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# PHEROMONES IN SMALL RODENTS AND THEIR POTENTIAL USE IN PEST CONTROL

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ABSTRACT: The paper reviews social interactions in small rodents in which pheromones have been reported to play a part. Some of the chemical messengers involved may have a potential use in control of rodent pests. Research in this field should be encouraged, because alternatives to the current control methods are highly desirable.

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In 1959, the German chemist Butenandt and his co-workers suggested the term "pheromones" to denote chemical messengers, which when emitted by an animal, release certain reactions in conspecifics (Karlson and Butenandt, 1959; Karlson and Luscher, 1959). By that time Butenandt had finished his 20-year long research that led to the isolation and identification of the sex attractant pheromone in the female silk moth, Bombyx mori. Since then more than a hundred insect pheromones have been identified, and several are now being used on a practical scale for forecasting population levels and in control programs.

Pheromonal effects are likely to occur in any animal phylum and are known to operate in such different groups as e.g. worms, snails, crabs, fish, and snakes, as well as in mammals such as rodents, deer, monkeys, and presumably humans.

Only in very few rodents are the chemical composition of pheromones known. These include a house mouse preputial gland pheromone (Spener et_ al., 1969) the ventral gland pheromone in the male Mongolian gerbil (Thiessen et_ al_., 1974), and a sex attractant in hamster vaginal secretion (Singer et_ al_., 1976).

The success insect pheromones have had in practical control work should stimulate an extensive exploration into the field of rodent pheromones and their potential use in regulating pest populations. However, the far more complex behavior of rodents as compared to insects constitutes an obstacle to the study of pheromonal effects and the practical use of pheromones in rodent control. A male moth after perceiving a female sex attractant has adequately been described as "a guided missile," homing in on the odor source. Mammalian behavior is much more complex, and rodents will not react that automatically to any pheromone, no matter how strong the lure may be.

But there is no doubt that pheromones play an important part with rodents. This can be illustrated by the fact that house mice will eat their own offspring if deprived of the olfactory bulb (Gandelman et_ al_., 1971). These animals are no longer capable of identifying their young in absence of the olfactory cues.

The use of chemical signals in communication offers at least two major advantages: the "message" can linger on long after the "sender" has left the stage, and communication works as well in total darkness as in broad daylight. In the restricted space of subterranean tunnels or runways in the bottom vegetation an odor is "trapped" for a much longer period than in the free. In many rodent species the bulk of the activity is restricted to such confined spaces. This is particularly true with populations living and multiplying under snow-cover.

In rodents, pheromones can be divided into two groups: (1) signal pheromones or releasers, i.e. substances that trigger immediate behavioral responses, and (2) primers, i.e. substances that produce effects that become manifest only after some time has passed, by working through some neuroendocrine pathway.

Mammals possess a great number of skin glands (Schaffer, 1940; Quay, 1968), and produce numerous odors (Lederer, 1950). Several scent sources are known or suspected to be involved in chemical communication in mammals: foot-sole glands, preputial glands, coagulation glands, anal glands, unspecialized sebaceous glands, salivary glands, urine, and feces.

In this paper I will give an outline of some pheromonal effects that have been shown to operate in small rodents, and speculate on the possible applicability of some of these pheromones in rodent pest control. Several reviews have been written on chemical communication of mammals in general (e.g. Rails, 1971; Eisenberg and Kleiman, 1972; Mykytowycz, 1972) and that of rodents in particular (e.g. Bronson, 1971; Schultz and Tapp, 1973). Several

books have good articles covering the topic (e.g. Sondheimer and Simeone, 1970; Johnston et al., 1970; Birch, 1975).

MARKING OF ENVIRONMENT

It is well established that a wide variety of mammals mark objects in their environment with their body odors, which serves several purposes. Schulz and Tapp (1973) point out that: it promotes group integrity and also provides a familiar geographical area which supplies the physical concomitants necessary for survival. Due to the familiar scent the animals can more safely and easily participate in their normal life processes.

Environmental novelty is likely to be the most important factor to elicit marking, as shown in house mice by Maruniak et al. (1975), who define a familiar environment for a male house mouse as one "in which he marks at a low rate because he is not perceiving novel olfactory cues."

House mice use urine to mark their environment. Other rodents utilize different techniques and sources of body odors for marking. Water voles, Arvicoia terrestris, stamp the exudate of their flank glands onto the ground by means of the sole of their hind feet (Frank, 1956). Golden hamsters rub their flank glands on the objects to be marked (Johnston, 1975). Mongolian gerbils utilize their ventral glands for marking objects or each other, and the active fraction of these glands has been identified as phenylacetic acid (Thiessen et al., 1974).

Rats leave visible tracks on objects in their environment, and the smell of these marks are investigated by the animals, as is the odor of their urine (Reiff, 1952; Richards and Stevens, 1974).

The marking behavior is in many cases connected with social dominance and territoriality, as in the Mongolian gerbils (Thiessen et: al., 1970), water voles (Frank, 1956) and house mice (Desjardins et al., 1973). The flank glands of the water vole have been shown to go through an annual activity cycle where the maximal output coincides with the breeding season (Stoddart, 1972), during which the dominant males defend their territories against intruders.

The act of territorial marking often involves aggressive behavior. During marking, several deer species behave as if they were fighting an enemy. Normally, the dominant animals mark most frequently, and often have more we 11-developed scent glands than the subordinate ones.

Territorial marking may help reduce overall fighting between neighboring animals of the same species once territories are set up. Rails (1971) provides a good review of scent marking in mammals.

GROUP AND INDIVIDUAL RECOGNITION

Olfactory cues can be utilized to distinguish between animals of different species or subspecies. Both bank voles, Clethrionomys (Godfrey, 1958; Rauschert, 1963) and deer mice, Perornyscus (Moore, 1962), are capable of this, and prefer their own kind for a mate. This discriminatory mechanism is considered important in isolation between subspecies and hence in formation of new species.

In social hierarchies of the type we find in many mammals, it is important for the individual to recognize the social status, sex, and sexual state of its conspecifics. House mice are capable of utilizing olfactory cues for this purpose (Chanel and Vernet-Maury, 1963; Bowers and Alexanders, 1967; Kalkowski, 1967; Scott and Pfaff, 1970; Davies and Bellamy, 1972). Rats possess similar capacities (Carr et al., 1965; Krames et al, 1969; Pfaff and Pfaffman, 1969; Krames, 1970; Stern, 1970; Lydell and Doty, 1972; Alberts and Galef, 1973).

Different strains and populations may be distinguishable by olfactory cues. Wild rats readily attack strange conspecifics (Barnett, 1963) a phenomenon that is probably at least partly due to differences in strain odor (Alberts and Galef, 1973).

The "olfactory environment" in which an animal is raised can influence the future behavior. House mice reared with rat "aunts" (i.e. foster mothers) will be attracted more, strongly to rat than to mouse odor (Paschke et al., 1970. Exposure to certain odors, even

artificial ones, may influence the future choice of juveniles as shown with food habits in deer mice (Drickamer, 1972), social development in rats (Marr and Gardner, 1965), and sexual preferences in mice (Mainiardi et al_., 1965). In young rats exposed to a single odor, the odor imprinting is visualized in a selective degeneration of the mitral cells of the olfactory bulb. A certain chemical substance will produce degeneration of specific zones of the mitral cell layer (Døving and Pinching, 1973; Døving pers. comm.). Degeneration of bulb mitral cells is found in wild bank voles (Døving and Christiansen, unpublished data).

## MATERNAL PHEROMONE

In the care of rodent pups by their mothers, both acoustic and olfactory communication play important parts. During the first 2 weeks of life pups of several rodent species emit ultrasonic calls which enables their mother to retrieve them (Zippelius and Schleidt, 1965; Sewell, 1967; Allin and Banks, 1972). When 14 day old rat pups are mobile enough to leave the nest. At this age, their mother starts emitting a pheromone, and the pups simultaneously become responsive to this odor. The emission, as well as the responsiveness of the pups, cease about when weaning of the young takes place (Leon and Moltz, 1972). The maternal pheromone is believed to be produced through bacterial decomposition of caecotrophe. The caecotrophe is produced and defecated in great quantities by lactating females, due to their high food consumption. The food intake is thought to be governed by the prolactin level in the females. Different diets produce different odors, and the pups apparently learn to distinguish and orient themselves against their own mother's diet specific pheromone (Leon, 1975). The possibility of imprinting siblings with a maternal pheromone or with other environmental odors may contribute to group cohesion, and to the creation of "clans." The young are likely to be marked by the maternal pheromone of their mother (Leon, 1975). It should be mentioned that different strains of house mice may have differences in group odor which can even be detected by the human nose.

## SEX ATTRACTANTS PRODUCED BY FEMALES

Pheromones that attract the opposite sex are found in both female and male rodents.

Receptive female rats range farther than usual from their burrows and leave scent marks, which are examined by males and used to track females (Calhoun, 1962). Both sexes can be trained to discriminate between odors of sexually active vs. inactive animals of the opposite sex (Carr and Caul, 1962). Sexually experienced male rats prefer the odor from receptive females over that from nonreceptive, whereas naive males or castrates show no such preference (LeMagnen, 1952; Carr et_ al_., 1965; Stern, 1970). The sex attractant is found in estrus urine. It is most likely present in the bladder and is hence not added by secretions along the urethral tract or within the vaginal orifice. The attractant capacity of estrus urine samples is lost within 24 h when stored at room temperature (Lydell and Doty, 1972).

Chemical sex attractants are not the only cues serving as stimuli for copulation, as intact males attempt to copulate with both anestrus and estrus females (Alberts and Galef, 1973).

In male mice removal of the olfactory bulb abolishes sexual behavior (Rowe and Edwards, 1972). Estrus female mice emit a sex attractant for the males. Sexually experienced male mice, but not sexually naive ones, prefer the odor of estrus females to that of diestrus females (Hayashi and Kimura, 1974).

Information concerning the source of this pheromone in mice is conflicting. Dixon and Mackintosh (1975) reported the presence of a factor in estrus urine which potentiates sexual behavior in males. However, Hayashi and Kimura (1974) found that female urine was not effective in eliciting either odor preference or mating behavior in male mice, whereas vaginal discharge from estrus females had this capacity.

Vaginal secretions are found to be highly attractive to male golden hamsters (see Johnston, 1972) as well as to male rhesus monkeys (Michael and Keverne, 1970). Dimethyl disulphide is an attractant component of the hamster vaginal discharge (Singer et_ al_., 1976).

## SEX ATTRACTANTS PRODUCED BY MALES

Both experienced and naive-receptive female rats prefer odor of normal males to that of castrated males, whereas naive-nonreceptive females show no such preference (Carr et al.,

1965; Jones and Nowell, 1974a). The attractant odor may originate from the preputial gland, as has long been suspected (Stanley and Powell, 1941; quoted from Brown and Williams, 1972).

Sexually experienced rats, both male and female, spent more time investigating homogenates of preputial glands than other tissue hemogenates of the opposite sex. The other test tissues (submaxi1lary salivary glands and foot pads) were not investigated more than control tissues, i.e. muscle, fat, and liver (Orsulak and Gawienowski, 1972). The cited investigation, however, did not study the reaction of males or females to the preputial gland odor of their own sex. It might well be that a similar reaction would be found.

In mice, a lipid soluble factor strongly attractive to sexually experienced females is present in the preputial gland (Bronson, 1966). The factor is also found in preputial gland homogenate and externally voided urine, but not in bladder urine or urine from preputialectomized males (Bronson and Caroom, 1971).

Sexual experience in female mice reinforces the olfactory preference for the preputial gland pheromone, whereas high levels of circulating progesterone (or natural pregnancy) block the preference (Caroom and Bronson, 1971).

The mouse preputial gland contains long-chain alkyl acetates, a group of chemicals known to exist as pheromones in certain butterflies (Spener et al., 1969).

AGGRESSION ELICITING PHEROMONES

Aggression in small rodents, such as mice, rats, voles, and lemmings is particularly overt in males. Dominant males defending their territories are likely to attack conspecifics. Females generally behave more submissively and seldom become objects of serious attacks. They can, however, be rather aggressive when pregnant or lactating, defending their home-sites and young toward intruders. Juvenile males are generally tolerated by adult males unti1 puberty.

Laboratory mice may live in hierarchical or amicable groups (Poole and Morgan, 1975). With two amicably cohabiting males, aggression can be provoked if the urine of a strange male is applied to one of the two (Mackintosh and Grant, 1966).

Urine from dominant males provokes considerable aggression in male fighter mice, when applied to the fur of castrated male opponents. Urine from subordinate males elicits less aggression and urine from castrates least. The graded levels of aggression support the assumption that the pheromone is androgen-dependent (Mugford and Nowell, 1970a). Female mice normally escape attacks from males because they lack the necessary androgen mediated aggression eliciting odor. When injected with androgens, however, they may provoke aggression from fighter males, even though they behave submissively themselves (Mugford and Nowell, 1970b). An increasing degree of androgenization of the females was paralleled by increasing preputial (clitoral) gland weights and an increasing degree of aggression in fighter males exposed to their urine (Mugford and Nowell, 1971).

The preputial gland in rodents is proposed as the source of a pheromone signalling maleness and aggressiveness, and is thought to play an important part in a population odor "language" (Brown and Williams, 1972). The importance of this pheromone is underlined by the finding of Hayashi and Kimura (1974) that sexually experienced males spent as much time investigating preputial (clitoral) gland homogenate as they spent on the vaginal discharge of estrus females.

It has been shown with mice that bulbectomy (i.e. removal of the olfactory bulb) may completely prevent intermale aggression, though not aggressive behavior in a competition for food situation (Rowe and Edwards, 1971). Anosmic male rats do not exhibit aggressive behavior against unfamiliar males, whereas normal males do (Alberts and Galef, 1973).

AGGRESSION INHIBITING PHEROMONE

In mice aggression between males is reduced if female urine is applied to one of them, which suggests that urine contains an odor with aggression inhibiting properties (Mugford and Nowell, 1970a; Dixon and Mackintosh, 1971). The aggression inhibiting effect is independent of the estrus state of the urine donor, and is unaffected by ovariectomy (Dixon and Mackintosh, 1975).

## AVERSIVE PHEROMONE

In mice an androgen-dependent aversive pheromone found in male urine discourages prolonged investigation of a treated area by other male mice, at least by subordinate ones. Castration of the urine donor eliminated the aversive effect of urine, testosterone therapy reestablished it (Jones and Nowell, 1973a). Dominant male urine is far more effective in producing this effect than subordinate male urine, which is no more effective than water (Jones and Nowell, 1973b). The authors suggest that the aversive pheromone of dominant males induces greater emotionality and lower activity in subordinates, and that the lower levels of androgen-dependent pheromones (aversive as well as aggression-promoting pheromones) in subordinates may be a result of the considerable stress suffered by the subordinates. Likewise, they point out that because only the most aggressive dominant males are likely to hold territories, it seems fitting that their urine should possess strong aversive properties.

Male mice of a certain strain did not react to aversive pheromones of other strains, nor from rats or hamsters. Grouping of donors resulted in a complete loss of the aversive effect (Jones and Nowell, 1974b).

The aversive pheromone may well be identical to the aggression-promoting pheromone found in the preputial gland, but serving a different function under different social situations.

## FEAR/ALARM PHEROMONE

In situations which bring forth a strong feeling of fear or anger, several animals produce substances with pheromone capacities. "Mental sweat" in humans is produced by glands different from those that produce the "normal" sweat, serving temperature regulation. In fearful situations, house mice discharge urine, which is claimed to contain a pheromone which other mice tend to avoid (Muller-Velten, 1966). It is, however, doubtful that the urine is the carrier of the alarm pheromone in mice (Rottman and Snowdon, 1972). Rats can reliably distinguish between odors of stressed and unstressed conspecifics (Valenta and Rigby, 1968). The rats appear to examine the odor from stressed individuals more thoroughly than that from nonstressed, and urinate more frequently in presence of the former odor (Stevens and Koster, 1972). They do not seem to avoid areas containing the odor of fecal material from fear conditioned rats. This suggests that the perceivable odor differences between stressed and nonstressed rats may not implicate an alarm-evoking pheromone (King et. al., 1975). Instead, the odor may just elicit curiosity.

An alarm substance for rats in conspecific blood and muscle tissue has been demonstrated by Stevens and Saplikoski (1973). Blood from rats of different strains, as well as mouse blood, elicited escape reactions in rats, whereas human blood did not (Hornbuckle and Beall, 1974).

## ADRENAL EFFECTS

The adrenal cortex produces a large number of hormones, comprising sex as well as stress hormones. Both aggression (Mackintosh and Grant, 1966) and activity (Ropartz, 1966) of mice increases when exposed to the odor of strange males. Neither odor from castrated nor from isolated males is able to increase activity (Roparts, 1967a). Experiments by Archer (1968) suggest that the increased activity may be associated with a decrease in the threshold for aggressive behavior induced by olfactory stimuli. Exposure to strange male odor leads to increased adrenal weights and increased adrenocortical function in male mice (Archer, 1969a, b). In isolated males the odor from a group of females produces adrenal hypertrophy (Ropartz, 1967b).

## ONSET OF PUBERTY

The onset of puberty in female mice can be regulated by social stimuli. If a female mouse is reared only with females, the puberty may be delayed (Vandenbergh et al., 1972; Drickamer, 1975). The presence of a male in contrast accelerates the puberty onset (Vandenbergh, 1967, 1969; Castro, 1967). The factor mediating these effects are found in the urine (Cowley and Wise, 1972). The pheromone in male mouse urine accelerating female puberty is androgen-dependent and does apparently not originate from the preputial gland. Male rat urine has the same effect on female mice as urine from male mice (Colby and Vandenbergh, 1974), whereas male human urine has not (Vandenbergh et. al., 1975). The active fraction is supposed to be a portion of a protein or of a substance bound to a protein,

it is not volatile and therefore is probably transmitted through direct contact with male urine (Vandenbergh et al., 1975).

ESTRUS CYCLING AND PSEUDOPREGNANCY

If female house mice are grouped in absence of males their estrus cycles may be suppressed and they enter a state of prolonged anestrus (Whitten, 1959), or they may develop pseudopregnancies (Lee and Boot, 1955, 1956). If a male is introduced to a group in prolonged diestrus, estrus cycling is induced and accelerated, and often a synchrony of estrus cycles appears within the group (Whitten, 1956, 1958). This "Whitten effect" can be produced by means of male mouse urine (Marsden and Bronson, 1964). The pheromone is volatile and acts through olfactory perception (Whitten et al., 1968; Zarrow et al., 1970). It is androgen dependent, as castration eliminates the effect (Bruce, 1965), and ovari-ectomized/testosterone-injected females produce urine with this potential (Bronson and Whitten, 1968). The Whitten effect cannot be produced by immature or castrated males (Zarrow et al., 1970). The pheromone is present in bladder urine free from any accessory gland secretion (Bronson and Whitten, 1968). Preputial gland homogenate applied to the nasal area failed to produce the effect (McKinney, 1972). The Whitten effect has also been demonstrated in wild house mice (Chipman and Fox, 1966).

It has been concluded that the pheromone promotes gonadotrophin release in the female, resulting in ovulation (Zarrow et al., 1970). In rats introduction of males to all-female groups do not produce such a striking Whitten effect as in mice, as only a small proportion of the females responded to the introduction with synchronized estrus cycles (Hughes, 1964). An acceleration of ovulation in rats by male urine has been demonstrated (Aron and Chateau, 1971).

DISRUPTION OF PREGNANCY

In laboratory house mice, implantation of ova may be prevented by exposure of the female to the odor of a strange male (Bruce, 1959; Bruce and Parrott, 1960). The pheromone mediating this effect is present in the urine (Dominic, 196A). The "Bruce effect" has also been demonstrated in wild house mice (Chipman and Fox, 1966), in deer mice (Eleftheriou et al., 1962) and also in an induced ovulator, Microtus agrestis (Clulow and Clarke, 1968). In inbred strains of house mice, the Bruce effect may be extinct (Marsden and Bronson, 1965) or may occur at a high rate (Bruce, 1966).

POTENTIAL USE IN PEST CONTROL

The priming pheromones -- i.e. those influencing puberty onset, estrus cycling and pregnancy -- may have a future potential in management of population. In this paper, however, I would like to limit the discussion to a couple of the releaser (signal) pheromones, which seem to be of more immediate interest to pest control. Those are the sex attractants, and the aggression eliciting pheromones.

The sex pheromone which is found in female rodent urine or vaginal discharge could be an important substance for attracting males to traps or to stations with toxic bait or chemosterilants. An attempt to evaluate this potential possibility has been made by Field (1971) who reported increased acceptability of chemosterilant bait by rats on treatment with estrus urine. However, more research is needed to quantify the attractant capacity of these pheromones, and to isolate and identify the chemical components that are responsible for this presumed attraction.

The males generally are more active than females in searching mates. Nevertheless, a male produced odor attracting females could be very useful in rodent control. As mentioned before the preputial glands in mice produce a factor that is strongly attractive to sexually experienced females, and a similar attraction may exist in rats.

The preputial gland is found in a great number of rodent species (e.g. mice, rats, and voles), but is absent in others (e.g. deer mice and ground squirrels). This large, paired gland is found under the skin close to the penis, its ducts opening to the surface of the prepuce. Females have a smaller, similar (clitoral) gland. A comprehensive review of the structure and function of the rodent preputial gland is given by Brown and Williams (1972), who suggest that the gland odor signals maleness. Sexually receptive females may react to this "message" which indicates the presence of a possible mate. The preputial gland has long served as a target organ for hormone studies and is known to increase in size with increasing levels of both testosterone and progesterone, and to decrease under influence of high levels of estradiol.

The production and/or output of the gland are correlated to the hormonal state and social status in mice (Bronson and Marsden, 1973). The perineal scent gland in guinea pigs shows a similar correlation to the social status (Beauchamp, 1974). It might well be that the differences in preputial gland odors between males and females are due to quantitative, not qualitative characteristics, as indicated by Brown and Williams (1972). Spener et al. (1969) found the same alkyl-acetates in males and females of a specific mouse strain, although the relative amounts showed differences. These acetates made up a larger proportion of the total gland contents in the males than in the females.

Brown and Williams (1972) have suggested a model for chemical communication in rodents. According to this model, three different chemical signals are utilized for the identification of an individual: (1) odors signalling familiarity or strangeness, (2) a female odor, and (3) an odor communicating maleness/aggressiveness. This last odor is likely to originate from the preputial gland. A combination of these three odors is thought to serve as a chemical "poster" for each individual, signalling its present social status to its conspecifics, who react to the total message according to their own social status and experience. For example, an individual with a familiar "group" odor, which lacks both the male and the female smell is perceived as a juvenile and is generally not subject to attack. In contrast, an animal that lacks the female smell, but has a strong preputial odor, is perceived as a dominant male, which is avoided by subordinate males and attacked by territorial males. Correspondingly, a pregnant or lactating female, with a strong female smell and a relatively strong clitoral gland odor, is avoided by males because of her possible aggressiveness.

This model could explain an important part of the social communication in say a vole population living in subterranean burrows or under snow cover.

Further speculation along this line is tempting: if the preputial odor signals aggression in a fluctuating vole population, this chemical signal may have an increasing effect on the animals as the population grows in numbers. In a dense population the aggression signal may be present everywhere, and might in the long run affect the physiological status of the animals. It is tempting to suggest that the permanent presence of an aggression signal might play an important part in creation of population "stress" and hence in the final breakdown of fluctuating vole populations. As mentioned above, the odor from a strange male mouse can increase the adrenal size and activity of other males.

I strongly feel that the role of the preputial gland in rodent communication should be object to intensive study by rodent pest control researchers, because of the possible potentials in manipulation of rodent populations.

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