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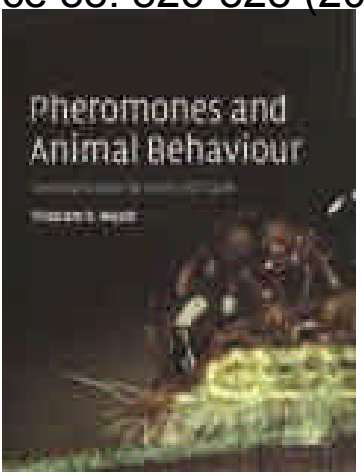

Pheromones and Animal Behaviour. Communication by Smell and Taste. Tristram D. Wyatt, Cambridge University Press, Cambridge, UK, 2003. 408 pp. Price: $50.

Beauty itself, as with faces, is not simple: perfumes can be handsome (Mitsouko), *graceful* (Calandre), *gorgeous* (Joy), *comely* (Shalimar), *radiant* (Tommy Girl), *exquisite* (Après l'Ondée), *stunning* (Angel). *Reader beware:* Paradox *is, to paraphrase something once said about Scriabin's music, a perfume of 'almost unbearable loveliness.'… What I find all the more irritating is that* Paradox *isn't even 'my type'. It is, after all, yet another fruit salad of the type that has kept perfumers gainfully employed since* Deci-Delà. *But this fruit salad does something that it has no right to do; break hearts.*

Luca Turin quoted in
The Emperor of Scent, Chandler Burr

He saw that there was no mood of the mind that had not its counterpart in the sensuous life, and set himself to discover their true relations, wondering what there was in frankincense that made one mystical, and in ambergris that stirred one's passions, and in violets that woke the memory of dead romances, and in musk that troubled the brain, and in champak that stained the imagination; and seeking often to elaborate a real psychology of perfumes, and to estimate the several influences of sweet-smelling roots and scented, pollen-laden flowers; of aromatic balms and of dark and fragrant woods; of spikenard, that sickens; of hovenia, that makes men mad; and of aloes, that are said to be able to expel melancholy from the soul.

The Picture of Dorian Gray
Oscar Wilde

The sense of smell has always evoked strong reactions, and this book seeks to tell us why.

This is the age of chemical ecology. The *Journal of Chemical Ecology* is now joined by *Chemoecology*, another specialist journal, and the contents pages of almost every biological journal reveal an increasing number of papers devoted to the chemical mediation of behavioural and ecological processes. The 2004 Nobel prize in Physiology or Medicine was also awarded to Richard Axel and Linda Buck for their pioneering work on the discovery of olfactory receptors and for providing a combinatorial schema for the neurobiology of odour perception. There is a palpable excitement in the air, especially for evolutionary ecologists, for we now have the tools to progress from primary reception to the ultimate processing of chemical signals with a whole range of fascinating and meaningful questions to be asked in between. From that time in the 1950s when Adolf Butenandt had to sacrifice 500,000 female silk moths to determine the identity of the first pheromone to today when the same can be achieved with a single silk moth, chemical ecology has come of age and is now a mainstream interdisciplinary field which merges chemistry with ecology, evolution, neurobiology, and animal behaviour into one exquisite whole.

Tristram Wyatt's book therefore comes at a very opportune moment and can make an important impact on young researchers looking for new and exciting problems. It is written as a textbook but provides a wealth of information on a variety of areas which embrace a wide range of interdisciplinary research that is possible within this field. Couched within an evolutionary framework, the book provides a comprehensive bibliography as well as suggestions for further reading and references to reviews that are most useful for a new entrant into the field. Below I will provide examples of some important areas covered by the book and also provide critiques of instances where I feel Wyatt should have provided more information or where he was not entirely accurate. With such a fast-moving field, it is, of course, inevitable that some of the information Wyatt provides is already out-dated.

First, a few examples of the amazing use of pheromones in communication that are also illustrative of the variety of mechanisms and situations in which pheromones are used in life processes: salamander males that inject pheromone via specialized teeth directly into the bloodstream of females that they are courting as part of the mating ritual; pigs that can smell out truffles because an active ingredient in truffle odour happens to be 3α-androstenol which is a steroid mating hormone contained in boar saliva; bolas spiders that lure moths towards them by mimicking moth pheromone; wild potatoes that produce aphid alarm pheromone on their leaves and thus repel potential aphid pests; male spiders who use female pheromones to find receptive females and once on the web of such a female, cut off the chemically-scented silken lure lines so that no other male spider can find her. What could be more beautiful than this example: the desert iguana *Dipsosaurus* lives in a temperature environment where highly volatile pheromones would be extremely short-lived; this lizard uses scent marks of higher molecular weight, and thus lower volatility, that strongly reflect (not absorb as Wyatt states) ultraviolet; this visual signal generated by the chemical compounds functions as a long-range attractant while the pheromone itself functions in the short range. The book has many such and even more wondrous examples that cannot but evoke enthusiasm for the field.

An important point made in the book is that chemical signals are honest signals. In evolutionary theory, only signals that cannot be deployed by cheaters can be honest indicators of good genes and therefore can be used successfully by females in mate choice; e.g. some moths feed on plants containing toxic pyrrolizidine alkaloids which are then sequestered within the body including within the spermatophores of the males; females choose males and their spermatophores based on their alkaloid content because eggs and developing embryos derived from such fertilizations would have greater alkaloid content and therefore more protection against predators; here, the alkaloid content of males is the signal and there is no question of cheating. Similarly indication of territory size by scent-marking also constitutes honest signalling since the presence, frequency of renewal of the pheromone marks, as well as the quantity of pheromone deposited will indicate true ownership of space.

The author also reviews the well-studied insect and vertebrate olfactory systems and makes an excellent point about how little is known about olfaction in birds. Birds were believed to have no sense of smell and it is only very recently that the whole new world of olfaction in birds has opened out to scientific investigation. Birds are now known not only to use olfaction in finding food and in homing but also in sexual display and ritualized mating sequences[1], and this appears to be more true of seabirds than those of other lineages, which warrants further investigation.

Although the author does have a valuable section on the vomero-nasal organ (VMO), it is unfortunate that he did not discuss the putative origin and evolution of the VMO. Although this organ seems to be restricted to the tetrapods, it does not occur in some groups such as birds and some mammals. Why is this so? Whether humans have a functional VMO is still mired in controversy, as is whether there are mood-altering human pheromones that are sensed using the VMO. Clearly the VMO will generate much interest in the years to come as will the role of the major histocompatibility complex (MHC) in mate choice. Wyatt ably reviews the prevalent evidence on the role of olfaction and the MHC on mate choice in rodents and humans and also discusses the phenomenon of the t-locus and t-haplotypes in the mouse. The t-locus, which is linked to the MHC, contains alleles that are lethal in the homozygous condition. Heterozygous females use olfactory cues to avoid mating with heterozygous males and seem to prefer wild type males. What causes the persistence of the t-alleles if females can use odour cues to discriminate against heterozygous males? It would have been useful if Wyatt had mentioned that these lethal alleles are maintained in the population because of the fact that they are also segregation distorters, which means that sperms containing the lethal alleles are disproportionately represented in the population.

The book has excellent sections on pheromone genetics, on the relationship between pheromones and speciation using the example of chemical isolation mechanisms in *Drosophila*, and on the possibility of olfactory aposematism. There is also a lucid exposition of olfactory recognition mechanisms that are especially important in social organization, e.g. how does a worker ant evaluate whether a conspecific worker belongs to the same or a different colony? Are these chemical signatures genetic or do they change with diet? Does the phenomenon of self-inspection of odour cues occur? Is there learning? There is an interesting section on the possibility of increasing olfactory sensitivity; e.g. a percentage of the human population cannot smell 5α-androstenone; however, such androstenone anosmics begin to smell this compound with repeated exposure; thus in humans and mice at least, olfactory experience seems to influence sensory perception. How this occurs is still unknown.

Pheromones are known to play an important role in insect sociality. Wyatt devotes substantial space to discussing this topic and does it very well. In many insect societies, the queen uses a pheromone to suppress the ovarian development of worker females; however, workers in many social insect species are known to lay unfertilized, and therefore, haploid eggs which develop into males. This conflict between queen and workers is often hypothesized to be resolved by the phenomenon of worker policing wherein workers destroy eggs laid by their uncooperative nestmates. Since the field is advancing so rapidly, it is worth remarking that although the book mentions that worker policing is mechanistically possible in honey bees because the queen's eggs can be differentiated from eggs laid by workers by a pheromone mark from the Dufour's glands of the queen bee, this is no longer thought to be true[2]. The phenomenon of worker policing is still highly controversial and a simple explanation of pheromone marking appears to be currently insufficient as an explanation[3].

Although Wyatt has covered important ground in this book, once the reader's appetite has been whetted, I as a reader, clearly wanted more. Therefore, a section on the topic of the first chemical signals would have been very valuable. Wyatt does mention in passing that microbes were the first to use chemical signals, but he does not develop this theme further. The literature is replete with examples of signalling and eavesdropping by microbes. For example, self-recognition molecules that allow *Amoeba proteus* to recognize members of their own clones as 'self', so that they do not engulf themselves, are also used as kairomones by the predatory ciliate *Euplotes*, to localize its amoeba prey[4]. Perhaps Wyatt should have quoted a source such as Bonner [5] to make the progression from the idea of cell-cell signalling to signalling between organisms using chemicals.

Unfortunately, the distinction between a signal and a cue has not been clearly made in the book. This is an important distinction in behaviour because a signal benefits the sender (e.g. an allomone, or a synomone, in current pheromone terminology) while a cue benefits the receiver to the detriment of the sender (e.g. a kairomone). Furthermore, there is also the use of the term odorant in the book without a clear differentiation between pheromones and odorants. As a matter of fact, perhaps the title of the book is in some sense a misnomer, because the book includes many examples of chemically-mediated behavioural and physiological interactions which are not mediated by 'pheromones' in the strict sense; therefore Infochemicals or Semiochemicals and Animal Behaviour might have been more appropriate as a title. However, to be fair, the author does raise the issue of pheromones versus semiochemicals right at the very beginning of the book, and clearly states that pheromones are only a subclass of semiochemicals; however, from a behavioural point of view, a discussion of communication using signals versus cues, which would include all types of infochemicals, is absolutely necessary. The title of the book advertises that it is also about communication by taste; however, taste features on only one page of the book, and there is really nothing about taste in the text, unless one considers the tongue-flicking behaviour of snakes, or the flehmen behaviour of some vertebrates such as the horse, which place the odorant molecules near the openings of the vomero-nasal organs, as belonging to this category.

A question that immediately follows is whether pheromones and odorants have the same detection mechanism. Are pheromones in vertebrates sensed by the VMO while other odorants are sensed by the regular olfactory epithelium? Do different mechanisms also occur in invertebrates? Since pheromones are also chemicals, should different mechanisms be expected, and if so, why? These and related issues have been raised by Christensen and Hildebrand[6] and more recently by Vogt[7]. It appears that there is no clear pattern over here and much more work needs to be done in these important areas. I would have liked to see a discussion of such issues in the book.

The book ends with a section on the practical application of pheromones and on pheromones in the human context. Considering that the threshold of detection in male moths for female sex phermones is lower than 10^4 molecules.cm^{-3}, for dogs the odour detection threshold is 10^6 molecules.cm^{-3} and for humans[8] the detection threshold is 10^9 molecules.cm^{-3}, it is no surprise that defence departments are looking closely at how insects smell, and that, for example, NASA is developing an Electronic Nose (ENose) that can be trained to recognize any compound or combination of compounds. Soon sniffer dogs and sniffer pigs may be sensors of the past, and will be replaced by sniffer insects or bionic noses, that will draw inspiration from the combinatorial wizardry of insect and vertebrate olfactory systems.

In summary then, this book is timely, extremely informative, and very readable. Biology and chemistry departments of all undergraduate and graduate colleges would do well to recommend this book to their students and to incorporate it into their curriculum. I learnt much from this book and will use it frequently both as a reference source and as a text.

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