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PHEROMONES AND ANIMAL BEHAVIOUR. By Tristram D. Wyatt. Cambridge, UK: Cambridge University Press. 2003. 391 pp. ISBN 0-521-48526-6. \$40.00 (paper).

This book is potentially of interest to many researchers in the social and life sciences, where new findings bearing on the evolution of chemical communication among animals occur at an accelerating pace. Because of this rapid pace, books on the topic of chemical communication can find themselves out of date or out of touch with pertinent literature. Neither is true of Wyatt's book.

In focusing on pheromones, the matter of definition is important for readers. In this regard, I found the book initially frustrating, and I must admit rereading

the first several pages in search of a concise definition, despite Wyatt's statement of his "broad and generous approach" (p. 2) on the matter. Wyatt considers a wide array of interactions to be pheromonal in nature, placing pheromones within a broader category of chemical signals (semiochemicals). To Wyatt, olfactory information-gathering does not qualify per se, although it may represent a stage in the evolution of pheromonal communication. After reading Chapter 1, readers may be inclined to believe that biochemical convergence in pheromones (elephant and moth pheromones are the example) is inevitable, simply because chemical signals are so widely used by all animals. Chemical by-products are the inevitable and omnipresent results of metabolic processes, so the exploitation of such by-products (as pheromones) may be fodder for natural

selection. This view makes biochemical convergence as well as the overlapping and/or interchangeable roles of some chemosensory systems all the more likely.

Chapter 1 sets the stage nicely for nonspecialists and tunes the reader toward Wyatt's evolutionary approach to the topic. Chapter 2 introduces nonspecialists to the methodologies (bioassays, electroantennogram, single-cell recordings, and gas-liquid chromatography). From here, the book changes pace and direction. Specifically, beginning with Chapter 3, the discussion turns sharply toward placing pheromones within the context of evolutionary biology, beginning with a thorough discussion of pheromones and mate choice. Wyatt includes a remarkable table of evolutionary mechanisms that select for male traits. The table invokes images of male ornamental plumage, advertising health benefits to females. But instead of visual stimuli, the table lists "odour based examples." These examples, which are some of the most interesting in the book, include chemical stimuli that advertise direct health or resource benefits to females, show indirect benefits ("good genes"), or are examples of runaway selection.

Chapter 4 discusses aggregation pheromones, with much discussion on insect behavior. Chapter 5 turns toward scent-marking in vertebrates. The perspective that scent-marking transcends territorial behavior (indicating social status and health of the signaler) is convincing. Chapter 6 focuses on pheromones and social organization. The chapter also deals with kin recognition, revisiting the topic of mate choice and discussing mother-infant bonds. Chapter 7 discusses pheromones and recruitment communication in insects. Chapter 8 is another highly successful effort, making the reader think about selective pressures on pheromonal communication. For instance, why would so many organisms from mammals to marine invertebrates risk releasing alarm pheromones, which could attract "eavesdropping" predators? Kin selection comes immediately to mind, and is discussed, but Wyatt details examples of such pheromones acting as signals among unrelated individuals. Both the signaler and respondent may be subject to different selective pressures within one context. For example, skin pheromones released by damaged skin of fish may confer no special advantage to the injured releaser, but it is adaptive for all around to respond by fleeing.

To some degree, Chapter 9 slows the pace of the book, discussing pheromonal communication at the molecular level. The chapter is largely successful, although the section on volatile vs. nonvolatile molecules and their respective importance to olfaction and vomeronasal organ (VNO) function is somewhat vague. Chapter 10 returns to some engaging behavioral examples, with a discussion of pheromones and orientation behavior. Renowned trackers (e.g., dogs) as well as swimming and flying followers of chemical trails are

discussed. "Eavesdroppers," including rather alarming examples of spiders and parasitic wasps, are discussed in more detail in Chapter 11. Chapter 12 turns to applied use of pheromones (priming pheromones for farm animals, and pest control). Chapter 13 is perhaps the most evocative, dealing with the subject of human chemical communication.

Students of natural selection, sociobiology, and evolutionary psychology will enjoy this book. Much of the subject matter is appealing to physical anthropologists, including considerations of influences of resources on invertebrate mating strategies, discussion of the major histocompatibility complex, mate choice in mammals, and a critique of human pheromone research. The ability of the researcher to build on some ideas while acknowledging contentious aspects of them (e.g., human pheromones, especially copulins) will be greatly enhanced by this book.

There were some minor points with which I disagree, primarily from the perspective of a morphologist. Wyatt indicates that the VNO opens into the nasopalatine duct in Old World primates (perhaps a typographical error intended as New World primates). A section entitled "Do We Have a Functional VNO?" summarizes the highly controversial topic of the human VNO quite well and succinctly. But later, issues regarding homology and function are blurred. Thus, Wyatt states, "If Old World primates do have a VNO then it would be easier to hypothesize the presence of one in humans." This specific issue is one of homology, not functionality. The absence of a VNO in most Old World anthropoids is not necessarily evidence against a functional human VNO. Wyatt's functional discussion details much more convincing evidence that the human VNO is a nonchemosensory organ.

Overall, such points are minor. This book focuses much more on the vehicle of communication than on the receptor organs. The elements that relate to pheromonal communication are selected from a vast literature and are well-integrated. Wyatt takes us much further than the mechanism, by providing a context of natural selection. This quality makes the book attractive to a broad group of scientists, including physical anthropologists. Wyatt has succeeded in his stated goal of the book: to bridge gaps among "biologists of many kinds and a rich diversity of chemists" (p. xiii).

TIMOTHY D. SMITH
School of Physical Therapy
Slippery Rock University
Slippery Rock, Pennsylvania

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