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Book Review

Pheromones and Animal Behaviour: *Communication by Smell and Taste* by Tristram D. Wyatt. Cambridge University Press, 2003. ISBN: 052148068X.

Reviewed by James V. Kohl

Tristram D. Wyatt's scholarly text intricately details ubiquitous chemical communication among animals from a diverse range of species. The Asian elephant shares a component of its female sex pheromone with140 species of moth. Thus, evolutionary theory provides the backdrop for an interdisciplinary approach to chemical communication that includes information from neurobiological, hormonal, behavioral and ecological research. The book's thirteen chapters conclude with "On the scent of human attraction: human pheromones?" We now know that humans produce pheromones and that they also respond to pheromones with changes in behavior. The link from animal pheromones to human behavior extends to humans a biological basis for behavior, which makes *Pheromones and Animal Behaviour* more pertinent to those who want to learn about human behavior.

Wyatt makes clear the fact that pheromones function in the context of other sensory input. Lizards see ultraviolet light that helps to guide them along a pheromone trail to their mate, and the alarm odor of the black-tailed deer is transmitted with auditory and with visual signals. In any species, this "signal redundancy" makes it more difficult to determine the relative functional importance of visual, auditory, tactile, or olfactory cues. In all species, chemical communication via pheromones seems likely to play the primary role in sexual behavior. The primary role of pheromones in sexual behavior is examined across a continuum of pheromone-induced effects that occur earlier or later in a sequence. Included in this sequence are aspects of social behavior like organization and aggregation, which precede sexual behavior.

The author's scope is substantially broad. Unfortunately, with regard to the continuum of pheromone-induced effects, he fails to include information about the physiological organization of the innate sexually dimorphic response to mammalian

pheromones. Thus, the reader is left with no information about the neuroanatomical basis for a neuroendocrine response that links mammalian pheromones from the social environment (i.e., nurture) to the genetic (i.e., nature) underpinnings of hormone-driven reproductive sexual behavior. For example, the gonadotropin surge in male mice that are exposed to pheromones is briefly mentioned, but without information about the biological origin of this response. Nevertheless, though there is a chapter on sex pheromones, it is important to note that this work does not focus on reproduction. Instead, the broad-based coverage is of multiple aspects of pheromonal communication.

The reader is introduced to subsets of pheromones like kairomones: used by predators to detect prey; allomones: used to lure prey, and synomones, that benefit both signaler and receiver. The coverage of insect pheromones dominates. Aggregation pheromones bring conspecifics together for defense against predation, and can also be important in synchronization of reproductive efforts to coincide with resource availability. Pheromones inhibit reproduction when food sources are unavailable, but also act to ensure that appropriate numbers of conspecifics are produced to thwart species' extinction by predators. Scent marking is used in conjunction with territorial behavior to separate the signaler from the receiver. This separation helps to ensure fewer physical threats to individual survival. (Even if the fight is won, both the winner and the loser might die from their wounds.)

Social groups are organized through pheromonal cues that provide information about species, colony, caste, age, gender, and reproductive status. Mother-infant recognition via pheromones plays a key role in bonding and in infant survival. Mammalian pheromones cause hormonal changes, which affect the success of pregnancy, alter the timing of puberty, modulate the female fertility cycle, and also modulate reproductive behavior and aggression. Pheromones are used to recruit conspecifics for a variety of collective purposes that include foraging, defense, and the building of nests. Alarm pheromones serve to alert conspecifics as well to alert individuals of other species to conditions that may benefit one and all. But alarm pheromones also may be detrimental when they attract additional predators.

A chapter on mechanisms of olfactory perception and interpretation may seem somewhat overwhelming; this is a difficult subject to master. But this book would not be complete without information on receptors that trigger a cascade of reactions leading to signal transduction. Indeed, when sensory input leads to behavior, the pheromonal signal may be the most important signal of all. The full scope of signal transduction/interpretation/affect is not yet known, but Wyatt offers an overview of the role that chemical communication plays in affective neuroscience.

The importance of orientation to a pheromonal signal is discussed in somewhat confusing context. "At first sight, many animals behave as if they are aiming for a 'goal' or target but, without other evidence, it is more accurate to de-

scribe their movements as responses to the stimuli received at or up to that point" (p. 207). Prefacing any statement on orientation to pheromones with "At first sight" and also incorporating "aiming," which requires a visual cue, provides an example of why many people might underestimate the importance of pheromonal communication. In context, "At first sight" is suggestive of visual input, but visual input is not required to elicit a response to pheromones. Still, as Wyatt indicates, we think about visual input and use terms that describe orientation to visual stimuli because we respond to pheromones without thinking. With exposure to pheromones, movements as responses to stimuli are due to affective reactions that occur below the level of consciousness. In some cases, Wyatt's terminology fails to make this clear. On the other hand, it is noted that dogs can detect a scent concentration difference in the air above two consecutive footprints, made 1 second apart, up to 20 minutes earlier. Clearly this ability to orient to pheromonal cues, used in tracking, cannot be confused with orientation to visual input—an animalistic ability that pales by comparison.

Visual input is thought to be more important to bird species than olfactory input. Fortunately, *Pheromones and Animal Behaviour* does not allow this thought to go unchallenged. "The protein-rich urine marks of voles are conspicuous in the ultraviolet part of the spectrum visible to birds…"(p. 232). The ubiquitous nature of pheromones in animal communication makes it likely that we will learn more about how birds incorporate them into avian behavior as is also noted in McClintock (2000).

A somewhat amusing analogy is discussed in light of the relationships of predators, guests, and parasites of social insects. Social insects recognize strangers and evict them or kill them. However, even parasitic strangers are allowed to colonize the nests of some other species, so long as they smell right. "The human equivalent might be to share our homes with alligators, which we insisted on feeding ahead of our own children and which ate our children unbeknown to us" (p. 245). Clearly this analogy goes too far by extending to humans aspects of social communication in insects. But it also alludes to some other interesting cross species comparisons in the use of pheromones.

Pheromones are used in insect pest management to monitor population size, disrupt mating, lure and kill, or to trap or otherwise manipulate insect behavior.

Pheromones are used to manage reproduction in domestic animals. Exposure to the boar pheromone androstenol can advance puberty in female pigs, and result in more cost-effective breeding practices. Pheromones also are used in cows, pigs, and sheep to synchronize ovulation for more predictable results from artificial insemination.

What then can be said in a chapter about human pheromones? The neuroendocrine mechanisms by which androstenol advances puberty in female pigs might be exemplified by the fact that androstenol exposure alters levels of lu-

teinizing hormone (LH) in women (Shinohara, et al. 2000). LH levels are important both in the onset of puberty and in the maintenance of an ovulatory fertility cycle in women. There are several studies that indicate human pheromones alter levels of LH. Berliner et al. (1996) indicated that a progesteronic pheromone alters LH pulsatility (and testosterone levels) in men. Stern and McClintock (1998) showed that the pheromones of women regulate ovulation in other women, presumably by affecting the LH/follicle stimulating hormone (FSH) ratio. Similarly, Shinohara et al. (2001) showed that axillary pheromones from women either in the follicular or in the ovulatory phase of the menstrual cycle differentially modulate pulsatile LH pulse frequency in other women. LH levels also have been repeatedly linked to mammalian reproductive sexual behavior, which includes human sexual behavior (see for review Kohl and Francouer, 1995). For example, Preti et al. (2003) showed that male axillary extracts increase LH levels and they also elevate mood in female recipients. Only this most recent study by Preti and his colleagues would have been unavailable to Wyatt during his literature review in the preparation for publication of *Pheromones and Animal Behaviour.*

Does the absence of some very recent information from human studies of putative pheromones and their effect on hormone levels (and mood) indicate that the author was remiss in his manuscript preparation? No, it merely indicates that the neuroendocrinology of the mammalian pheromone response (see Kohl et al., 2001) was not intended to be included in this comprehensive review. However, it is disturbing that within the first 8 pages of his chapter on human pheromones, Wyatt cites 15 times either individual or collective works by Schaal and/or Porter. Perhaps Wyatt did not give thorough consideration to the available information on human pheromones because he relied on limited information sources. Thus, to the extent that cross species comparisons are valid, this book may fail readers who are more interested in the role of pheromones in human behavior than in the role of pheromones in the behavior of other animals.

To his credit, Wyatt does include a great amount of information about human pheromones and integrates information presented in earlier chapters with information about the role of human pheromones in mate choice for genetic diversity, which is a requirement for species survival. Mate choice for genetic diversity in other species is a function of olfaction and pheromones. Thus, Wyatt brings home the point that human olfactory acuity and specificity correlates well with the ability that tracking dogs exhibit after being trained (as mentioned above). Simply put, humans are able to detect differences in "tissue type," a fact that is often overlooked when human olfactory abilities are compared with the abilities of other animals. Indeed, "What human beings lack in acuity… they make up in powers of discrimination, which rival those of any other mammal" (Dobb, 1989, p. 51).

Women appear to prefer the scent of genetic diversity when they are most likely to get pregnant. Men appear to prefer the scent of women when women are most likely to get pregnant. The pheromones of women affect hormone levels in

other women. The pheromones of men influence hormone levels in women. Since the influence of pheromones on hormone levels in other animals is essential to properly timed reproductive sexual behavior, human correlates help to stress the need for more research on the function of human pheromones in human sexuality. Meanwhile, pheromones have been commercialized and incorporated into fragrance products since the early 70's. The successful marketing of pheromone-containing fragrances continues, despite no peer-reviewed data to support advertising claims that human pheromones cause rapid behavioral changes that lead to increased opportunities for sexual activity. This disparity among data, claims, and marketing success, suggests that some people may intuitively "know" more about human pheromones than what can be scientifically supported. Wyatt offers considerable scientific support for the concept of human pheromones.

Further reading at the end of each chapter will assist those who wish to know more about the topic of pheromones. Appendices provide additional information on the chemical structure of pheromones. The text is sufficiently referenced and well indexed. It would be hard to overstate the importance of this book for its contribution to the understanding of animal behavior. And Wyatt repeatedly leaves room for extrapolation from results in other species to potential explanations of human behavior.

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References

Berliner, D. L., Monti-Bloch, L., Jennings-White, C., and Diaz-Sanchez, V. (1996) Functionality of the human vomeronasal organ (VNO): Evidence for steroid receptors. *J. Steroid Biochem. Mol. Biol*. 58, 259-265.

Dobb, E. (1989) The scents around us. *Sciences,* November-December, 46-53.

Kohl, J. V., and Francoeur, R. (1995) *The Scent of Eros: Mysteries of Odor in Human Sexuality*. Continuum, New York.

Kohl J. V., Atzmueller, M., Fink ,B., and Grammer, K., (2001) Human Pheromones: Integrating Neuroendocrinology and Ethology. *Neuroendocrinol. Lett*. 22, 309-321.

McClintock, M. K. (2000) Human Pheromones: Primers, Releasers, Signalers, or Modulators? In Wallen, K., and Schneider, J. E. (eds.), *Reproduction in Context*. Cambridge, MA: MIT Press, 355-420.

Preti, G., Wysocki, C. J., Barnhart, K. T., Sondheimer, S. J., and Leyden, J. J. (2003) Male axillary extracts contain pheromones that affect pulsatile secretion of luteinizing hormone and mood in women recipients. *Biol. Reprod*. 68, 2107-2113.

Shinohara, K., Morofushi, M., Funabashi, T., Mitsushima, D., and Kimura, F. (2000) Effects of 5alpha-androst-16-en-3alpha-ol on the pulsatile secretion of luteinizing hormone in human females. *Chem Senses*. 25, 465-467.

Shinohara, K., Morofushi, M., Funabashi, T., and Kimura, F. (2001) Axillary pheromones modulate pulsatile LH secretion in humans. *Neuroreport*. 12, 893-895.

Stern, K., and McClintock, M. K. (1998) Regulation of ovulation by human pheromones. *Nature*. 392, 177-179.