution that each of them has made. I am proud that they are willing to claim me as an advisor. They are David Edwards, Ana Jurcak, Maryam Kamran, Sara Lahman, Tim Ludington, Alex Neal, Kathryn Rapin, Juliet Slutzker, Molly West, and Sarah Wofford. My undergraduate students have also read the book and provide me with sets of eyes that are most closely aligned with my intended audience. They are Elli Kantonen, Florence Montarmani, Zach Morris, and Kaitlyn Trent.

I would like to thank Janet Slobodien and Eric Hardy of Springer for bringing these thoughts to print and for taking a chance on this book. Finally, a constant source of inspiration and joy is my family. Without their help and support, I wouldn't be in a position to write a book. Jen, Meghan, and Connor, you have been essential to my sanity through the scientific journeys of my life.

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# Chapter 1
# An Introduction

## The Hidden Odor World

It is an early spring morning in Northwest Ohio as I prepare for my morning run. The air still has the crispness and moisture that reminds me of the past winter, but there are signs of warmer days ahead. Having rained last night, there is a hint of freshness to the smell of the morning air. These signs of spring will help me pass the time as I follow my normal route. As much as my body longs for the comfort of my bed, I force myself to set off at my usual slow pace.

As I approach the house on the corner, I see brilliant red Darwin tulips are emerging from their winter slumber in my neighbor's garden. Sprinkled in and around the red are bright yellows, deep purples, and oranges, reminiscent of a living Monet painting. Standing tall like a multi-hued army, these colors serve a far greater purpose than to please this runner's eyes. The petals act as showy advertisement to the local insect community. "Come and sample the sweet nectar" they call. In exchange for the advertised meal, the diner will help spread the pollen needed to propagate the next generation of flowers.

Looking around, I can see other signs of spring which can be found in the trees. Small green buds are appearing and beginning to add a touch of contrast color to the brown branches. A flash of orange and black crosses in front of me and lands on the oak tree to my left—an oriole sporting its bright vest and black coat looking for nest material. The proud cardinal stands out from the green shrubs wearing its formal dress just like its human namesake. I enjoy these colorful distractions on my journey. They take my mind off of my heavy breathing and stimulate me to think about nature and biology even in this small urban setting.

Colors are not the only stimuli that accompany me on my run. Above the din of my footfalls, nature greets me with her melodies, tweets, and chatter. Half a mile down the road from the cardinal and oriole sightings, I hear the familiar coo of a mourning dove that often greets me on my lonely runs. The mourning doves often sit on the power wires across from my house and softly call as I stretch out my stride to warm my muscles for the rest of my run. As most of the world around me sleeps, we share a connection only early risers can feel. A haunting sound, but I have come to welcome their song as an integral part of my morning routine. A loud and angry



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argument wakes me from short introspection. Two squirrels chatter to each other as a brown squirrel chases a black one up, down, and around a large Maple tree. As a behaviorist that studies aggression, I am fascinated by their interactions. Their loud clicks are a sure sign that one is an interloper being forcefully escorted from the other's territory. Despite an intense interest to stop and watch, I move on.

At the end of the road, I leave the hard pavement for a small path leading through a stand of trees to a protected meadow. This is the favorite part of my morning ritual. Although I live in a small town, in these woods, I am immersed in the natural world. There are no sounds from cars, cyclists, or people leaving their homes for a morning commute. The only sights or sounds are those produced by nature herself. As I attempt to run more quietly on the dirt and wood chip path, I can focus more closely on the natural world around me. About 300 yards into the forest, I hear a crash followed by a series of slight footsteps. Over to my right, I catch a glimpse of a young deer. Upon hearing my heavier footfalls, the deer freezes. As we catch each other's eyes, we have a long staring contest. I imagine that the deer is attempting to figure out if I am dangerous threat or simply something to ignore. The outcome of that decision is clear as the graceful deer dashes away from me, easily clearing any downed trees in its pathway.

I emerge from the forest to the bright sunlight that has engulfed the small meadow. The ground is still muddy from a rain 2 days past, and there are patches of standing water forming small aquatic ecosystems. Although a petite meadow by any measure, the meadow is teaming with life, and I immediately notice one of its most familiar members. Perched high atop the large reeds that serve as sounding posts is a red-winged blackbird. Named for the brilliant sergeant-at-arms patches on its shoulders, this beautiful bird is performing a common spring ritual for many animals; the male is trying to establish a home territory in hopes of attracting a female and raising a family. As I continue along the path, the bird slowly hunches its back, displaying even more prominently its red stripe, and gives a loud "braaaaack" call. Off in the distance and out of my line of sight comes a return response. Another blackbird has heard the first call and is attempting to negotiate where to draw the line on their adjacent territories. The bird closest to me quickly flutters over to another reed. Presumably closer to his competitor. Over and over again, these two engage in a series of calls in an attempt to have as large of a territory as possible. With each call, the birds are hoping to warn other males that this area is its home and they should stay away. Other birds have begun to respond in kind to the first two and soon the whole meadow is alive with their songs.

As my legs begin to tire and my breath becomes ragged, I sadly leave this little paradise and begin my trek along a series of sidewalks that lead to my own home. The return trip is far less stimulating, providing me with ample opportunity to reflect on the morning's sights and sounds. The springtime sounds of birds singing to establish territories or attract mates, the slow greening of the world as the trees awaken from their winter slumber, and the colorful show of flowers are the signs that indicate spring is upon us.

As visual and auditory beings, we humans relish these springtime harbingers. The bright red tulips and the calls of the blackbird remind us that warmer days are

**Fig. 1.1** Running meadow of odors

coming. These visual and auditory cues signal time to pack away the winter coats and find lighter clothing to enjoy the warmth outside. Similar to the tulips and blackbirds, we communicate with each other using words, phrases, and sounds. Music and language are key elements of human society. Images on the television, in movies, and in photographs are used to convey information, evoke feelings, and entertain. For most of us, we perceive the world through our eyes and ears. Our other senses, such as smell, taste, and touch, act as supporting cast members to the leading roles of hearing and vision. The natural world, such as the one experienced on my run, often brings these minor players to the forefront. Yet, to treat our noses and tongues as second class sensory citizens is like walking through The Louvre with sunglasses on. Imagine studying the Mona Lisa through polarized shades. Certainly, one could see the painting, but the total sensory experience is undercut unless all of our vision is used.

Just imagine that we have invented special glasses that give us the power to see the odorous world the way that other organisms perceive it. Put your pair on and walk outside for just a moment. As the bright sunlight hits our eyes, we would encounter a world far different from what we would normally expect. The air is full of molecules carried by breezes. Chemical signals would flood our eyes just as surely as sounds overwhelm our ears at a cocktail party. Stare at any plant and you would see compounds being released into the air from leaves, bark, and roots. A squirrel in a tree exudes carbon dioxide and other compounds with each breath. Glance along its brown body and notice that specific points (scent glands) appear to be slowly releasing chemical signals. If we could translate these signals into language, we would see phrases, sentences, statements, songs, and other messages waiting to be intercepted and interpreted. Taking in the scene as a whole, we would see a symphony of chemicals being played by the creatures of nature in their daily conversations (Fig. 1.1).

One of my favorite examples of the symphony (called chemical communication) comes from the work of Dr. Michael Breed and his coworkers at the University of

Colorado. For years, he has studied various forms of recognition in social insects. (The reasons why these insects need social recognition are explained in Chap. 6.) Focusing on Neotropical ants in Panama, Dr. Breed has discovered that these ants have sentries posted at entranceways into their colonies. The sentries perform a thorough "smell" check of each ant that enters the colony. In many ways, these ants have evolved their own TSA agents whose smell check is as thorough as any whole body scan at any airport. If the ant passes the test, it is allowed access to the colony, but if the wrong odor is detected, the sentries forcibly carry the offending individual out of the anthill to the outskirts of the colony's territory. Each colony has its own odor, called a "label," and the odor can arise from a genetic basis; it may be given to the workers from the queen ant or may arise from specific foods that are present in a particular colony.

The genetics of social insects are rather interesting because only the queen produces eggs. The entire colony is related genetically. The unique nature of the ant's genetics doesn't stop there. The queen of the colony produces two types of eggs. One set of eggs are fertilized and produce females and those not fertilized produce males. All males within the colony will have an identical genetic makeup and all of the females will share at least 50 % of their genes. Different colonies will have different queens and, if the recognition pheromone is based on the genetics of the queen, then the colony will have a unique odor signature.

This nestmate recognition serves to keep intruders out and helps to ensure the survival of the colony. With patience and keen observation, Dr. Breed and his coworkers noticed some ants taking food out of one colony and transporting it to a nearby colony. These ants were discovered to be thieves that were stealing food from one colony and taking it to their home colony. But how could these thieves penetrate the chemical recognition of nestmates performed so thoroughly by the sentries? It appears that through repeated attempts to gain entry and the subsequent rebuffs by sentries, the nestmate chemical gets transferred to the interloping ants. When enough interactions with the sentries have been performed, the thieving ant smells sufficiently like a nestmate ant to the guards. This acquired chemical camouflage now allows the intruder ants to sneak in, take food, and secure safe passage back to their home colony.

This chemical camouflage and name tags are just a glimpse into the hidden world of chemical communication so prevalent in nature, and yet we are oblivious to it. Chemical communication is an ancient art, first performed when two single celled organisms exchanged chemicals in the primordial soup. Through the ages, the use of chemicals as a form of communication has proliferated to such a degree that there is not a single organism on earth that does not use some aspect of it. This can be attributed to the chemical nature of life itself; every single organism must take in, transform, produce, and release chemicals. Consequently, nature is full of chemicals, all with secret information about the inner workings of the organism that produced them. What species is it? What sex is it? Is it healthy, sick, dominant, or ready for reproduction? These are just a few of the questions that can be answered by smelling the world. Every organism is capable of detecting and responding to chemical signals, and they only differ in the degree to which chemical communication plays a role in gathering and transmitting information.

It is impossible to make such lofty claims about the nature of any other sense. There are numerous examples of organisms that do not use vision, from cave fish to bats. The ability to produce and receive sounds occurs in a surprisingly few number of organisms. Virtually all of life uses chemical signals. Even the lowly bacteria communicate to each other chemically. But despite the importance and prevalence of chemical communication through nature, the richness to which organisms have developed the ability to communicate using signature molecules is often underappreciated, even within the academic community. A recent informal survey of the latest textbooks in animal behavior, physiology, neurobiology, and ecology shows that there are 20 times as many pages devoted to vision and hearing as there are to chemical communication.

To illustrate how extensive and diverse nature's chemicals are, let us return to my morning run, but this time with our special glasses on. Retracing the same steps, our glasses should reveal to us our chemical world. Remember those red, yellow, and purple tulips, brilliantly calling to the insect world? Those colors represent only part of the picture. As we know, many flowers produce exquisite scents. And in spite of what we might like to think, flowers did not develop those scents to add ambience to our homes, but rather as a way to communicate to the insect world that great bounties can be reaped within their petals. Flowers have developed scents to attract all types of creatures, such as bats, flies, bees, and moths. As we shall see in later chapters, an odor that is irresistible to a fly or bat would not make a good scented candle used in our homes. The Titan Arum flower, for example, has evolved a scent similar to that of rotting flesh mixed with burnt sugar. A distinctive odor that is hard to imagine as a fragrance. The flower uses this foul odor to deceive sweat flies that normally lay eggs in carrion. The Titan Arum's "perfume" serves to attract the flies to its massive bloom in order to ensure pollination and continuation of the species.

My jog continued past the gardens and on to the small forest before the meadow. This small forest is a mixture of trees dominated by oaks, often used as symbols of strength and might. Yet the massive plants can be devastated and denuded by tiny insects. Unable to defend themselves, how do our mighty oaks fend off these voracious attacks? Once an oak tree has been attacked, the tree begins to produce a distasteful chemical sequestered in its leaves. This compound, often called a secondary metabolite, makes the leaves less desirable to hungry insects driving them to other trees. Although if you are an oak tree within a large forest, there is a good chance that the neighboring trees may be related as either your offspring or your parents. What good does it do to send off all of your insect enemies to eat your family and friends? Obviously, the oak tree should tell the neighboring oaks about this potential threat, but how do you communicate if you are a tree? Nature again has solved this dilemma using chemical communication. The oak tree that has been attacked, not only produces a compound that makes its leaves less palatable, it also produces a compound that is sent through its roots to the surrounding trees. The surrounding trees detect the presence of this compound and begin to produce the anti-herbivory chemical in their leaves also.

Remember that young deer running away from my footfalls? A quick glance with our new glasses reveals a whole array of chemical signals. Carbon dioxide, a sure sign of life, emerges from its nostrils. Just below the eyes, the forehead glands