

between social behaviour and life history evolution. What's more, I cannot even make my usual complaint about price, since, for once, the paperback price is very reasonable and represents a sound investment for anyone's personal library.

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Pheromones and Animal Behaviour. Communication by Smell and Taste. By TRISTRAM D. WYATT. Cambridge: Cambridge University Press (2003). Pp. xv+391. Price £75.00 hardback, £27.95 paperback.

Compared with visual and acoustic signalling, olfaction has long been the poor relation in the study of animal communication, recognition of its importance being hampered by methodological limitations and our own sensory biases. This book neatly summarizes the substantial ground regained over the half-century since bombykol, the female silk moth pheromone, became the first pheromone to be characterized. Wyatt adopts a broad definition of pheromone, thus encompassing chemical cues that may not elicit specific responses or physiological changes in receivers but that none the less communicate information that influences their behaviour. This definition permits inclusion of, for example, odours involved in kin discrimination, such as those mediated by the major histocompatibility complex (MHC), and those produced as scent marks for territorial defence. The similarly catholic selection of examples from across a wide range of taxa ensures that this is a comprehensive and well-balanced account of the role of olfactory signals in behaviour across the animal kingdom.

Having been introduced to the origins and diversity of chemical signals, and constraints on their design, we then learn about the techniques and approaches used to identify pheromones and describe their effects, including chromatography and bioassays. Each of the following six chapters covers particular categories of behaviour in which odour plays a key influence. The first of these tackles sex pheromones, including those that coordinate gamete release, induce scramble competition for mates and that are used in contests over mates, before a larger section on odours involved in mate choice. Selection on these chemical signals may also contribute to reproductive isolation and speciation, and the potential for this is illustrated with research on pheromones of moths and *Drosophila*. The next chapter reviews aggregation and host-marking pheromones. Pheromones promote aggregations in species where individuals gain benefits from being in larger groups (Allee effects); for example, female

mosquitoes are attracted by pheromones to common oviposition sites where they benefit from dilution of predation risk, while marine invertebrates depend on coordinated settlement after the larval dispersal phase for successful reproduction. Host-marking pheromones, seen in parasitic insects, help females avoid laying eggs in the same host twice, or in hosts already parasitized by others. Wyatt now turns to the use of scent marks to defend territories. Explanations for how scent marks achieve this function, how territory owners deploy their marks in an economic manner, and what information is available in marks overmarked by others, are addressed. The following chapter deals with the role of odour in kin and individual recognition, and primer pheromones that influence reproduction in social groups. The first section is rightly dominated by recognition systems in colonial insects, although mammalian examples are also discussed. The second describes the use of primer pheromones to mediate caste changes within insect colonies or to suppress reproduction in subordinates, and draws parallels between the mechanisms involved in regulation of reproduction in social insects and many mammals. Different pheromone mechanisms used by colonial insects to recruit group members for foraging and nest building are reviewed next and shown to be a key feature of their success. The final chapter to deal with specific behaviour categories reviews alarm pheromones. While many examples can be explained by kin selection, alarm pheromones are more problematic in unrelated groups and several adaptive explanations are offered.

Four more chapters cover more general aspects of pheromonal communication. The first examines mechanisms of odour perception by the brain and the behavioural and physiological responses that result. Second, mechanisms for localizing and approaching the odour source are described. The third discusses the costs of signalling incurred by interception of odour signals by eavesdroppers or by responding to deceptive mimics. Lastly, various ways in which our understanding of pheromonal communication can be applied to increase success in animal husbandry, conservation and pest management are discussed.

The final chapter contains an intriguing discussion of the role of odour in human behaviour. Recent evidence suggests that we are more influenced by odours than we previously realized, notable examples including self and kin recognition capabilities, effects on memory and mate choice, and detecting cues to ovulation. True pheromone effects include induction of menstrual synchrony in women as a response to male and female odours, although evidence for true pheromonal effects remains highly controversial (e.g. Hays 2003). The source and structure of human odour molecules is discussed, as are mechanisms of perception; there is also a section on medical and forensic uses of odour perception.

Wyatt's book is a remarkable summary of a growing and exciting field of discovery. His writing is clear, the book is fully referenced, and helpful figures and summary boxes are provided throughout. A particular strength is the concise presentation of the theoretical background to each major topic, enabling readers unfamiliar with the topic to appreciate fully how the pheromones under scrutiny have evolved. In addition, the appendices provide some basics of the molecular structure of pheromones, for those of us who struggled

with chemistry at school. Those interested in the sense of taste may be disappointed by the predominant focus on smell, but this reflects the functional significance of taste in feeding rather than communication. For those interested in olfaction, this book is excellent both as an introduction to the field and as a refresher of a vast, growing and exciting literature.

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The Ethology of Domestic Animals: An Introductory Text. Ed. by P. JENSEN. Wallingford: CABI Press (2002). Pp. ix+240. Price \$40.00 paperback.

Per Jensen has assembled some well-known scientists from the world of applied animal behaviour and put together a compact overview of the field. The book is aimed at students of biology, veterinary medicine and animal science taking introductory courses in animal behaviour or applied zoology. The 200-page volume is divided into two roughly equal-sized sections. Part A opens with a historical background to the modern study of ethology and its applications. Five further chapters deal with biological elements of behaviour and, to an extent, how this knowledge is used in the broad discipline of applied ethology. These chapters cover the genetics of behaviour, motivation and organization, learning and cognition, social and reproductive behaviour and the use of behaviour as an indicator of animal welfare. Part B contains seven chapters describing the behaviour of individual domestic species. These sections deal with the behaviour of fowl, horses, cattle, sheep and goats, swine, dogs and cats and finally, rabbits and rodents.

The opening chapter, by Jensen, introduces the historical background to the modern study of ethology, beginning with Palaeolithic cave art and working up to Nobel laureates Lorenz and Tinbergen. To define the scope of ethological study he invokes Tinbergen's questions of causation, function, ontogeny and phylogeny, and also notes that modern ethology is becoming more concerned with the subjective experiences of animals. Jensen raises just a few areas of application for the science of ethology: welfare assessment, animal production, control of behaviour and treatment of behaviour disorders. This introduction, while very coherent, is rather brief. I would have liked to see him take fuller advantage of the opportunity to stimulate the interest of beginning students in the field, with a little more depth of discussion and perhaps incorporating anecdotes or specific research examples.

The second chapter, also by Jensen, introduces the genetics of behaviour, showing how genes shape behaviour and how it is thus influenced by evolution and domestication. This includes the evolutionary history of domestication and the influence that domestication can have on the behaviour of species. It is a mistake to assume

that domestication has done much to change the perceptual and cognitive abilities of these animals or diminished their capacity to suffer in inadequate environments. What artificial selection has done is to create strains that are adequately productive for human purposes despite the conditions imposed upon them. In general, Jensen argues that, given the freedom to express it, there are only subtle differences in behaviour between domestic animals and their wild counterparts. He concludes with a message of central importance for students in this discipline. The apparent differences between the behaviour of domestic animals and their wild counterparts occur precisely because they are very responsive to their environment. Managed agricultural environments are frequently inadequate to allow the expression of a full repertoire of normal behaviour. As we now understand rather well, deviation from normal behaviour is an important indicator of the extent that the environment constrains the biological and cognitive functioning of an animal, and is thus intimately related to its state of well-being.

The chapter on the physiology, motivation and organization of behaviour by Toates gives as clear an explanation of motivational processes as I have read. He also gives a succinct account of some key components of nervous system physiology. I found this to be perhaps the most cogently written chapter in the book. The author takes care to point out that a mechanistic description of behaviour in terms of competing hierarchies of motivation does not replace discussion of 'wants', goals and cognition.

Forkman's chapter, 'Learning and Cognition', begins with the idea that learning is all about predicting and controlling the future. It is as well that he flags learning as the major component of the chapter to follow, because cognition per se is mentioned only in passing. That said, he gives a well-written account of the basic learning processes and the associated terminology. Careful reading of this chapter could obviate the need for a whole lecture just to explain these terms and thus save teaching time for more interesting matters.

I found the chapter on reproductive behaviour by Weary & Fraser both enjoyable and informative. Unfortunately, references are particularly sparse in this chapter. Hamilton's rule is explained at some length without citing the original work. Ideas as important as these deserve full attribution, and should be on every student's further reading list. The text also tells us that in the 1920s 'an ethologist' described peck order in fowl. Again, this is too important an idea not to be properly attributed. Yet another nameless 'ethologist', we are told, played begging calls to parental swallows. It surely would have done no harm to name these individuals.

Part A concludes with a chapter on behavioural disturbances, stress and welfare by Keeling & Jensen. Animal welfare has long been important to applied ethologists. In fact, it is rapidly becoming the central issue for many workers in the field. I am happy to see the authors make one simple yet very important point here. Abnormal behaviour can be what the majority of animals show when conditions are inadequate. To invoke stereotypic behaviour as evidence of poor welfare is to court controversy. Scientists in this field are divided as to the significance of a stereotypy for an animal performing it, but tend to agree that high levels of stereotypic behaviour are indicative of deficiencies in the animal's environment or management. It is not clear whether, given predisposing conditions, an individual stereotyping animal is