
CHEMICAL SIGNALS IN VERTEBRATES

4

Ecology, Evolution, and
Comparative Biology

Edited by

David Duvall
Dietland Müller-Schwarze and
Robert M. Silverstein

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PREFACE

This volume reviews recent developments in our understanding of chemical signaling in vertebrates. After sections dealing with general principles and chemical aspects of vertebrate pheromones, it follows a taxonomic approach, progressing from fish to mammals. The editors asked a diverse, international group of leading investigators, working on a wide array of vertebrate taxa and specific issues, to consider their efforts from comparative, evolutionary, and ecological viewpoints. The relative number of manuscripts in each part does not necessarily reflect current intensity of research, since the editors invited speakers who together would provide a balanced and comprehensive overview, while avoiding duplication. Still, the part on mammals is the longest.

Fourth in a series dating from 1977, this volume illuminates current trends and likely future developments in the field of chemical signaling in vertebrates. Going back even farther, the first chapter, a personal account of the past quarter century by Dr. Mykytowycz recalls the most important milestones, such as symposia, or the founding of societies and journals. He also credits those investigators who stand out by their seminal studies.

Some new trends can be discerned. First, more taxa, even those with hitherto only microsmatic reputation, such as birds (papers by Wenzel and by Mason and Clark) are examined for their olfactory involvement. This wider coverage allows application of evolutionary lines of thought that may aid in further hypothesis testing (e.g., Smith; Houck; Dawley; Gosling; Graves et al.; and Keverne and Rosser). Second, the primer pheromones have emerged as the vertebrate pheromones with the most consistent effects. For this reason, a number of laboratories worldwide are attempting to exploit these effects for livestock breeding (e.g., Albone et al.). After decades of effort, the first primer pheromone has been chemically identified (Jemiolo et al.). Third, the search for applications is taking new routes. For example, Sullivan and Crump explore the responses of pest rodents to predator odors.

Finally, we now know that the isolation and identification of biologically active vertebrate odor components, while in many ways similar in procedure to that so successfully applied in insects, poses a greater challenge. As in insects, several constituents usually must act together for the effect to occur. However, in vertebrates, odors functioning in recognition of species, group, individual or physiological state may consist of dozens of compounds. Instead of the "response-guided strategy" (Albone, 1984), where the bioassay follows successive fractionation steps, investigators of mammalian pheromones now speak of "odor images," "patterns," or "profiles," meaning that active constituents may occur in many or all fractions and that fractionation actually destroys the biological effect. The effect of various components of such an odor image may be additive, synergistic, or redundant (Muller-Schwarze et al.). An example of processing of chemical

signals by humans (Doty) concludes the review. Needless to say, this field is more important than a single contribution can convey.

As this collection of essays testifies, the exploration of chemical signals has become more firmly embedded in behavioral ecology and socio-biology. Current research has been stimulated by the studies of insect pheromones and is guided by evolutionary concepts.

These papers were presented at the Fourth International Symposium on Chemical Signals in Vertebrates, held at the University of Wyoming, Laramie, from 27-30 July 1985. Our meeting was affiliated with the 10th International Symposium on Comparative Endocrinology, organized by Charles Ralph and held the previous week at Copper Mountain, Colorado. We thank the Union Carbide Corporation and the University of Wyoming Office of Research and College of Arts and Sciences for financial support. Richard Doty, Robert Jenkins, Walter Eggers, and Joan Wadlow deserve greatest thanks for their help in obtaining this support. The helpful counsel of John G. Vandenberg, Ben S. Goodrich, and D. Michael Stoddart is also gratefully acknowledged.

Laramie "locals" who helped immeasurably with the actual presentation of the conference include Brent Breithaupt, Matt Goode, Al Redder, Brent Graves, Steve Buskirk, Bill Gern, Charles Ralph, Mike King, Geoff Carpenter, Mary David, Ruby Sanchez, Pat Beintema, Chuck Cooper, and our dedicated "army" of student volunteers. Brent Graves, Matt Goode, Al Redder, and Jeanne Trupiano-Duvall helped with proofreading. Mary David deserves special thanks for typing the entire camera-ready volume with so much patience and talent. Finally, our thanks to Jeanne Trupiano-Duvall for help with the indices and for her patience and support.

Laramie, Wyoming
Syracuse, New York

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Summer, 1986

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A QUARTER OF A CENTURY OF STUDIES OF CHEMICAL

COMMUNICATION IN VERTEBRATES

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The purpose of this article is to give a brief outline of the events and processes which have taken place over the last twenty five years which have led to the emergence of a new biological discipline - namely that of chemical communication in vertebrates.

The simplest way of doing this is to recall my own involvement in it. Naturally, in adopting this approach, there is always the chance that the final picture may be somewhat biased.

References are made to the more important meetings and publications and to the formation of societies devoted to the promotion of interest in the field. In conclusion, the needs for future research are suggested.

THE NEED TO STUDY COMMUNICATION IN ANIMALS

In the early '50s we in Australia, for practical reasons, undertook a series of studies of various aspects of the biology of free-living European wild rabbits, Oryctolagus cuniculus. The hope was that the knowledge gained would enable us to control more efficiently the numbers of these animals which represent a serious agricultural problem. My personal task, originally, was to study the diseases of the rabbit. In the course of this work, however, I developed an interest in behaviour and became convinced of its importance in the population dynamics of free-living animals. At that time, the behaviour of animals ceased to be a trivial, theoretical subject; ethology became acknowledged as a separate discipline. This provided a legitimate excuse for me to enter into this new realm of biology.

In the course of our ethological studies, it became obvious that to preserve their characteristic pattern of behaviour and to assure an orderly coexistence, rabbits have to communicate with one another.

Like other mammals, rabbits probably make use of all modalities to exchange information. However, such behavioural activities as regular olfactory exploration of their surroundings and conspecifics, "chinning," the formation of "dung-hills," "tail-flagging" and the enurination of other individuals suggested that for wild rabbits, odour signals derived from

the anal, chin, and inguinal glands and from urine are particularly important means of communication.

A search through the literature showed that the existence of the odour-producing glands mentioned above had already been recorded by anatomists and histologists, but in view of a complete absence of information on the behaviour of the species, the question of their functions was wrongly interpreted or completely ignored. Thus, there was an obvious need to clarify the role of the odoriferous skin glands in the European wild rabbit.

The scenario just outlined was not confined to the study of rabbits. A similar necessity appeared at about the same time for other species, as interest in mammalian behaviour, and the role of olfaction in it, grew rapidly.

FACTORS STIMULATING EARLY STUDIES OF OLFACTORY COMMUNICATION

Apart from the rise of ethology, there were other factors which stimulated interest in olfactory communication in vertebrates.

First of all, the early success of chemists in their research on insect pheromones, and the discussion and speculation which developed from it, provided strong encouragement and hope that "mammalian pheromones" may be just as easy to study. This would be of benefit to man in his efforts to manage populations of both free-living and domestic animals.

We now know that the early expectations of the practical importance of insect pheromones proved to be too optimistic. In any case, direct comparison of the behaviour of insects and higher animals leads to a misleading simplification. Also, modern analytical techniques of gas chromatography and mass spectrometry, which became commonly available during the mid-'60s, were soon found to be inadequate to solve the complexity of mammalian odours. The lack of suitable behavioural assays was another hampering factor.

On the other hand, it was perhaps fortunate that at this early stage of interest in olfactory communication of mammals those involved were not aware of all these problems; otherwise, the enthusiasm of many of them would surely have been dampened. Incidentally, the belief that the responses of mammals to odour signals are stereotyped and genetically controlled prevailed for a long time. This oversimplification, even today, often confuses many workers without previous experience in behavioural studies.

Exciting observations on the effects of odour on the timing of oestrus and the blocking of pregnancy in laboratory mice, which came to light around the mid-'50s, was another factor which inspired interest in olfactory communication.

Another stimulus which generated interest was the progress in understanding the physiology of olfactory systems for which we are indebted to such workers as E. D. Adrian, C. Pfaffmann and Y. Zotterman. The availability of electrophysiological techniques, which allowed the measurement of the electrical responses of the olfactory bulbs and peripheral olfactory systems to odour stimulation, promised easier experimentation.

EARLY SOURCES OF INFORMATION

In this early period of marshalling of ideas which eventually formed the foundation for the new field of interest, R. W. Moncrieff's book

"Chemical Senses" (1951, 2nd edition) contained all the information on olfaction available at that time and was of great help to the beginner.

An early interest shown by perfumers and natural product chemists in the secretions from mammalian skin glands did not stimulate attention as their studies were completely unrelated to the animal's behaviour. Nevertheless, the paper by Kingston (1965), summarising their achievements, proved a useful reference for further chemical studies.

Naturally, one could not afford to ignore the fairly numerous reports on the occurrence and histology of odour-producing skin glands throughout the animal kingdom. Some of them hinted at the possible role of skin glands in the communication of information related to reproduction. Subsequently, our own histological studies showed very clearly that social status - i.e., behavioural status of an individual, is reflected in the histological appearance of odoriferous glands which function for communication purposes (Mykutowycz, 1970).

FIRST STEPS TOWARDS THE ORGANIZATION OF GROUP MEETINGS

Even scientists cannot afford to live and work in complete isolation. As a result of the increasing interest in chemical senses generally, a number of meetings of workers in this field took place in the '50s (McCartney, 1968). Of special importance to us, however, was the First International Symposium on Olfaction and Taste which was held in Stockholm in 1962 as a satellite meeting to the International Congress of Physiology organised by Y. Zotterman. The program of this and subsequent triennial meetings, known as ISOT, although centered around physiology, also provided an opportunity to those interested in behaviour to meet and exchange ideas (Zotterman, 1963).

There were, however, few who were ready to take advantage of this opportunity. Only two or three contributions on the program of the first ISOT were directly related to the problems of the communicatory role of smell. In subsequent meetings, this area was somewhat more strongly represented. Nevertheless, what was important was the indication of the emerging awareness that there was a need to study chemical signaling in the olfactory behaviour of animals.

In 1962, sensory physiology itself was still in an early stage of development and this was very clearly expressed in the opening address by E. D. Adrian. He remarked that ... "Our subject has reached the right stage for serious discussion and we must get down to it. It concerns fundamental problems where physiology and psychology meet (at that stage behavioural matters were still the domain of psychology, not ethology), in fact we are in one of those borderlands which are the most fertile regions for the scientific advance...".

Although Adrian directed his remarks mainly toward his fellow physiologists, they were and still are appropriate to all those interested in olfactory communication in mammals.

During the first ISOT, only Jacques LeMagnen, the founder of the field of olfactory-endocrine relationships, whose later work linked animal and human studies, hinted at future developments. In his paper he remarked that ... "Electrophysiological investigation of olfactory and gustatory afferent fibres does not allow us to analyse the discriminatory process itself. Only behavioural data can actually reveal the differential effects of the given stimuli on the olfactory system. Thanks however to the work of Adrian, Pfaffman and of the Swedish and other workers, modern electrophysiological

evidence has given us an idea of both the physiochemical and the intrinsic nervous mechanisms which at different levels account for the phenomena demonstrated by behavioural methods."

While the first ISOT in 1962 merely indicated the trends, the end of the '60s saw the appearance of separate groupings of workers interested in the study of chemical communication in animals.

It was most timely that the only known mammalian semiochemicals which fit nicely into the concept of insect pheromones - two steroids present in the saliva of the domestic boar (5 α -androst-16-en-3-one and 3 α -hydroxy-5 α -androst-16-ene) - were isolated by Patterson (1969), just at the time when interest in olfactory communication was rising.

The first ever conference organised at the international level, which gathered together all those interested specifically in the chemical communication of animals, took place in June (27-28) 1968 at Auburn, Massachusetts. It was organized mainly by D. J. Moulton in cooperation with J. W. Johnston, and A. Turk (Johnston et al., 1970). The Auburn symposium brought together chemists, biologists, insect physiologists, mammalian endocrinologists, experimental psychologists, animal behaviourists and zoologists, as well as other specialists. This cocktail of different specialists was the best indication that a new, important biological discipline, chemical communication in animals, had emerged.

Most appropriately, E. O. Wilson, a founder of sociobiology, was invited to give the introductory speech. He already had at least ten years experience in the field of olfaction, having published a number of papers in which he not only summarised the achievements in the field of entomology, but also ventured into the mammalian world. Wilson's (1963) paper, published in "Scientific American," served as a key reference for many who contemplated entering the new niche of ethology.

During the '60s a further two ISOT and Gordon Conferences on the Chemical Senses were held. The Japanese Association of Taste and Smell (JUST) was formed in 1968. In the same year, the Commission on Chemoreception of the International Union of Physiological Sciences was organised. Its status and nature were formalised in 1972. The traditionally physiologically oriented program of the third ISOT held in New York in 1969 was augmented by papers on olfaction and behaviour of fish, birds and mammals. The speakers included J. E. Bardach, Bernice M. Wenzel, W. K. Whitten and T. G. Schultze-Westrum.

In 1968, another important event took place when the Ambrose Monell Foundation provided funds to create, in Philadelphia, a unique research and teaching center devoted exclusively to studies of the chemical senses. M. R. Kare was appointed as its Director and the late D. J. Moulton, who devoted his entire research career to the study of olfaction, contributed significantly towards its initial organisation.

The Monell Chemical Senses Center, originally a division of the University of Pennsylvania, was an exercise which proved to be highly successful. It has grown rapidly into a complex multidisciplinary institute in which major emphasis is placed on studies of the structure and behavioural function of chemical signals as well as on the physiology of their reception in mammals, including humans. Apart from M. R. Kare and D. J. Moulton, many others who figure prominently in the field of chemical communication became associated with the Monell Center - notably G. Eppler, R. L. Doty, G. K. Beauchamp, G. Preti and A. B. Smith, III.

THE EXCITING '70s

While the main activities unfolded on the American continent, colleagues in Europe did not lag behind. In 1970, at the International Summer Course on Odour Perception, held in Utrecht, Netherlands, the European Chemoreception Research Organisation (ECRO) was inaugurated due to the efforts and support of M. Beets - a successful scientist and industrialist - and the enthusiasm of E. P. Köster. Although started as a European venture, ECRO opened its membership to colleagues from other parts of the world. In 1982, ECRO had over 400 members from more than 30 countries. Its function is to promote and support research and exchange information on all aspects of chemical senses. ECRO's activities include organising mini-symposia and congresses. Although it is oriented more towards physiology, there are also opportunities for those interested in chemical communication in animals to use its forum.

Thus, at the start of the '70s, students of various aspects of olfaction found themselves well organised into separate groups with fairly discrete, strongly defined mutual interests. The formation of these groups was aided not only by common professional backgrounds, but also by personal contacts and affinities. Those eager to solve the questions related to the behavioural role of olfaction in vertebrates no longer had to feel that they worked in isolation. Their numbers grew constantly. This was well demonstrated by frequent, smaller local and international meetings devoted specifically to chemical communication and by the appearance of special journals, newsletters and new books. The interest in olfactory communication widened beyond the laboratory species and those few which were the subjects of investigation initially.

There was always interest in the role of olfaction in man. In the past, physicians, psychiatrists, criminologists, anthropologists and others periodically touched upon this question, but their statements were not based on adequate systematic research data. This has been emphasised by McCartney (1968) in his useful publication, already mentioned above.

The advances in the studies of the effect of "primer pheromones" on oestrous cycles, cycles among women living in close proximity to one another. others, F. H. Bronson and W. K. Whitten, also inspired interest in olfaction in humans. The works of J. G. Vandenbergh and L. C. Drickamer added considerably to this.

The likelihood of the existence of human pheromones became the subject not only of more frequent speculation, but also of more systematic observation after Martha McClintock (1971) reported on the synchronisation of menstrual cycles among women living in close proximity to one another. Subsequently, specifically designed studies substantially strengthened the supposition that olfactory signals perceived subconsciously are responsible for this (Russell et al., 1980).

The studies of R. P. Michael and associates of the importance of the odour of vaginal discharge in communicating the reproductive states of rhesus monkeys, Macaca mulatta, also contributed towards the growth of interest in the possible role of olfaction in the behaviour of humans. W. Montagna was one of those who reinforced this trend through his studies of the histology of skin glands in primates, through his leadership at the Oregon Regional Primate Research Center and as an organiser of the Annual Symposia on Biology of the Skin. For example, during the 22nd Symposium of this series, a talk by myself and B. S. Goodrich as coauthor on the behavioural role of skin glands in animals, was meant to acquaint the participants, predominantly dermatologists, with a possible new function of

the integument. Among other speakers, was F. J. Ebling who, through his own work and that of his associates on the hormonal control of skin glands, contributed significantly towards a better understanding of chemical communication.

Those concerned with the reproduction of animals were amongst the very first to pay attention to the importance of odour. No wonder reports on the effect of urine odour on the timing of oestrus and blocking of pregnancy in laboratory mice were inductive.

In 1972, during the 3rd International Symposium on Comparative Reproduction entitled "Environment and Reproduction in Mammals and Birds" held in Edinburgh, one session chaired by Hilda M. Bruce was devoted to olfaction. The decision to include this topic into the program was made under the influence and advice of A. S. Parkes, the noted British reproductive physiologist who, right from the very early stages, generated the awareness that olfaction was an important extrinsic factor influencing reproduction.

Information on the importance of the odour of the salivary steroid in the reproduction of domestic pigs, which J. P. Signoret effectively continued to disseminate, also provided a powerful stimulus among those with a practical approach to the study of reproduction in animals.

On the program of the 8th International Congress on Animal Reproduction and Artificial Insemination, which was held in Krakow, Poland in June 1976, there was a session entitled "Role of Pheromones in Reproduction" (Myktyowycz, 1976). Among the participants were colleagues representing Australia, Canada, France, India, U.K., Poland and U.S.A.

The first ever gathering of researchers interested exclusively in the behavioural role of olfaction in vertebrates, predominantly in mammals, took place in 1976 at Saratoga Springs, New York (see Muller-Schwarze and Mozell, 1977). This first Symposium on Chemical Signals in Vertebrates was attended by 140 participants. Its objective was to bring together the physical and the biological scientists so that they might develop a greater understanding of one another's theoretical concepts and practical problems. Almost all laboratories involved in work on vertebrates were represented. This meeting gave a much needed impetus to an evolving interaction between researchers who were just beginning to approach chemical reception in higher animals, rather as integrated teams than as specialists, in separate disciplines working in parallel.

The Saratoga Springs Symposium provided a forum for the clarification of some newly emerging fundamental questions such as the suitability of the concept of "pheromones" in work with mammals, the question of learning in chemical communication, of diet in shaping odour profiles and the effects upon chemical communication of the multisensory context in which it must operate. Also, the question of the chemical complexity of odour signals received attention.

The Symposium in Saratoga Springs, as well as subsequent ones of this series held in Syracuse in 1979 and in Sarasota in 1982, were organised mainly by D. Muller-Schwarze in association with R. M. Silverstein. The organisation of this current symposium in Laramie, Wyoming in July 1985 has already involved colleagues of the younger generation, particularly David Duvall.

Physiologists, acting on the suggestion made by Lord Adrian referred to earlier, asked Wes Whitten to organise a symposium on olfaction during the International Physiological Congress held in Paris in July 1977. F. H. Bronson, M. Novotny, G. Raisman, J. P. Signoret and J. G. Vandenbergh