



Social odours in mammals

Volume 1

Edited by

Richard E. Brown and
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Preface

Generations of countryfolk, naturalists, and huntsmen have wondered at the acute sense of smell which opens a dimension to the lives of many other mammals, but from which we are barred. Some have doubtless cursed, rather than marvelled, at the sense which drives the once reliable dog besotted for a far-off bitch, or which thwarts the stalker at the whim of a breeze. It does not take a training in science to recognize our nose-blindness, or to hunger for a knowledge of what Kenneth Grahame, in *The wind in the willows*, called the mysterious fairy calls from out of the void, for which 'we have only the word smell, to include the whole range of delicate thrills which murmur in the nose of the animal night and day, summoning, warning, inciting, repelling'.

The realization that our own species is dismally ill-equipped to notice, far less to decipher, this profusion of mammalian odours, seems not to have deterred, but rather to have spurred biologists to excesses of curiosity. The result has been, over the past decade or so, a rapid expansion of information on these scents which function in mammalian communication, and which we shall call social odours. However, information on these social odours, their nature, sources, deployment, and functions, is widely scattered in the scientific literature and has become, in two senses, unusually fragmented. The first reason for this fragmentation is that the strength and the weakness of studies of olfactory communication is that they can be launched from diverse perspectives, involving the expertise of biologist or chemist, ecologist or histologist, field naturalist, endocrinologist or experimental psychologist. There is thus the opportunity for the fruitful combination of interdisciplinary forces in the common quest, or for their artificial division along the barriers of jargon. One practical consequence of these varied inputs is that it is not always obvious where to look in order to read about either recent advances or established background.

The second sense in which information on social odours is fragmented is a combined result of the tendency for biologists to study intensively only a few species, and the fact that members of thousands of mammalian species are each endowed with several sources of social odours. In consequence, a survey of current publications concerning social odours often gives an imbalanced impression of the prevalence of olfactory communication amongst mammals, disguising the fact that existing studies have tackled only the tip of the iceberg. Furthermore, the same focus on only a few species fails to direct the reader to the enormous variety of relevant snippets of information on a much wider array of mammals.

The growth of theoretically exciting ideas concerning social odours, the scattered publications and expertise, the feeling that a systematic review of literature on the whole Class could provide a realistic perspective and a useful

reference work all prompted us to produce this two volume book. The structure of the book very much reflects our aims, as elaborated in our introductory chapter (pp. 1-18). Briefly, the two volumes are organized taxonomically, each chapter dealing with one or more orders. We hope it has an encyclopaedic quality which will be enduring useful, in that a vast store of literature is summarized in the text and, particular, in the summary tables. The possibilities for reference use are enhanced by comprehensive species and author indexes. At the same time, there is also an emphasis on reviewing modern ideas and even, in some chapters, otherwise unpublished data.

One of the most exciting fields of modern biology is the study of social behaviour; and the role of social odours in mammalian societies could hardly be more forcefully emphasized than in the chapters which follow. Indeed, we would argue that odours are a fundamental part of mammalian sociality and adaptation. While the secretions of the mammary glands may legitimately have pride of place, the scent-producing glands of the skin do not rank far behind in the list of qualities that are essentially mammalian.

We gratefully acknowledge all those who have helped in the production of these two volumes. In particular, at Dalhousie and Oxford, we were aided in proof-reading by Geoffrey Carr, Stefen Natynczuk, Jenny Ryan and Lilyan White, and in indexing by Gillian Kerby and Colin Pringle, together with Peter King and Dierdre Harvey of the Kellogg Health Sciences Library at Dalhousie. The composite drawings in Chapters 3, 6, 9, 10, 11, 12, 13, and 15 are by Priscilla Barrett.

Halifax and
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August, 1984

R.E.B.
D.W.M.

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Introduction: The pheromone concept in mammalian chemical communication

DAVID W. MACDONALD and RICHARD E. BROWN

Apart from man, most other animals think through their noses. If we too were olfactory animals there would be no bird watchers, but in their place we would have mammal smelling societies.

Nisbett (1976, p. 30).

The importance of mammalian scent glands was first noted by perfumers who used three odours from mammalian scent glands: musk, civet, and castor. Musk is taken from the preputial glands of the musk deer (*Moschus moschatus*); civet from the anal glands of the civet (*Viverra civetta*), and castor from the castor gland of the beaver (*Castor canadensis*). A fourth mammalian source of perfume odour is ambergris, produced in the intestines of the sperm whale. According to Ellis (1962) the use of ambergris and musk is 'almost as old as civilization itself' (p. 40) while civet and castor were not used in Europe until the fifteenth and sixteenth centuries.

Although there are some early descriptions of mammalian scent glands, such as that of Pallas (1779), scientific study did not begin until the nineteenth and early twentieth centuries. Histological analysis and classification of mammalian skin glands were first conducted by Graff (1879) and Ranvier (1887). Later surveys of scent glands were published by Brinkmann (1912), Schiefferdecker (1922), and Eggeling (1931). From 1910 to 1945 R. I. Pocock described the scent glands of mammals kept in the London Zoological Gardens, and his prolific articles (listed in Hindle's (1948) bibliography) remain as the only descriptions of the scent glands of many species. The most complete modern reference for the skin glands of mammals is Schaffer's (1940) monograph, which is, unfortunately, difficult to obtain.

Some works on specific groups of mammals, such as Ewer's (1973) book on the Carnivora, contain chapters on scent glands and some reviews on the general aspects of skin glands have recently been published including those of Ortmann (1960) on the anal glands, Gabe (1967) on the research history and classification of skin glands, and Adams (1980) on the odour-producing organs of mammals; no attempt has been made to summarize all the information on mammalian scent glands since Schaffer's (1940) monograph. Today such a summary needs to be made in the context of evolutionary and ecological theory which did not exist in Schaffer's time. One aim of the authors of this book has been to compile such a summary.

Social functions of odours

A second purpose of this book is to examine the social functions of the odours produced by mammals. In *The descent of man* (1877) Darwin discussed two functions for scent glands and odours in communication: defence and reproduction. He states that:

With some animals, as with the notorious skunk of America, the overwhelming odour which they emit appears to serve exclusively as a defence. With shrew-mice (*Sorex*) both sexes possess abdominal scent-glands, and there can be little doubt, from the rejection of their bodies by birds and beasts of prey, that the odour is protective; nevertheless, the glands become enlarged in the males during the breeding season.

Darwin (1887, p. 528).

Darwin associated scent glands with reproduction because he noted that secretions occur more often in males than females, are more abundant in the breeding season, do not commence until adulthood and are inhibited by castration. He also noted species differences in scent glands among closely related animals.

It was clear to Darwin that the odours produced by the mammalian scent glands were important for sexual selection:

In most cases, when only the male emits a strong odour during the breeding season, it probably serves to excite or allure the female . . . The odour emitted must be of considerable importance to the male, inasmuch as large and complex glands, furnished with muscles for everting the sack, and for closing or opening the orifice, have in some cases been developed. The development of these organs is intelligible through sexual selection, if the most odoriferous males are the most successful in winning the females, and in leaving offspring to inherit their gradually-perfected glands and odours.

Darwin (1887, p. 530).

After Darwin, the role of odorous secretions in courtship and sexual selection was emphasized as the primary function of the scent glands of mammals. Pycraft (1914), for example, gives the following anecdote

That these secretions play an important and perhaps variable part in the selection of mates seems demonstrated in the case of an incident related to me by my friend Mr. John Cooke, who some time ago was watching a flock of some three hundred sheep while it was being driven by the shepherd and his dogs into a field. As soon as they were securely shut in, and the shepherd had gone, three rams who were included in the flock at once began a three-cornered fight. One, presumably the youngest, was soon vanquished. The other two soon settled their differences, and the clashing of horns was at once followed by a very different performance. The master ram began to run in and out among the ewes, sniffing at each, and driving out those whose odour most pleased him. Having at last satisfied himself with a harem of about one hundred, the second ram was allowed to make a like choice, and behaved in a like manner, leaving the remainder to the ram which was first vanquished.

Pycraft (1914, pp. 69-70).

While many early zoology textbooks mentioned the scent glands of mammals and suggested possible functions for the odours of these glands, they were mainly speculative in nature. In *The Cambridge natural history*, for example, Beddard (1923) states the following:

It seems to be possible that the function of these various glands is at least two-fold. In the first place, they may serve, where predominant in one sex, to attract the sexes together. In the second place, the glands may be useful to enable a strayed animal of a gregarious species to regain the herd. It is perfectly conceivable too that in other cases the glands may be a protection, as they most undoubtedly are in the Skunk, from attacks. In connexion with the first, and more especially the second, of the possible uses of these glands, it is interesting to note that in purely terrestrial creatures, such as the Rhinoceros, the glands are situated on the feet, and would therefore taint the grass and herbage as the animal passed, and thus leave a track for the benefit of its mate. The same may be said of the rudimentary glands of Horses if they are really glands. The secretion of the 'crumen' of Antelopes is sometimes deposited deliberately by *Oreotragus* upon surrounding objects, a proceeding which would attain the same end. One may even perhaps detect 'mimicry' in the similar odours of certain animals. Prey may be lured to their destruction, or enemies frightened away. The defenceless Musk-deer may escape its foes by the suggestion of the musky odour of a crocodile. It is at any rate perfectly conceivable that the variety of odours among mammals may play a very important part in their life, and it is perhaps worthy of note that birds with highly-variegated plumage are provided only with the uropygial gland, while mammals with usually dull and similar coloration have a great variety of skin glands. Scent is no doubt a sense of higher importance in mammals than in birds. The subject is one which will bear further study.

Beddard (1923, pp. 13-14).

The role of olfaction in sexual selection in humans was examined by Havelock Ellis (1920) who concluded that smell plays only a small role in sexual selection in humans, except for some rare cases:

As the sole factor in sexual selection olfaction must be rare. It is said that Asiatic princes have sometimes caused a number of the ladies to race in the seraglio garden until they were heated; their garments have then been brought to the prince, who has selected one of them solely by the odor. There was here a sexual selection mainly by odor. Any exclusive efficacy of the olfactory sense is rare, not so much because the impressions of this sense are inoperative, but because agreeable personal odors are not sufficiently powerful, and the olfactory organ is too obtuse, to enable smell to take precedence of sight.

Ellis (1920, p. 66).

Ellis's major contribution to the study of olfactory communication in man lay not in his discussion of sexual selection, but in his identification of the sources of human odours and their information content. Ellis also noted differences in human odours due to race, sex, and age and made the important observation that a person's odour could be altered by his emotional state and by hormonal changes at puberty.

It is a significant fact, both as regards the ancestral sexual connections of the body odors and their actual sexual associations today, that, as Hippocrates long ago noted, it is not until puberty that they assume their adult characteristics. The infant, the adult, the aged person, each has his own kind of smell, and, as Monin remarks, it might be possible, within certain limits, to discover the age of a person by his odor. In both sexes puberty, adolescence, early manhood and womanhood are marked by a gradual development of the adult odor of skin and excreta, in general harmony with the secondary sexual developments of hair and pigment. Venturi, indeed, has, not without reason, described the odor of the body as a secondary sexual character. It may be added that, as is the case with the pigment in various parts of the body in women, some of these odors tend to become exaggerated in sympathy with sexual and other emotional states.

Ellis (1920, p. 63).

While there are many examples of changes in odour associated with sexual arousal in mammals, there are fewer examples of odours associated with other emotions but Bedichek (1960, p. 139), for example, states that:

There is a lot of evidence that the odour generated by fear in the human body stimulates the dog to attack. Cowboys, generally, believe that the odour of fear exhaled by the human body excites and often renders a horse unmanageable.

That physiological changes due to emotional, hormonal, and genetic factors could lead to changes in bodily odour was clearly pointed out by Bethe (1932) in his article on 'neglected hormones'. Bethe discussed the findings that there are species, family, and individual differences in odours, examined the changes in the odours of female mammals when they come into heat and discussed the role of odours in mother-infant attachment.

Scent marking

Another function of this book is to examine the social function of scent marking in mammals. The early ethologists recognized the importance of odour marks in an animal's environment: 'territory marking' using urine, faeces and the secretions from skin glands was described for pine martens by Goethe (1938), for bears and dogs by Bilz (1940) and for other mammals by Hediger (1944, 1949). According to Hediger (1950) scent marks make an animal's territory familiar as well as warding off intruders. Hediger (1955) summarizes the importance of these scent marks as follows:

A particularly important type of locality in the animal's territory should not be overlooked, the so-called demarcation places, found with deer, and many other mammals. These exist usually on prominent twigs or branches, or tree stumps, or stones, to which the owner of the territory applies its own property marks, so to speak, in the form of a self-produced scent. We must remember that most mammals are macrosmatic, i.e., they have a literally superhuman sense of smell, by means of which they recognize faint traces of scent, which are quite beyond our powers of detection, as conspicuous signals.

Whilst human beings usually demarcate their buildings and homes optically

by means of signboards and street numbers, macrosmatic animals naturally use scents. These are produced in parts of the body varying with the species concerned. In deer and among antelopes, the gland above the eye, the so-called antorbital gland, produces a strong-smelling, oily substance, a small quantity of which is rubbed off on to branches and the like. In this way the whole living space is virtually impregnated with the individual scent of the owner. Any other member of its own species is thus warned off by these scent signals, as soon as it enters an occupied territory.

Hediger (1955, p. 19).

The value of scent in warning off intruders was referred to very explicitly by Hediger (1955, p. 23):

Scents, whether of dung, urine, or glandular secretion, are detachable from the body. They can literally be separated to act as place-reservations. The particle of dung, or the trace of secretion on the marking place, becomes as Bilz shows, the *pars pro toto* (part for the whole), and continues to be efficacious even in the absence of its author.

Bilz, discussing the demaraction behaviour of bears and dogs (1940, p. 285), states: 'Excrement and the image conveyed by it, frighten and even terrify the intruder'. It was this concept of territorial marking and the implied aggressiveness of the scent marks which attracted the interest of the classical ethologists. Tinbergen (1953), for example, made only one reference to olfactory communication in mammals and that is in a chapter on fighting:

Not all threat is visual. Many mammals deposit 'scent signals' at places where they meet or expect rivals. Dogs urinate to that purpose; Hyaenas, Martens, Chamois, various Antelopes and many other species have special glands, the secreta of which are deposited on the ground, on bushes, tree stumps, rocks, etc. The Brown Bear rubs its back against a tree, urinating while it does so.

Tinbergen (1953, pp. 58-9).

Lorenz (1954) viewed scent marking in the same way as Tinbergen, stressing the relationship between scent marking and aggressive motivation:

The leglifting of a dog has a very definitive meaning which is, paradoxically, exactly the same as that of a nightingale's song: it means the marking of the territory, warning off all intruders by telling them as clearly as their senses can perceive it that they are trespassing on the ground owned by somebody else. Nearly all mammals mark their territory by means of scent, as being one of their strongest sense faculties.

Lorenz (1954, p. 94).

This theme is expanded by Lorenz (1963) in *On aggression*:

Among mammals, which 'think through their noses', it is not surprising that marking of the territory by scent plays a big role. Many methods have been tried; various scent glands have been evolved, and the most remarkable ceremonies developed round the depositing of urine and faeces; of these the leg-lifting of the domestic dog is the most familiar. The objection has been raised by some students of mammals that such scent marks cannot have anything to

do with territorial ownership because they are found not only in socially living mammals which do not defend single territories, but also in animals that wander far and wide; but this opinion is only partly correct. First, it has been proved that dogs and other pack-living animals recognize each other by the scent of the marks, and it would at once be apparent to the members of a pack if a non-member presumed to lift its leg in their hunting-grounds. Secondly, Leyhausen and Wolf have demonstrated the very interesting possibility that the distribution of animals of a certain species over the available biotope can be effected not only by a space plan but also by a time plan. They found that, in domestic cats living free in open country, several individuals could make use of the same hunting-ground without ever coming into conflict, by using it according to a definite timetable, in the same way as our Seewiesen housewives use our communal washhouse. An additional safeguard against undesirable encounters is the scent marks which these animals—the cats, not the housewives—deposit at regular intervals wherever they go. These act like railway signals whose aim is to prevent collision between two trains. A cat finding another cat's signal on its hunting-path assesses its age, and if it is very fresh it hesitates, or chooses another path; if it is a few hours old it proceeds calmly on its way.

Lorenz (1963, p. 27).

Eibl-Eibesfeldt (1970) has emphasized both the threatening function of scent marks and their function in reassuring the territory owner:

The scent marks are chemical property signs. They aid the territory owner, first of all, as signs of recognition. They help in orientation and make the area familiar. A badger that becomes agitated or frightened in a strange environment can be calmed by letting it sniff an object that it had marked previously. A male hamster that enters the territory of a female during the mating season will mark this strange territory before it actually begins to court. It is probable that this also has a repelling function for others. Strange scent marks have an aggression-releasing effect in hamsters, which show threat behavior when sniffing strange scent marks.

Eibl-Eibesfeldt (1970, p. 311).

While most ethologists emphasized the role of odours in territory marking, aggressive and sexual encounters, Schloeth (1956) described the importance of olfactory investigation between mammals encountering strangers for the first time. Schloeth defined three basic patterns of olfactory investigation of conspecifics: naso-anal, naso-genital, and naso-nasal (see Fig. 1), and pointed out that animals had specific 'contact points' at which olfactory investigation most often occurred. Schloeth considered the investigation of scent marks to be an 'indirect' olfactory investigation as opposed to the more direct naso-anal, naso-genital, or naso-nasal postures.

Recent years have seen mounting acknowledgement, and somewhat increased understanding, of the complexity of mammalian societies. Nevertheless, proof of some enduring interpretations of the functions of social odours has remained sparse (e.g. the *pars pro toto* model, cf. Gosling (1982)). Olfactory communication turns out to be as complex and flexible as are the societies within which it operates: Kruuk (1972), for example, found that spotted hyaenas, *Crocuta*