

BOOK REVIEWS

Tristram D. Wyatt. 2003: *Pheromones and Animal Behaviour: Communication by Smell and Taste*. Cambridge University Press, Cambridge. 391 pp., Paperback: \$40.00, Hardback: \$100.00. ISBN 0-521-48526-6.

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More than half a century of chemical communication research has served a key role in promoting awareness and expansion of knowledge in theoretical and applied problems in organismal biology. Tristram Wyatt's *Pheromones and Animal Behaviour* is an accessible textbook that offers advanced undergraduate and graduate students a data-based, integrative, and broadly comparative synthesis of this field. Crossing back and forth between invertebrate–vertebrate boundaries more freely than any other text in this area, Wyatt grounds behavioral, ecological, and biochemical observations of pheromonal communication in an evolutionary context. A broadly recognized caveat to workers in this field, derived from the primary literature and in this and other texts, is the willing acceptance and repetition of 'just so' evolutionary stories from researchers who contend to have identified absolute functions of pheromonal communication.

Thirteen chapters fill the text. In several chapters, boxes and tables filled with straightforward and well situated summaries provide a ready reference location for students to check vocabulary terms and fundamental concepts. Careful production of the book is apparent, with very few typographic errors detected by this reviewer.

Determining the optimum sequence for the chapters is a problem most textbook and course designers share. Wyatt's sequence moves from pheromone definitions and examples (Chapters 1 and 2) to behavioral and ecological discussions of pheromonal phenomena in six chapters (Chapters 3–8). Chapters 9 and 10 shift to chemoreception systems and transduction mechanisms and to biophysical problems faced by organisms attempting to locate pheromonal sources in the environment. Many instructors would likely place these problems after the first two introductory chapters, and then follow with the behavioral ecology issues of Chapters 3 through 8. Under such a rearrangement, Chapter 11, an interesting chapter on 'pheromonal fraud,' logically follows the behavioral ecology chapters. Chapters 12 and 13, 'Applications' and 'Human Pheromonal Biology', respectively, provide some attractive engagement, a strong theoretical and empirical foundation having been built in Chapters 1–11.

An overview of the definitions and terminology used in chemical communication, and a synopsis of the diverse sources and functions of pheromones, are presented in Chapter 1. Regarding the latter, particularly compelling is a synthetic conceptual figure presenting as a spectrum, rather than as a dichotomy, the range of pheromonal functions between immediate behavioral 'releasers' and physiological 'primers'. There are 10 other figures in this chapter, two tables and two text boxes. Two of the figures include data.

Several of the behavioral and chemical analyses used to identify pheromones are discussed in Chapter 2. Here arises the complexity that pheromonal effects are often based on responses to precise mixtures of component chemicals, observations that make this field so challenging to reduce to its essentials. Two of the six figures contain data, whereas three figures and a text box describe chemical analysis methodology.

A strongly comparative approach to analyzing pheromonal communication in finding and choosing mates is used in Chapter 3. Though the attempt to develop an integrative synthesis on chemical communication's role in sexual selection and speciation is admirable, it is perhaps too uncritical, lacking prominent cautions necessary because of small sample sizes and impossibly confounded experimental designs, especially in field studies of vertebrate animals. Ten of the 15 figures feature empirical data, others show organisms and behavioral interactions, along with integrated summaries contained in one box and one table.

Pheromonal communication related to aggregation and parasite–host interactions is presented in Chapter 4. The discussion includes sharing of resources, facilitation of mating, swamping of predators,

and avoidance of super-parasitism. One of the three figures includes data, whereas the others and two boxes provide an overall biological context for aggregation.

Fundamental questions about scent-marking behaviors are featured in Chapter 5. Much of the discussion focuses on responses of invaders and challengers intruding on scent-marked areas, and considers a few questions about the motivation to scent mark an area, alluding to what might be considered to be the self-confidence of animals in the areas or territories they have marked. Six figures and two boxes illustrate and explain scent-marking behaviors, without presenting any substantive data.

Social organization in invertebrates and vertebrates is the emphasis of Chapter 6. The rich resources of chemical information along the sociality continuum is effectively communicated in Figure 6.1. Prominent treatment is given to the role of learning to identify the odors of conspecifics in one's own social unit. The only other figure in this chapter is a cartoon of naked mole rates, but the four boxes are richly endowed with data and explanations of recognition mechanisms and social insects.

Social animals, mostly invertebrates, persuade one another to achieve joint enterprises such as finding food, group travels, and nest construction, as described in Chapter 7. There are seven figures, one with data, two tables on trail pheromones, and three boxes, on tent caterpillars, recruitment mechanisms, and one on trail-following behaviors.

Focusing on alarm pheromones, Chapter 8 emphasizes communication between genetic relatives as the original foundation for the development of alarm signaling, but also considers how alarm pheromone release can benefit the source animal, perhaps by confusing predators. Two of the seven figures include empirical observations, and one table includes chemical structures of alarm pheromones.

Chemosensory transduction and associated neuroanatomical problems of pheromone responsiveness occupy Chapter 9. The dual chemosensory pathways of vertebrates (olfaction vs. chemoreception by the vomeronasal organ) and of insects (feeding vs. pheromone responses) are fully described, from the level of biophysical receptors to the level of central neural pathways. The problem of use-dependent changes in chemoreception and response is addressed concisely and accurately. The 12 figures summarize information in cartoon style, without showing much data. There are five summative or integrative boxes and a table with chemical structures.

Solutions to the biophysical problem of locating pheromone sources are described in Chapter 10. There are 14 figures, most portraying behaviors of chemo-transducing animals, but only a couple of these include the foundational data. Two of the three boxes portray biophysical analyses and a third provides a reference list of orientation descriptors.

Chapter 11 has some fun with pheromonal eavesdropping and fraud, with special emphasis on predators capitalizing on the pheromonal communication systems of their prey. Consideration is given to the competing needs for communication with conspecifics vs. attraction of exploiters. There are 10 figures, two of which have data, and two tables of summary information.

An impressive list for the potential application of pheromonal communication is delivered in Chapter 12. In addition, there are fair and accurate descriptions of the many failures in our attempts to capitalize on our chemical knowledge. Three of the five figures include data, and the two tables list known commercial applications and pheromonal lures.

The cultural and experiential problems associated with pheromonal communication in humans appear in the final chapter. Three of the seven figures include data. There are five tables, including lists of scent sources of human and non-human primates, psychophysical olfactory capacities to detect potential pheromones, and odors that indicate diseases. Two descriptive text boxes are included, one on human sebum and sweat, and the other on commercial products claiming to include pheromones.

Wyatt's text allows students in an advanced class on pheromones to build a strong foundation of knowledge, and its readable and engaging style will launch many productive arguments along the way. Deeper discussions to interpret data are also possible, especially for instructors who supplement the text with primary literature.

Sommer, U. & Worm, B. (eds). 2002: Competition and Coexistence. Springer-Verlag, Berlin. 221 pp., \$79.95. ISBN 3-540-43311-2.

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How species-rich communities can be maintained through time and the role of competition in structuring those communities has been a central question in ecology since Gause's demonstration of competitive exclusion in the 1930s. As the editors of this volume point out, growing anthropogenic

threats to some of the most diverse communities on the planet (e.g. coral reefs and tropical rainforests) currently make these questions both of academic and practical importance. This volume is an attempt to review and synthesize recent research on competition–coexistence relationships as in previous reviews by Schoener and Connell in the 1980s. Chapter 1 is a short, concise review of the historic development of ideas underlying the competition–coexistence field and is a good starting point for those not familiar with this area of ecology. The following two chapters focus on theoretical models of competition in systems where resources and potential competitors are well mixed, like those encountered by plankton, or in systems that are spatially structured, like those for sessile organisms like plants and intertidal invertebrates. Ethologists may find these chapters of interest primarily in stimulating them to draw analogies to animal systems. For example, the discussion of how the ability to store resources over time, as plants and plankton do in chemical form, alters competitive outcomes has direct parallels with the relative ability of animals to store and retrieve food from caches. Likewise, the lowered ability for well-mixed models to accurately predict the outcome of competitive interactions as the number of resources or competitors increase, and the tendency for such systems to develop their own internally driven, non-equilibrium, and potentially chaotic oscillations (Ch 2), has important implications for ethologists attempting to model behavioral outcomes in situations where animals can potentially use large numbers of competing behavioral strategies. Sections of these chapters on predator–prey interactions, and the effects of various foraging strategies on model predictions, are likewise relevant to the role of behavior in influencing competitive interactions. Chapters 4, 6 and 7 summarize empirical studies on plankton, rocky intertidal invertebrates and terrestrial vegetation, respectively. Although many of these chapters are excellent, the ethologist will be challenged to find strong analogies to animal systems in which individuals can modify their behavior and move widely through heterogeneous environments.

More relevant is Chapter 5 by Mark Ritchie, which specifically focuses on competition among mobile animals. In this chapter, Ritchie argues that coexistence is promoted when each species can exploit an exclusive set of resources, and that the abundance of these exclusive resources ultimately determines relative abundance of each species. However, in Ritchie's view, what any one species views as exclusive resources depends upon how spatial and temporal heterogeneity interact with the scale at which habitat is viewed by that species. For example, smaller bodied animals may see the environment in fine-grained form, with greater spatial heterogeneity in the abundance of resources than a large-bodied animal that would essentially 'average' small-scale heterogeneity over a larger area. One prediction of this view is that fine scale foragers should leave patches with lower resource densities, while larger bodied species leave patches with overall higher densities but search more area. Finally, Ritchie reviews evidence that fractal distributions may better represent resource distributions in space than random or uniform distributions assumed by many previous models. Although I was familiar with many of the original papers cited in this chapter, I found Ritchie's synthesis clear and stimulating. I believe it would be so for many readers interested in foraging behavior and habitat selection and how those behaviors may be modified by varying resource distributions and the presence of potential competitors.

Overall, I found this book easy to read, with a concise and consistent style across chapters. Figures were clearly presented and effectively described. I would recommend this as a good introduction to current models and empirical studies of the role of competition in structuring communities for those not already familiar with the topic.

Hughes, R. N. (volume ed.). 2002: *Reproductive Biology of Invertebrates, Volume XI: Progress in Asexual Reproduction*. Adiyodi, K. G. & Adiyodi, R. G. (series eds), John Wiley and Sons Ltd, Chichester, UK. 337 pp., \$165. ISBN 0-471-48968-9.

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The defenders of homeland security showed little interest in understanding asexuality among the invertebrates. The lead agent called it 'an unusually dense book', and returned my copy of Roger N. Hughes' edited volume, *Reproductive Biology of Invertebrates XI: Progress in Asexual Reproduction*. The armed team at Denver International had extracted it from my backpack with extreme prejudice, and although resembling C4 explosive under X-ray, the contents of this compact volume with its smooth umber jacket were judged non-incendiary. I confess, I must agree. However, after reading this volume's 10 diverse chapters, I was forced also to concede that the information it contains, although at

times unforgiving, leads to an inescapable conclusion; current behavioral perspectives on the costs, benefits and even the very details of asexual reproduction are at best too simplistic, and at worst, simply wrong. Incendiary, perhaps not, but sufficiently thought provoking to change my views on what asexuality really means.

Most behaviorists are comfortable with the notion that sexual lineages experience the twofold cost of meiosis (Maynard Smith 1971). That is, sexuals must divide their genome in half for each offspring they produce, and must produce sons as well as daughters. Asexuals simply place exact copies of their genome into each asexual daughter. All things being equal, asexual lineages are expected to numerically outcompete sexual lineages, unless the cost of sex is overcome by other mitigating factors, such as the inability of asexuals to eliminate deleterious mutations, or to respond to variable environments. Thus, sex may persist because environmental variation is common, or because pathogens and disease favor genetically diverse progeny (West 2002), or as proposed recently, because differential opportunities for mating within populations favor individuals with minute gametes, whereupon sexual selection not only purges mutations expressed by males, but also generates sufficient fitness variance to overwhelm the cost of sex (Agrawal 2001). Given the high frequency of anisogamy among sexual species, as well as elegant data consistent with the Red Queen hypothesis (Lively & Dybdahl 2000; West 2002), the question, "why sex?" may seem largely solved. One may then ask, "when asexuality?" particularly in diploid species that undergo periodic if not frequent sexual reproduction.

With one exception, neither question is specifically addressed in this book, although it is immediately clear that asexual reproduction is far more prevalent and considerably more complex than is explained in most behavior textbooks. Braig, Turner, Normark, and Stouthamer provide a detailed synopsis of microorganism-induced parthenogenesis, and convey the eerie sense that prokaryotic hegemony is already well established. Rollinson and Stothard review patterns of clonal and sexual reproduction in parasites. E. Davis Parker's chapter on geographic parthenogenesis in terrestrial invertebrates asks the specific question, "under what ecological genetic and phylogenetic circumstances do we find species which have eliminated recombinational sex for their reproduction?" (p. 93). Martinez considers the incidence of senescence and immortality among asexual lineages. Boero, Bouillon, Piraino, and Schmid consider asexual reproduction by the medusa stage of certain hydrozoans, a stage normally considered sexual and therefore a form of asexuality distinct from budding. Genetic mosaics and chimeras arising by asexuality are considered by Hughes himself. Forbes discusses the issue of resource allocation in asexual invertebrates. Lasker and Sanchez investigate the development of the colony form in modular organisms using fractal geometry, an approach that could be useful in understanding behavioral ontogenies and decision trees. Karlson reviews population processes in modular invertebrates. Lastly, Okamura, Freeland, and Hatton-Ellis consider the importance of metapopulation models for describing asexual and clonal animals.

In these chapters, asexual reproduction is shown to variously involve binary and multiple fission, as well as vegetative growth, embryonic growth, and fragmentation. Among parasites, yet unknown mechanisms within apparently asexual lineages create genetic variation. We learn that asexual propagules may arise from sexually or asexually derived tissues with different genetic consequences, and parthenogenesis may be initiated by female parents, or forced by male-killing endosymbionts. By now, there can be little doubt that all things are *not equal*, but things get curiouser still. At the populational level, asexual lineages may be indistinguishable from sexual lineages in their tendency to undergo senescence (or not), as well as in their patterns of resource allocation (or not). They appear to be mutually exclusive in their timing within life cycles, as well as distinct in their tendency to retain or lose genetic variation by drift, with predictable biogeographic patterns in disturbed and undisturbed habitats. However, depending on one's perspective, the consequences of asexuality on gene flow and metapopulation structure either fit or do not fit expectation. Clonal reproduction and subsequent selfing appear to cause considerable population structure, but the unusual ability of asexual individuals to recolonize vacated space also appears to eliminate the expected relationship between geographic distance and genetic divergence.

The scope of this book spans molecular to populational processes and it is a trove of information. As the latest issue of the well-known *Progress Series*, conceived by Kenneth and Rita Adiyodi, and designed to highlight research developments in invertebrate reproduction; *Volume XI* is clearly written by and for invertebrate zoologists. Although persistence pays off for readers able to tolerate or decode its unapologetic use of terminology, like most books of its kind, its treatment of issues important to researchers in animal behavior is only peripheral, and it generates more questions than answers. However, its central message is clear. Among animals, asexuality is seldom as simple as the mere production of clones. Therefore, this book is important and worth reading by all of us who think we understand what asexuality is and how it persists, as well as, when sex is favored and why.

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Kappeler, P.M. & Pereira, M.E. (eds). 2003: *Primate Life Histories and Socioecology*. University of Chicago Press, Chicago. 416 pp., \$30 or £21 (paperback). ISBN 0-226-42464-2.

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This volume is derived from papers presented at a conference in December 1999 at the German Primate Center. The chapters address the relationships among the ecology, social behavior, and life history characteristics of primates. Specifically, the authors examine the relationships among socioecological factors and length of gestation, number and size of offspring, length of lactation, age and size at weaning, pattern of growth after weaning, size and age at sexual maturity, interbirth interval, and lifespan among different primate taxa. The volume is divided into three main parts. The first is a set of five chapters dealing with basic issues regarding life history and socioecology. The second and third parts each contain three chapters and deal with developmental patterns among primates and the evolution of primate brains, respectively. The focus of most chapters was on how and why primates live so 'slowly' relative to other mammals.

In the first section, readers are presented with interesting and thorough analyses of phylogenetic relationships of primate life histories, as well as analyses regarding phenotypic plasticity and the use of matrix models for life history analysis. There is an excellent and thought-provoking chapter by Janson on predation pressure and selection on life history characteristics. Several chapters in the first section presented 'comparative' examples from other taxa, but those sections did not seem as strong as those in which the behavior, ecology, and life history 'strategies' of different primate taxa are compared.

The section on development provides some very basic and important insights into the timing and mode of development and focuses on the relative 'speed of life' with regard to differences in developmental rates across primate taxa. These include analyses of the trajectory of attaining final body mass as well as endocranial volume and a detailed presentation of data on dental development. Finally, there is a very interesting chapter dealing with the unusually long post-reproductive period of human beings, especially females. Hawkes et al. argue that the long post-reproductive period of human females has resulted from the evolution of disproportionate longevity rather than a premature cessation of reproduction, as proposed by Williams (1966). The chapter includes a thought-provoking set of hypotheses regarding the adaptive value of post-reproductive females (i.e. 'grandmothering') during a period of significant ecological change during human evolution.

The final section deals with the very interesting topic of the evolution of the primate brain. This is an especially interesting topic because of the fundamental importance of primate brains in sociality and resource exploitation as well as the disproportionate energy demands of the large brains of primates. In these three chapters conflicting data regarding the relationships among large brains, 'slow' life histories, and complex social systems are presented. Data from Deaner et al. show a positive relationship between brain size and life span, but not between brain size and other life history traits or social behavior. However, Ross, using a different and nonphylogenetic analytical approach, argues that relative brain size is correlated with age at first reproduction and social group size. She also argues that brain size is positively related to juvenile growth rate and duration of the juvenile period. Finally, Dunbar argues that large social group size selected for large brains among apes. While the issues about brain size, life history, and social behavior were not resolved in these chapters, readers gained valuable insights into the different analytical approaches used to address these questions.

Overall, 'Primate Life Histories and Socioecology' provides the reader with several thought-provoking and interesting chapters regarding the adaptive significance of primate life histories, ecology

and social behavior. Some chapters are fairly descriptive and/or focused on analytical techniques. However, most chapters are quite well done and thorough and a great deal of useful information is amassed in this volume. Anyone interested in primate life histories should own a copy of this book.

Reference

Williams, G. C. 1966: *Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thought*. Princeton Univ. Press, Princeton.