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SCENT MARKING IN MAMMALS

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Abstract. This paper reviews experimental and field studies on scent marking behaviour. The occurrence and effects of scent marking are considered in particular, and a number of areas for further research are made apparent. Marking behaviour in mammals is often stated to be 'territorial' or, more specifically, to play a role in territorial defence. In fact there is a shortage of evidence to support this view; many of the relevant observations are anecdotal or interpreted with preconceived notions of function in mind. While marking is clearly associated with aggressive behaviour in many species and may therefore be related in some way to territorial behaviour, its role in aggression is not understood. Moreover, there is evidence to support a number of other theories of function some of which are unrelated to territory. It seems that, as with any other mode of communication, scent marking has become adapted for use in a variety of contexts. It probably has more than one function in any one species and different functions in different species.

Scent marking is behaviour by which glandular secretions are deposited on the ground or onto objects in an animal's environment. Specialized cutaneous glands, producing apparently odoriferous secretions, are found in a majority of mammals (see Schaeffer 1940; Grassé 1955; Fiedler 1957, 1964; Tembrock 1968; Ewer 1968a) and detailed studies of the occurrence of glands within certain taxonomic groups have been carried out (see, for example, Pocock 1910; Dalquest & Werner 1954; Quay 1962, 1965, 1968; Quay & Tomich 1963; Doty & Kart 1972). The marking behaviour of a number of species has been described, and it is clear that there is a great deal of variation between species in the action patterns involved. This is partly due to the various positions on the body in which the glands may occur. The deposition of urine and faeces, carrying secretions of the sex accessory glands or anal glands, can also constitute marking behaviour (see Ewer 1968a; Mykytowycz 1970; Ralls 1971). Kleiman (1966) suggested a definition of scent marking which stated that odour can be dispersed by urination, defaecation and the secretion of glandular material. The latter is usually associated with some form of body rubbing and in all cases marking should be distinct from normal actions such as grooming or elimination by virtue of qualitative and quantitative changes in the behaviour. However, the latter point excludes the incidental deposition of scent as, for example, from the interdigital glands found in many ruminants (see Pocock 1910; Müller-Schwarze 1971), or the possibility that some small mammals may mark burrows or runways as they run through them (as in the shrew, *Blarina brevicauda*, see Pearson 1946). Schenkel (1966) suggested that the term 'marking' should be used when a mark is set which persists and can be perceived by other members of the species and therefore make possible an indirect contact between them. This review is concerned with the occurrence and effects of these deposits.

The chemical composition of scent marks has in no case been fully determined. A number of authors have suggested that a pheromone is involved in 'territorial marking' (Kirschenblatt 1962; Wilson & Bossert 1963; Gleason & Reynierse 1969; Michael & Keverne 1968). However, they disagree over the effect such a pheromone might bring about. It is clear from the data examined in this review that scent marks can transmit various olfactory messages, some of which may be found to involve the action of pheromones. However, to suggest that there is a pheromone specifically associated with scent marking is probably misleading. Bronson (1971) has recently stressed that the term 'pheromone' (Karlson & Lüscher 1959) should only be used in those cases where it is reasonable to suppose that a single substance brings about a specific effect. Thus, in the case of scent marking, use of the term is probably inappropriate as the responses to scent marks are not clearly defined and it remains possible that the effects of scent marks are brought about by a variety of olfactory cues. The composition of mammalian scent substances is probably complex. The essential components (from the point of view of the perfume trade) of the secretions of the civet, *Viverra civetta*, and the musk deer, *Moschus moschiferus*, have been identified but they have been used very little

in behavioural studies (Wilson & Bossert 1963). Some progress in the analysis of the substances used in mammalian olfaction has been reported recently (see Brownlee et al. 1969; Curtis et al. 1971; Müller-Schwarze 1971).

Theories of Function

Marking behaviour is often referred to as 'territorial marking ' (for example, Thiessen, Friend and Lindzey 1968; Mykytowycz 1968), although, as Schenkel (1966) has pointed out, the relationship between marking and territory is rarely stated. In some cases it may be that marking bears no relation to territory. For example, the black rhinoceros, *Diceros bicornis*, has a well defined marking behaviour but is not territorial (Schenkel 1966). However, the function of marking is often described as one of territorial defence, i.e. warning other animals away (Hediger 1950, 1955; Lorenz 1953, 1966; Ropartz 1968a; Harrison-Matthews 1969; Mykytowycz 1970). This idea, besides being well established, is one of long standing. It is sometimes attributed to Goethe (1938) or von Uexküll (1934), but is also to be found in Merriam's (1884) account of the otter, *Lutra canadensis*, in which he referred to property marks acting as a warning to rivals to keep away. However, contrary to the claims of some authors (for example, Ropartz 1968a), there is a lack of evidence to support this explanation of scent marking. In fact, marking might play a part in any field of olfactory communication, and there have been a number of other suggestions as to its communication value. The most frequently proposed ones are listed below; they have been raised by various authors, with the exception of the last one where reference is cited. Scent marks might act as:

(i) a deterrent or substitute for aggression, to warn conspecifics away from occupied territory;
(ii) a sex attractant or stimulant;
(iii) a system of labelling the habitat for an animal's own use in orientation or to maintain a sense of familiarity with an area;
(iv) an indicator of individual identity, perhaps including information on sexual status, age, dominance, etc.;
(v) an alarm signal to conspecifics;
(vi) Wynne-Edwards (1962) has proposed that marking has an epideictic function: an indicator of population size.

None of these possibilities has been fully investigated and for most of them there is little experimental evidence. In the review which follows, data from field and laboratory studies of marking behaviour are evaluated with respect to these theories. The material is organized into three sections: (1) The location of scent marks. (2) The frequency of marking according to the motivational state of the animal or the prevailing stimulus conditions. (3) The effects of scent marks on the behaviour of animals encountering them.

(1) The Location of Scent Marks

If scent marks acted as a means of territorial defence it might be expected that they would occur most frequently at the territorial boundaries. Hediger (1949) commented that many species deposit scent where they meet or expect rivals; this would tend to be near the territory borders. This is supported by Lindemann's (1955) report that the European lynx, *Lynx lynx*, and the wild cat, *Felis silvestris*, bury urine and faeces within the territory but deposit them conspicuously near the boundaries. In most cases, however, scent marking is not confined to the borders of the territory. In the beaver, *Castor canadensis*, for example, most marking points are at the edge of the territory but some are near the lodge (Aleksiuk 1968). Richards (1967) stated that the European beaver, *C. fiber*, marked the territorial boundaries but he also recorded that marking points occurred throughout the territory. In the rabbit, *Oryctolagus cuniculus*, Mykytowycz & Gambale (1969) have shown that marking points are found within the territory as much as round it, but are more frequent in the direction of a neighbouring colony. Mykytowycz (1965) said that the marking behaviour of the rabbit probably saturates the territory with smell. Marking the whole area of the territory in this way is probably common. It has been reported that scent marks occur within the territory in the case of the European hamster, *Cricetus cricetus* (Eibl-Eibesfeldt 1953) and the water vole, *Arvicola terrestris* (Stoddart 1970), and Goddard (1967) reported that the scent marks of the rhinoceros, *Diceros bicornis*, were located more or less at random throughout the home range. It is also possible that, in some species, a female with young may mark the nest or home site in particular. There has been no direct observation of marking behaviour in this respect, but Rosenblatt, Turkewitz & Schneirla (1969) showed that

kittens of the domestic cat could find their way back to the nest using olfactory cues which were deposited in and around the nest, presumably by the mother. Rat pups have also been found to be capable of orientation towards odours coming from their nest (Gregory & Pfaff 1971).

It might be argued that the saturation of territory with the animal's own scent (Mykytowycz 1965) serves to make the area familiar. Ewer (1968a) believes that an important function of scent marks may be that their presence provides a sense of security and 'increases confidence'. In some instances scent is deposited to serve in orientation within the territory. Goddard (1967) showed that the rhinoceros was able to lay and follow faecal scent trails, and rats and mice are known to use urine trails (Eibl-Eibesfeldt 1950a; Reiff 1951).

It is important to note that marking behaviour does not occur only within the animal's territory. This is evident from the fact that an animal will mark in novel, laboratory situations (for example, the golden hamster, *Mesocricetus auratus*; the gerbil, *Meriones unguiculatus*, various authors) and also from observations in the field. Eibl-Eibesfeldt (1953) recorded that the male European hamster marked when in a female's territory, and Myers & Poole (1961) and Kykytowycz (1965) observed that rabbits marked in neighbouring alien territories which they sometimes visited.

Marking on Other Animals

Scent marks are sometimes placed on other animals. Mykytowycz (1962, 1965) recorded that the male rabbit will mark a female and, less frequently, the female will mark the male and also the young. The female occasionally engages in what appears to be self marking by rolling on dung hills (Mykytowycz & Gambale (1969). Mykytowycz suggested that this behaviour serves to identify individuals by a group odour. Marking on other animals has been reported in lemurs, *Lemuridae* (Petter 1965), in the sugar glider, *Petaurus breviceps papuanus* (Schultze-Westrum 1965), the tree shrew, *Tupaia belangeri* (Martin 1968), the mongoose, *Helogale undulata rufula* (Rasa 1973), and other examples may be found in Ewer (1968a) and Tembrock (1968). Spraying a conspecific with urine (enurination) appears to be fairly common in the rodents and lagomorphs (see review by Kleiman 1971). Kleiman suggested that it acts as a form of reassurance by giving the other animal a familiar smell and it might thus help to resolve the approach/avoidance conflict of an encounter.

The location of marking points is thus not necessarily related to the boundaries and defence of territory. In some cases their distribution suggests that scent marks might be for the animal's own use. They may act as a means of orientation or could have a psychological effect on the animal's 'sense of confidence'. The marking of other animals may be connected with the maintenance of group identity. More detailed studies are required, in the manner of that carried out by Mykytowycz & Gambale (1969), on the distribution of scent marks within an animal's territory or home range.

(2) The Frequency of Marking Behaviour

Ewer (1968a) stated that the factors which evoke marking are obscure. There is, however, some data on the effects of several factors on marking frequency. These can be broadly classified as those relating to aggressive behaviour, to sexual behaviour, and to novel stimuli; these are discussed below. Marking, aggression and sexual behaviour have a common physiological basis to the extent that they are all dependent on the sex hormones. The size and secretory activity of the scent glands in several species are influenced by the sex hormones (see, for example, Kupperman 1944a; Martan 1962; Mykytowycz 1962, 1965, 1966; Glenn & Gray 1965; Dryden & Conaway 1967; Stoddart 1972). In the gerbil, *Meriones unguiculatus*, the frequency of marking behaviour in both the male and the female is controlled by the sex hormones (Thiessen, Friend & Lindzey 1968; Thiessen & Lindzey 1970). Androgens affect marking through the hypothalamus (Thiessen & Yahr 1970). Experiments in which the olfactory bulbs of the gerbil were ablated showed that olfactory stimuli were also essential to the maintenance of marking behaviour (Baran & Glickman 1970; Thiessen et al. 1970).

There has been very little investigation of the frequency of apparently spontaneous marking; perhaps because it seldom occurs in the laboratory. Marking by the golden hamster in a familiar home cage appears to be infrequent in both the female (Richards 1966) and the male (Johnston 1970). A similar finding has been reported for the gerbil (Higgins, Glickman & Isaacson 1967). However, the absence of marking may be an effect of the laboratory situation; it is probably more frequent in a natural environ-

ment. There is evidence that a dominant animal may mark several times an hour during periods of activity in the case of the duiker, *Cephalophus maxwelli* (Ralls 1969), the rabbit (Mykytowycz 1965; Mykytowycz & Gambale 1969), and the mongoose (Rasa 1973). However, more data on the frequency of apparently spontaneous marking is required.

Marking and Novelty

Marking behaviour has been observed when an animal is introduced to a new cage in the case of the tree shrew (Martin 1968), the green acouchi, *Myoprocta pratti* (Morris 1962), and in the bushy-tailed woodrat, *Neotoma cinerea acraia* (Egoscue 1962). Marking also occurs when a novel object is introduced into the home cage. Martin (1968) reported, for example, that the tree shrew marked an object placed in the cage at once with the throat gland or with urine; initially marking was intensive but it rapidly diminished. Similar behaviour has been observed in the brush tail possum, *Trichosurus vulpecula* (Kean 1967), the marsupial mouse, *Sminthopsis crassicaudata* (Ewer 1968b), and in the gerbil, *M. unguiculatus* (Gallup & Waite 1970).

The frequency of marking as a response to novelty has been the subject of some laboratory studies on the gerbil. Baran & Glickman (1970) observed male gerbils in a neutral novel area, measuring 60 × 80 cm, and reported a positive acceleration in marking rate during the first 10 min, followed by a levelling off for the remainder of a 15-min trial. However, on exposure to the test situation on the following day, marking frequency reached a peak after 5 to 7 min and then declined. Thiessen, Blum & Lindzey (1970) tested gerbils for 5 min on each of 11 consecutive days in an area measuring 100 cm^2. They found that marking by both males and females increased over the 11 days, particularly between days 1 and 5. They also found that the frequency of marking, within the 5-min period, changed as testing proceeded. During the first day, marking occurred most towards the middle and end of the test period, but this pattern changed so that by day 5, most marking occurred during the first minute and the frequency subsequently declined. Thus it appears that marking occurs as a response to novelty, probably with maximum marking at some moderate level of novelty. These observations lend support to the idea that marking might serve to make an area familiar to an animal by a system of olfactory labelling.

Marking and Sex

Marking appears to be related to several factors which suggest it might have a sexual function although in what way is not clear. These are discussed below.

Development of marking. In a number of species it has been found that the development of the scent glands coincided with sexual maturity. It was reported, as early as 1914, by Johnsen to be the case in the shrew. Marking behaviour also first appears at this time. The male golden hamster, for example, becomes sexually mature at about 35 days of age, and the flank glands become apparent between the 30th and 35th day (Kupperman 1944a, b). Marking behaviour starts as early as day 25 but does not develop fully until about day 30 (Dieterlen 1959; Rowell 1961).

Sexual dimorphism of marking. The scent glands and marking behaviour generally appear to be sexually dimorphic; both sexes usually mark but males do so more frequently. The flank gland of the male golden hamster, for example, is more developed than that of the female (Kupperman 1944a; Lipkow 1954), and it appears from the observations of Payne & Swanson (1970) that males mark about three times more often than the females. In the case of the gerbil, males mark about twice as often as the females (Thiessen 1968), while in the rabbit, males mark ten times more than the females do (Mykytowycz 1962).

Seasonal variation in marking. Gland activity and marking behaviour have been reported to increase during the breeding season in some cases. An increase in gland activity is said to occur in the European hamster, *Cricetus cricetus* (Eibl-Eibesfeldt 1953), and in the Siberian hamster, *Phodopus* (Vorontsov & Gurtovoi 1959). Stoddart (1972) showed that this was also the case in the water vole, *Arvicola terrestris*. Mykytowycz (1965, 1966) reported that the gland activity and marking behaviour of the rabbit increased during the breeding season and Townsend (1953) found that during the summer the beaver showed a peak of marking activity in July, although it is not clear how this relates to their breeding cycle.

In other cases, however, marking activity is reported to show no seasonal variation. Erlinge (1967, 1968) reported that the otter, *Lutra*

lutra, which mates mainly in the late winter or early spring, continued to mark throughout the year with a decline during the summer months (May to August) when the animals were observed to be generally less active. It has been stated that the scent glands of the shrew, *Blarina brevicauda* (Pearson 1946), and the gerbil, *Rhombomys opimus* (Sokolov & Skurat 1966) are active throughout the year and are therefore not connected with breeding. In the squirrel, *Sciurus caroliensis*, Taylor (1968) stated that peaks of marking activity occurred outside as well as within the breeding season. It thus seems that there is considerable variation between species in this respect. The point is well illustrated by the observations of Quay (1953) on the scent glands of five species in the genus *Dipodomys* (kangaroo rats). He found that gland size showed a clear seasonal cycle related to breeding cycle in two species, but in the others there was no seasonal change in gland activity, or, a seasonal cycle with no relation to the cycle of breeding activity.

Thus, while in some species marking may be related to breeding activity, in others it is not confined to the breeding season and it probably has other functions. There is, however, a lack of data on cyclic variation in marking behaviour (as opposed to gland activity) for the majority of species.

Oestrus and marking. It has been shown that oestrous state may be communicated by olfactory cues (for example, in the rat, Le Magnen 1952; Carr & Caul 1962), and it is possible that the scent marks of females carry this information. If this were so, cyclic variation in the marking activity of females, related to their oestrous cycle might occur. Beach & Gilmore (1949) found that the urine marks of the female domestic dog indicated her oestrous state to the male and that she urinated more frequently when in heat. Kleiman (1966) lists several other species in the family Canidae in which the female only marks at the time of oestrus, or with greater frequency during oestrus. Grassé (1955) stated that, in many species, the glands of the female secreted most at the time of sexual receptivity.

There appears to be no full investigation of marking frequency and the oestrous cycle in any species. However, there are a number of statements on this topic which are typical of the state of much of the marking behaviour literature in that they are not accompanied by supporting data and show some disagreement. In the golden hamster, for example, it has been stated that the female produced less flank gland secretion when in oestrus and did not exhibit marking behaviour (Brust 1953; Dieterlen 1959). This was also reported to be the case in the shrew (Pearson 1946), and possibly in the rabbit (Mykytowycz 1966). However, the contention of Brust (1953) and Dieterlen (1959) was contradicted by Whitney (1963) who stated that the flank glands of the female hamster produced a secretion only when she was in oestrus. Grassé (1955) also said that the female hamster marked particularly when in oestrus, but with glands in the genital region and not the flank glands. Dieterlen (1959) recorded that the female hamster marked with genital glands as well, though he claimed that these glands were sometimes active in anoestrous females as well as those in oestrus.

It is clear that there is a need for a more adequate investigation of this aspect of marking behaviour. [Data included in papers by Tiefer (1970) and Payne & Swanson (1970) appeared to show that the female hamster marked least when sexually receptive. However, in both these studies, females were tested in the presence of males as the primary interest lay in the interaction between males and females. Thus receptive females may have shown less marking behaviour because they spent the duration of the trial copulating.]

Marking is thus apparently related to several sexual factors which suggests it might have some sexual function. However, it has been shown that in the golden hamster (see Kirkman & Algard 1964) and the gerbil (Mitchell 1967) the scent glands, and therefore presumably the scent they produce, are not essential to mating as it is accomplished successfully even after the gland has been excised. There appears to be no published data on the frequency of marking in the course of mating although some statements on the subject have been recorded. Eibl-Eibesfeldt (1953) commented that the male European hamster scent marked on entering a female's territory prior to mating, and Whitney (1963) stated that the flank gland of the male golden hamster became damp with secretion when he was sexually excited. Marking during sexual excitement is reported to occur in the rabbit (Myers & Poole 1961), the agouti, *Dasyprocta aguti aguti* (Roth-Kolar 1957), and in several of the lemurs (see Petter 1965; Jolly 1966). There is also some evidence that enurination in several species of rodents and lagomorphs occurs particularly during courtship (Kleiman 1971).

It may be, however, that while marking is related to sexual status (i.e. sex, sexual maturity, and, in some cases, oestrous and seasonal cycles) its function is not necessarily associated directly with mating.

Marking and Aggression

The mediating role of olfactory cues in aggression has been demonstrated in mice (see Mackintosh & Grant 1966; Ropartz 1968b, and the review by Bronson 1971), and it is possible that such cues occur in the scent gland secretions, and thus the scent marks, of other species. An association between marking and aggression and dominance has been reported for a large number of species. Marking behaviour is related to dominance status; for example, in the rabbit, dominant animals mark more than those of lower social status (Mykytowycz 1965) and the same is true of the gerbil (Thiessen et al. 1971). Mykytowycz (1965) recorded an increase in marking activity when rabbits engaged in aggressive encounters. Sometimes marking may serve as a threat or warning in lieu of aggression, as in the account given by Lockley (1961) of a dominant rabbit marking immediately before it chased off a subordinate. Other observations which support the suggestion that marking and aggression are closely related, have been reviewed by Ralls (1971) to whom the reader is referred for further details. Some additional examples are to be found in Ewer (1968a). Ralls (1971) concluded that animals appear 'to mark frequently in any situation where they are both intolerant of and dominant to other members of the same species'. The occurrence of marking in conjunction with aggression suggests that it plays some part in threat display, and thus, perhaps, in territorial threat. However, it is important to note that its effect in aggressive encounters has not been determined. In some cases it is used independently of any territorial context as, for example, in the observations of Mykytowycz (1965) and Lockley (1961) referred to above, where marking occurred in encounters between colony members as much as between territorial rivals. Further discussion of the role of marking in territorial defence will be found in the account of the responses of animals to scent marks.

Marking as a response to an encounter with a conspecific is perhaps closely related to scent emission as a reaction to an individual of another species, perhaps as a means of defence. The well-known example of this use of scent is found in the behaviour of skunks and it also occurs in certain species of civet and mongoose (Bourlière 1955). According to Koenig (1957) and Münch (1958) the marmot, *Marmota marmota*, releases a secretion from the anal glands as a means of defence, and Hediger (1959) recorded the case of a captive lemur which marked in response to someone approaching its cage.

In some cases gland secretions may be deposited as a response to a predator with the effect of signalling alarm to conspecifics. It has been reported that the mouse and the rat can discriminate between the odours from stressed and unstressed animals (Müller-Velten 1966; Valenta & Rigby 1968; Carr, Martorano & Krames 1970; Carr, Roth & Amore 1971). Olfactory cues of this type might be deposited in scent marks. Müller-Velten (1966) found that mice avoided the odour from the urine of stressed mice, and Donovan (1969) has claimed that the domestic dog will avoid the anal gland secretion from a frightened dog. Müller-Schwarze (1971) found that the black tailed deer, *Odocoileus hemionus columbianus*, released scent into the air from the metatarsal gland when frightened but he also suggested that scent may be deposited from the interidigital gland when the animal is in flight. There is, however, no experimental evidence that scent marking is used to communicate alarm; in fact, volatile scent emitted directly from the frightened animal might be expected as this would provide a more rapid means of communication and the signal would not persist for as long as a scent mark might.

Thus scent marking may be used as a threat to other species as well as to conspecifics or might, in some cases, function as an alarm signal. There is a shortage of information, however, on the effects of scent marks in these respects.

(3) The Responses of Animals to Scent Marks

Response to Scent Marks of the Opposite Sex

Olfactory cues may serve to attract sex partners to each other (see Le Magnen 1952; Godfrey 1958; Carr & Caul 1962; Bronson 1971). or may act as stimulants to sexual behaviour (for example, in the golden hamster, Murphy & Schneider 1970). Noble (1939) suggested that scent marks might make an animal's territory sexually stimulating to the opposite sex; however, there is little evidence available for either attractive or stimulating properties of scent marks.

Michael (cited in Michael & Keverne 1968) stated that a female cat in oestrus showed the patterns of behaviour typical of her response to a male if she was placed in a cage recently occupied and marked by a male. It has been suggested for several species, that scent marks of females attract males to them (for example, the slow loris, *Nycticebus coucang*, Seitz 1969, and the grey squirrel, Taylor 1966). Beach & Gilmore (1949) showed that urine from female dogs in oestrus was more attractive to males than urine from anoestrous females and Donovan (1969) found that the anal gland secretion of an oestrous bitch stimulated mounting by the male. Both these signals would be deposited at the urination and defaecation points of an animal. Rowe (1970) found that mice, *Mus musculus*, were attracted to traps by olfactory cues left by an animal of the opposite sex which had previously occupied the trap, and Moore (1965) showed that the deer mice, *Peromyscus maniculatus* and *P. polionotus*, were attracted to a box which had previously contained a female. These observations show that a scent mark can act as an attractive stimulus to a member of the opposite sex; however, there is no evidence to show that they do act in this way in a natural situation. As with the use of scent as an alarm signal, it would seem to be more adaptive to attract a mate by a volatile signal rather than a scent mark so that the animals are attracted to each other directly rather than to the general area in which they are living. Scent trails could be used in this context but this has not been observed in any species. Beach & Gilmore (1949) suggested that this might occur in the case of the dog.

In opposition to the idea that scent marks might serve to attract mates, it has been suggested that a receptive female may be inhibited from marking and thus cease to warn other animals away (Harrison Matthews 1952). The information on this aspect of marking is inconclusive and, once again, further research is needed. There seems to be a particular lack of data on the marking behaviour of females.

Response to Scent Marks of the Same Sex

The observations reported in the literature of the behaviour of males when the scent marks of other males are encountered, are reviewed below divided into five categories of response.

Avoidance of a scent-marked area. It is sometimes suggested that scent marks warn other animals to keep out of occupied territory. However, there appear to be no observations of animals withdrawing after encountering an alien scent mark. Leyhausen (1965) said that there was no evidence for a deterrent effect of scent marks in cats, and it is well known that the domestic dog does not withdraw from an area scent marked by another dog (Scott 1967). It was suggested by Leyhausen & Wolff (1959) that scent marks might act 'like railway signals' to minimize encounters between individuals by signalling how recently an animal has passed. There is some evidence that this occurs in the cheetah, *Acinonyx jubatus*, in which there are no fixed territories but each group of animals appears to avoid encountering other groups (Eaton 1970). The scent marks of the otter may also have this sort of effect (Erlinge 1968) where intrusions, even to the centre of a neighbouring territory, are probably common. In fact, invasions of this sort into marked territory have been observed in several cases. Eibl-Eibesfeldt (1953) stated that a marking point of the European hamster, while probably acting as a warning, was never observed to frighten another animal away and territorial intrusions did occur. In the rabbit, also, visits are made into the neighbouring territories (Myers & Poole 1961; Mykytowycz 1965). Thus withdrawal from a scent-marked territory is clearly not the usual response. A more likely territorial effect of scent marks is suggested below.

Modification of behaviour in response to a scent mark. Some observations have been recorded which show that when an animal enters alien territory, a general modification of behaviour may occur. The predisposition for an animal on home ground to win in an aggressive encounter, and for the intruder to flee, has been known in the context of the laboratory cage for some time (see Dice 1929; Crawford 1939; Nice 1941). In the field Mykytowycz (1965, 1968) has described how a rabbit, upon entering alien territory, becomes alert, moves with an altered posture, ceases to feed and will flee from an occupant of the territory regardless of the rabbits dominance status within its own colony. Similar observations have been reported for the marmot (Münch 1958), and in an experimental study of the behaviour of the gerbil in the presence of alien scent marks, Thiessen et al. (1970) reported that the animals appeared to become more hesitant and cautious. These changes in behaviour might be due to olfactory cues, particularly the scent marks, of the territory occupier, but could also be a response to any novel environment or to the absence of the

animals own scent marks. The relative importance of these factors has not been investigated. It seems probable, however, that although scent marks do not cause avoidance, they may signal that an animal is in foreign territory and predispose withdrawal in the presence of the resident animal. It is thus reasonable to suppose that in the course of repeated territorial encounters, scent marks of another animal might acquire aversive properties through a learning process. This has not been investigated experimentally, but there is some support for the idea to be found in the results of Nyby, Thiessen & Wallace (1970).

Approach to a scent mark. There are several accounts in the literature of males approaching the marking points of other males. This phenomenon is familiar to us in the behaviour of the domestic dog and cat, but it also occurs in species which appear to maintain a more exclusive territorial system. An interesting example of this is provided by the method of trapping beavers related by Audubon & Bachman (1847) in which beaver castor (the preputial secretion used in marking) is used as an effective bait in the traps. Audubon & Bachman also stated that beavers visited the marking points of their neighbours, and Erlinge (1968) reported that the otter made journeys which had the apparent goal of investigating the scent left by other animals at marking points. A laboratory test to determine whether alien scent marks were approached or avoided, was carried out by Baran & Glickman (1970). Male gerbils were found to show a preference for shredding paper impregnated with alien sebum compared to either neutral paper or paper carrying their own sebum. Baran & Glickman concluded that approach rather than aversion to alien sebum was indicated by this result. In support of this, Thiessen, Lindzey & Nyby (1970) reported that male gerbils, but not females, showed 'obvious interest' in a pad impregnated with sebum from another male compared to a neutral stimulus. Rowe (1970) found that male house mice were attracted to traps previously occupied by unfamiliar males.

Thus the evidence suggests not only that male scent marks probably do not bring about avoidance by other males, but that the converse may be true, i.e. that they have attractive properties.

Marking behaviour as a response to a scent mark. In conjunction with an approach to a scent mark, a marking response has been observed in a number of cases. This is, once again, well illustrated by the domestic dog and is also reported in other members of the Canidae (see Heimburger 1959), and in the domestic cat (Leyhausen 1965). An animal may also mark when alien marking material is presented to it artificially. Aleksiuk (1968) found that the beaver marked when it encountered alien castor which had been placed in its territory, and Martin (1968) reported that objects already marked by tree shrews seemed to produce intense marking when presented to others. Rasa (in press) observed that if a mongoose was placed in an alien cage it immediately marked at the alien marking points. That this sort of response is elicited by the alien mark rather than by other properties of the marking site, and is not the same as a marking response to novel stimuli discussed earlier, is demonstrated in the case of the sugar glider by the observations of Schultz-Westrum (1965). He found that a group of sugar gliders marked an object more when it had been previously marked by another group of animals than if it was presented as a clean, novel stimulus. A similar finding was reported for the golden hamster (Johnston 1970) and the mongoose (Rasa 1973). The increase in marking observed when an animal entered a cage already marked by another, unfamiliar animal, was found to be greater than that which occurred after introduction to a similar clean cage.

Experiments with the rabbit showed that if alien faecal pellets were placed in the rabbit's home territory or cage, they elicited intense marking (Mykytowycz 1968; Mykytowycz & Hesterman 1970). However, if a rabbit was placed in the completely unfamiliar territory of another rabbit, it did not mark, although it did mark in a socially neutral, novel area. In addition, it has been reported that when a rabbit enters a territory which it regularly visits, some marking activity continues to occur (Myers & Poole 1961; Mykytowycz 1965). These observations suggest that the response to an alien scent mark may vary according to the context in which it is encountered. This may be an important consideration for the inerpretation of laboratory studies in the absence of field studies. It has been shown by Nyby, Thiessen & Wallace (1970) that gerbils may learn to modify their marking frequency, apparently in response to olfactory cues associated with attack and defeat.

In some species, however, it seems that an alien scent mark may be the primary stimulus for marking behaviour. This possibly applies

to the development and maintenance of the communal marking sites of colonial species, as, for example, in the desert cavy, *Microcavia australis* (Rood 1970), several Heteromyid rodents (Eisenberg 1963, 1964), the rabbit (Mykytowycz 1965; Mykytowycz & Gambale 1969), several species of zebra, *Equus* (Klingel 1967, 1968), and the mountain goat, *Creamnos americanus* (Geist 1964). In these cases the same marking points are used by all members of the group. Of greater interest, however, are the cases in which it has been observed that common marking sites are used by animals living in separate territories. Audubon & Bachman (1847) included a description of how the scent marking sites of the beaver were located on the borders of neighbouring territories; animals from both territories were alleged to contribute to them. Erlinge (1967, 1968) reported that established scent marking sites were common to all individuals in the district; animals visiting them deposited their own scent after investigating that left by others, and Eaton (1970) observed that a group of cheetahs encountering the scent marks of another group, inspected them and then marked the same place. Jolly (1966) reported that lemurs, *Propithecus verreauxi*, would mark a place which had been marked some time before by the members of another troop. Goddard (1967) found that the rhinoceros was mainly solitary but the home ranges of individuals overlapped and several animals used the same dung hills as marking points. A form of communal marking is also reported in the spotted hyaena, *Crocuta crocuta*. Harrison Matthews (1939) recorded a case of a latrine site of the hyaena which covered an area of a quarter of an acre. The social relations of the animals using this site was not stated but presumably a large number of animals was involved. Kruuk (1966) has stated that single packs of hyaenas containing as many as 100 animals had been seen.

The establishment and use of marking points common to a large number of animals would appear to give support to the idea that they act as loci for the general exchange of information, as suggested by Seton in 1910. Odour is used as a means of identifying individuals in the mouse (Bowers & Alexander 1967), and the gerbil (Dagg & Windsor 1971), and Kalkowski (1968) has shown that mice can discriminate between the individual scent traces left by others. Rasa (1973) found that mongooses could be trained to discriminate between the anal gland secretions, which are deposited as scent marks, of different individuals. It may also be inferred that information concerning individual identity is contained in the scent marks of other species from the observation that when, for example, two golden hamsters meet they investigate, in particular, each other's flank glands. This led Petzsch (1951) and Lipkow (1954) to suggest that a cue for individual identity was present in the secretion of the gland. Behaviour whereby attention is paid to the scent glands when two animals meet, has also been reported in the European hamster (Eibl-Eibesfeldt 1953) and in the black tailed deer in which the tarsal gland is the subject of investigation (Müller-Schwarze 1971). It is probable that the communication made through this behaviour also occurs when the glandular secretions are encountered in the form of a scent mark. Hesterman & Mykytowycz (1968) found that human subjects could discriminate between the anal gland secretions (which coat the faecal pellets used in marking) from different rabbits, on the basis of the intensity of the odour, with respect to age, sex, breeding condition and social status. Scent marks may thus signal a number of pieces of information about the animal which deposited them.

A further explanation of the communal nature of scent marks was given by Wynne-Edwards (1962). He suggested that 'the establishment of special points to which animals go to deposit their scent and seek that of their fellows' had an epideictic function. There is some evidence that the frequency of marking may, in fact, vary with changes in population density. Erlinge (1968) reported that otters increased their marking activity at times of high density. In 1 year, for example, the density of otters was one per 3·6 km of river and about 80 per cent of the marking points were being visited regularly; in the following year the density fell to one otter per 5·0 km and only about 40 per cent of marking sites were regularly visited. It is also interesting to note that Kock, Stoddart & Kacher (1969) in their study of lemmings, *Lemmus lemmus*, during a population peak, observed that large latrines were formed along the migration routes. These measured 20 to 30 cm in diameter and were a few centimetres high, sometimes occurring at intervals of several metres. It is not known if an increase in marking activity by all individuals was involved or if the size of the latrines was simply related to the number of animals passing them. Clearly the presence of the faeces

of other animals was a stimulus for an animal to deposit its own. Mykytowycz & Gambale (1969) showed that the number of dung hills in a rabbit colony appeared to be related in some way to changes in population size; this was not, however, the only factor affecting their frequency. In another study on density and marking, this time with the chin gland of the rabbit, Myers et al. (1971) reported some ambiguous results which appeared to show that marking increased when fewer rabbits were present in a limited area. Also, it was reported by Thiessen et al. (1971) that gerbils, housed in various densities, showed a decrease in marking activity in a test situation, as the number of animals housed together was increased. The results of these studies are difficult to interpret but they suggest that the relationship between marking frequency and population size may be an interesting area for further investigation. It has been suggested that marking could affect the breeding condition of a population of animals through the distribution of primer pheromones (see Ralls 1971).

Threat as a response to a scent mark. There are some observations of a threat display in response to alien scent marks; they support the view that marking itself contains an element of threat. For example, Eibl-Eibesfeldt (1953) reported that the European hamster ground its teeth in a characteristic expression of threat upon smelling the scent mark of another animal. Similarly, Aleksiuk (1968) observed that the beaver hissed when smelling an alien mark in a manner which he believed to be associated with aggressive threat. A threat display in response to alien scent from the cheek gland of the mongoose is also reported to occur (Rasa 1973). In some instances the threatening behaviour patterns occur together with marking behaviour.

From the preceding sections it is clear that a number of events can occur in response to an alien scent mark. Approach, investigation and marking behaviour are probably the most usual. The nature and strength of the response made to a scent mark may depend on the social relations and experience of the animals and perhaps also on factors such as the time of year.

The Response of an Animal to its Own Scent Marks

Finally, it is also relevant to consider the effects an animal's own scent marks may have on itself. An animal's own scent might act to 'increase its confidence' (Ewer 1968a). It has been suggested that this effect of scent, after it has been released as a response to novelty or fear, may have been fundamental to the origin of scent marking behaviour (see Morris 1956; Kleiman 1966; Ewer 1968a). It is often said that scent marks could provide a sense of 'homeliness' for an animal (for example, Eibl-Eibesfeldt 1953; Mykytowycz 1968), but there appears to have been no experimental investigation of the response of an animal to its own scent marks. The observations of the use of scent trails already mentioned, show that scent marks do sometimes act as cues to the animal that deposited them. The idea that scent marks might increase an animal's confidence is supported by an anecdote related by Eibl-Eibesfeldt (1950b) in which a badger, *Meles meles*, frightened by a strange environment, was calmed by the presentation of an object which had its own scent on it.

Discussion

It will be clear from the content of this review that there is a shortage of data relating to the occurrence and functions of marking behaviour, and that there is a great deal of scope for experimental work. There is some evidence to support a number of different explanations of the function of scent marks.

Marking is associated with aggression and dominance in many species and this suggests that it is involved in some way with threat or with territorial motivation. However, its exact role in this context has not been determined. In some cases scent marks possibly occur more frequently at or near territorial boundaries, but they do not appear to cause withdrawal or warn intruders away. It may be that they bring about a general modification of behaviour, in particular a predisposition to flee, and it is possible, moreover, that scent marks might acquire aversive properties; but these are both untested hypotheses.

There is a limited amount of evidence to support the idea that scent marks might act as alarm signals, in that marking may occur in some species when an animal is frightened.

Scent marks may have some function associated with sexual activity but in what way has not been determined. Marking is found to be connected with several factors related to breeding (sexual dimorphism, sexual maturity, possibly the oestrous cycle), and in some cases it may be related to the cycle of reproductive activity. In other cases it is not confined to the breeding

season and therefore some function unrelated to breeding is implied.

The fact that marking often occurs as a response to novelty and that an animal may scent mark throughout its territory or range, lends some support to the idea that marking is acting to make the habitat familiar. There are also observations which show that scent marks are sometimes used in orientation, through the formation of scent trails, and perhaps also in the orientation of young animals to the home site.

In many species it is found that common marking sites are used by several individuals and marking points may be sought out and appear to elicit marking behaviour. This might be interpreted as indicating that scent marks act as sites for a general exchange of information. It seems likely that scent marks can be used to indicate individual identity and status, and in some cases, where they are used to mark other animals, a group odour may be involved. In this respect scent marks might play a role in the territorial organization of a community. The observation that marking may occur as a communal activity and also that the frequency of marking may vary with changes in population size, raises the possibility that marking might be involved in some way in the regulation of population density.

Thus it appears that marking behaviour can have a number of functions. In this review a variety of species have been used to illustrate the points made and it is probable that marking serves different functions in different species. This is suggested, for example, by the variation found between species in the relationship between cyclic changes in marking activity and breeding.

Many species have more than one source of scent secretion, any of which might be used in scent marking (for example, in the sugar glider, Schultze-Westrum 1965; the tree shrew, Martin 1968; the rabbit, Mykytowycz 1968; and many rodents have glands at more than one location, see Quay 1965, 1968; Quay & Tomich 1963). Marks originating from different sources may have different effects. It was noted by Pocock (1910) that even to a human observer, the odour of four separate glands of the gazelle, *Gazella dorcas*, were distinct. There is experimental evidence to show that different glands in the case of the black tailed deer (Müller-Schwarze 1971) and the mongoose (Rasa 1973) have separate functions. Moreover, there is no reason why a single scent mark should not, for example, signal 'home' to the marking animal, act as an identity check for another member of the colony, and signal threat to a foreign male or the presence of a potential mate to a female. A common misconception seems to be that all scent marking behaviour can be treated as analogous whereas in reality it is obviously a diverse behaviour and scent marks can have many functions.

The deposition of odoriferous secretions, urine or faeces, to form a scent mark, is a part of an animal's system of olfactory communication. It is distinct from the release of a volatile scent directly from an animal, in that scent is deposited by specific action patterns, but it is not necessarily distinct by any functional criterion. In fact the relative permanence of a scent mark compared to a volatile release of scent, would result in it being particularly adaptive in certain contexts, for example, in scent trails or in the maintenance of social organization perhaps through labelling territory. However, the term 'territorial marking' is often not appropriate because in many instances marking behaviour is clearly unrelated to territory and in no case has its communication value with respect to territorial organization been determined.

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