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Animal Scent Marking

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Preface

The focus of this eBook is on scent marking and the source of the scent of some wild mammalian species in order to provide compiled information on role of scent in their sexual communication, behaviour of territory and dominance, role of scent marking in communication behaviour and movement tracks. Scent marking is a special pattern of behaviour where by animals transmits chemical communication signals into their immediate environmental objects. Scent marks are a form of status signal, advertising territory ownership, and condition dependent signals of quality and competitive ability. Since likely with the variation of behaviour, scent-marking mechanisms of species of mammals also varies from species to species, thus, this eBook will provide some information on mechanisms and different strategies of scent marking positions by different groups of mammals.

The author would like to acknowledge all-important source of reading materials cited in this eBook.

Chapter I

Introduction

Scent marking is a special pattern of behaviour whereby animals transmit chemical communication signals into their immediate environmental objects.[1] Scent marks are a form of status signal, advertising territory ownership, and condition dependent signals of quality and competitive ability.[2] In common with animal signals in other sensory modalities, scent marks provide a means of assessment,[3,4] which informs receivers about the signaler's quality.[5] Information about the location, density, freshness and chemical properties of scent marks are likely to contribute to the appraisal of the signaler by the receiver before the participants meet.[5,6] In a territorial context, the product of this appraisal may be a decision to avoid the risk of meeting the signaler by withdrawing from the territory.[7] Mammalian scent marking is often associated with territorial defence.[2,8,9]

Secretions of specialized integumentary glands of various types play a major role in this behaviour. In addition to secretions of specialized integumentary glands, urine, faeces, saliva, vaginal secretions and even sweat play some roles in the transmission of species specific chemical messages.[1,6,10] Mammalian scent marks typically comprise of a complex mixture of volatile and nonvolatile components, although not all of these may be involved in signaling, particularly in the cases where animals use excretory products (urine or faeces) for scent marking.[3] Scent marking has been considered as an integral part of the repertoire of behaviours involved in aggressive behaviour.[5] It would appear that the presence of scent marking odours increases the confidence of own territory and decrease the confidence of intruders.[11]

The perception of a strong odour, the production and deposition of scent are closely correlated in every mammalian species[10] in which olfaction is one of the dominant sensory systems.[12] The olfactory stimulus, which releases scent marking, can be any strange foreign odour, thus, exploration of a new environment is often coupled with an increase in the frequency of scent marking.[13] The occurrence of scent glands in several species of mammals indicates the salient role in the chemical communication systems of mammals. The locations of such glands at specific body sites of behavioural relevance facilitate an easy transfer of the secretions on to the objects in their environment.[14]

According to Lazaro-Perea et al., [6] scent marking in mammals has been frequently related to within group social and reproductive dominance and to defence of territory and resources. Due to the diversity of information that can be coded in a single signal, chemical cues can often serve different functions at the same time.[2] Alternative hypotheses, however, have been proposed for scent marking in mammals: identification of species, subspecies, group, or individuals, signaling social and reproductive status or promoting synchronization of reproductive cycles, attracting members of the opposite sex, labeling resources, and reassurance/confidence.[6,10,15,16]

Lazaro-Perea et al.,[6] proposed various hypotheses regarding the possible functions of scent marking in mammals. These basically fall into five categories such as: the first hypothesis is the territorial demarcation, which explains the scent marks act as a form of advertisement of ownership of their territories and conflicts are avoided by convention. A crucial component of this hypothesis is that home ranges are in fact true territories, with little or no overlap. Moreover, this hypothesis predicts that scent marking occurs more in perimeter of the territory. Pumas incorporate scent secretions from glands between the toes scratches on standing tree and maintain their territories (Figure 1).

Figure 1 Puma scent marking on a tree.[17]

The second is the ownership hypothesis. According to this hypothesis, animals scent mark to identify and claim ownership of food resources within a home range, and to indicate a priority of use of the resource. Thus, food trees are predicted to be marked more often than nonfood resources. The third hypothesis, mate attraction hypothesis suggests that females may scent mark as a way to advertise reproductive state and provoke male to male competition. If females use scent marks to attract mates, they are expected to scent mark at higher rates during the mating season or periods of estrus.[18] A fourth hypothesis suggests that scent marking is a form of non-combative fighting.[19] If scent marking is a form of non-combative fighting between groups, then animals are expected to scent mark more during intergroup encounters and when individuals or groups have overlapping home ranges. The final hypothesis, self advertisement hypothesis predicts that animals scent mark on unmarked substrates to avoid any blending or masking effects that might occur with scent marks that over mark another individuals scent mark.

Scent marking is a complex form of communication that is used by adults both within and between groups. This type of signals may serve different functions for different individuals.[6] During agonistic encounters and territorial defence, mammals over mark the competitors scent mark.

Scent over marking refers to cases in which the scent mark of one individual partially overlaps or completely covers the scent marks of another individual.[12] Scent over marking occurs when an animal deposits its scent mark on top of the scent mark of a conspecifics. Over marking may provide advantages in the transfer of information to the individual whose scent is on top but not to the individual whose scent is at the bottom.[20]

Over marking has been reported in numerous species of mammals in a variety of social contexts, mostly during agonistic encounters, during territorial disputes, on prominent objects and near the habitat of a potential mate.[2] Studies on golden hamsters (*Mesocricetus aurutus)* and meadow voles (*Microtus pennsylvunicus)* show that animals exposed first to an over mark, respond preferentially and display a better memory for the odour of the top scent donor than that of the bottom scent donor.[12] This preference for the top scent suggests that these animals treat the odour of the top scent donor as being more important or having greater value than that of the bottom scent donor.[20]

Over marking can be sighted when an animal urinating over a faecal or urine mark of another animal.[21] Virtually, all terrestrial mammals have at least one type of scent marking behaviour by which individuals deposit scents from specialized glands, other secretions (e.g., saliva), or excretory products, e.g., urine or faeces.[7,12] Sillero-Zubiri & Macdonald[22] have revealed that, the Ethiopian wolves vigorously over mark neighbors' scent marks. Over marking could be a form of competition between rivals in which individuals can target specific individuals by covering their scent marks.[12] Such competition is likely to be energetically expensive because rivals are likely to respond in kind, calling for a counter response, as each individual is likely to have several rivals.[21] Empirical studies have led to the formulation of three hypotheses and predictions about the role of over marking in mammals.[20] The first hypothesis states that animals over mark to announce their presence in an area; essentially, over marking creates a community bulletin board. The community bulletin board hypothesis predicts that individuals will over mark the scent marks of all conspecifics. The second hypothesis states that animals over mark to form a group scent that is unique to that population. The group scent hypothesis predicts that animals will over mark the scent marks of group members more often than those of novel individuals. The third hypothesis states that animals over mark the scent marks of competitors. The competition hypothesis predicts that animals will over mark the scent marks of align individuals more often than those of group members. Studies on rodents suggest that over marking may be a form of competitive olfactory communication.[12]

Most mammals scent mark by depositing faeces, urine and secretions of specialized skin glands on objects in their environment.[5] This behaviour has often been related to territorial defence.[2] In the context of intraspecific competition, the abundance and distribution of resources within a territory could produce different spatial patterns of scent deposition, which aim to maximize the defencibility of limiting resources within territories and reduce the costs of their defence.[19] Many mammals use scent marks to advertise territory ownership.[18,23] Territorial marking is a behaviour used by animals to identify and demark their territories.[23] Most commonly, this is scent marking, accomplished by depositing strong smelling chemicals such as urine and faeces at prominent locations within the territory.[13] Scent marks in the environment continue to provide information to conspecifics when the owner is absent, and are used by territory owners to demonstrate their competitive superiority by ensuring that their own marks are the most abundant in their territory.[7] This is a reliable signal of competitive ability, because success in defending the territory is a prerequisite for maintaining scent marking coverage of the defended area.[8] Thom & Hurst[7] in their investigations of individual recognition by scents suggested that for territory marks to demonstrate ownership and competitive ability effectively, they must contain an individuality signal that allows potential competitors and females to recognize the territory owners. Without this identity information, all the benefits of scent marking are lost. For this reason, territorial scent marks are an ideal cue in which to look for individual identity signals.[18] Scent marking possibly plays a role in territory defence and may be involved in dominance behaviour.[13] Gray Wolf and red fox defend their territories from other packs through scent marking, which involves urination and defecation (Figure 2A) (Figure 2B). Often the scent contains carrier proteins, such as the major urinary proteins, to stabilize the odours and maintain them for longer.[24] Not only does the marking communicate to others of the same species, but it is also noted by prey species and avoided.[10,25] For example, leopards and jaguars mark by rubbing against vegetation. Some prosimians, such as the red-bellied lemur, also use scent marking to establish a territory. Many ungulates, for example the blue wildebeest, use scent marking from two glands, the pre-orbital gland and hoof glands.[26]

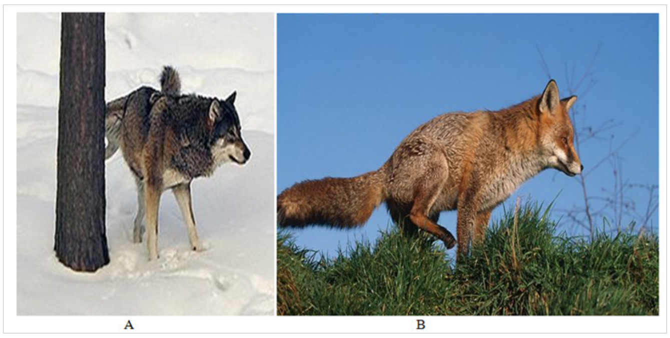

Figure 2 (A) Gray wolf (*Canis lupus*) and Red fox (*Vulpes vulpes*). **(B)** Scent marking their territory.[27]

Chapter II

The source of scent

In most mammalian species, individuals use several sources of odours for communication.[10] The sources include urine, faeces, vaginal secretions, saliva, and skin glands.[10,12] Mammals use urine, faeces, or the secretion of specialized skin glands to mark their territories. These sources can carry different information and thus, have different functions.[8] As it is stated by Eisenberg & Kleiman[10], species specific odours as well as community odours arise from several sources. The active components of scent gland secretion, urine and faeces may differ due to genetically controlled metabolic variations for a species or population.[7] Each scent source provides many different messages or types of information about the sender and that different scent sources have overlapping information but also can have some unique information.[28] A glandular secretion does contain a pheromone and even if there is a specific receptor protein, specialized receptor cells, or both for this pheromone and there are neural pathways in the central nervous system for response to this chemical, the pheromone will still be perceived in the context of the odour quality of the mixture.[12] For example, if a male rodent smells the urine from another member of its own species, it might have hard wired sensory mechanisms for one or more individual compounds, but in addition, it will also perceive information on the basis of the overall quality of the odours, e.g., individual identity, major histocompatibility type, or genetic relatedness (kin or nonkin).[10]

Johnston[12] suggested that mammals have discrete sources of chemical signals in specific locations on the body and that different sources contain signals or information that differs to some extent. The secretions may be generated in a gland and then spread by the sender on another part of its own body. Alternatively, the substances may be deposited on specific loci in the environment, such as branches of trees through active scent marking. The glandular secretions may also diffuse from the body of the sender into the air and to a partner,[8,10] a process known as passive marking.

Origin of scent particles

There are different sources of odours in mammals. Odour may comprise chemicals provided by food, synthesized by the animal or produced via bacteria. Often, scent organs are moist, warm and anaerobic, perfect conditions for bacterial development.[29] Species' metabolic products contain signal compounds, including amines, aldehydes, ketones, carbohydrates, alcohols, phenols, fatty acids and esters, all of which may be biologically meaningful.[21,30] Johnston[12] on the study of rodents demonstrated that body odour is influenced by major histocompatibility complex (MHC). The MHC region is the most variable region of the genome. This variability is related to the variability of the proteins produced and value of such variability is that the greater the variety of proteins, the greater the range of responses to pathogens. Odour can reveal much information about an individual, including sex, diet, social status, individual and group identity, reproductive condition, age, health and emotional states.[31] Among these, social odours are pheromones, chemicals that trigger innate behaviours and physiological responses.[32] Animals can often gain information about the quality of potential mates from the quality of their odours, allowing them to discriminate against individuals of low social class, poor health or unsuitable genotype.[15] Many vertebrates produce odours, scents or pheromones in association with many important functions.[25,32] House shrew, striped hyena and black tailed deer produce scents under stress; other mammals mark territories and their habitat with scent. The scent is released in many ways, along with urine, faeces and saliva. They are also produced through specialized glands.[10,33]

Urine: The use of urine in scent marking behaviour has long been recognized in carnivores, such as canids.[34] In rodents, however, most research on scent marking has involved, species that use secretions from specialized glands, e.g., the gerbil (ventral gland) and the hamster (flank gland).[12] Male and female degus scent mark with urine using two methods.[34] The first involves urination on inanimate objects (e.g. a rock or the substrate). The most common use of urine is to identify or scent mark core area, home range or territory. Some animals use urine for identifying pathways, resting grounds, feeding grounds and sleeping sites. In this type of urine marking, urine is expelled which, the hindquarters move from side to side. The resultant urine spot often looks like a long wavy line.[34] The second method of urine marking (termed enurination) occurs during social investigation, usually when two animals are in an antiparallel position. One individual will spray urine on the partner's flank using a leg-lift posture; enurination often precedes separation of the pair.[34] Urine odours are also transferred from individual to individual through dust bathing in sand, which contains urine.[10]

According to Hardesty[35], urine contains urea, which is toxic to mammals and constantly being filtered out of the bloodstream by the kidney. Once outside of the body of the mammal as a component of urine, certain bacteria use urea as a source of energy. The byproduct of these bacteria using urea as fuel is ammonia, the all too familiar odour associated with the accumulation of urine. For instance, wild cats of both sexes mark their ranges by depositing faeces in prominent locations and leaving scent marks through urine spraying, cheek rubbing, and scratching the ground.[34]

Proteins also have implicated in communication among laboratory house mice.[12] One prominent feature of mouse urine is the presence of large amounts of proteins, called mouse urinary proteins. Mouse urinary proteins do bind with smaller molecules and promote the slow release of these substances, thus prolonging the effectiveness of urine marks.[12]

Faeces: Faeces may represent an ideal substance for marking, because it has a minimal energetic cost to the signaler, and can continue to indicate possession of a territory when the owner is occupied in activities other than territorial defence.[2] However, because faecal marking is constrained by faecal production, territorial individuals should prioritize the marking of positions that have the highest value as territorial signals. African civets uses defecation sites and invariably deposit their faeces in fixed places but do not bury them.[36,37]

The male hippopotamus marks its pathways between aquatic resting place and grassy feeding ground, by the deposition of dung at places along the trail, usually close to some conspicuous objects.[38] As hippopotamus defecates while walking on the trail, it keeps moving its tail rapidly from side to side, as a result faeces are splashed out and get deposited all over the vegetation above ground level, and places it at the nose height to make it more noticeable by conspecifics. Tigers select specific places and mark their territories by their droppings. Besides the observer abilities, some factors influence the marks and signs left by animals. Soil characteristics, vegetation, and local climate determine sign and mark conditions. Sandy and loamy soils preserve better footprints than soft soils with thick organic maters of layers, and stony areas. However, stony areas, dry ecosystems, and frozen ecosystems provide the best preservation for faeces.[38]

Saliva: Saliva is also been found to have odoriferous qualities.[7,12] Saliva is a secretion available to all mammals, which has been used as a scent marking agent by bears, dogs, pigs and a number of other animals.[33] Most marsupials deposit saliva on twigs by chewing them and this marking the foliage of their territory. Lesser hedgehog first salivates on the object to be marked and then scratches it. In addition, females of mammals lick their babies to scent mark them with saliva for recognition, as in the case of female wildebeest.[33]

Vaginal secretion: Chemical communication plays major roles in mammalian social life and reproduction.[39,40] In many species, males can detect the reproductive status of females either by urine or scent marks facilitating a successful mating.[7,41] The odours of vaginal secretions are sufficient to attract males over short distances. Vaginal secretions are one of the primary cues that elicit male courtship calling, and small quantities of vaginal secretions deposited by females in vaginal marks are sufficient to elicit ultrasonic calling and attract males over short distances. Thus, it is likely that vaginal scent marking and ultrasonic calling by females interact to facilitate attraction and location of mates during courtship.[39]

Skin glands: Social functions of skin glands are either related to hierarchic signaling, with dominant individuals using marks to reinforce their status over subordinates.[42] Mammals are well equipped with odour producing skin glands.[22] The odour they produce seems to be closely linked with sex, and may also be involved in other behavioural contexts. Skin glands occur in many parts of the body of mammals depending on the way of life of the species.[1] Thus, on the head they may be located in the frontal, occipital, temporal, buccal, infraorbital, submandibular areas, in the lips or in the eye orbit.[43] Furthermore, many species possess glands on various parts of the limb, like intradigital, metacarpal and metatarsal.[44,45] On the trunk of the body, there are dorsal, intercostal, supracaudal, abdominal, thoracic and anal glands. For instance, European rabbits (*Oryctolagus cuniculus*) have three pairs of scent glands used in scent marking. These are chin glands, anal glands and inguinal glands. As rabbits are territorial, they use these glands to define their territories.[43,45]

The size of the glands and the amount of marking behaviour are related to the level of sexual activity of each individual. Male rabbits mark more frequently than females, and dominant rabbits mark more frequently, most often in the presence of subordinates.[33]

Scent glands are found in the genital area of most mammals and in various other parts of the body, such as the underarms of humans and the pre-orbital glands of deer and muskox. They produce a semi-viscous fluid, which contains pheromones. These odour messengers indicate information such as the dominance status, territory, and sexual status.[33] Scent glands include, apocrine glands, such as sebaceous glands in the armpits of humans, tarsal glands of deer or cranial surface glands of the red-bellied lemur, flank glands of voles or shrews, anal scent glands found in most carnivores and castor in beavers. The development and use of scent glands by mammals is associated with sexual maturity and the presence of gonadal hormones. Dominant males tend to scent mark more frequently than other age/sex categories.[22]

African palm civets have two sets of scent glands that secret strong smelling substances, found between the third and forth toes on each foot, and on the lower part of their abdomen. These glandular secretions are primarily used for marking territories and are involved in mating.[36] Marmoset scent mark using a complex mixture of scents from several sources, including secretions from the apocrine and sebaceous glands, urine, genital tract secretions, and faecal material.[46] They deposit scent using recycling scent marking behaviours.

Chapter III

Mechanisms of scent marking

Methods by which mammals mark their territories vary with the species.[47] Some mammals mark not only locations but also other members of their own species. Among ungulates, scent marking of pathways and territorial locations is well developed. Some species either mark areas by urination and defecation, separately or in combination.[47] Urine and faeces contain metabolic wastes that serve as chemical signals. Many kinds of mammals are highly specific; a stereotyped routine is associated with urination and defecation.[48] Smith[46] found that tigers use various marking types interchangeably depending on the habitat and situation. They leave more scrape marks in open grasslands, compared to thick forest where numbers of scent marks are higher. This could be due to low detectibility of scrapes in thick forest and lack of marking trees in grasslands. The different types of marking mechanisms are discussed below.

Urination

Urination is the ejection of urine from the urinary bladder through urethra to outside of the body.[24] Urination often serves a social purpose beyond the expulsion of waste material. Dogs and felids mark territories by urine. Rodents such as rats and mice mark familiar paths with their urine.[12] The urine and urination of animals of differing physiology or sex sometimes have different characteristics.[24] For example, the urine of birds and reptiles is whitish, consisting of a paste-like suspension of uric acid crystals, and discharged with faeces, whereas in mammals urine is yellowish in colour, with mostly urea instead of uric acid, and discharged separately. A male fox raises one of its hind legs and urine is sprayed forward in front, whereas a female fox squats down its urine so that urine is sprayed on the ground between the hind legs. Four-legged animals usually kneel, or lift or spread one or more legs, to complete full urination.[24]

Black-Decima[49] suggested that both males and females of brocket deer bend the hind legs to assume a squatting posture with the hind legs extended (Figure 3A), but there is considerable individual variation in the degree to which the hind legs are bent.

Defecation

Clapperton[25] studied the ferret (*Mustela furo* L.) in which defecation is an obvious action with the animal sniffing at the chosen site. The animal would then turn around and back into position, and stand still for five seconds or longer, with the body slightly stretched out and with the tail curled right over the body.[28] The squatting posture is usually somewhat less pronounced than in urination, but the tail is raised, showing the white underside almost completely (Figure 3B). Rhythmic up and down movements of the tail often occur in both urination and defecation.[49] Some mammals defecate in discreet individual latrines as do hyenas and collared anteaters (*Tamandua tetradactyla)* in the Brazilian.[38] Among carnivores, the secretion produced by the anal gland adheres to the faeces during defecation. The secretion of each species has a characteristic and complex odour and it supplies intra and inter-specific information of an individual's territory, sex, reproductive state, and movements.

Thrashing

Thrashing is the beating of vegetation with the horns. The deer contacts a bush or a branch with its forehead and moves the head laterally and medially, maintaining contact with the branch (Figure 3C). Occasionally, the movement can become violent and appear as an attack on the bush. Thrashing commonly accompanied by pawing the ground with the forefeet.[49] Through thrashing, mammals leave their scents on vegetation, which demonstrate their presence or ownership capability.

Glandular rubbing

Glandular rubbing is a well-known behaviour in many mammalian species, including primates, in which a scent marking function frequently assumed as body surfaces used in rubbing usually have skin glands with odoriferous function.[1,22,42,50,51] For example, deer rubs its forehead against a branch or the trunk of a sapling. It then scrapes the area with its lower incisors (Figure 3D). A visible scar is left on the tree and the forehead of the deer appears wet and has small pieces of bark on the hairs. Hirano et al.,[42] studied rubbing behaviour in howlers, all rubbing behaviour episodes (repeated contact of any body part on a substrate). Such glandular scent marking patterns are well pronounced among several mammals.[1,2,10,12,43]

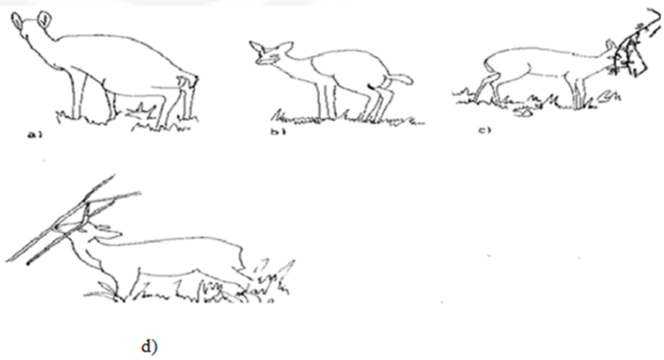

Figure 3 Postures of brocket deer while scent marking. (A) Urination position. (B) Defecation position. (C) Thrashing position. (D) Glandular rubbing positions.[46]

Fuctional role of scent marking

The role of scent marking in mammals is well-studied.[1,2,15,19] Scent recognition may help animals determine how best to avoid competitors and intercept kin or potential mates by reducing the costs of agonistic encounters between neighboring territory owners.[21,52]

Scent marking is more frequent when animals are adult, male, and dominant or territorial, especially during the breeding season. Eisenberg & Kleiman[10] in their extensive review of olfactory communication of mammals described the function of release and deposition of scents. It permits the exchange of chemical information among animals that live with overlapping home ranges but tend to move and forage alone. It also gives information with respect to age, sex and reproductive status. One particular feature of scent marks deposited in the environment is that they can provide chemical signals over a comparatively long period, in the absence of the signaler.[1,3,5,31] Animals also use scent marks to attract a mate,[2,15] provide information on the female's reproductive status or to initiate courtship.[10,40]

According to Lazaro-Perea et al.,[6] scent marking involves an animal's deposition of chemical signals throughout the habitat. Animals scent mark with urine, faeces, glandular secretions and other bodily substances.[1] It is not only olfactory but also visual, enabling wide ranging, potentially competing members of species like leopards[17] to position themselves temporally and spatially within their habitat. The advantages are twofold: marking transmits scent messages to other leopards, facilitating mutual avoidance and preventing unwanted encounters and fighting.[3] Marking odourants are also a vital "bulletin board" for leopards, announcing their social and reproductive status to potential breeding partners. Unlike bobcats and house cats, pumas are not known to spray urine as part of their scent marking repertoire.[17] Nevertheless, most of the proposed functions for scent marking in social animals make specific predictions about, frequency of marking by different group members, behavioural context in which the signal is deposited, distribution of marks over the home range, temporal variation of scent marking, and variability in frequency and pattern among groups of different social composition.[42] Scent marks play in territorial maintenance is considered specifically in terms of how they may achieve the goal of limiting intruders from exploiting defended resources.[53,54]

Lazaro-Perea et al.[6] based on their study of scent marking behaviour in wild groups of common marmosets proposed three main functions of scent marking in mammals these are marking related to use or defence of the home range and resources within the home range, marking related to social status and marking related to reproduction. The frequency and pattern of scent marking of a species or population may vary, however, depending on the social system (group size and composition, and intergroup relationships) and the type as well as distribution of resources. Mammalian scent marking is usually related to territorial and social functions. A territorial role is assumed when marking behaviour is related to intergroup encounters and home range boundaries, with marks used to signal the use of resources or area by members of their group.[42]

However, when home ranges are very large to preclude group members from effective marking of boundaries, territorial marking can predominate in the core area. The scent increases the confidence of the animals. For instance, African elephant, when facing a rival, during the breeding season turn his trunk around and smell his own temporal gland. This appeared to increase the confidence to attack the rival.[33]

Individual recognition

The ability to recognize individuals or their genetic relatedness plays an important role in mammalian social behaviour.[55] Individual recognition requires the ability to discriminate multiple animals according to their unique features. Individual information might be coded in a number of ways, although scent appears to be the primary modality for individual recognition in many species. Any individual cue, whether it is based on incidental information or an evolved signal, should exhibit certain key characteristics in order to fulfill the requirement for reliability.[7] It should be relatively independent from other background variations. It should be sufficiently distinctive to be easily and reliably distinguished from all other types of information. Identity cues should exhibit temporal stability. While age, reproductive status, health and social status vary through time, identity (species, sex, individual) remains constant. In order to maintain the association between the individual animal and its identity signal, the signal must remain stable despite variation in other characteristics reflecting the animals current status and environment. Animals release odours from many sources including a wide range of scent glands and in faecal and urinary excretions.[15]

In many cases, scents are deliberately placed in the environment in the form of scent marks to provide information over prolonged period. The ability to discriminate between individuals is an essential prerequisite for patterns exhibited by primates, including dominance interactions, territorial behaviour, and inter and intra-group relations together with offspring, parent and mate recognition.[46] Some species of mammals are known to discriminate between individuals of their species entirely by scent.[48]

Eisenberg & Kleiman[10] provided a summary statement of the role of olfactory communication in mammals. They regarded scent as a means of exchanging information, orienting the movements of individuals, and integrating social and reproductive behaviour. The capacity to recognize individuals by scent alone is probably important in nocturnal species or those that form large colonies. In particular, the ability of a mother returning from foraging bouts to locate her offspring by scent in a large colony has obvious fitness benefits.

Ungulates are frequently on the move in search of food. They also congregate in large numbers to give birth in synchrony, thereby decreasing the risk of dangers. They give birth to precocial young, capable of following the mother shortly after birth. Mothers have limited supplies of milk and selection favours the ability to recognize their own young from among the many unrelated young in the herd. Mothers recognize their offspring by scent and allow them to suckle, while rebuffing unrelated young.[48,56]

Hamsters habituate to different odours from the same individual, indicating that scent from multiple sources potentially reveals individual identity.[12] The vomeronasal organ apparently aids discrimination of odours. Non-volatile scent stimuli are detected via the vomeronasal system, example Major Urinary Proteins while air borne volatiles are detected through the main olfactory system. The development of odour preferences normally begins with the mother- offspring bond. For the parturient female, the initial similarity between the odour of the neonate and the odour of her own birth fluids may make the neonates attractive. 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 odour between mother and young.[10]

The chemical basis of individual identity

Mammals release an enormous variety of molecules into the environment that contribute to their chemical profile, and which could potentially be used to recognize the identity of individuals of the producer.[57] Chemicals that convey information about individual identity do not generally elicit a direct response, but provide information that may bias the current response or a future response of an individual.[7] Nevertheless, the finding of specific classes of chemosignal, and sensory responses that appear to be adapted to convey individual information suggests that such odours are likely to have important influences on behaviour.[57] Two genetic regions are principal candidates for the basis of individual odours, owing to their polymorphic nature and expression in scent marks.

The first is the Major Histocompatibility Complex (MHC), known in mice as H-2. Mice and rats discriminate between individuals differing only at MHC.[15] Discrimination is mediated by varying proportions of volatile carboxylic acids in urine and influences preferences for mates.[19] MHC has been identified as a locus influencing disease resistance, mate choice, and kin recognition in mammals.[58] In addition to immunological role at the cellular level, MHC genotype can determine individual identity at the behavioural level.[55]

The main olfactory system is able to integrate the pattern of volatile molecules produced by an animal into an overall odour signature for that individual. However, many of the constituent molecules will be subjected to environmental influences, such as changes in diet, or microbial flora, and may prove unreliable cues for recognizing the individual on subsequent occasions. There is a strong argument that reliable cues for individual discrimination and recognition should be based on differences in individual genotype.[55] Brennan & Kendrick[55] had studied MHC dependent mate choice in congenic strains of mice differing only in their MHC genotype. When given the choice between two individuals, under laboratory conditions, mice generally choose to mate with the MHC dissimilar individuals. Two strains that are identical except for allelic differences at a particular locus are called congenic strains, and any measurable characteristic that differs between the two congenic strains must be ascribed to the genes at that locus. Congenic strains of mice and rats that differ only in alleles at the MHC have been used in several different experimental paradigms to examine whether the MHC is associated with specific odour signatures.[7] Inbred strains consist of animals that are genetically uniform and homozygous for all their genes (i.e., each chromosome pair is identical).[59] Unrelated individuals are all likely to express different MHC types. It has widely been assumed that MHC also provides the main source of variation in odours that are used for individual recognition.[7]

The second region contributing to individual identity is the polymorphic multi gene family coding for Major Urinary Proteins (MUPs). Urine is the primary source of scent cues in mouse and rat. Animals of both sexes use urine marks for conspecific communication.[60] It is made up of metabolic byproducts and chemical components specifically manufactured and added to urine to act as chemical signals. MUPs are mostly synthesized in the liver under hormonal influence, then transported via blood and secreted in urine.[60] MUPs appear to have ideal characteristics for providing a stable and persistent individual identity cues. The pattern of MUPs expressed in urine is a fixed, genetically determined characteristic that remains the same throughout adult life regardless of status changes or alterations in food resources.

Unlike MHC and other genes that influence the profile of metabolites in urine, their only known role is in chemical signaling.[7] Highly polymorphic non-volatile components such as the MUPs in the urine of house mice appear to have evolved to provide a specific and highly stable chemical signal of individual identity, which is a fixed characteristic of the individual expressed independently of other factors, and is stable and persistent when deposited in scent marks.[55] However, non-volatile scents are undetectable at a distance and pumping them to the vomeronasal organ requires investigation through physical contact with the scent source, but this is more dangerous particularly if these are competitors.[7,58]

Conclusion

Mammalian scent marking behaviour is usually related to territorial and social functions. Territoriality appears where resources are limited and so in energetic terms, it is important for individuals to minimize the energy expended in defending it, whilst still maintaining an effective defence. Defence of a territory using scent dramatically reduces the chances of direct contact or conflict between rivals.

Urine, faeces, saliva, vaginal secretions and skin glands are sources of odours in most mammalian species. These sources can carry different information and thus have different functions.[8] Patterns of mammalian scent marking varies between species. The role of scent marking as a tool for olfactory signaling in the social communication of mammals is widely variable, because the function of scent marking may vary with different ecological and social conditions. Discrimination of their own species from other closely related species is essential not only for reproductive purposes but also in the context of competition for resources and anti-predator behaviour. This provides an exciting opportunity to learn more about chemical, behavioural, endocrine, and ecological levels of analysis so that a fully integrated picture can be obtained.

The recognition of individuals depends on learning their chemosensory profile, which involves changes at all levels of neural processing. Mammals produce complex mixtures of chemosignals that are still poorly understood. Single molecules can act as pheromones exerting specific control over physiology and behaviour, while genetically determined cocktails of molecules enable the recognition of individuals. There is no single means of signaling individuality information, but rather a variety of complementary systems, based on highly polymorphic genetic loci that are adapted for use in different behavioural contexts, such as mate choice or in territoriality. Understanding the function of scent marking patterns may provide valuable information for monitoring population estimates based on sign surveys, and thus could be of help in the process of conservation activities.

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