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.