Chemical Ecology of Vertebrates

Chemical Ecology of Vertebrates is the first book to focus exclusively on the chemically mediated interactions between vertebrates, including fish, amphibians, reptiles, birds, and mammals, and other animals, and plants. Reviewing the latest research in three core areas: pheromones (where the interactions are between members of the same species), interspecific interactions involving allomones (where the sender benefits) and kairomones (where the receiver benefits) This book draws information into a coherent whole from widely varying sources in many different disciplines. Chapters on the environment, properties of odour signals, and the production and release of chemosignals set the stage for discussion of more complex behavioral topics. While the main focus is ecological, dealing with behavior and interactions in the field, it also covers chemoreception, orientation and navigation, the development of behavior, and the practical applications of chemosignals.

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PREFACE

Chemical ecology is developing by leaps and bounds. Thousands of growing points involve all organisms and offer ample opportunities for collaboration of chemists and biologists. The biological aspect draws on diverse fields, ranging from molecular genetics, anatomy, histology, and genetics to endocrinology, animal behavior, and systems ecology. Given this confluence of many strands of science, it is little wonder that there is not a textbook for chemical ecology courses.

While plant and insect studies dominate chemical ecology, the percentage of papers on vertebrates in the *Journal of Chemical Ecology* has held steady at 10–19% since its inception in 1975. Most papers on vertebrates deal with mammals, and birds have only recently attracted the attention of chemical ecologists (Müller-Schwarze, 2005). Chemical ecology is both a basic and an applied science. Fundamental questions include reproductive interactions in fish, olfactory imprinting, chemistry and functions of scent marking in mammals, olfactory foraging in seabirds, self-medication in animals, and protein chemistry. Practical applications consider, for example, challenges in fish migration, sea turtle conservation, pest control, and animal husbandry. To succeed in solving practical problems, we first have to establish the basic natural history, behavior, and ecology of a species: To lure brown tree snakes to scented traps, we need first to know what food odors or pheromones these animals attend to. In contrast to insects, much behavior of mammals is under multisensory control, and applications of repellents and attractants based on natural behavior are yet to be realized. Attractants are still in the art stage, much the same way as hunters and trappers have always used them. Sometimes we rediscover in the scientific literature what practitioners knew all along. After we published a paper on the existence and histology of the tail gland of reindeer (Müller-Schwarze *et al.*, 1977), Swedish Saame told us how they avoid contaminating reindeer meat with this smelly gland, which was well known to them.

Our field has progressed from studying simple responses within a species to study of more complex ecological relationships. Research began with identifying the chemicals responsible for chemosensory communication: the classical pheromones. Now more complex ecological relationships are emerging for vertebrates. Investigations into predator–prey systems describe interactions between two species: predators cueing in on pheromones of their prey. Further, white-tailed deer presumably use wolf scent marks to orient and stay within the relative safe border areas of wolf territories. Increasingly more levels and larger pieces of the ecosystem are being studied: foraging seabirds cue in on dimethyl sulfide that is liberated when plankton feed on smaller organisms. Certain vultures spy on other vulture species that have detected carcass odors. Honeyguides and honey badgers form an effective partnership to exploit bee colonies. Such tripartite relationships are already well known for insects and other invertebrates.

The vast and diverse scope of the book precludes completeness. I had been advised to limit the book to pheromone communication, or just to mammals. However, interspecific interactions such as herbivory and plant and animal defenses have always been at the heart of chemical ecology, and the chemical ecology of most other vertebrates has just begun. As an animal behaviorist, I emphasize animals and their interactions with members of their own and other species. (By contrast, the *Journal of Chemical Ecology*, for example, "is devoted to an ecological understanding of the origin, function and significance of *natural chemicals* [italics mine] that mediate interactions within and between organisms.") This hybrid of textbook and review does not address methods. Good compendia of methods exist; that of Millar and Haynes (1998) is the best example. To avoid misleading conclusions from still fragmentary and unsettled research, I have refrained from textbook-style selectivity and generalizations. In this sourcebook, I present original data and consciously avoid premature generalization of studies still in flux. Birds' incorporation of fresh aromatic plants into their nests comes to mind as an example.

The chapters on pheromones, allomones, kairomones, orientation, and applications are the core of the book. The other chapters on environment, molecular properties, and chemoreception serve in supporting roles, always with animals in mind. I have deliberately included speculative ideas and open questions, both to encourage further research and to stimulate discussion in courses. For example, p. 365 suggests that mammals' wallowing, pawing, and urine soaking may be more adaptive in animals inhabiting cold countries. It is left to the reader to ponder why. Some ingenious stepping-stones show the path to today's knowledge: pioneer work on fish alarm pheromones, dog tracking, or palatability of birds. A certain planned redundancy keeps each chapter directly accessible; earlier ones need not be consulted.

I accumulated and honed the book's material during 14 years of teaching a course entitled *Chemical ecology of vertebrates* to graduate students and advanced undergraduates. Biology students have a complex relationship to chemistry.

I try to make chemistry interesting and relevant to a biologist. I emphasize ecology with a chemical twist, and not ecological chemistry. Because of its multidisciplinary nature, chemical ecology serves as a wonderful "capstone course" for graduate and advanced undergraduate students. They are challenged to remember disparate facts and principles from a variety of courses, such as the 12 cranial nerves, terpene classification, clay types, toxic plants, parasitism, carnivore ecology, fish migration, conditioned aversions, symbiosis, protein structure, bird behavior, nutrition, human health, livestock reproduction, behavior development, and much more. In examinations, students have listed numerous practical applications they have learned in this course. Responses included drinking tea with milk, eat dirt when poisoned, be wary of pufferfish, know estrogen mimics on livestock pasture, use chemical bird repellents, failure of chemical defenses vis-à-vis introduced species, and to make a car salesman take off his jacket (it could be artificially scented to boost sales). My heartfelt thanks go to the many friends and colleagues who helped by reviewing and providing information, suggestions, discussions, and constructive criticism over many years. I fondly remember countless discussions over decades with Drs. Robert M. Silverstein and the late John B. Simeone, both good friends. My wife Christine has participated in this project the longest, by searching literature and always looking out for new developments in the world of odors. I am especially indebted to Drs. Lee Drickamer, Donald E. Moore III, Tsutomu Nakatsugawa, Lixing Sun, Max M. Mozell, and Robert Mason for reviewing all or parts of the book. My colleagues Dr. José Giner, Dr. Neil Price, Christopher Sack, and Mangesh Goundalkar proofread chemical structures and names. Over the years, exchanges with former graduate students, Drs. Peter Houlihan, Bruce Schulte, Axel Engelhart, and Jan Herr, have enriched this work. I also benefited from the questions and comments by many students taking the course over the years. Even a single-author book depends on a team. I thank Cindi Gamage for essential keyboard help with references and both Cindi and Joyce Buczek for keeping track of the permissions for reproducing figures, and Dr. Jane Ward at Cambridge University Press for her tireless dedication and excellent editing. Jennifer Cheshire helped to track down numerous literature references.

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