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.

**Dietland Müller-Schwarze** is Professor of Environmental Biology at the State University of New York.
Chemical Ecology of Vertebrates

DIETLAND MÜLLER-SCHWARZE
State University of New York
CONTENTS

Preface xix
Acknowledgements xii

1 The odorsphere: the environment for transmission of chemical signals 1
1.1 Air 3
1.2 Water 15
1.3 Water–air interface 17
1.4 Influence of setting 17

2 Properties of vertebrate semiochemicals 20
2.1 Functional groups 20
2.2 Polarity 22
2.3 Solubility 22
2.4 Isomers and enantiomers 22
2.5 Volatiles 22
2.6 Non-volatiles 24
2.7 Multicomponent pheromones 26
2.8 Sex differences 31
2.9 Life expectancy of chemical signals 32
2.10 Spatial range of odor signals 33
2.11 Interaction of olfactory and visual signals 33

3 Odor production and release 36
3.1 Signals in excretions 36
3.2 Glandular secretions 38
3.3 Body odors and body region odors 48
3.4 Diet influences on odor production and venoms 49
3.5 Hormonal control of odors in urine and secretions 52
3.6 Microbial odors 53
3.7 Reservoirs 54
## CONTENTS

3.8 Pheromone transport 54
3.9 Environmental odors for communication 55
3.10 Supporting structures: osmetrichia, muscles 56
3.11 Special adaptations for broadcasting chemosignals 57

4 Chemical cues in orientation and navigation 60
4.1 Fish 61
4.2 Amphibia 68
4.3 Reptiles 69
4.4 Birds 71
4.5 Mammals 80

5 Chemoreception 82
5.1 Encounter and exposure: orientation, sniffing, licking, tasting 82
5.2 Receiving molecules: chemosensory organs 84
5.3 Structure–activity relationships 110
5.4 Neural pathways and decoding 112
5.5 Odor detection thresholds 113
5.6 Hormonal influences on chemoreception 119
5.7 Chemoreception and age 120
5.8 Interaction between chemical senses 121

6 Signaling pheromones I: discrimination and recognition 124
6.1 Familiarization with environment and objects 125
6.2 Familiar versus non-familiar social odors 125
6.3 Recognizing kin 129
6.4 Individual odors 133
6.5 Odors in parental behavior 136
6.6 Species and population discrimination 142
6.7 Modulating behavior by status signals 144
6.8 Competition between conspecifics of the same sex 144
6.9 Liquid assets: marking territory and home range with urine and secretions 151
6.10 Scent marking in mammals 153

7 Signaling pheromones II: sex and alarm pheromones and evolutionary considerations 171
7.1 Sex pheromones: attracting and stimulating 171
7.2 Alarm and alert odors 191
7.3 Trail odors 196
### Contents

7.4 Information about food .................................................. 197
7.5 Evolutionary considerations .......................................... 198

8 **Intraspecific signals: priming pheromones** .......................... 203
8.1 Fish reproduction ......................................................... 203
8.2 Amphibia ...................................................................... 207
8.3 Reptiles ...................................................................... 207
8.4 Mammals ..................................................................... 207
8.5 Priming pheromones in humans? ..................................... 224

9 **Development of intra- and interspecific chemical communication** .......................... 227
9.1 Fish ............................................................................ 227
9.2 Amphibia ..................................................................... 228
9.3 Reptiles ...................................................................... 228
9.4 Birds .......................................................................... 231
9.5 Mammals ..................................................................... 231
9.6 Learning .................................................................. 241

10 **Allomones I: chemical defense by animals** ......................... 246
10.1 Fish ............................................................................ 246
10.2 Amphibia ..................................................................... 250
10.3 Reptiles ...................................................................... 256
10.4 Birds .......................................................................... 259
10.5 Mammals ..................................................................... 262
10.6 *Pars pro toto*: decoy odors .......................................... 264
10.7 Invertebrate allomones that deter vertebrate predators ...... 264
10.8 Recycled animal and plant materials ................................. 265
10.9 The question of coevolution between predator and prey ...... 268

11 **Allomones II: plant chemical defenses against herbivores** .......... 270
11.1 Classes of plant defense compound .................................. 271
11.2 Physiological effects of secondary plant metabolites ....... 284
11.3 Chemical defense strategies by plants ............................... 299
11.4 Feeding or avoiding? herbivores vis-à-vis plant defenses ...... 303
11.5 Plant responses to herbivory ............................................ 332
11.6 The question of coevolution of plants and herbivorous mammals .... 334
CONTENTS

12 Kairomones and synomones 338
12.1 Predator–prey interactions 338
12.2 Host odors used by parasites 371
12.3 Eavesdropping 374
12.4 The self-anointed: chemical mimicking 376
12.5 Evolutionary considerations 377
12.6 Plant chemicals used by vertebrates 378
12.7 Animal chemicals benefitting plants 383
12.8 Synomones 383

13 Practical applications of semiochemicals 391
13.1 Fish 391
13.2 Reptiles 393
13.3 Birds 394
13.4 Non-human mammals 397
13.5 Humans 418

Glossary 423
References 428
Index 530
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 source-book, 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.
ACKNOWLEDGEMENTS

Publisher and author thank the following publishers for permission to reproduce illustrations:

Alliance Communications Group/Allen Press:

American Association for the Advancement of Science:
Fig. 4.1. From: Scholz, A. et al. (1976). Science 192, 1247–1249.
Fig. 5.7. From: Mori, K. et al. (1999). Science 286, 711–715.
Fig. 6.3. From: Desjardins, C. et al. (1973). Science 182, 939–941.

American Society for Ichthyology and Herpetology:

American Society of Mammalogists:
Fig. 8.1. From: Batzli, G.O. et al. (1977). Journal of Mammalogy 58, 583–591.

Annual Reviews:
Fig. 5.6. From: Buck, L. (1996). Annual Review of Neuroscience 19, 517–544.

Elsevier:
Fig. 3.14. Reprinted from Zeitschrift für Säugetierkunde, 21, Ortmann, R. Über die Musterbildung von Duftdrüsen in der Sohlenhaut der weissen Hausmaus (Mus musculus albinus), 138–141, copyright 1956, with permission from Elsevier.
ACKNOWLEDGEMENTS

W.H. Freeman Publishing:
Fig. 1.5. From: Moen, A. (1973). *Wildlife Ecology*, p. 71.

The Herpetologists’ League, Inc.:
Fig. 7.4. From: Greene, M.J. and Mason, R. T. (2000). *Herpetologica* 56, 166–175.

Journal of Herpetology:
Fig. 4.8. From: Chelazzi, G. and Delfino, G. (1986). *Journal of Herpetology* 20, 451–455.

McGraw Hill Education:
Figs. 3.4 and 3.5. From: Duellmann, W. and Trueb, L. (1986). *Biology of Amphibians*.

Nature Publishing:
Fig. 2.3: From: Böcskei, Z. *et al.* (1992). *Nature* 360, 186–188.

Oxford University Press:
Fig. 5.9b: From: Rasmussen, L.E.L. and Hultgren, B. (1990). *Chemical Signals in Vertebrates*, vol. 5, p. 155.


Sigma Xi, The Scientific Research Society:

Smithsonian Institution:
Fig. 3.3. From: Weitzman, S.H. and Fink (1985). *Smithsonian Contributions to Zoology*, 421, 1–121.

Springer (including Academic Press, Plenum):


Fig. 7.9. From: Frisch, K. v. (1941). *Zeitschrift für vergleichende Physiologie* 29, 46–145.

xv 

ACKNOWLEDGEMENTS

Fig. 12.2. *Journal of Chemical Ecology* 21 (1995) p. 1357, Responses of beaver (Castor canadensis Kuhl) to predator chemicals, Engelhart, A. and D. Muller-Schwarze, fig 4. With kind permission of Springer Science and Business Media

**Thomson Publishing Services:**
Fig. 5.2. From: Bond, Carl E. (1979, 1996). Biology of Fishes.

**John Wiley and Sons:**
Fig. 3.8. From: Albone, E.S. (1984). Mammalian Semiochemistry, p. 43.
Fig. 5.5. From: Albone, E.S. (1984). Mammalian Semiochemistry, p. 245.

Fig 10.8. With kind permission of the Zoological Society of London.