# OLFACTORY COMMUNICATION IN MAMMALS  4034

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## INTRODUCTION

In the broad perspective chemical communication has been the subject of several recent reviews (Wilson 138; Johnston, Moulton & Turk 59; Wilson 137). The present review will be more restrictive; we will deal with one aspect of chemical communication in one class of vertebrates, i.e., olfaction in the Mammalia.

For the purposes of this review, olfactory communication is defined as the process whereby a chemical signal is generated by a presumptive sender and transmitted (generally through the air) to a presumptive receiver who by means of adequate receptors can identify, integrate, and respond (either behaviorally or physiologically) to the signal. It is assumed that the sender-receiver relationship is in some way the result of natural selection so that signal production by the sender leads to an increased likelihood that the sender or the species will benefit from the transmission of the message; the whole process of communication is subject to the pressures of natural selection.

A chemical signal which serves to trigger a response in a conspecific receiver is generally referred to as a *pheromone* (Wilson 137)—in contrast to an *allomone,* which is a signal used to communicate with a member of another species (Brown 16). By thus defining olfactory communication, we have eliminated from consideration in this review problems of food selection, habitat selection, etc, which do involve the chemical senses but which result from different sorts of interactions of the organism with the environment.

Olfactory communication has certain advantages, since it allows a receiver to assess certain parameters of its social environment very specifically. There is a disadvantage to chemical communication since in general there is no inherent directionality in the propagation of the signal and, in order to orient toward the source of chemical information, the presumptive receiver must make use of a gradient. The "active space" of a chemical signal has been the subject of extensive discussion by Wilson (137) and Wilson & Bossert (139). A tremendous advantage of using chemical signals instead of visual and auditory ones is that chemical traces persist for some period of time

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in the absence of the sender. The deposition of discrete chemical substances is generally referred to as *marking behavior* and will be treated as a separate section of this review.

In the literature on marking behavior and olfactory communication, the motivation of behavior associated with the deposition of odoriferous sub- stances and the function(s) of the odors are often inadequately separated; this is confusing, especially when a term like *territorial-marking* is used. We will try to clarify some of this confusion in the final section of the review. Also, most reviews on the subject of olfactory communication have concen- trated on the specialized movements associated with some kinds of odor de- position (*scent-marking*) but have ignored the release or deposition of excre- tory products as major features of olfactory communication. We hope to give a balanced treatment to all functional aspects of odor release and deposition.

## THE PERCEPTION OF CHEMICAL SIGNALS

The perception of chemical substances by mammals is generally mediated through three different classes of receptors (for a recent review, see Pfaffmann 100). Nerve endings in the nasal mucosa are responsive to a variety of chem- ical substances and, although these receptor organs exhibit a high threshold, their reaction properties are very similar to those of the olfactory neurons themselves. In the nasal cavity, the general chemical sensitivity of unspecial- ized nerve endings which eventually lead to the trigeminal nerve has been reviewed in part by Beidler (9). Mammalian taste receptors, incorporated within the taste buds of the tongue, respond to five limited classes of chemi- cal substances, but only when the chemical substances are in solution and are brought directly into contact with them. Taste receptors generally connect with the seventh, ninth, and tenth cranial nerves (see Beidler 8).

Olfaction involves only those specialized receptor neurons located in (*a*) the olfactory mucosa or epithelium at the rear of the nasal cavity which con- tains neurons forming the first cranial nerve and terminating in the olfactory bulb of the brain, and (*b*) olfactory epithelium discretely organized in many mammalian species into a vomeronasal organ. The structure and function of the olfactory epithelium has been reviewed by Moulton & Beidler (89) and Moulton (87, 88). In general, olfaction is a specialized form of chemical reception since the stimulus molecules are airborne and are drawn into the nasal cavity, interacting in an as-yet-undefined manner with the cell mem- branes of the primary olfactory receptors.

The manner in which the olfactory neural-receptor is activated by a chemical substance is still subject to discussion (see Amoore 3, Wright 141, and Lettvin & Gesteland 71). Regardless of lack of information concerning the activation mechanism and the imprecise conceptualization of how chemi- cal information is integrated within the olfactory bulb, it is undeniable that chemical substances are perceived by mammals and influence their behavior.

## THE VOMERONASAL ORGAN

The vomeronasal organ, or Jacobson's organ, is a little-known anatomical structure which is involved in chemoreception (Kerkhof 61). In the Squamata it consists of a section of olfactory epithelium enclosed in a cartilaginous capsule shut off from the nasal cavity and opening into the mouth cavity. Burghardt (22) has reviewed the function of the Jacobson's organ in perception of chemical stimuli by snakes and lizards; however, its function in mammals has been debated during the past 70 years. Among mammals, the vomeronasal organ is an encapsulated structure on each side of the nasal septum near the floor of the nasal cavity. It is strongly developed in the Insectivora, Rodentia, Marsupialia, Artiodactyla, and Perissodactyla. In the higher primates (Pongidae and Hominidae), some Chiroptera, and many aquatic mammals (Cetacea), the organ may be reduced or entirely absent (Weber 132). The epithelium on the medial side of the blind pouch is rather thick and is similar in structure to the sensory epithelium of the olfactory organ, while the lateral wall is characterized by cuboidal epithelium. At the anterior end of the cartilaginous pouch which contains the olfactory epitehlium there is generally a canal leading to the upper, middle, or lower segment of the naso-palatine duct. In some forms (e.g., *Equus*), the naso-palatine duct does not connect with the nasal cavity at all and, in that case, the Jacobson's organ communicates independently with the nasal cavity (Sisson & Grossman 117). For many species, the exact anatomical relationship between the Jacobson's organ and the nasopalatine duct, the nasal cavity, and the buccal cavity is unclarified. Thus, in a number of mammals the Jacobson's organ can communicate either directly with the nasal cavity or indirectly with either the nasal cavity or the buccal cavity via the naso-palatine duct.

The olfactory epithelium of the Jacobson's organ connects with the olfactory bulb of the brain by means of a special nerve, the vomeronasal nerve (*nervus terminalis*); in some mammalian species there is an accessory lobe of the olfactory bulb to which this nerve connects. The path of the *nervus terminalis* is often lined with serous glands interspersed with epithelial cells. Recent research by Winans & Scalia (140) has demonstrated that in the rat (*Rattus norvegicus*) neural input from the vomeronasal organ proceeds to the accessory olfactory bulb and from there to the amygdaloid nucleus. Since the amygdaloid nucleus projects to the hypothalamus, the authors suggest that the vomeronasal organ has the potential for influencing sexual and feeding behavior.

The cavity of the Jacobson's organ itself is almost always filled with fluid, and there is an ampulla-like structure containing numerous blood vessels which apparently can engorge to momentarily increase the pressure within the organ, thus forcing out the fluid within the capsule. Diminishing the swelling can draw the fluid back into the cavity. These are often referred to

as "pumping bodies" [e.g., *Schwellkörper* (Weber 132)]. Hence, although enclosed, the organ has a mechanism for flushing itself out and for taking up from the mouth or nasal cavity fluids which may contain chemical substances in solution.

In contrast to Adrian's (1) earlier work performed with the rabbit (*Oryctolagus*), Tucker (127) found the vomeronasal epithelium to be as sensitive as the olfactory epithelium. Müller (91) was able to demonstrate that the sensory epithelium of the Jacobson's organ in the mouse (*Mus*) responded to chemical solutions. Hence, the physiological activity of the vomeronasal organ in the mouse and rabbit can no longer be doubted. However, more research on a variety of mammalian species is needed to establish the universality of this function.

The function of the vomeronasal organ in mammals has been the subject of recent studies. Poduschka & Firbas (101) describe the anatomical relationship of the vomeronasal organ to the mouth and nasal passages in *Erinaceus*, the hedgehog, and Verberne (131) discusses the possible relationship of the activity of the vomeronasal organ to the phenomenon of *Flehmen* in Felidae.

Classically, *Flehmen* was described as a definite facial expression shown by Perissodactyla, Artiodactyla, and some species of the Carnivora after scenting various olfactory stimuli, especially the urine of females (Schneider 110). In the ungulates, the external manifestation of *Flehmen* consists of lifting or curling the upper lip to expose the upper incisors (in the Perissodactyla and Tylopoda) or the cartilaginous plate (in the Cervidae and Bovidae). Later, Schneider noted a similar lip retraction phenomenon, involving a lateral lip movement, in cats.

For Schneider, the genesis of this facial expression was the most important problem. It is now recognized, however, that upon the perception of specific odors, animals show a much broader class of behavior patterns. This was well pointed out by Poduschka & Firbas (101). In essence, the general phenomenon consists of an animal (*a*) sniffing an odoriferous substance, (*b*) perhaps licking it, and then (*c*) lifting its head while either retracting the lip musculature or lifting the upper lips (in those forms where the lip is mobile). When the nose is proboscis-like (e.g., *Solenodon*), the nose may be lifted dorsad. But, equally important are the associated phenomena of relaxing the lower jaw, protruding or moving the tongue, licking the lips, salivating, and altering the breathing rate. Often, there is a cessation of breathing, followed by expulsion of the breath in short spurts. The nostrils of the animal may range from partial closure to dilation during the breath expulsion phase.

Knappe (66) suggested that the phenomenon of *Flehmen* was associated with stimulation or activation of Jacobson's organ. Poduschka & Firbas (101) actually demonstrated that, in *Erinaceus*, licking at a substance, lifting the nose, opening the mouth, and salivating did stimulate the Jacobson's organ since the tongue tip was actually pushed up to the dorsal opening of the naso-palatine canal in the buccal cavity. Thus, potentially odoriferous sub-

stances are transferred in solution to the vomeronasal organ by the naso-palatine canal. The associated activity of *Selbtsbespucken* (self-anointing), where excessive saliva is spread on the quills of the hedgehog's body, is now considered an activity derived from *Flehmen* and the stimulation of the Jacobson's organ (Poduschka & Firbas 101).

Activation of the Jacobson's organ may be a widespread phenomenon in mammals that possess a functional vomeronasal organ which connects either to the buccal cavity or to the nasal cavity. Tongue movements, excessive salivation, and changes in breathing apparently accompany the stimulation of this organ. The assumption of a lip-curling expression is peculiar to those species that possess a mobile upper lip, and it appears either to widen the canal leading to the vomeronasal organ (in phyllastomatid bats (Mann 81) or to aid in nostril closure, thus assisting the retention of air in the nasal cavity as it is slowly expelled (Dagg & Taub 34). Although Dagg and Taub deny that lip curling in giraffes is a mechanical aid in the stimulation of the Jacobson's organ, they do draw attention to one very important feature in *Flehmen* by artiodactylans. This involves the alteration in breathing and the temporary retention of air in the nasal cavity before successive expulsions. Dagg and Taub do not convincingly demonstrate, however, that *Flehmen* in artiodactylans is unrelated to the stimulation of the Jacobson's organ itself. They attempt to do so by attacking Knappe's (66) original hypothesis. Although Knappe was probably incorrect in the details of his mechanical interpretation, his general hypothesis may yet be valid. Surely much more anatomical and physiological, as well as behavioral, research is needed. The idea that the Jacobson's organ may be intimately involved in the perception of sexual pheromones was advanced by Whitten in an unpublished speech in 1963 (referred to in Bronson 11).

## THE SOURCE OF CHEMICAL SIGNALS

Given a receptor as sensitive to such a wide variety of inputs as is the olfactory epithelium, it is fair to say that the whole *corpus* of a presumptive mammalian sender can generate a bewildering variety of chemical signals. Despite this, it is possible to delineate specific by-products of metabolism which have a role in chemical communication.

The urine and feces of mammals are used as chemical signals. The body posture and movement patterns associated with defecation and urination have been reviewed by Altmann (2), together with information concerning associated behavior patterns, including scattering movements. In addition, she summarizes for each species relevant information concerning the localization of urination and defecation sites and the social significance of urination and defecation in a broad variety of contexts. Unfortunately, experimental evidence confirming the presumptive information content in urine and feces and many of the implied social relationships is lacking in all too many cases.

Glandular exudates are also involved in olfactory communication; Mykytowycz (97) has recently reviewed the role of glands in communication.

Glands associated with the eye (Quay 102) may secrete during social encounters [e.g., *Dinomys, Microgale, Setifer* (Collins & Eisenberg 33, Eisenberg & Gould 44)]. Glands associated with the buccal cavity (Quay 103) may be involved in marking behavior when the lips are rubbed on the substrate. The sex accessory glands, also involved in olfactory communication in many mammals, have been especially well studied in swine (Sink 116, Signoret 115). The various skin glands and their distribution and morphology were first systematically reviewed by Schaffer (108); the glands associated with mammals' anal region were the subject of a subsequent review (Ortmann 98).

In Table 1, olfactory communication in two unrelated mammalian species, the black-tailed deer, *Odocoileus hemionus* (Müller-Schwarze 93, and the marsupial sugar glider, *Petaurus breviceps* (Schultze-Westrum 112), is compared. Six specialized gland areas in the deer are involved in the transmission of information concerning sex, age, identity, and mood. The secretions may be generated in a gland and then spread by the sender on another part of its own body, or alternatively, the substances may be deposited on specific loci in the environment, such as branches of trees. The glandular secretions may diffuse from the body of the sender into the air and to a partner. In addition to the six glandular areas, excreted substances such as urine and feces are involved in the transfer of chemical information. A similar use of urine, feces, and several glands may be noted for the marsupial *Petaurus* (Schultze-Westrum 113), in which five glands have been identified, two of which function only in the male and one only in the female.

In several cases the exact functional significance of these substances has not been elucidated, and in only two instances has a mammalian secretion been isolated with respect to some of its active components (Müller-Schwarze 92; Brownlee, Silverstein, Müller-Schwarze & Singer 17; Michael, Keverne & Bonsall 85). In the first case, a gamma lactone was identified as one of the more active agents in the tarsal gland secretion in *Odocoileus hemionus*. In the second case, short-chain aliphatic acids were suggested to be the active components of the vaginal secretion of the rhesus monkey *(Macaca mulatta)*. Sink (116) has proposed that androgen derivatives (i.e., androstenols, which possess musky odors) may act as sex pheromones in the swine *(Sus scrofa)*, and he outlines some possible biosynthetic pathways by which an odoriferous androstenol could be produced from a blood-circulating steroid.

Table 2 lists glandular secretions involved during contact-promoting behavior between a male and a female prior to copulation among four species of tenrecs. Here, glandular secretions from five body areas are important in the coordination and potentiation of courtship and copulatory behavior. It should be stressed that these glandular secretions need not be deposited in the environment to function in a partner. In Part B of Table 2, the same four species are now considered with respect to the deposition of secretions from some of the same glandular areas, as well as the deposition of saliva, urine, and feces. Here it is seen that, although saliva, urine, and feces may provide

TABLE I. PRODUCTION OF OLFACTORY SIGNALS FOR AN EUTHERIAN AND A MARSUPIAL

| | Source of chemical substance | Mode of deposition or transfer | Implied function or context |
|---|---|---|---|
| *Odocoileus h. hemionus* (Müller-Schwarze 93) | Gland area | | |
| | Tarsal gland | Through the air or transferred to head by self marking | Sex and age identifier |
| | Metatarsal gland | Through the air or by contact with the ground | Discharges when frightened |
| | Pre-orbital gland | Gland is vestigial | ? |
| | Forehead "gland" | Rubbed on branches | Secondary marking of tarsal gland secretions |
| | Tail gland | Through the air | ? |
| | Interdigital gland | Deposited while walking | ? |
| | Excreted substances | | |
| | Urine | Deposited on ground or sprayed on tarsal gland | Specialized urination in thwarting context (i.e., "rub" urination) |
| | Feces | Deposited on ground | ? |
| *Petaurus breviceps papuanus* (Schultze-Westrum 113) | Gland area | | |
| | Sternal gland (♂ only) | Rubbed on partner or substrate | Community odor establishment |
| | Frontal gland (♂ only) | Rubbed on partner | Community odor establishment |
| | Uro-genital area | | |
| | Proctodeal gland | Substrate marking | Contributes to fecal scent |
| | Paraproctal gland | Through the air | Warning signal to predators |
| | Pouch gland (♀ only) | Through the air | Attracts newborn young |
| | Excreted substances | | |
| | Urine | Deposited at discrete loci | Contributes to community odor |
| | Saliva | On substrate or on body | ? |
| | Feces | Deposited at discrete loci | ? |

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TABLE 2. FORMS OF OLFACTORY COMMUNICATION IN THE TENRECIDAE[a]

Glandular areas involved in contact-promoting behaviors

| Gland area | Species |
| --- | --- |
| Axillary | H, M, S, E |
| Inguinal | H, M, S, E |
| Head gland | H |
| Ear glands | H, M, S, E |
| Cloacal glands | H, M, S, E |

Forms of deposition

| Type of substance | Locus of deposition | | | |
| --- | --- | --- | --- | --- |
| | Object | Substrate | Self-marking | Marking a partner |
| Eye secretions | H, M, S, E | — | — | — |
| Glands associated with the cloaca | H, M, S, E | H, M, S, E | — | H, M, S, E |
| Saliva | H, M, S, E | — | E | ? |
| Urine | — | H, M, S, E | — | ? |
| Feces | — | H, M, S, E | — | — |

[a] H = *Hemicentetes semispinosus;* S = *Setifer setosus;* M = *Microgale talazaci;*
E = *Echinops telfairi* (From Eisenberg & Gould 44).

information concerning the identity and sex of the depositor, they need not be involved in intimate contact behavior once two individuals have come together. This leads us then to a consideration of marking.

## THE DEPOSITION AND RELEASE OF CHEMICAL TRACES

The deposition of chemical substances must be, but has not always been, considered in five contexts: deposition on a specific object in the environment, deposition on the substrate without reference to a particular object, deposition on a social partner, deposition from one part of the sender's body to another part of its own body (self-marking), and finally, release of scent from the body surface into the surrounding air.

### OBJECT-MARKING

In object-marking some glandular area of an animal's body is actually rubbed over a specific locus or urine and feces are deposited at discrete loci in the environment. Object-directed marking movements are often quite complicated and may involve the assumption of rather unusual postures in order to deposit the scent at a reasonable height above the ground, presumably enhancing the "active space" of the point source of the scent (Wemmer 133). Figure 1 illustrates the probable evolutionary pathways of marking-postures in viverrid carnivores.
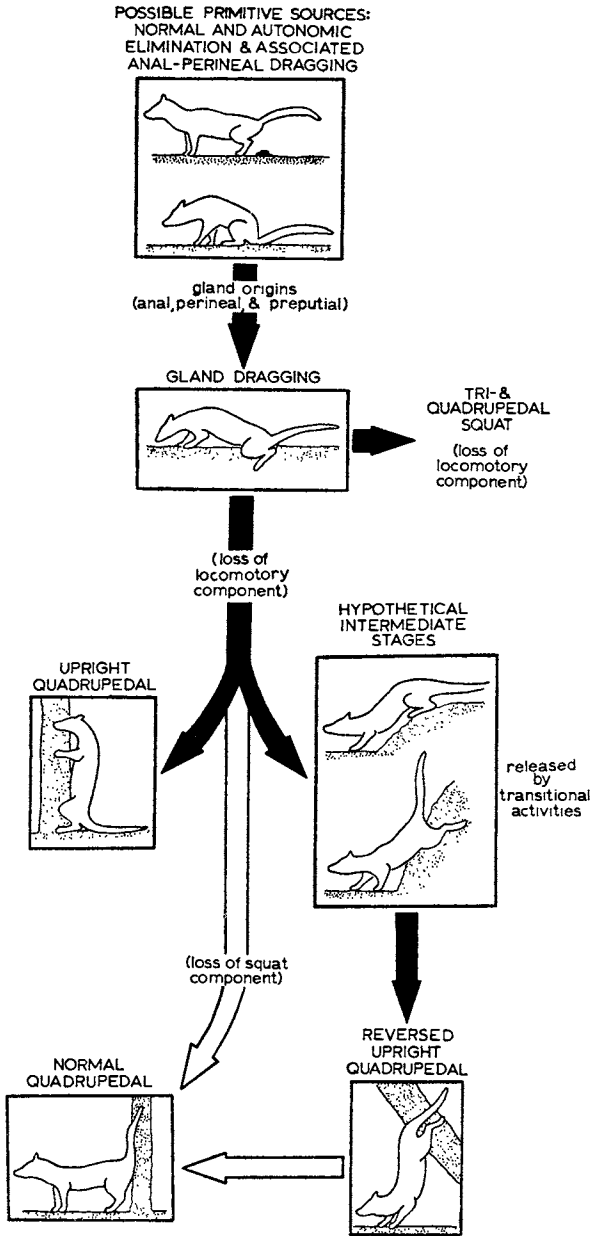
**FIGURE 1.** A derivational scheme of some stances employed by viverrid carnivores during scent-marking. Each arrow points to a specific stance exhibited by extant species and a hypothetical intermediate stage. Black arrows designate logical evolutionary pathways of stances in which glandular contact with the substrate is mediated by variations on the squatting theme. The white arrows designate two possible (but less logical) sources of the normal quadrupedal marking stance from a squatting stance (Wemmer 133).

Perhaps one of the better illustrations of marking phenomena in mammals is provided in the paper by Tschanz, Meyer-Holzapfel & Bachmann (126). In this paper the rubbing behavior of the European brown bear (*Ursus arctos*) is considered. Male bears will rise on their hind legs while rubbing their backs and neck regions on specific loci, such as tree trunks, or they may assume a frontal position to rub their chests while biting and clawing at the bark. Such rubbing behavior by males reaches a minimum in the fall and a maximum in May just prior to the breeding-season. Individual males have preferred marking loci, some of which are used only by a single male, while others are used in common by several males. Females have spots separate from those of the males, but they may also use the communal loci used by the males. Each individual animal has in its living space a fixed marking pattern with set points which are used in a routine fashion. Young bears avoid the loci marked by a foreign adult male. Males can distinguish the sex of the marker.

In addition to rubbing posts, bears also communicate with each other by scenting urine and feces. Fecal scents are apparently not very important, but the male can distinguish the scent of female urine from that of male urine. Similar marking behavior patterns can be discerned for other mammals (Kleiman 62); we have used the example of the bear only because it is a rather complete study. The functional significance of such marking patterns will be deferred until a later section.

It should be mentioned that some activities of mammals are related to marking behavior but do not necessarily involve deposition of scents from their own bodies; rather they render an area of the environment conspicuous through disturbance and release of odor. Scratching up the earth, although it may involve the deposition of pedal gland scent, can also attract an animal's attention through the smell of the fresh earth itself (e.g., scratching behavior by the Felidae after scent-marking). Breaking branches or scarring the bark of trees with tusks, horns, or claws can also attract a social partner's attention by the sap flow from the tree rather than from any odor trace left by the tusks, horns, or claws of the marker (Eisenberg & Lockhart 45).

The visual conspicuousness of the scent-marking postures of some species, as well as the conspicuousness of the scented area itself, suggests that orientation to certain chemical traces may be based on vision as well as olfaction. The former may act particularly in species living in social groups (e.g., leg-lifting in wolves), while the latter may be important in more solitary mammals. The relative importance of visual stimuli and olfactory stimuli in orienting an animal to an odor site has not been investigated.

## MARKING A SOCIAL PARTNER

This behavior is widespread within the Mammalia and may involve simply crawling over a partner while dragging the ano-genital region and/or urinating on the partner's body, as in *Rattus* (Steiniger 120). Specialized mark-

ing movements may, however, be involved. For example, in *Petaurus* (as described by Schultze-Westrum 112), the frontal gland of the male may be actively rubbed on the body or in the sternal gland area of the female.

## SELF-MARKING AND RELATED PHENOMENA

It is well-known that some species of mammals may respond to an odor source by spreading the scent upon various parts of their bodies. This has been well described in the necksliding response of *Civettictis* by Wemmer (133). Another form of self-marking includes transferring urine or secretions from one part of the animal's body to another part, such as the black-tailed deer reaching forward with its hind leg and smearing tarsal gland secretions upon its own head (Müller-Schwarze 93).

Yet another pattern of self-marking involves the self-anointing (*Selbtsbespucken*) reaction of the hedgehog (*Erinaceus*). In this behavior pattern, an odoriferous substance is contacted and licked. Excessive saliva is produced and impregnated in part with the odor of the licked substance; this saliva is then spread alternately on the sides of the animal's body by tongue movements. A similar self-anointing behavior has been noted in the spiny tenrec, *Echinops telfairi;* the animal wipes its forepaw in the saliva and then spreads the saliva on alternate sides of its body (Eisenberg & Gould 44). The functional significance of such self-marking movements will be considered later.

## SUBSTRATE-MARKING AND PELAGE-DRESSING

Sand-bathing as a means of dressing pelage is a widespread behavior pattern, especially among desert dwelling mammals (Eisenberg 43). Sand-bathing typically involves digging in the substrate, followed by a species-specific series of rubbing movements, often including both side and ventral rubs. While sand-bathing, the animal leaves behind on the substrate traces from various diffuse and localized glands. Occasionally the sand-bather may urinate on the bathing spot and subsequently impregnate his fur with urine. Sand-bathing, then, defies simple classification, since it is at the same time a pelage-dressing activity and a marking movement. As a marking movement, sand-bathing may have elements of both substrate-marking and self-marking. Furthermore, since sand-bathing may involve multiple use of a single locus by several individuals, it may result in the reciprocal exchange of glandular secretions (Eisenberg 43).

## RELEASE OF SCENT INTO THE AIR

Because we are so used to observing a specific behavior pattern associated with the deposition of chemical traces or observing the result of that chemical release (e.g., as a visible scent mark, urine, or feces), we tend to disregard mammals' ability to release scent without there being any visible sign of it. Indeed, this is the case in many species which produce specific odors when frightened [e.g., the black-tailed deer metatarsal scent (Müller-Schwarze

93)]. This type of scent release has been ignored, and more research is needed in this area.

## THE FUNCTION OF OLFACTORY SIGNALS

In discussing the functions of olfactory stimuli and their effects on the receiving organism, we must distinguish between the amount of information potentially inherent in a signal and the information actually perceived; perhaps a visible response is given to only a fraction of the total assimilated content. These conceptual distinctions are important because a given chemical stimulus may contain more bits of information than can be perceived or will be responded to at any one time. The perception of the response to a chemical substance will depend upon the condition of the organism when the stimulus is received—i.e., its age, sex, reproductive state, and mood. For example, it is well known that the ability of women to perceive the odor of exaltolide varies with the menstrual cycle, the greatest sensitivity to the odor being at ovulation; men typically cannot perceive it (LeMagnen 70).

In this and the following section, we will review the types of information known to be transmitted in chemical signals and the effects of these signals on the organism.

### INFORMATION TRANSMITTED IN CHEMICAL SIGNALS

*Species and racial identity.*—The early work of Godfrey (53) demonstrated quite clearly not only that bank voles (*Clethrionomys*) could distinguish between the odors of their own and another subspecies but also that the males of each subspecific group preferred the odors of closely related females; thus olfactory cues could act as reproductive isolating mechanisms. Later work by Moore (86) on two species of *Peromyscus* (*P. maniculatus* and *P. polionotus*) indicated that *P. maniculatus*, which lives in sympatry with other species of the same genus, prefers the odor of a conspecific to that of *P. polionotus*, while *P. polionotus* individuals (which are geographically isolated) show no preferences. Another study (Bowers & Alexander 10) on *Mus musculus* showed that house mice, using only olfactory cues, can discriminate between conspecifics and another rodent species (of *Peromyscus*). Recently Dagg & Windsor (35) demonstrated that gerbils (*Meriones unguiculatus*) can distinguish the odors of conspecifics from those of four other species of small rodents.

The ability of *Mus* to distinguish between their own and a different mouse strain was also demonstrated by the pregnancy block or Bruce effect. Parkes & Bruce (99) and Dominic (37) showed that the pregnancy of a recently inseminated female mouse can be blocked if the female is exposed to the odor of a male of another strain. In this work it was clearly shown that no visual, auditory, or tactile contact with the strange male was necessary for the block to be effective; the scent of the male's urine or shavings from his living quarters were sufficient. Although the Bruce effect is operative in other myomorph genera [*Microtus* (Clulow & Clarke 32), *Peromyscus* (Bronson &

Eleftheriou 13, Terman 123)], it has not been shown conclusively that olfactory stimuli alone produce the effect. However, it is likely that both *Microtus* and *Peromyscus*, like *Mus* and *Clethrionomys*, can differentiate between conspecifics of different strains or even populations on the basis of odor.

The existence of a group or community odor in social mammals has also been demonstrated. Both the common marmoset (*Callithrix jacchus*) (Epple 47) and the sugar glider (*Petaurus breviceps*) (Schultze-Westrum 112) can discriminate group members from outsiders on the basis of odor. Young sugar gliders assume a defensive posture when presented with a known animal covered, in succession, with the frontal, sternal, and ano-genital gland secretions of a stranger; thus, all three glandular regions produce a community-specific odor.

Species-specific and strain odors, as well as community odors, probably arise from several sources. First, the active components of scent gland secretion or urine and feces may differ due to genetically controlled metabolic variations for a species, strain, or population. There might be differences, not only in the chemical composition of secretions and excretions, but also in the ratios of the active components within a substance. Either way, different odors would be produced by the different species, strains or populations. Second, variations may result from environmental factors; populations in slightly different habitats are likely to vary in their diet. Thus, differences in waste products (i.e., urine and feces) are to be expected.

Finally, individual genetic differences in the production of chemical substances can add to community odors in social species; frequent body contact between individuals, through sleeping and resting in a cluster, transfers and mixes the individual odors of group members, thus creating a homogeneous odor. Moreover, there are specific behavior patterns for transferring chemical secretions and urine to conspecifics. In rabbits, *Oryctolagus cuniculus*, and *Petaurus* the dominant male marks group members with glandular secretions (Lyne, Molyneux, Mykytowycz & Parakkal 75, Mykytowycz 96, Schultze-Westrum 113). In lagomorphs and caviomorph rodents (Kleiman 64), males often urinate on conspecifics, especially females, during social encounters. With one individual marking all the others, some homogeneity of odor may be produced.

*Sexual identity and the identification of reproductive state.*—Bowers & Alexander (10), using a discrimination test, have shown that the mouse can identify the sex of a conspecific by odor, and Dagg & Windsor (35) have found the same ability in the gerbil. It has also been demonstrated that duikers (*Cephalophus maxwellii*), black-tailed deer (*Odocoileus hemionus*), the collared peccary (*Dicotyles tajacu*), and the brown bear (*Ursus arctos*) respond differently to the odors from glandular secretions depending upon whether the secretion is from the same or the other sex (Ralls 105, Müller-Schwarze 93, Sowls 118, and Tschanz, Meyer-Holzapfel, & Bachmann 126). Other studies have mainly concentrated on the discrimination and prefer-

ences of males and females for the odor of other males and females in different reproductive states. The earliest studies were by LeMagnen (69) and Beach & Gilmore (6), who demonstrated, respectively, that male rats and male dogs can distinguish and prefer the odor of an estrous female to that of an unreceptive female.

Recent studies on macaques [*Macaca mulatta* (Michael & Keverne 84; Michael, Keverne & Bonsall 85), *Macaca radiata* (Rahaman & Parthasarathy 104)] indicate that olfactory signals rather than acoustical or visual ones are of major importance for the male in discriminating between estrous and anestrous females. Michael & Keverne (84) showed an increase in the level of copulatory activity in normal male rhesus when paired with ovariectomized females who had had extracts of vaginal secretions from an estrogen-treated female administered to the vagina. They also showed a decline in copulatory behavior when males were rendered anosmic (Michael & Keverne 84). Rahaman & Parthasarathy (104) observed an increase in auto-erotic behavior and general arousal of bonnet males who were allowed to smell females during several estrous cycles, but were in visual, acoustic, and tactile isolation from them.

The experiential and hormonal factors influencing the development of the discrimination of and preferences for the homo- and heterotypical sex odor have also been studied, especially by Carr and co-workers. Carr's earlier work demonstrated convincingly (Carr & Caul 23) that both intact and ovariectomized females could discriminate intact from castrated males, and conversely, intact and castrated males could discriminate diestrous from estrous females. Thus, the presence or absence of gonads did not influence the ability to discriminate between a reproductively active or inactive member of the opposite sex.

In later papers by Carr and other workers (Carr, Loeb & Dissinger 25; Carr, Loeb & Wylie 26; Wylie 142; Carr, Wylie & Loeb 28; Stern 121), olfactory preference tests were used instead of discrimination tests. In this work, the sex, experience, hormonal condition, and age of the subjects were varied, as were the test odors. Schultz & Tapp (111), in a recent review of the research on odor preferences among rodents, have found that using one subject and two odorant animals makes possible 80 nonredundant test combinations. Less than half of the possible combinations have been tested. Of the 34 combinations that have been tested, preferences were found in 13; but where two investigators have tested the same combination, there have often been differences in the results. Despite the discrepancies, these studies suggest that males show demonstrable preferences more often than do females and that both sexual experience and hormonal condition contribute to the preferences shown. Thus, in several mammalian species, it has been established that individuals can distinguish between both the sex and the reproductive state of the partner via olfactory signals alone, that there are preferences for odors of both the homo- and the heterotypical sex, and that these preferences alter

with the age and reproductive state of the receiver.

The discrimination of sex is probably based on several factors. In some mammals, scent glands are better developed in males than females [the rabbit (Mykytowycz 96); the ring-tailed lemur, *Lemur catta* (Evans & Goy 48); the hamster, *Mesocricetus auratus* (Lipkow 74)]. Thus, discrimination can be based upon the presence or absence of a particular secretion or differences in the concentration of the secretion. For the discrimination of reproductive state, a similar mechanism might be operating, since glandular activity may vary seasonally (see Mykytowycz 97); in both cases, the production of the scent will be under hormonal control. There may also be genetically based differences between the chemical compositions of the secretions of males and females.

The discrimination of reproductive state, however, may also be dependent on the differential excretion of just those steroids which are affecting the reproductive system, thus producing variations in the odor of waste products, especially urine. It is known that several androgen metabolites have a quite musky odor (Sink 116). Variations in the concentrations and combinations of excreted steroids can arise from two sources: (*a*) a change in the metabolism of the steroids so that there is a differential excretion of the metabolites during separate phases of the reproductive cycle, and (*b*) a change in the production of actual steroid types during the reproductive cycle (e.g., the variation in progesterone and estrogen levels during the estrous cycle is well documented).

Another source of odor which may be used to detect reproductive state, especially in females, arises from uterine and vaginal secretions. Recently, Michael, Keverne & Bonsall (85) isolated and identified some of the active substances found in the female rhesus monkey's vaginal secretions which are attractive to males.

*Discrimination of individuals.*—The demonstration that mammals can discriminate between individuals, using solely the olfactory sense, was first seen in the work of Bowers & Alexander (10) on mice. Carr, Krames & Costanzo (24), although interested in the odor preferences of sexually satiated and unsatiated male rats, also indicated that males could distinguish between two receptive females, with one of which they had already mated. Recently Dagg & Windsor (35) have shown that gerbils can discriminate between the urine odors of two individuals of the same sex even if the urine is diluted 1000 times.

*Discrimination of age.*—It is evident that most mammals can distinguish between the smell of prepubertal and mature individuals, since the functioning of many scent glands and the associated scent-marking behaviors are known to be hormone dependent. Mykytowycz (97), for example, has found that the odor from the chin gland of the rabbit gets stronger as the animal

ages. In male dogs and cats, the adult patterns of urinating (i.e., leg-lifting and spraying backward) do not develop until the animal is sexually mature. If the differences in odor between sexually mature and juvenile animals are based on the multiple effects of circulating hormones, then one cannot, in fact, consider this more than the discrimination of relative age. There is as yet no evidence that mammals can distinguish between other adults on the basis of absolute age rather than with respect to either reproductive state or individual characteristics.

*Identification of mood.*—There is evidence now indicating that mammals can identify the mood and social status of a conspecific solely on the basis of odor. Both mice and rats have been shown to be capable of recognizing an odor of stress or fear (*Angstgeruch*) in conspecifics. This ability is not based upon individual recognition (Valenta & Rigby 128, Müller-Velten 94, Sprott 119). In the mouse, Müller-Velten (94) found that this odor (which arose from the urine) remained potent for 7 to 8 hours (it induced an avoidance response), but was no longer active after 24 hours. Müller-Schwarze (93) has hypothesized that the odor of the metatarsal gland in black-tailed deer is indicative of alarm since it is released in fear-inducing circumstances (e.g., when the deer encounters a dog). Moreover, deer show reduced frequency of licking the caretaker's hand and feeding when the scent from another deer's metatarsal gland is first presented to them.

In the mouse studies, the donor odor arose from animals frightened in nonsocial conditions (e.g., from electric shock), but there are also data demonstrating that when "fear" is induced through agonistic encounters, the mice also produce odors which conspecifics can identify (Carr, Martorano & Krames 27).

In rats living in stable dominance hierarchies (thus, in conditions where a sudden alarm reaction is not produced), more time is spent sniffing the odor of an unknown submissive male than that of a dominant male in a preference test (Krames, Carr & Bergman 67). Thus rats can discriminate between the odor of a submissive animal and that of a dominant one even when the individuals producing the odors have not been recently involved in an agonistic encounter.

The release of scent during stress situations is well documented in the Mammalia, the classic and most specialized response being that of skunks (*Mephitis mephitis*) in the secretion of scent from the anal glands while in a hand-stand posture. Other mammals produce strong odors from scent glands when under stress—e.g., the house shrew, *Suncus murinus* (Dryden and Conaway 41) and the black-tailed deer, *Odocoileus hemionus* (Müller-Schwarze 93). Moreover, urine and feces are often excreted in fear-inducing conditions as an autonomic response, but in some species the response has come under greater voluntary control. Chinchillas (*Chinchilla laniger*) and guinea pigs (*Cavia porcellus*) squirt urine at human handlers when disturbed (see Kleiman 64 for a review). This specialized release of odor when frightened may

not only act as a warning signal to neighboring conspecifics but also may act as an antipredator mechanism (e.g., in the skunk).

### PHYSIOLOGICAL AND BEHAVIORAL EFFECTS OF ODORS

Olfactory stimuli have classically been put into two categories. Some substances act as *releasers* in that they will immediately elicit a very specific response. Among mammals, however, there are few odors which seem to act in this fashion. The second type of substance has traditionally been referred to as a *primer* since its effect is delayed or not behaviorally visible. Most studies of primers have dealt with reproductive processes (e.g., the Bruce, Whitten and Lee-Boot effects, to be discussed below). However, the behavior of an individual can also be affected by primers since all odors which identify the species, race, sex, and mood of an organism more or less set the stage for an encounter by allowing the receiver to prepare itself for a specific type of interaction. For example, Müller-Schwarze (93) refers to a 7-month old black-tailed doe which immediately went to a female fawn when presented with a male deer whose hocks had been covered with the tarsal gland secretion of a female fawn. Recognition of the age and sex of the scent caused this female to move toward an animal which best fit the odor perceived.

Within the category of primers, we must also recognize a wide class of substances which will simply arouse the individual and prepare him for a change in the environment. For example, the presentation of foreign odors often produces an increased activity level in captive mammals, probably by virtue of the odor's novelty. Although these substances are not involved in communication, a similar mechanism may be operating with respect to conspecific odors, since nonspecific arousal may result from the perception of certain olfactory stimuli arising from conspecifics, because of their novelty to the receiver.

Along these same lines, we must also stress that the same substance can have both priming and releasing effects. A chemical substance which causes the release of a specific behavior pattern is also likely to be acting on the reproductive state, mood, or general level of arousal of the receiver, thus having both long- and short-term behavioral consequences. Because of the probable multiple effects of some olfactory stimuli, we will divide the following discussion into functional categories.

### REPRODUCTION

*Reproductive function.*—One of the first studies indicating that odors had a significant effect on reproductive processes was that of Bruce (18); it was demonstrated that the introduction of a strange male to a recently inseminated female mouse inhibited the successful completion of pregnancy by blocking implantation. Later it was found that this effect was mediated solely through odor (Parkes & Bruce 99, Dominic 37) and that prepubertal castration of the introduced male (Bruce 19) or rendering the female anosmic (Bruce and Parrott 21) prevented the pregnancy block.

It is thought that these olfactory stimuli eventually affect the hypothalamus; the release of pituitary prolactin is prevented, and the release of FSH and LH is stimulated, thus inducing the recurrence of a normal estrous cycle (see Bronson 11). It has recently been shown that LH is released from the pituitary of recently inseminated female mice after exposure to alien males (Chapman, DesJardins & Whitten 30). Exogenous prolactin (Bruce & Parkes 20, Dominic 40), an ectopic pituitary graft (Dominic 39), or exogenous progesterone (Dominic 38) administered during the post-coital period prevents the pregnancy block effect.

The adrenals have also been implicated and may be one route through which the hypothalamus is affected. Environmental conditions in which pregnancy block ordinarily occurs (i.e., in high density populations) are also those conditions in which adrenal size and functioning is affected (Christian 31). The pregnancy block has also been found in the deermouse, *Peromyscus maniculatus* (Bronson & Eleftheriou 13) and *Microtus agrestis* (Clulow & Clarke 32), but it has not as yet been conclusively demonstrated for other mammals.

A second priming effect of olfactory stimuli is seen in the Lee-Boot and Whitten effects (see Whitten 134, Whitten & Bronson 135). Female mice (*Mus*) or deermice (*Peromyscus*) caged together show irregular estrous cycling and often exhibit pseudo-pregnancy, but the presence of a male, the urine of a male, or the smell of an adult male (Whitten, Bronson & Greenstein 136, Bronson & Dezell 12, Bronson & Marsden 14) rapidly brings the females into estrus and synchronizes their cycles. The presence of a male has been found to be important in the induction of estrus in several other species—e.g., the green acouchi, *Myoprocta pratti* (Kleiman, personal observation); the wild guinea pig, *Galea musteloides* (Rood & Weir 106); and sheep and goats (see Whitten & Bronson 135)—but whether estrus induction is accomplished solely through olfactory stimulation in these species is not known. Recently a third, but not surprising, effect of male urine odor or the presence of a male on reproduction has been demonstrated (Vandenbergh 129, 130). When housed with adult males or exposed to their odor, female mice reach puberty earlier. Terman (122) has demonstrated that maturation is advanced and reproduction enhanced in pairs of deermice, *Peromyscus maniculatis bairdii*, reared on shavings from populations which have themselves reached such high densities that reproduction is inhibited. Deermice reared on shavings from bisexual pairs or on clean shavings do not show this early maturation. Thus, the pheromone or pheromones which inhibit pregnancy in high-density conditions enhance reproduction within a given pair. The occurrence of early maturation has also been demonstrated in female swine (Brooks & Cole 15), but it has not been shown that this effect is mediated solely through smell.

It is possible that the reproductive-priming pheromones which inhibit pregnancy, induce estrus, and advance puberty in mice could be the same substance present in the urine of all adult males. Presumably the effects on

the female will be dependent upon her reproductive condition at the time the olfactory stimulus is perceived as well as upon her early olfactory experience (see below).

*Sexual behavior.*—It has long been recognized that the odor of a female during estrus is one of the prime stimuli indicating her condition to the male (see Hafez 54 for a summary concerning domestic mammals). The greater time spent sniffing odors of estrous over anestrous females in dogs (Beach and Gilmore 6) and rats (LeMagnen 69) indicates not only the ability to discriminate between the odors but also a preference for estrous female odor over all other scents. Moreover, one of the basic interactional patterns during the precopulatory period involves sniffing the glandular regions by both partners, especially the ano-genital region.

To act as a releaser of sexual behavior, an odor not only must be perceived and preferred, but its absence must lead to a significant decrease in or to the elimination of sexual behavior. Such an importance of olfactory stimuli for mating has been shown only for the golden hamster, *Mesocricetus auratus* (Murphy & Schneider 95), and the rhesus monkey, *Macaca mulatta* (Michael & Keverne 84, 85); whereas it has not been shown to eliminate mating behavior in the dog (Hart & Haugen 56); the rat, *Rattus norvegicus* (Heimer & Larsson 58, Larsson 68); or the ram (Lindsay 72, Lindsay & Fletcher 73). In species where anosmia does not completely eliminate mating behavior in the male, some deficits (e.g., rat and ram) have been observed.

The importance of olfactory stimulation for the mating behavior of the female has not been examined in detail since the tactile input from the male during mounting and palpation is thought to be extremely important in inducing lordosis. However, studies of estrous female swine (Hafez & Signoret 55, Signoret 115) indicate that the presence of boar odor is very important in eliciting the "mating stance" from females who are touched lightly on the back by a human handler. Only 48% of estrous sows assume the mating stance in isolation from any type of male stimulation; this number increases to 81% if the females are exposed to boar odor. The preputial glands have been implicated in boar sex odor (Dutt, Simpson, Christian & Barnhart 42).

*Maternal behavior.*—As with sexual behavior, it has been generally accepted since the work of Beach & Jaynes (7) that maternal behavior is under multisensory control. Visual, auditory, tactile, and olfactory cues from the young are necessary to induce and maintain the appropriate maternal responses. Most recent work has supported this assumption [sheep (Lindsay & Fletcher 73), goats (Klopfer (65)], but two recent studies on mice, *Mus* (Gandelman, Zarrow, Denenberg & Myers 51), and rats, *Rattus* (Fleming 50), have demonstrated that the loss of the olfactory sense can completely eliminate maternal responses, resulting in the young being either cannibalized or ignored.

## SOCIAL BEHAVIOR

*Withdrawal and submission.*—It has already been mentioned that mice (*Mus*) exposed to the odor of conspecifics frightened in nonsocial conditions show an avoidance response (Müller-Velten 94) and that black-tailed deer exposed to metatarsal scent exhibit inhibited activity (Müller-Schwarze 93). For odors released during social interactions, only discrimination and preference tests have been staged to assess the effects. However, it is revealing to review the work of Carr, Martorano, & Krames (27) on the odor preferences of mice (*Mus*) exposed to pairs of odors drawn from three classes of test subjects: (*a*) conspecifics stressed in social interactions (i.e., defeated in a fight), (*b*) nonstressed conspecifics (i.e., victorious or isolated animals), and (*c*) mice stressed in nonsocial situations. One must assume in these experiments that a preference for one odor may also indicate an avoidance of a second odor. With this assumption in mind, it was found that in all but one of the experiments in which one test odor was from a mouse which had either been defeated in an encounter or shocked, the experimental animal preferred the second odor, and this was true for both dominant and the subordinate test mice. The only experiment in which the odor of a victim or a stressed mouse was preferred was when a defeated mouse was exposed to the odor of that particular conspecific which had defeated him. These results suggest that the odor of a defeated or shocked mouse almost inevitably produced avoidance (i.e., a preference for another odor). Thus, the *Angstgeruch* may also be produced during social encounters by defeated animals and thereafter result in avoidance by conspecifics. It should be mentioned that the results of a similar experiment on rats (*Rattus*) in Carr's laboratory (Krames, Carr & Bergman 67) were the reverse of that found with mice, since the rats spent more time sniffing the odor of an unknown defeated male than an unknown dominant. There is no evidence than an *Angstgeruch* (which produces avoidance in mice) is produced in rats, although rats can identify the odor of a conspecific stressed in a nonsocial situation (Valenta & Rigby 128). Of course, it is extremely difficult to experimentally distinguish among attraction to, avoidance of, or indifference to one or both odors or any combination of these, when the measure is only the amount of time spent sniffing two odors; however, the results of Carr's experiments are certainly suggestive.

*Aggression and dominance.*—There are few documented cases of mammals responding to the odor of an absent conspecific by exhibiting aggressive behavior in the absence of a conspecific. Brush-tailed possums (*Trichosurus vulpecula*) exhibit threat displays when sniffing only the anal gland secretion of another adult male (Thomson & Pears 125), and flying phalangers show increased aggression towards males in neighboring cages when presented only with the odor of a strange adult male (Schultze-Westrum 112). In other species, a change in aggressive behavior has mainly been shown during paired

encounters or in groups. The species used most often has been the mouse (*Mus*).

One of the earliest investigations (Mackintosh & Grant 76) demonstrated an increase in the frequency of agonistic interactions in familiar pairs of male mice (*Mus*) when one member was removed and his ano-genital region covered with the ano-genital secretions of a strange male. Conversely, there were fewer agonistic interactions when two strange males were introduced if one was first rubbed against a conspecific familiar to the second, rather than if they were introduced after the first was rubbed with moistened cotton as a control. Dixon & Mackintosh (36) demonstrated a reduction in aggressive behavior in pairs of mice if one was rubbed with the urine of a female before the introduction. Increases in aggression have also been found by Archer (4) in established groups of mice exposed to strange male odor. Mugford & Nowell (90) showed that when castrated male mice were covered with the urine of aggressive, submissive, and castrated mice, there were successively fewer agonistic responses after the introduction to a strange male. Using another technique, Ropartz (107) obliterated agonistic behavior by removal of the olfactory bulbs and significantly reduced it by scenting both mice of a pair with a strong perfume.

Thus it would appear that adult male mice produce a substance, probably in their urine, which increases the tendency to fight when paired for the first time. Whether this pheromone is identical to that producing the reproductive effects already described is not known since the active substances have not been isolated. However, it seems unnecessary to postulate separate substances; only a sexually differentiated response to the odor needs to be present.

Until now, we have mainly considered the effects of an alien conspecific odor. We must, however, consider the effects of personal odor on aggression and dominance. For most mammals the odor most typically encountered is one's own or that of a familiar conspecific; the odors arise from secretions emanating from the body surface and those scent marks (in the form of glandular secretions, feces, and urine) that are encountered during routine movements in the home range. It has been suggested that these odors "reassure" the individual (Ewer 49), since they maintain a certain level of confidence in an animal as it traverses its territory. This increased confidence when in the presence of personal odor partially explains the common observation that animals on their home territory win fights more often than they lose.

*Scent-marking.*—The perception of a strong odor and the production and deposition of scent are closely correlated in practically every mammalian species in which olfaction is one of the dominant sensory systems. The olfactory stimulus which releases a bout of scent-marking can be any strange foreign odor; thus, exploration of a new environment is often coupled with an increase in the frequency of scent-marking.

The organism's own personal odor or that from a strange or familiar conspecific also may release scent-marking behavior. Marking in response to personal odor occurs regularly and probably at a definable frequency which varies little. For example, in the slow loris, *Nycticebus coucang* (Seitz 114), the frequency of urine-marking is directly related to the normal activity pattern; during periods of intense activity there is a higher frequency of marking. These marks aid in orienting the individual in its environment.

In both males and females of many species, the odor of a foreign or familiar conspecific increases the frequency of scent-marking. Adult males especially mark in response to the odor of other adult males (see Ralls 105).

*Arousal.*—A number of immediate and long-term effects of olfactory stimuli relating to several different categories of behavior have been described. One effect of odor cannot be dealt with in this framework, and that is the general arousal effect which may result from the perception of certain odors. It is probable that in communication, some species-specific odors may act solely to arouse the recipient; of course, those odors which contain information about species, sex, mood, etc, will also have arousal properties. Increased arousal can be expressed in a number of ways through scent-marking, aggression, grooming, etc. Unfortunately, few researchers have attempted to determine whether all behavior patterns increase in frequency as a response to odors, or just the one they were studying.

*Development of odor preferences.*—The development of species recognition and species or subspecific odor preferences has been investigated in some detail; it has recently been referred to as *olfactory imprinting* (Carter & Marr 29). The earliest work on the development of olfactory preferences was described in a series of papers by Mainardi (77, 78) and Mainardi, Marsan & Pasquali (79, 80); it was followed by Kennedy & Brown (60). In these studies it was shown that young female mice (*Mus*) reared with both male and female parents eventually prefer to mate with males of a different strain, thus rejecting the odor of the male with which they were reared. However, in the absence of a male parent, the female will mate with males of her own strain. In further studies it was shown that young females whose odor was artificially altered by administering perfume to the littermates during the preweaning stage exhibited preferences for mice carrying that same odor when they reached maturity. The phenomenon was not found in males, since adult males reared in a perfumed environment showed no preferences for either normal or perfumed females as adults. Since Mainardi's work, similar effects have been found in rats, *Rattus* (Marr & Gardner 82, Marr & Lilliston 83), and guinea pigs (Carter & Marr 29). In these studies the subjects were reared under either normal or artificial odor conditions and then tested for a preference. The rat and guinea pig work also examined, in part, later odor preferences as a function of the age of initial exposure to an artificial odor, the duration of that exposure, the length of time since the last exposure at test-

ing, and the type of odor used. It was found that the age of exposure (rat and guinea pig) and duration of exposure (guinea pig) affected later preferences. Not surprisingly an early, long exposure produced the greatest effects at adulthood. However, in the guinea pigs the presence of the artificial odor during rearing did not create a permanent change in preferences, since all animals, whatever their early experience, eventually preferred the odor of normal individuals. It was also of some interest that the guinea pigs showed a natural preference for one of the two artificial odors used; i.e., they preferred ethylbenzoate to acetophenone (Carter & Marr 29).

The development of odor preferences normally begins with the mother-offspring bond. For the parturient female, the initial similarity between the odor of the neonate and the odor of her own birth fluids may make the neonates attractive (Klopfer 65). Later, contact with the young during nursing and frequent grooming by the mother which transfers the mother's saliva onto the young may maintain the similarity in odor between mother and young. In several species, the lactating female is known to exhibit increased secretory activity in some glandular regions [e.g., the muzzle gland in the serotine bat, *Eptesicus serotinus* (Kleiman 63), and pouch glands in *Petaurus* (Schultze-Westrum 113)]. The preference of the young for the odor of the mother (from which sexual selection can arise) undoubtedly results from a conditioning process whereby the mother's (and littermates') odors are initially associated with warmth, food and security, and later are preferred because they are most familiar.

## SUMMARY

Having reviewed both the information transmitted by chemical traces and the effects of these on behavior and physiology, we should now return to some of the more classical hypotheses concerning the function of marking behavior and scent marks themselves.

From extensive observations in zoological gardens and in the wild in Africa, Hediger (57) hypothesized that depositing excretory products or glandular secretions in specific loci was strongly associated with the possession of a territory; the implicit assumption was that such marking behaviors were involved with territorial defense. That this may be the case for many species of mammals is not to be doubted; transient individuals may withdraw from areas which are heavily impregnated with the odor of a conspecific. On the other hand, there is little information in the literature to indicate that conspecifics avoid the marked spots of their neighbors. This is especially true for those species which show broad overlap in adjacent home ranges. If anything, the marked spot is a locus at which any individual within a given community can deposit scent (Eisenberg & Lockhart 45). The frequency with which an animal will cover the scent of a conspecific with his own scent attests to this. Marking behavior need not necessarily be the prerogative of territory holders nor need it be shown only in a territorial context. As Schenkel (109) points out, and Goddard (52) corroborates, in species that show spacing—such as

the black rhinoceros (*Diceros bicornis*)—with no active defense of space toward known neighbors, spacing with respect to transients may be promoted through marking, but classical, territorial defense need not be shown. Moreover, the extensive marking behavior shown by female mammals before and during estrus is obviously not territory related, nor is the scent release commonly observed in frightened individuals.

The release and deposition of scent serves many functions. It permits the exchange of chemical information among animals that live with overlapping home ranges but tend to move and forage alone. It gives information with respect to age, sex, and reproductive condition, and a receiver's response to a scent mark depends in part on the location and mood of the receiver and the qualitative properties of the mark itself. Ewer (49), in her extensive review of scent marking, distinguishes between an individual perceiving its own scent mark and the perception of a foreign mark. In her tabulation she does not, however, consider responses to different kinds of foreign marks (familiar or unfamiliar conspecific, sex, age, etc) or the physical position or psychological security of the receiver. A potential receiver moving through the social space of another individual already exhibits decreased confidence and increased readiness to flee before it perceives the mark of the resident. Schulze-Westrum (113) clearly indicates in his study of *Petaurus* that not only the type of mark perceived but the mood of the receiver very much determines the reaction tendency. Hence, clear-cut demonstrations of avoidance behavior upon reception of a conspecific's scent are scarce in the literature; there is a multiplicity of variables that must be isolated before a definite response pattern can be shown.

Thus, we must divorce ourselves from considering scent marks as a means of territorial defense; rather, we should think of scent as a means of exchanging information, orienting the movements of individuals, and integrating social and reproductive behavior.

## THE MOTIVATIONAL BASIS FOR SCENT DEPOSITION AND RELEASE

In using the term *motivation*, one is basically asking the question "why?" In the literature on marking behavior, many pronouncements and inferences have been made concerning why animals mark. Unfortunately, this question can be asked at a number of levels of analysis, and few people bother to define at which levels they are working when they discuss the problem. One of the more frequent mistakes is to ascribe a motive to an animal once a presumed function is found.

On one level, the study of motivation can involve an analysis of those external or internal stimuli which affect the occurrence of either the form or the frequency of the behavior pattern. Studies of the hormonal regulation of scent-marking behavior (e.g., Thiessen & Yahr 124) come into this category as do studies of the sensory and neural control of marking (Baran & Glickman 5). Using the same approach, one can manipulate the environment and

determine what external circumstances influence the occurrence of the behavior. We know that marking is often a normal response to a novel environment with foreign odors. Although this type of research is clearly concerned with the causation of the behavior, either through its physiological mechanisms or its stimulus control, the terms *motive* and *mood* are rarely used.

In contrast, much research has been directed toward ascribing moods or motives to a marking animal and classical ethological methods have been applied to the analysis of the motivation of marking behavior. This has been done rather well by Ralls (105), who concludes that scent-marking is primarily motivated by an aggressive tendency. She cites several studies showing that marking is most vigorously performed by dominant animals when they are intolerant of conspecifics and likely to attack. Scent marking is temporally associated with attack and occurs under stimulus conditions where attack is likely. Unfortunately, she considers mainly those situations which produce higher than normal levels of marking and basically skirts the question of the motivation of less vigorous marking ["... it may be entirely different" (Ralls 105)]. The rhythmicity of the urine-marking of the slow loris (Seitz 114), varying as it does with the activity cycle, cannot be motivated by an aggressive tendency. Nor can the urine-marking of male jackals (*Canis aureus*) and male leopards (*Panthera pardus*) during routine daily patrols of the home range (Eisenberg & Lockhart 45). Although these observations deal primarily with urine-marking, similar trends can be seen in the deposition of glandular secretions.

This points up another limitation of Rall's review. By concentrating on the deposition of glandular secretions on objects or conspecifics, she largely eliminates from consideration the motivation of self-marking and the nondirected release of odor into the air, as well as the use of urine and feces in olfactory communication. As we have seen, the release of odor into air is most often associated with stimulus situations producing fear and withdrawal. Moreover, it has been argued elsewhere (Kleiman 62, 64) that the specialized urine-marking patterns of some species of mammals are probably derived in an evolutionary sense from autonomic urination induced by fear. It would be unlikely that a behavior initially motivated by fear would, after becoming specialized, be motivated by aggression.

Finally, we must point out Rall's emphasis on marking behavior in males, to the exclusion of females. In female mammals, scent gland activity and associated marking patterns, as well as urine-marking, may vary with the reproductive cycle. Again, there is an increased marking rate which bears no direct relationship to attack propensities.

It is true, however, that marking with specialized skin glands is often a sexually dimorphic phenomenon. Males of many species exhibit functional skin glands which are nonfunctional or reduced in females [e.g., *Oryctolagus* (Mykytowycz 96), *Mesocricetus*, (Lipkow 74), *Elephas* (Eisenberg, McKay & Jainudeen 46)]. In these species the active gland in the male is often sensitive to androgen, and castration will result in glandular atrophy as well as the

abolishment or reduction of the marking behavior (Thiessen & Yahr 124).

What has been established then is that some marking patterns by males of some species necessitate that the male be intact and possess a high androgen titre in its blood stream. We may infer that these males possess the potential for showing significant amounts of aggressive behavior in the appropriate environment. Some of the marking may well be performed when the animal is aggressively motivated, but it does not follow that marking, itself, is aggressive in its expression.

One way in which we can approach the motivation of scent-marking is to consider that for each individual—depending upon his age, sex, mood, and reproductive state—there is an optimum odor field which will provide the optimum level of security. This odor field is composed of a combination of olfactory stimuli emanating from the individual, the environment, and conspecifics. The ratios of these separate olfactory stimuli and their overall intensity (i.e., the level of odor saturation) influence the animal. If a disturbance in the odor field occurs (a) through a change in physiological state which alters the sensitivity of the individual and his perception of the optimum odor field, (b) through the introduction of a foreign odor, or (c) through a change in the odor field caused by the dissipation of scent previously deposited, then the individual will attempt to restore the previous balance by the release and deposition of scent. The changed odor field may also arouse the individual, depending upon the nature of the change, and other behavior patterns may be initiated.

We can take a few examples to illustrate the point. In many female mammals, a low level of scent-marking behavior is seen until the female begins to approach estrus, when the rate of urine-marking increases dramatically. Instead of considering this behavioral change a result of aggressive, territorial, or sexual tendencies (which is not likely if there are no other indications of aggression, territoriality, or receptivity), one can hypothesize an alteration in the female's perception of her olfactory milieu. The high level of conspecific odor may become less tolerable and a new balance in the ratio of conspecific to personal odor may be required to achieve an odor field which provides the maximum security. In this case, the optimum odor field for a female is affected by her hormonal state.

The social status of an individual may also affect the optimum odor field through the physiological changes that relate to social rank. Dominant male individuals may have a low tolerance for foreign-male conspecific odor or even to known-male conspecific odor. Thus, one sees a basal high level of marking which increases upon the introduction of foreign odor. Subdominant or subordinate males may tolerate high levels of nonpersonal odor, but will show increased rates of scent release when they are placed in a changed odor field.

It should, of course, not be assumed that the numerous odoriferous substances produced by each species of mammal affect scent-marking behavior in a similar way. Some substances are associated with specialized responses

that may not produce changes in the level of scent-marking behavior. For example, the *Angstgeruch* certainly affects the odor field of a mouse, but the response is one of avoidance. There may be a complete inhibition of scent-marking under these conditions.

Moreover, scent may be released and deposited by an individual for reasons which are unrelated to the prevailing odor field. For example, sensory feedback from full scent pouches (e.g., in viverrids) may result in the release of glandular secretions (Wemmer 133). Autonomically induced urination, if it occurs under conditions of electric shock or after a defeat, is another case in point.

It should be clear from the above that even though we have suggested a motivational basis for some marking behavior, we are not attempting to present a general theory that would cover all contexts in which odor is released. No single motivational state underlies all scent release and deposition and no single stimulus situation can account for the elicitation of all possible behavior.

## LITERATURE CITED

1. Adrian, E. D. 1955. Synchronized activity in the vomeronasal nerves with a note on the function of the organ of Jacobson. *Pflügers Arch. Gesamte Physiol. Menschen* 260:188–92
2. Altmann, D. 1969. *Harnen und Koten bei Säugetiere.* Wittenberg Lutherstadt: Ziemsen Verlag. 104 pp.
3. Amoore, J. E. 1966. Psychophysics of odor. *Cold Spring Harbor Symp. Quant. Biol.* 30:623–37
4. Archer, J. 1968. The effect of strange male odor on aggressive behavior in male mice. *J. Mammal.* 49:572–75
5. Baran, D., Glickman, S., 1970. Territorial marking in the Mongolian gerbil: a study of sensory control and function. *J. Comp. Physiol. Psychol.* 71:237–45
6. Beach, F. A., Gilmore, R. W. 1949. Responses of male dogs to urine from females in heat. *J. Mammal.* 30:391–92
7. Beach, F. A., Jaynes, J. 1956. Studies on maternal retrieving in rats. III. Sensory cues involved in the lactating female's response to her young. *Behaviour* 10:104–25
8. Beidler, L. M. 1954. A theory of taste stimulation. *J. Gen. Physiol.* 38:133–39
9. Beidler, L. M. 1966. Comparisons of gustatory receptors, olfactory receptors, and free nerve endings. *Cold Spring Harbor Symp. Quant. Biol.* 30:191–200
10. Bowers, J. M., Alexander, B. K. 1967. Mice: individual recognition by olfactory cues. *Science* 158:1208–10
11. Bronson, F. H. 1968. Pheromonal influences on mammalian reproduction. *Reproduction and Sexual Behavior,* ed. M. Diamond, 341–61. Indiana Univ. Press.
12. Bronson, F. H., Dezell, H. E. 1968. Studies on the estrus-inducing (pheromonal) action of male deermouse urine. *Gen. Comp. Endocrinol.* 10:339–43
13. Bronson, F. H., Eleftheriou, B. E. 1963. Influence of strange males on implantation in the deermouse. *Gen. Comp. Endocrinol.* 3:515–18
14. Bronson, F. H., Marsden, H. M. 1964. Male-induced synchrony of estrus in deermice. *Gen. Comp. Endocrinol.* 4:634–37
15. Brooks, P. H., Cole, D. J. A. 1970. The effect of the presence of a boar on the attainment of puberty in gilts. *J. Reprod. Fert.* 23:435–40
16. Brown, W. L. 1968. An hypothesis

concerning the function of the metapleural glands in ants. *Am. Natur.* 102:188–91

17. Brownlee, R. G., Silverstein, R. M., Müller-Schwarze, D., Singer, A. G. 1969. Isolation, identification, and function of the chief component of the male tarsal scent in black-tailed deer. *Nature* 221:284–85

18. Bruce, H. M. 1960. A block to pregnancy in the mouse caused by proximity to strange males. *J. Reprod. Fert.* 1:96–102

19. Bruce, H. M. 1965. Effect of castration on reproductive pheromones of male mice. *J. Reprod. Fert.* 10:141–43

20. Bruce, H. M., Parkes, A. S. 1960. Hormonal factors in exteroceptive block to pregnancy in mice. *J. Endocrinol.* 20:xxix–xxx

21. Bruce, H. M., Parrott, D. M. V. 1960. Role of olfactory sense in pregnancy block by strange males. *Science* 131:1526

22. Burghardt, G. M. 1970. Chemical perception in reptiles. *Advances in Chemoreception*, ed. J. W. Johnston, D. G. Moulton, A. Turk, 1:241–308. New York: Appleton Century Crofts

23. Carr. W. J., Caul, W. F. 1962. The effect of castration in rats upon the discrimination of sex odours. *Anim. Behav.* 10:20–27

24. Carr, W. J., Krames, L., Costanzo, D. J. 1970. Previous sexual experience and olfactory preference for novel vs. original sex partners in rats. *J. Comp. Physiol. Psychol.* 71:216–22

25. Carr, W. J., Loeb, L. S., Dissinger, M. L. 1965. Responses of rats to sex odors. *J. Comp. Physiol. Psychol.* 59:370–77

26. Carr, W. J., Loeb, L. S., Wylie, N. R. 1966. Responses to feminine odors in normal and castrated male rats. *J. Comp. Physiol. Psychol.* 62:336–38

27. Carr, W. J., Martorano, R. D., Krames, L. 1970. Responses of mice to odors associated with stress. *J. Comp. Physiol. Psychol.* 71:223–38

28. Carr, W. J., Wylie, N. R., Loeb, L. S. 1970. Responses of adult and immature rats to sex odors. *J. Comp. Physiol. Psychol.* 72:51–59

29. Carter, C. S., Marr, J. M. 1970.

Olfactory imprinting and age variables in the guinea-pig, *Cavia porcellus. Anim. Behav.* 18:238–44

30. Chapman, V. M., DesJardins, C., Whitten, W. K. 1970. Pregnancy block in mice: Changes in pituitary LH and plasma progestin levels. *J. Reprod. Fert.* 21:333–37

31. Christian, J. J. 1963. Endocrine adaptive mechanisms and the physiologic regulation of population growth. *Physiological Mammalogy,* ed. W. Mayer, R. G. van Gelder, 1:189–353. New York: Academic

32. Clulow, F. V., Clarke, J. R. 1968. Pregnancy-block in *Microtus agrestis*, an induced ovulator, *Nature* 219:511

33. Collins, L., Eisenberg, J. F. 1972. The behavior and breeding of pacaranas (*Dinomys branickii*) in captivity. *Int. Zool. Yearb.*

34. Dagg, A. I., Taub, A. 1970 Flehmen. *Mammalia* 34:686–95

35. Dagg, A. I., Windsor, D. E. 1971. Olfactory discrimination limits in gerbils. *Can. J. Zool.* 49:283–85

36. Dixon, A. K., Mackintosh, J. H. 1971. Effects of female urine upon the social behaviour of adult male mice. *Anim. Behav.* 19:138–40

37. Dominic, C. J. 1964. Source of the male odour causing pregnancy-block in mice. *J. Reprod. Fert.* 8:266–67

38. Dominic, C. J. 1966. The inhibition of the olfactory block to pregnancy in mice by administration of exogenous progesterone. *Naturwissenschaften* 53:310–11

39. Dominic, C. J. 1966. Observations on the reproductive pheromones of mice, II. Neuro-endocrine mechanisms involved in the olfactory block to pregnancy. *J. Reprod. Fert.* 11:415

40. Dominic, C. J. 1967. Effect of exogenous prolactin on olfactory block to pregnancy in mice exposed to urine of alien males. *Indian J. Exp. Biol.* 5:47–48

41. Dryden, G. L., Conaway, C. H. 1967. The origin and hormonal control of scent production in *Suncus. J. Mammal.* 48:420–28

42. Dutt, R. H., Simpson, E. C., Chris-

tian, J. C., Barnhart, C. E. 1959. Identification of preputial glands as the site of production of sexual odor in the boar. *J. Anim. Sci.* 18:1557

43. Eisenberg, J. F. 1963. The behavior of Heteromyid rodents. *Univ. Calif. Publ. Zool.* 69:1–100

44. Eisenberg, J. F., Gould, E. 1970. The tenrecs: A study in mammalian behavior and evolution. *Smithson. Contrib. Zool.* 27:1–137

45. Eisenberg, J. F., Lockhart, M. 1972. An ecological reconnaissance of Wilpattu National Park. *Smithson. Contrib. Zool.* 101:1–118

46. Eisenberg, J. F., McKay, G. M., Jainudeen, M. R. 1971. Reproductive behavior of the Asiatic elephant (*Elephas maximus* L.). *Behaviour* 38:193–225

47. Epple, G. 1970. Quantitative studies on scent marking in the marmoset (*Callithrix jacchus*). *Folia Primat.* 13:48–62

48. Evans, C. S., Goy, R. W. 1968. Social behaviour and reproductive cycles in captive ring-tailed lemurs (*Lemur catta*). *J. Zool. London* 156:181–97

49. Ewer, R. F. 1968. *Ethology of Mammals.* London: Logos xiv + 418 pp.

50. Fleming, A. 1971. *Olfactory and experiential factors underlying maternal behavior in the lactating and cycling female rat.* PhD thesis. Rutgers Univ., Newark, NJ. Unpublished

51. Gandelman, R., Zarrow, M. X., Denenberg, V. H., Myers, M. 1971. Olfactory bulb removal eliminates maternal behavior in the mouse. *Science* 171:210–11

52. Goddard, J. 1967. Home range, behaviour, and recruitment rates of two black rhinoceros populations. *East Afr. Wildl. J.* 5:133–50

53. Godfrey, J. 1958. The origin of sexual isolation between bank voles. *Proc. Roy. Phys. Soc. Edinburgh* 27:47–55

54. Hafez, E. S. E., Ed. 1969. *The Behavior of Domestic Animals.* Baltimore: Williams & Wilkins. 2nd ed. 647 pp.

55. Hafez, E. S. E., Signoret, J. P. 1969. The behaviour of swine. See Ref. 54, 349–90

56. Hart, B. L., Haugen, C. M. 1971. Scent marking and sexual behavior maintained in anosmic male dogs. *Comm. Behav. Biol.* 6:131–35

57. Hediger, H. 1951. Observations sur la Psychologie Animale dans les Parcs Nationaux du Congo Belge. *Explorations des Parcs Nationaux du Congo Belge, Mission H. Hediger-J. Verschuren* (1948). Fascicule 1:1–195. Brussels

58. Heimer, L., Larsson, K. 1967. Mating behavior of male rats after olfactory bulb lesions. *Physiol. Behav.* 2:207–9

59. Johnston, J. W., Moulton, D. G., Turk, A. See Ref. 22, Chemical Communication in Animals

60. Kennedy, J. M., Brown, K. 1970. Effects of male odor during infancy on the maturation, behavior, and reproduction of female mice. *Develop. Psychobiol.* 3:179–89

61. Kerkhof, H. 1924. Beitrag zur Kenntnis des Baues und der Funktion des Jacobsonschen Organ. *Z. Mikrosk. Anat. Forsch.* 1:621–38

62. Kleiman, D. 1966. Scent marking in the Canidae. *Symp. Zool. Soc. London* 18:167–77

63. Kleiman, D. G. 1969. Maternal care, growth rate and development in the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*), and serotine (*Eptesicus serotinus*) bats. *J. Zool. London* 157:187–211

64. Kleiman, D. G. 1971. The courtship and copulatory behavior of the green acouchi, *Myoprocta pratti. Z. Tierpsychol.* 29:259–78

65. Klopfer, P. H. 1971. Mother love: What turns it on? *Am. Sci.* 59:404–7

66. Knappe, H. 1964. Zur Funktion des Jacobsonschen Organs. *Zool. Garten* 28:188–94

67. Krames, L., Carr, W. J., Bergman, B. 1969. A pheromone associated with social dominance among male rats. *Psychonomic Sci.* 16:11–12

68. Larsson, K. 1969. Failure of gonadal and gonadotrophic hormones to compensate for an impaired sexual function in

anosmic male rats. *Physiol. Be-hav.* 4:733–37

69. LeMagnen, J. 1952. Les phéno-mènes olfacto-sexuels chez le rat blanc. *Arch. Sci. Physiol.* 6:295–331

70. LeMagnen, J. See Ref. 22, Con-clusion, Communication by Chemical Signals, 393–404

71. Lettvin, J. Y., Gesteland, R. C. 1966. Speculations on smell. *Cold Spring Harbor Symp. Quant. Biol.* 30:217–26

72. Lindsay, D. R. 1965. The impor-tance of olfactory stimuli in the mating behavior of the ram. *Anim. Behav.* 13:75–78

73. Lindsay, D. R., Fletcher, I. C. 1968. Sensory involvement in the recognition of lambs by their dams. *Anim. Behav.* 16:415–17

74. Lipkow, J. 1954. Uber das seiten-organ des goldhamsters (*Meso-cricetus auratus auratus* Wat-terh.). *Z. Morph. Oekol. Tiere* 42:333–72

75. Lyne, A. G., Molyneux, G. S., Mykytowycz, R., Parakkal, P. F. 1964. The development, structure, and function of the submandibular cutaneous (chin) gland in the rabbit. *Austr. J. Zool.* 12:340–48

76. Mackintosh, J. H., Grant, E. C. 1966. The effect of olfactory stimuli on the agonistic behav-iour of laboratory mice. *Z. Tierpsychol.* 23:584–87

77. Mainardi, D. 1964. Interazione tra preferenze sessuali delle fem-mine e predominanza sociale dei maschi nel determinismo della selezione sessuale nel topo (*Mus musculus*). *Rend. Accad. Naz. Lincei* 37:484–90

78. Mainardi, D. 1965. Un esperi-mento nuovo sul determinismo delle preferenze sessuali nella femmina di topo (*Mus muscu-lus domesticus*). *Boll. Zool.* 32:1–6

79. Mainardi, D., Marsan, M., Pas-quali, A. 1965. Causation of sexual preferences of the house mouse. The behaviour of mice reared by parents whose odour was artificially altered. *Atti Soc. Ital. Sci. Natur. Mus. Civ. Stor. Natur. Milano* 54:325–38

80. Mainardi, D., Marsan, M., Pas-quali, A. 1965. Assenza di pre-ferenze sessuali tra ceppi nel maschio di *Mus musculus do-mesticus. Ist. Lombardo (Rend. Sci.)* 99:26–34

81. Mann, G. 1961. Bulbus olfactorius accessorius in Chiroptera. *J. Comp. Neurol.* 116:135–44

82. Marr, J. N., Gardner, L. E., Jr. 1965. Early olfactory experience and later social behavior in the rat: preference, sexual respon-siveness, and care of young. *J. Genet. Psychol.* 97:167–74

83. Marr, J. N., Lilliston, L. G. 1969. Social attachment in rats by odor and age. *Behaviour* 33:277–82

84. Michael, R. P., Keverne, E. B. 1968. Pheromones in the com-munication of sexual status in primates. *Nature* 218:746–49

85. Michael, R. P., Keverne, E. B., Bonsall, R. W. 1971. Phero-mones: isolation of male sex at-tractants from a female pri-mate. *Science* 172:964–66

86. Moore, R. E. 1965. Olfactory dis-crimination as an isolating mechanism between *Peromys-cus maniculatus* and *Peromys-cus polionotus. Am. Midl. Na-tur.* 73:85–100

87. Moulton, D. G. 1966. Differential sensitivity to odors. *Cold Spring Harbor Symp. Quant. Biol.* 30:201–6

88. Moulton, D. G. 1967. Olfaction in mammals. *Am. Zool.* 7:421–29

89. Moulton, D. G., Beidler, L. M. 1967. Structure and function in the peripheral olfactory system. *Physiol. Rev.* 47:1–52

90. Mugford, R. A., Nowell, N. W. 1970. Pheromones and their effect on aggression in mice. *Nature* 226:967–68

91. Müller, W. 1971. Vergleichende elektrophysiologische Unter suchungen an den Sinnesepithe-lien des Jacobsonschen Organs und der Nase von Amphibien (*Rana*), Reptilien (*Lacerta*) und Säugetieren (*Mus*). *Z. Vergl. Physiol.* 72:370–85

92. Müller-Schwarze, D. 1969. Com-plexity and relative specificity in a mammalian pheromone. *Nature* 223:525–26

93. Müller-Schwarze, D. 1971. Phero-mones in black-tailed deer

(*Odocoileus hemionus columbianus*). *Anim. Behav.* 19:141–52

94. Müller-Velten, H. 1966. Über den Angstgeruch bei der Hausmaus. *Z. Vergl. Physiol.* 52:401–29

95. Murphy, M. R., Schneider, G. E. 1970. Olfactory bulb removal eliminates mating behavior in the male golden hamster. *Science* 167:302–4

96. Mykytowycz, R. 1965. Further observations on the territorial function and histology of the submandibular cutaneous (chin) gland in the rabbit, *Oryctolagus cuniculus* (L.). *Anim. Behav.* 13:400–12

97. Mykytowycz, R. See Ref. 22, The role of skin glands in mammalian communication, Communication by Chemical Signals, 327–60

98. Ortmann, R. 1960. Die Analregion der Säugetiere. *Handbuch der Zoologie,* Band 8, Lieferung 26. 68 pp.

99. Parkes, A. S., Bruce, H. M. 1962. Pregnancy-block in female mice placed in boxes soiled by males. *J. Reprod. Fert.* 4:303–8

100. Pfaffmann, C., Ed. 1969. *Olfaction and Taste. Proc. 3rd Int. Symp.* Rockefeller Univ. Press

101. Poduschka, W., Firbas, W. 1968. Das Selbstbespeicheln des Igels, *Erinaceus europaeus* Linné, 1758, steht in Beziehung zur Funktion des Jacobsonschen Organes. *Z. Säugetierk.* 33: 160–72

102. Quay, W. B. 1954. The Meibomian glands of voles and lemmings (Microtinae). *Misc. Publ. Mus. Zool. Univ. Mich.* 82:1–24

103. Quay, W. B. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. *J. Mammal.* 46:23–36

104. Rahaman, H., Parthasarathy, M. D. 1971. The role of olfactory signals in the mating behavior of bonnet monkeys (*Macaca radiata*). *Comm. Behav. Biol.* 6:97–105

105. Ralls, K. 1971. Mammalian scent marking. *Science* 171:443–49

106. Rood, J. P., Weir, B. J. 1970. Reproduction in female wild guinea pigs. *J. Reprod. Fert.* 23:393–409

107. Ropartz, Ph. 1968. The relation between olfactory stimulation and aggressive behavior in mice. *Anim. Behav.* 16:97–100

108. Schaffer, J. 1940. *Die Hautdrüsenorgane der Säugetiere.* Berlin: Urban & Schwarzenberg

109. Schenkel, R. 1966. Zum Problem der Territorialität bei Säugernam Beispiel des Schwarzen Nashorns und des Löwens. *Z. Tierpsychol.* 23:593–626

110. Schneider, K. M. 1930. Das Flehmen. *Zool. Gart.* (Leipzig) 3: 183–98. 4:349–64. 5:200–26. 5:287–97

111. Schultz, E. F., Tapp, J. T. Olfactory control of behavior in rodents. *Psych. Bull.* In press

112. Schultze-Westrum, T. G. 1965. Innerartliche Verständigung durch Düfte beim Gleitbeutler *Petaurus breviceps papuanus. Z. Vergl. Physiol.* 50:151–220

113. Schultze-Westrum, T. G. 1969. Social communication by chemical signals in flying phalangers (*Petaurus breviceps papuanus*). *Olfaction and Taste,* ed. C. Pfaffman, 268–77. Rockefeller Univ. Press

114. Seitz, E. 1969. Die Bedeutung geruchlichen Orientierung beim Plumploris *Nycticebus coucang* Boddaert 1785 (Prosimii, Lorisidae). *Z. Tierpsychol.* 26:73–103

115. Signoret, J. P. 1967. Attraction de la femelle en oestrus par la mâle chez les porcéns. *Rev. Comp. Anim.* 4:10–22

116. Sink, J. D. 1967. Theoretical aspects of sex odor in swine. *J. Theor. Biol.* 17:174–80

117. Sisson, S., Grossman, J. 1953. *The Anatomy of the Domestic Animals.* Philadelphia: Saunders. 4th ed. 972 pp.

118. Sowls, L. K. 1971. Social behavior of the collared peccary (*Dicotyles tajacu* L.). *Proc. 1st Int. Conf. Behav. Ungulates and its Relation to Management,* Calgary

119. Sprott, R. L. 1969. "Fear communication" via odor in inbred mice. *Psychol. Rep.* 25:263–68

120. Steiniger, F. 1950. Beiträge zur Soziologie und sonstigen Biolo-

gie der Wanderratte. *Z. Tierpsychol.* 7:356–79

121. Stern, J. J. 1970. Responses of male rats to sex odors. *Physiol. Behav.* 5:519–24

122. Terman, C. R. 1968. Inhibition of reproductive maturation and function in laboratory populations of prairie deermice; a test of pheromone influence. *Ecology* 49:1169–72

123. Terman, C. R. 1969. Pregnancy failure in female prairie deermice related to parity and social environment. *Anim. Behav.* 17:104–8

124. Thiessen, D. G., Yahr, P. 1970. Central control of territorial marking in the Mongolian gerbil. *Physiol. Behav.* 5:275–78

125. Thomson, J. A., Pears, F. N. 1962. The functions of the anal glands of the brushtail possum. *Victoria Natur.* 78:306–8

126. Tschanz, B., Meyer-Holzapfel, M., Bachmann, S. 1970. Das Informationssystem bei Braunbären. *Z. Tierpsychol.* 27:47–72

127. Tucker, D. 1963. Olfactory, vomeronasal and trigeminal receptor responses to odorants. *Olfaction and Taste,* ed. Y. Zotterman, 45–69. Oxford: Pergamon

128. Valenta, J. G., Rigby, M. K. 1968. Discrimination of odor of stressed rats. *Science* 161:599–601

129. Vandenbergh, J. G. 1967. Effect of the presence of a male on the sexual maturation of female mice. *Endocrinology* 81:345–49

130. Vandenbergh, J. G. 1969. Male odor accelerates female sexual maturation in mice. *Endocrinology* 84:658–60

131. Verberne, G. 1970. Beobachtungen und Versuche über das Flehmen Katzenartiger Raubtiere. *Z. Tierpsychol.* 27:807–27

132. Weber, M. 1927. *Die Säugetiere.* Jena. 2 vols.

133. Wemmer, C. 1972. *The behavior of* Genetta tigrina *and related genera.* PhD thesis. Univ. Maryland, College Park. Unpublished

134. Whitten, W. K. 1966. Pheromones and mammalian reproduction. *Advances in Reproductive Physiology,* ed. A. McLaren, 1:155–77. New York: Academic

135. Whitten, W. K., Bronson, F. H. See Ref. 22, The role of pheromones in mammalian reproduction, Communication by Chemical Signals, 309–26

136. Whitten, W. K., Bronson, F. H., Greenstein, J. A. 1968. Estrus-inducing pheromone of male mice: Transport by movement of air. *Science* 161:584–85

137. Wilson, E. O. 1968. Chemical systems. *Animal Communication,* ed. T. Sebeok. Indiana Univ. Press

138. Wilson, E. O. 1970. Chemical communication within animal species. *Chemical Ecology,* ed. E. Sondheimer, J. E. Simeone, 133–55. New York: Academic

139. Wilson, E. O., Bossert, W. H. 1963. Chemical communication among animals. *Recent Progr. Horm. Res.* 19:673–716

140. Winans, S., Scalia, F. 1970. Amygdaloid nucleus: New afferent input from the vomeronasal organ. *Science* 170:330–32

141. Wright, R. H. 1964. *The Science of Smell.* New York: Basic Books. xii + 164 pp.

142. Wylie, N. R. 1968. Neonatal castration modified responses to sex odors. *Proc. 76th Ann. Conv. APA,* 291–92