# Pheromones and Animal Behavior

## Chemical Signals and Signatures

SECOND EDITION

Pheromones and other kinds of chemical communication underlie the behavior of all animals. Building on the strengths of the first edition, widely recognized as the leading text in the subject, this is a comprehensive overview of how pheromones work.

Extensively revised and expanded to cover advances made over the last ten years, the book offers a thorough exploration of the evolutionary and behavioral contexts of chemical communication, along with a detailed introduction to the molecular and neural basis of chemosensory perception. At a time of ever increasing specialization, Wyatt offers a unique synthesis, integrating examples across the animal kingdom. A final chapter critically considers human pheromones and the importance of olfaction to human biology. Its breadth of coverage and readability make the book an unrivaled resource for students and researchers in a range of fields from chemistry, genetics, genomics, molecular biology, and neuroscience to ecology, evolution, and behavior.

A full list of the references from this book is available for download from www.cambridge.org/pheromones.

**Tristram D. Wyatt** is a researcher at Oxford University's Department of Zoology, and an Emeritus Fellow of Kellogg College, Oxford. He is interested in how pheromones evolve throughout the animal kingdom, at both molecular and behavioral levels. These broad interests give him a unique vantage point, enabling him to draw together developments across the subject.

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*To Robert*

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# PREFACE TO THE SECOND EDITION

This book is designed to bring together people already working on chemical communication and to encourage others, especially chemists (who have a vital role in this research), to take up the challenge. My aim has been to make an evolutionary understanding of chemical communication, including pheromones, accessible to a broad scientific and lay audience.

Pheromone research brings together scientists with many different areas of expertise, from a rich diversity of chemists to biologists of many kinds. Each area of expertise has its own jargon and concepts – a behavioral ecologist speaks a different language from a neuroscientist. The book recognizes that every scientist is a novice outside their own subject, even science close to their own, so I try to explain ideas in terms understandable by non-specialists while at the same time aiming to be up to date and detailed enough for the specialist. I also wanted to write a book that could be enjoyed by the majority of the world's scientists whose first language is not English and thus also clearer for everyone.

Pheromones offer exceptional opportunities to study fundamental biological problems. The rapid progress of the last decades comes from the convergence of powerful techniques from different areas of science including chemistry and animal behavior, combined with new techniques in genomics and molecular biology. These allow us to investigate questions at every level: molecular, neurobiological, hormonal, behavioral, ecological, and evolutionary. The discoveries from molecular biologists have greatly expanded our knowledge of the evolutionary biology of olfactory communication. Equally, molecular biology only makes sense in the context of evolution.

I wrote the first edition to provide the overview of chemical communication we were then missing, covering the whole animal kingdom, integrating approaches from ecology to neurobiology, and all with an evolutionary perspective. I have kept the same overall structure for the book in the new edition. As before, the book is organized around themes such as sex, speciation, and social organization, rather than taxonomically. The book also covers the perception and processing of chemosensory information. In each topic I have aimed to integrate examples from across the animal kingdom. In the same paragraph you may read about nematodes, moths, snakes, and mice. I explore the often convergent ways evolved by different kinds of animals to solve the same communication needs.

All chapters have been comprehensively updated and most chapters have been completely rewritten. The changes are perhaps most significant, as you might expect, in those parts involving molecular biology, especially in the chapter on perception of pheromones. Recent results include the surprising discovery that insect chemoreceptors have evolved independently of vertebrate ones. However, there has also been much new to discuss in evolution and ecology, including results coming from the application of molecular techniques as well as detailed field work.

Different parts of the book emphasize examples from different taxa. As in the first edition, mammals feature more strongly than invertebrates in the sections on individual variation and hormonal effects of pheromones for example, but invertebrates dominate the sections covering mechanisms of searching behavior.

Chapter 1 defines pheromones and looks at evolution of pheromones as signals. I raise a pragmatic distinction between pheromones and the chemistry of individual or colony odors. I also look at the role pheromones play in speciation. The importance of both common ancestry and convergence in molding chemical signals is a key theme.

Chapter 2 is about the development of analytical tools and how these are changing the study of chemical communication, allowing us to identify types of molecules previously hard to work with. New genomics techniques can be used to identify genes involved in both production and perception of molecules and not just in model organisms such as *Drosophila*. On the behavioral side I emphasize the importance of proper randomization of treatments and "blinding" of experimenters wherever possible. Progress will depend on productive partnerships between chemists and biologists.

The following six chapters cover different aspects of pheromones in the ecology and behavior of animals. Chapter 3 is about the evolution of pheromones in sexual selection, drawing out the many parallels between animals in a wide range of taxa. Among the new material featured in the chapter is work on *Drosophila* and moths as well as developments in evolutionary theory.

Chapter 4 covers Allee effects and the roles pheromones have in spacing organisms, bringing them together, and keeping them apart.

Chapter 5 reviews territorial behavior, largely in terrestrial vertebrates. The discovery of the male mouse pheromone, darcin, offers fascinating insights into female mouse behavior (Roberts *et al.* 2010, 2012). Darcin prompts her to learn the individual odor of the territorial male and where the scent mark is.

The parallels between complex social behaviors mediated by chemical communication in social insects and social mammals are explored in Chapter 6. The queen pheromones of an increasing number of social insects are being identified. It seems, however, that mammals do not use pheromones to "suppress" reproduction by subordinate members of the group.

Recruitment in social insects for foraging and nest building and for defense are covered by Chapters 7 and 8 respectively. One major change in our understanding is a clearer distinction between alarm pheromones and cues. The molecules involved in fish alarm are likely to be cues rather than pheromones.

Chapter 9 explores how olfaction works and how the olfactory receptors themselves evolve, in enormous variety. Vertebrates and invertebrates are similar in the way they detect and process chemical cues, by combining inputs from neurons carrying different olfactory receptors, but they achieve this with quite different receptor families, which evolved independently.

The mechanisms that animals have evolved to find an odor source are discussed in Chapter 10. We understand more about the mechanisms that fish and birds use than when the first edition was written. There are some interesting uses of genetically manipulated *Drosophila* larvae to explore the ways they orientate in chemical gradients.

Broadcast signals can be eavesdropped. Chapter 11 covers a world of deception and spying, including new players and a clearer understanding of selection in some classic examples.

Chapter 12 discusses how an understanding of chemical communication can be used for agriculture and to control disease vectors. Whereas insects formed the main examples of pheromone control, pheromones are showing promise for the possible control of vertebrate pest species, notably the sea lamprey.

Chapter 13 covers the roles of chemical communication in human beings. I discuss the smells we produce and the ones we can perceive. One of the most surprising things that has emerged from genomics studies on humans is the enormous variation between us as individuals in what we can smell. Our olfactory receptor repertoires are individually quite different: it is likely that we each experience unique olfactory worlds. I conclude the chapter by exploring some of the limitations of current research on human pheromones and how we could take it forward.

Finally, the appendix explains the common chemical terminology you will come across.

While some of the molecules important in chemical communication are shown in the figures, there are too many mentioned in the text to illustrate them all. Instead, you can see them on sites such as www.chemspider.com, which allows you to search by common name and shows synonyms as well as the systematic names. Many pheromone molecules, together with some background, are included on Pherobase www.pherobase.com (El-Sayed 2013).

## Choice of literature for the second edition

This book necessarily offers a selective distillation of an enormous literature. I have attempted to reflect our consensus understanding of each topic. For reviews, I have generally used the most recent I could (though I reference earlier reviews if they continue to be influential). The papers cited have been chosen to reflect both their contributions to the subject but also because they offer good entry points to the literature (do use Google Scholar™ or Web of Science™ to find papers citing these leads). Sometimes you will find a review and a particular experimental paper both referenced, for example (Cardé & Haynes 2004; Liénard *et al.* 2010), which will be obvious, I hope, when you look them up. The references for this edition are also available at www.cambridge.org/pheromones.

Wherever possible, I have chosen sources that you will be more likely to be able to find. Where I have had a choice between equally good papers I have gone for the one in an open access journal or one that the authors have made available on the web, for example on their own website. It may be worth searching on an article title to see if it is available. If an article is not available and you do not have institutional access to the journal, you might courteously write to the author to see if they have a PDF to send. Most people are pleased to be asked – I know I am.

## Wikipedia™

Have you considered helping edit Wikipedia's entries in our subject? It might seem surprising for a textbook to recommend its readers to consider contributing their expertise to Wikipedia, the world's largest online encyclopedia, but this is where the greatest influence for our subject will be. As Wikipedia is where most people look first, Bateman and Logan (2010) encourage scientists to seize the opportunity to make sure that Wikipedia articles are understandable, scientifically accurate, well sourced, and up to date. Bond (2011) makes such a call to his fellow ornithologists and presents many advantages of getting involved. Pheromones and some aspects of chemical communication are briefly covered in Wikipedia but not to the depth and range of many other areas of science. You might be able to improve this. Logan *et al.* (2010) give tips for getting started and guidance on good practice.

If you would like Microsoft PowerPoint™ slides of the illustrations in the book for teaching or talks, do email me, tristram.wyatt@zoo.ox.ac.uk, letting me know which chapters' figures you would like.

# ACKNOWLEDGMENTS

I would particularly like to thank the following for generously reading the whole book in draft: Bruce Schulte, Jagan Srinivasan, Joan Wyatt, and Vivian Wyatt. I am also grateful to many other friends and colleagues for help with various chapters and recent writing projects, which helped me develop ideas explored in the book, including Olle Anderbrant, Richard Benton, Thomas Breithaupt, Patrizia d'Ettorre, Monica De Facci, Dick Doty, Heather Eisthen, Maud Ferrari, Jean-François Ferveur, Kevin Foster, Tom Getty, Stephen Goodwin, Alan Grafen, Christina Grozinger, Penny Hawken, Matthieu Keller, Jae Kwak, Jean-Marc Lassance, Darren Logan, Jocelyn Millar, Dan Rittschof, Benoist Schaal, Peter Sorensen, Számadó Szabolcs, Robert Taylor, Kevin Theis, Martin Thiel,Tobias Uller, Marc Weissburg, Tom Wenseelers, Danielle Whittaker, Brian Wisenden, and Ben Wyatt.

Any remaining errors are mine of course, and I would welcome comments and suggestions for corrections. You can contact me at tristram.wyatt@zoo.ox.ac.uk.

I would like to thank all the scientists in addition to those listed above who advised me on their areas of expertise and kindly sent reprints and pre-prints of their work. The book would not have been possible without their help and generosity. In keeping the range of animal groups represented as wide as possible, I have had to be selective. Inevitably I have not been able to include many examples that I would have liked to. I apologise to authors whose research I was not able to describe here despite its high quality.

Many colleagues generously helped me with high-resolution copies of their illustrations. I would like to give additional thanks to colleagues who produced new or especially adapted figures for me, including Christina Grozinger, Harland Patch, Troy Shirangi, Jagan Srinivasan, and John Terschak.

It is a pleasure to thank Martin Griffiths, Megan Waddington, Abigail Jones, Kath Pilgrem, Vania Cunha, and other colleagues at Cambridge University Press for their encouragement and assistance at all stages of producing the second edition.

I would like to thank the publishers and societies listed at the end of the book for permission to reproduce figures and tables, particularly those which did not charge fees.

# SI PREFIXES

| Factor | Name | Symbol |
|---|---|---|
| $10^{-2}$ | centi | c |
| $10^{-3}$ | milli | m |
| $10^{-6}$ | micro | μ |
| $10^{-9}$ | nano | n |
| $10^{-12}$ | pico | p |
| $10^{-15}$ | femto | f |

# ABBREVIATIONS

| | |
|---|---|
| 2MB2 | 2-methyl-but-2-enal |
| AOB | accessory olfactory bulb |
| AOS | accessory olfactory system |
| BNST | bed nucleus of the stria terminalis |
| cAMP | cyclic adenosine monophosphate |
| cGMP | cyclic guanosine monophosphate |
| CHC | cuticular hydrocarbon |
| CNG | cyclic nucleotide-gated channel |
| CNV | copy number variant |
| cVA | *cis*-vaccenyl acetate |
| ESP1 | exocrine gland-secreting peptide 1 |
| GC | gas chromatography |
| FPR | formyl peptide receptor |
| GABA | $\gamma$-aminobutyric acid |
| GPCR | G-protein-coupled receptor |
| GR | gustatory receptor (invertebrates) |
| GSN | gustatory sensory neuron (insects) |
| GUR | gustatory receptor (*Caenorhabditis elegans*) |
| HPLC | high-performance liquid chromatography |
| iGluR | ionotropic glutamate receptor |
| IR | ionotropic receptor |
| JH | juvenile hormone |
| MHC | major histocompatibility complex |
| MGC | macroglomerular complex |
| MOB | main olfactory bulb or OB |
| MOE | main olfactory epithelium |
| MOS | main olfactory system |
| MOT | medial olfactory tract |
| MTMT | (methylthio)methanethiol |
| MUP | major urinary protein |
| MPOA | medial pre-optic hypothalamus |
| OB | olfactory bulb (MOB) |
| OR | olfactory receptor |
| ORCO | olfactory receptor coreceptor (insects) |
| OSN | olfactory sensory neuron (also termed olfactory receptor neuron, ORN) |
| SEM | scanning electron micrograph |
| SEM | standard error of the mean |
| SNP | single nucleotide polymorphism |
| SPME | solid phase micro extraction |
| T1R | taste receptor type 1 |
| T2R | taste receptor type 2 |
| TAAR | trace amine-associated receptor |
| TRC | taste receptor cell |
| TRPC2 | transient receptor potential channel 2 (= TRP2) |
| V1R | vomeronasal receptor type 1 |
| V2R | vomeronasal receptor type 2 |
| VNO | vomeronasal organ |
| VNS | vomeronasal system (= accessory olfactory system) |