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OLFACTORY AWARENESS.

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Abstract

Awareness is defined here as a state in which complex brain analysis is used to process sensory stimuli or constructs based on memory. Awareness is described using five headings: unaware, perceptual awareness, cognitive awareness, assessment awareness and executive awareness. Examples are given and awareness in man and other animals compared. The mechanisms of olfactory awareness are briefly reviewed and then the relevant effects of primer pheromones, releaser pheromones, identity semiochemicals, pheromones modifying aggression and fear pheromones are described. It is concluded that olfaction plays a major role in animal awareness and that this should not be overlooked when attempting to improve welfare.

INTRODUCTION - Definitions.

"Are animals 'conscious' or 'aware' or 'rational'?" ask those concerned with animal welfare and ethics. The zoologist's answer is different from the philosopher's and rarely do two people agree because these terms are often used colloquially to embody a variety of ambiguous and overlapping meanings. We believe that a concensus is possible provided that the protagonists agree upon definitions of "awareness" or "consciousness". Awareness is perhaps the preferable term since it is less likely to have overtones of "mind" or "soul" thrust upon it.

We use the term "aware" to mean that an individual is sensible to stimuli. This implies that not only has a sensory stimulus been perceived but processing has involved higher levels of brain function. However, an individual can also be aware of an idea or a mental image triggered by memory rather than current sensory input. The definition used here is: awareness is a state in which complex brain

analysis is used to process sensory stimuli or constructs based on memory (Broom in press). The term "complex brain analysis" implies that there is some degree of interpretative thought over and above perceptual processing. We propose that there is a gradation in awareness which may be described under five headings. An observer may assign a particular degree of awareness on the basis of physiological or behavioural responses to stimulation.

It is impossible to be certain of the degree of awareness in any organism other than oneself but we hope that a consensus of probability is achievable when dealing with vertebrates and using the definitions proposed below.

Unawareness and four proposed degrees of awareness in ascending order of degree

1. Unaware but responsive.

The afferent and efferent nervous system is intact but, following some sensory input, either no brain processing takes place, eg. a spinal reflex in a decerebrate frog, or there is no higher level processing, for example those effects of a primer pheromone which elicit no immediate response from the individual but modify its subsequent physiological functioning.

2. Perceptual awareness.

A perceived stimulus results in an automatic response which the individual may or may not be capable of modifying voluntarily. Examples include: a. (response not modifiable) the spinal reflex response to pain in an intact animal; blinking when an object passes close to the eye; b. (response sometimes modifiable) scratching to relieve irritation and the effects of a releaser pheromone.

The responses to stimuli described under headings 1. and 2. are used clinically to assess the "level of consciousness" in order to gauge the depth of anaesthesia or extent of neural damage.

3. Cognitive awareness.

Brain processing of sensory inputs or of constructs based on memory results in a flexible response. Very many effects of sensory input fall into this awareness category. They are often modified by the memory of similar stimuli and responses. Examples range from the subliminal appreciation of

stimuli whilst driving a car in 'auto pilot' mode, to a mother recognising her offspring and an individual responding to a known competitor, ally, dwelling place or food type. Humans, and probably all vertebrates, are cognitively aware of much sensory input which follows a predicted pattern and they respond to this in an appropriate but largely automatic way. If an unpredicted event occurs, however, they immediately modify their response.

4. *Assessment awareness.*

The individual is able to assess and deduce the significance of a situation in relation to itself over a short time span. Assessment and deduction are indicated by a complex sequence of responses extending over time. Examples include complicated feeding procedures such as blue tits opening milk bottles; vertebrate prey responding to predators and vice versa and many human social responses. Self awareness is a kind of assessment awareness since it requires an appreciation of the qualities of and integrity of the self as an entity in the environment.

5. *Executive awareness.*

The individual is able to assess, deduce and plan in relation to long term intention. This may involve deductions about the feelings of others, imagination, and the mental construction of elaborate sequences of events. Examples include complex communication with conspecifics in humans and possibly other social mammals and the making and using of tools in an original way.

The Uniqueness of Man?

Man can have all the degrees of awareness described above. It is debatable whether there is any qualitative distinction between the executive awareness of man and that of apes. There is certainly a quantitative distinction. Human language provides an unique medium of communication and it is used to convey abstract thought.

Jeremy Bentham, in "Principles of Morals and Legislation" (1789), maintained that what matters morally when considering man's attitudes to other species, is not their degree of awareness so much as their capacity to suffer. Potentially, suffering can be associated with all the degrees of awareness but its nature changes. Physical pain is experienced using **perceptual** awareness and, provided that

one knows the species-specific pain signals, its assessment is entirely feasible. We propose that frustration involving **cognitive** awareness will result from confinement in restricted environments, i.e. those where the animal is unable to carry out its natural behaviour patterns. **Assessment** awareness is of relevance when considering many contentious issues of animal welfare. For example, animals which are aware in this way may feel fear or anxiety in an unfamiliar situation or when they remember a similar scenario which resulted in a bad experience. They may also be disturbed when they identify changing and less desirable relationships between themselves and their environment, for instance, other individuals.

Some philosophers may claim self awareness to be a peculiarly human attribute. This does not fit our definition. We assert that the human concept of 'I' or 'me' is a linguistic artefact and the use of these pronouns does not necessarily imply a concept of self any greater than that which an ape or other social mammal might have.

Suffering at the **executive** level of awareness involves, for example, long-term under-achievement which, in humans concerned with abstract thought, can lead to psycho-somatic disorders. It may be that such awareness is absent in other species although similar symptoms of abuse can occur. It is possible that those able to operate with this degree of awareness may actually suffer less when confronted with adverse physical situations. Man is able to anticipate the limited time scale of the suffering, for example when travelling in difficult conditions, and does not become unduly concerned. Secondly, man may be able to transcend cognitive awareness in pursuit of executive awareness, for example, when painting pictures or composing music in a cold attic without enough food. We propose that this is a good reason for not using human suffering as a model to deduce the degree of suffering in other animals. The danger of extrapolation may be to under-estimate the suffering of the animal because it may be aware only of current discomfort and have no hope of amelioration or reward.

The ability to anticipate a sequence of events and, on that basis, formulate long term plans requires executive awareness. Such ability is linked to “imagination” and “theory of mind” the general existence of which, in animals other than man, is hotly debated. Evidence suggests that chimpanzees

are probably aware at an executive level. Wolves and dogs modify their behaviour as if extrapolating their feelings and thoughts to others and so they may have executive awareness. However, it could be that a relatively anosmic species like man misses a lot of canine information sources. Perhaps their appropriate changes in behaviour are based entirely upon evidence conveyed by body and chemical language and so do not qualify as executive awareness. Here is another good reason for caution when extrapolating from our own condition. The result of an insult to an animal's olfactory environment may be worse than a human can readily believe.

Although it is always impossible to prove how much another suffers, it is possible to provide a means of assessment which can be generally agreed upon. We contend that establishing a defined degree of awareness in a specified animal under specified conditions can be useful in predicting a level of suffering. These defined degrees of awareness have no direct quantitative relationship to the suffering which may result from compromised welfare. The potential for suffering at the perceptual level of awareness is as great as at the assessment level. The relationships between awareness, feelings and welfare are discussed further by Griffin (1981), Dawkins (1993) and Broom (1996, in press).

OLFACTORY AWARENESS

The term used to encompass all signals perceived by organs of taste and smell is 'semiochemical' from the Greek *semio* meaning a signal. Semiochemicals are subdivided on a functional basis. A pheromone is a substance produced by one animal which conveys information to other individuals by olfactory means (Albone, 1984; Fraser and Broom, 1990) and usually passes between members of the same species. Some pheromones have a delayed effect on reproductive physiology and these are termed "primer pheromones". Since there is no immediate behavioural evidence that a primer pheromone has been perceived, the animal cannot be described as being 'aware' of the signal but since such signals are essential for normal physiological functioning, we shall include them. Other pheromones affect the behaviour of an animal immediately it perceives them and these are termed "releaser pheromones".

All vertebrates depend to some extent upon their sense of smell to monitor their environment. The odour sensitive receptors in the nasal mucosa are functional neurones and their axons project to the olfactory bulb for primary processing. From the olfactory bulb, direct connections pass through the limbic system to the hypothalamus whose functioning may be influenced by some primer pheromones without involving higher cortical processing. There is no evidence that primer pheromones evoke awareness at any level although they may profoundly affect the physiology of the reproductive system and hence subsequently alter the animal's behaviour. Another corollary of the limbic level of olfactory processing is that an odour may rapidly elicit a largely standard behavioural response typical of what is termed a 'releaser' pheromone. Such a response would come within our definition of perceptual awareness.

Although no releaser pheromones have been demonstrated in humans, smells and tastes often have strong emotive associations related to a memory of some sort but one not easily recalled unless triggered by that sensation. An example is the madeleine-triggered childhood memory recounted by Proust (1932) in "Remembrance of Things Past". Smells are evocative but can only be described indirectly by similes. These phenomena are also probably related to the limbic rather than cortical nature of primary olfactory processing and contrast markedly with human visual experiences which can be described directly and precisely.

Most vertebrates have a well developed smell and taste organ, the vomeronasal or Jacobson's organ, situated above the hard palate and communicating by a small duct with, usually, both oral and nasal cavities. A small vomeronasal organ responsive to skin steroids has recently been described in the adult human and is well developed in the human foetus. It is probable that the foetal vomeronasal organ monitors amniotic fluid and fulfils an important function in establishing maternal offspring bonding (Hepper, 1992; Van Toller and Kendal-Reed, 1995). Young rabbits show dietary preferences based on the prenatal maternal diet (Semke *et al*, 1995). Receptor cells line the walls of a well-vascularised sac into which fluid can be drawn from the mouth or vapour from the nasal cavity. Nerves from these receptors run to the accessory olfactory bulbs lying just behind the main olfactory bulb. This accessory system seems to monitor high molecular weight pheromones in fluids such as urine or skin secretions. A mammal typically touches the sample with its lips and then holds

up the head and displays 'flehmen' which is a type of grimace with the lips rolled back or, in the case of the pig, a yawn or, in the case of the cat, the mouth held a little open. The fluid presumably enters the vomeronasal sac by a combination of capillary action and a pumping action caused by the blood vessels in its wall contracting and dilating. D'Hospital and Hart (1985) demonstrated that fluid moved from the oral to the vomeronasal cavity during flehmen in the goat. Flehmen is most often seen when a male ungulate encounters urine from an oestrous female conspecific. In equines the vomeronasal duct runs into the naso-palatine duct with an oral opening at the back of the mouth and the function of flehmen may be to close the nostrils and facilitate the entry of air born odour into the vomeronasal sac under pressure. All classes of domestic horse show flehmen in response to the taste and smell of a variety of substances but it is seen far more frequently in the stallion in response to the smell of horse urine and faeces (Stahlbaum and Houpt, 1989). Cats, large and small, respond to conspecific urine scent marks in this way. The vomeronasal is the major pathway involved in the pheromonal modulation of reproduction (Meredith & Fernandez-Fewell, 1994).

In fish, amphibians, reptiles and mammals, pheromones are used to affect reproductive condition, to signal reproductive state and social status, to find food and mates and to navigate. Alarm pheromones signalling danger are extensively used in shoaling fish and herding mammals. Birds do not seem so dependent upon olfaction but smell is used to detect and monitor food in several species such as chickens, gulls and vultures. Chicks can be trained to discriminate odours and pigeons, starlings and swifts use local environmental scents for navigation (Papi 1992).

Most mammals have several anatomical sources of semiochemicals. Pheromones may be metabolites in faeces or urine and saliva or secretions from glands in the urogenital system, anus and skin. Each pheromone is used in a particular context, for instance, to indicate or influence reproductive state, to proclaim social status, to mark territory, to label self and kin. The source of the pheromone and the way it is employed is species-specific and its effect usually restricted to conspecifics. The chemical identity of most mammalian pheromones is still unknown although a number of compounds are known from carnivore anal glands (Albone and Gronneberg, 1977; Banks *et al.*, 1992) and fluids or secretions used for marking such as the circumgenital glands of tamarins (Belcher *et al.*, 1988).

The presence of a substance in an active secretion is not proof of its activity and behavioural bioassays have often proved negative despite compelling analytical evidence. The boar pheromone, androstenone, is an exception, possibly because activity is restricted to a few related compounds rather than depending upon the synergistic influence of many components. Androstenone was the first mammalian pheromone to be chemically identified (Patterson, 1968; Perry *et al*, 1972).

Primer pheromones

Primer pheromones have been intensively investigated in the mouse and pig. The reproductive physiology of the female mouse is largely governed by these although the identity of only two of the compounds is known. Volatiles in adult female urine suppress oestrus cyclicity in cohabiting female mice- the 'Whitten' effect (Whitten, 1959). If an adult male or its urine is introduced, the oestrous cycles become more frequent (Whitten, 1958). A testosterone dependant mixture of a brevicomin and a toliudine compound together with another unidentified component of male urine, induce oestrus acceleration and synchronisation (Jemiola *et al*, 1985). If male urine or female urine from oestrous or pregnant lactating mice is smelled by immature female mice, the onset of puberty is advanced (Vandenbergh, 1973). If recently mated female mice are exposed to urine volatiles from a male of a different strain from the one that mated with them, pregnancy is blocked and 70-80% return to oestrus - the 'Bruce' effect (Bruce, 1959). More recently, pheromones have been shown to exert even more complex and subtle effects on reproduction and aggression in free living mouse colonies (Hurst *et al.*, 1993; Hurst and Nevison, 1994).

Male and female pheromonal stimulation of oestrus is a common phenomenon in mammals occurring in rodents, artiodactyls and primates. In cattle, male urine will accelerate puberty in heifers, which is useful to obtain early season calves. Herds of cows without a bull show a higher incidence of "silent heats" than those with a bull (Vandenbergh, 1983). A pheromone in the urine and cervical mucus of cows will tend to synchronise oestrus in the herd. In sheep and goats a male pheromone has the effect of synchronising oestrus (Schinckel, 1954a, b). In the anoestrous ewe, the induction of a circulating luteinising hormone (LH) peak and ovulation 18 to 25 days after introduction of a ram is known as the 'ram effect'. The pheromone involved can be extracted from rams' fleece and is a synergistic combination of 1,2-hexadecanediol, 1,2-octadecanediol and an as

yet unidentified component in the acid extract of fleece. Oestrous ewes exposed to fleece extracts from high performance rams also produce more lambs per birth than control ewes (al-Merestani & Bruckner, 1992). Unlike the rodent and bovine, the urine has no pheromonal activity in the sheep. Bulbectomised ewes still respond to direct contact with a ram by a rise in LH so cues other than odour must be sufficient (Cohen-Tannoudji *et al.*, 1986). The source and identity of the male goat pheromones is not yet known but it is not 4-ethyl octanoic acid which is responsible for the typical 'billy' odour (Sugiyama *et al.*, 1981).

Little is known about primer pheromone effects in the horse but stallions show a higher rate of flehmen response to the products of pro-oestrous and oestrous mares than any other class of horse and this is followed by marking rather than courtship behaviour. Female pheromones could be important for reproductive priming in the stallion (Stahlbaum & Houpt, 1989).

Boar contact advances and synchronises puberty in immature gilts, the "boar effect" (Kirkwood and Hughes, 1979; Pearce *et al.*, 1988). It also induces an early lactational oestrus in recently farrowed sows (Petchey & English, 1980). The source of the pig pheromone is adult boar saliva and activity is found predominantly in an androgen metabolite, 5 α -androst-16-en-3-one [androstenone] (Patterson, 1968). Booth (1975) found that high concentrations of another active androgen metabolite, 3 α -androst-enol, and androstenone began to accumulate in the submaxillary salivary glands of pubescent boars. These steroids have a smell and are partly responsible for 'boar taint' which renders meat from mature boars, unappetising. There is a sexual dimorphism in salivary gland production and olfactory sensitivity to these pheromones; adult female pigs detect them at a fivefold lower dilution than boars (Dorries *et al.*, 1995). A similar sexual dimorphism for androstenone detection has been claimed for humans but not corroborated by others (Doty *et al.*, 1981). The endogenous circulating androgen levels are lower in females than males and this difference in olfactory background may account for the higher sensitivity in female detection. Other claims made for this versatile pheromone are that it affects the female sex cycle in cattle (Sokolov *et al.*, 1995) and possibly humans (Comfort, 1971). It has no known effect on female sheep or goats (Claus *et al.*, 1990). Oestrous sows can also advance and synchronise puberty in contact gilts but the effect is not so marked as in boar contact (Pearce and Pearce, 1992; Peacock and Hughes, 1995).

Gilts and sows housed in long-term close proximity to a boar may become habituated to the boar stimulus via olfactory and auditory signals and exhibit silent oestrus (Signoret, 1970; Hemsworth and Barnett, 1990). However, the company of the female pig is also important for the development of normal sexual behaviour in the male. The male pig deprived of female contact at puberty shows irreversible deficiencies in sexual behaviour while the mature boar shows some depression but behaviour returns to normal after four weeks of renewed sow contact (Hemsworth, 1992). Some of these effects may be mediated by tactile, auditory and visual signals but it seems likely that there is a pheromonal involvement too.

Oestrus synchrony occurs in colonies of female cats and seems to be controlled by valeric acid and possibly other fatty acids present in oestrous vaginal secretion (Bland, 1979). Valeric acid from any source, for example the root of *Valeriana officinalis*, induces oestrogen-dependent sexual behaviour in female cats and restless searching behaviour in the male (Brown, 1874; Bland, 1979).

In mammals which live in social communities or two generation family groups, for instance marmosets, pheromones from the reproductive pair often suppress reproductive activity in the adult offspring (Epple, 1978). Some degree of pheromonal sexual suppression of young group members is common throughout rodents (Brown, 1985).

Releaser Pheromones and Reproduction.

Releaser pheromones are important in vertebrate reproduction for inducing sexual arousal in males and females and initiating mating behaviour. They ensure that mating occurs at peak female fertility. For instance, a male arousal pheromone is secreted from sweat glands in the vulva and perineal region of oestrous cattle. The pheromone attracts the sniffing and licking attentions of bulls four days before "standing" oestrus occurs and is also detected by other cows but not until two days before oestrus. There may be a sexual dimorphism in detection threshold or more than one pheromone involved. Dogs and rats have been trained to detect a change in vulva and milk odour associated with bovine oestrus (Hawk *et al.*, 1984).

A functionally similar pheromone seems to occur in oestrous ewes although Bland *et al.*, (1992), analysing urine and vulvovaginal secretions, failed to identify an active fraction by gas chromatography. This suggests that the pheromone may be produced by perineal skin glands as in the cow. Anosmic rams are able to pick out oestrous ewes and to respond by a rise in sex hormone levels so cues other than odour must be sufficient (Lindsay, 1965).

Feral stallions pay particular attention to the faeces and urine of mares, sniffing and overmarking them. In the breeding season urine is voided frequently by both sexes and as a mare approaches oestrus, the stallion will repeatedly sniff her urine and show flehmen. Geldings treated with gonadotrophin releasing hormone and testosterone, but not testosterone alone, show similar behaviour in response to an oestrous mare. Although there is little recorded information, this activity is probably essential for oestrus detection and mating behaviour (McDonnell and Diehl, 1989). Foals from one week to five months old show coprophagy usually eating their mother's faeces. This may be stimulated by a maternal pheromone and serve a nutritional need for deoxycholic acid and gut flora inoculation (Crowell and Houpt, 1985).

Courtship in pigs involves a lot of muzzle sniffing with the boar slavering frothy saliva and 'blowing' at the sow. Both androstenone and androstenol elicit lordosis (standing-still-for-mating response) in pro-oestrous and oestrous sows (Perry *et al.*, 1972; Booth, 1975). In the absence of a boar, an aerosol spray of such compounds is now used, together with back pressure, to test sows' readiness for artificial insemination. Typical of the speed of a releaser effect, oestrous sows will adopt a rigid standing posture as soon as 5 seconds after smelling the pheromone.

The vaginal secretion of oestrous bitches releases a 'calling' pheromone that is attractive to male dogs and somewhat attractive to male foxes and wolves. The active principle may be methyl p-hydroxybenzoate but there is some dispute about this. The scent of urine from an intact male causes some oestrous female felids, for example the domestic cat and tiger, to adopt a mating stance (Michael, 1973; Todd 1963). One candidate for a pheromonal precursor is feline [amino-hydroxy-dimethyl-thiaheptanoic acid]. Female urine contains a fifth of the amount found in the urine of intact tom cats and ocelots but it is not found at all in the urine of lion, tiger and puma (Bland, 1979;

Hendriks *et al.*, 1995). The mating behaviour of tom cats is little affected by bulbectomy but pheromones play an important part in controlling oestrus and mating behaviour in the female. The well known investigative and sexual behaviour induced in cats, small and large, by the scent of nepetalactone in catmint [catnip] is independent of intact sexual status. It does depend upon an autosomal dominant gene and is possibly the response to an hallucinogenic agent rather than a pheromone (Jackson and Reed, 1969).

The rabbit doe secretes a labile "nipple search" pheromone which guides the blind pups to a nipple (Hudson and Distel, 1986). The restricted suckling time (about four minutes a day) and sibling competition make this pheromone physiologically essential. Similar nipple search pheromones occur in cats (Larson and Stein, 1984) and pigs (Morrow-Tesch and McGlone, 1990) and probably other multiparous species although not yet demonstrated. In pigs and dogs, the young tend to recognise a particular nipple at which they always suckle. This may depend upon marking labels in their saliva (Jeppeson, 1982).

Identity Semiochemicals

Olfactory identity signals form the basis of territorial and personal scent marking which is a common feature of vertebrate communication and is particularly well developed in mammals. The constant component of odour identity signals is linked to genes in the major histocompatibility complex so that monozygous twins share a very similar odour signature (Sommerville *et al.*, 1995). However, some components of the odour spectrum allow identical twins to be distinguished. This has been demonstrated experimentally using dogs to identify humans by odour (Kalmus, 1955; Sommerville *et al.*, 1990). Hepper (1988) found that dogs were unable to distinguish T-shirts worn by identical twin infants while they were breast-fed by the same mother but could distinguish them as soon as the infants were weaned. Diet must determine part of an individual's odour spectrum. Dietary preferences can be established on the basis of prenatal olfactory experience in the rat and rabbit (Hepper, 1986; Semke *et al.*, 1995) and this is likely to happen in other species.

Social mammals generally use their noses as well as their eyes and ears to establish the identity of conspecifics. For example, deer have specialised secretions and the odours from them elicit adaptive

behavioural responses (Müller-Schwarze and Müller-Schwarze 1975, Broom and Johnson 1980). This cognitive awareness is essential for maintaining social hierarchies and other relationships. In the rodent, dog, pig and parturient sheep olfaction is the most important sense in this context. Mammals, even man, depend upon individually specific combinations of semiochemicals for mother-offspring bonding. Post-parturient ewes are attracted to the smell of their own lamb's amniotic fluid for the first four hours after birth. Outside this time window, they find the smell aversive (Levy & Poindron, 1984). The ewes use this odour on their lamb for bonding and to distinguish it from other newborn lambs which they will not allow to suckle (Herscher *et al*, 1963). Parturient cattle and goats are also attracted to the smell of amniotic fluid. The newborn lamb uses vision and hearing to initiate contact with its mother but it already has prenatal experience of the scent of its dam and olfaction plays an important part in its bonding (Vince, 1993).

As well as the odour of amniotic fluid, the ewe also uses genetically related odour cues to identify her lambs. This is shown by allowing bonding with only one lamb of a multiparous birth. On subsequent presentation of another lamb, the ewe tolerates a monozygous sibling better than a heterozygous one. After the amniotic odour has gone, both mother and offspring must depend on other identity labels for bonding. Olfactory cues originating from the ewe's inguinal wax help the lamb to locate the teat (Vince, 1993).

Olfactory awareness in feral horses seems largely concerned with competition between stallions. Dominant stallions defaecate strategically near resources such as water holes and trails but will only defend a territory in rare cases of high density populations where resources are scarce (Rubenstein, 1981). A stallion with a harem will over-mark faeces and urine deposited unselectively by subordinate males, mares and juveniles, with his own faeces and urine. When challenged by another stallion, a great deal of counter marking and sniffing of contested dung heaps takes place, sometimes escalating into a fight. Stallions can differentiate the sex of another horse on the basis of faeces but not urine which may explain the function of their faecal marking behaviour (Stahlbaum and Houpt, 1989). Mutual grooming, rubbing on posts and rolling are popular activities in groups of horses and they normally all rub and roll on the same site so these could be ways of imposing a common identity odour on the group.

A sow can recognise at least 20 conspecifics and is aware of the array of its competitive and friendly relationships with them (Mendl *et al.*, 1992). Studies of salivary cortisol levels and the incidence of fighting show that mixing a batch of strange pigs is stressful until a familiar social structure has developed. This takes several days. Similarly, strange gilts introduced into a stable group of sows attract aggression. Both these situations may be ameliorated by allowing the pigs to have olfactory contact through bars during a five day pre-exposure period before mixing (Kennedy and Broom, 1994). When gilts are introduced into a group of sows, fighting is reduced if the sows have been previously exposed to either the smell of bedding from the gilts' pen or the sounds of the gilts (Kennedy and Broom 1996).

Dogs have developed a remarkable olfactory acuity through the need to identify conspecifics (or human surrogate-conspecifics) in a socially complex pack system and the need to track prey. Conspecifics are directly identified by the odour of mouth, face and anus. Dogs, particularly males and oestrous bitches, use urine to scent mark. The prime purpose is identity and status communication since dogs do not mark out territories. Dominant dogs and bitches mark more than subordinates and marking frequency increases when there is visual or olfactory evidence of a strange dog or after victorious aggressive encounters (Macdonald, 1985). Overmarking other dogs' scent marks commonly occurs. The anal gland secretion accompanying faeces is a rich source of identity and sexual information and scratching up earth with the hind feet frequently occurs after defaecation but the significance of this is uncertain. It may be to give a visual guide to the scent mark.

Dogs can accurately distinguish and identify a large number of people by general body scent alone (Settle *et al.*, 1993; Schoon and de Bruin 1994). In standard competition trials, bloodhounds can follow the trail of a person who walked over rough moorland 24 hours before and identify the person they have tracked. If a dog approaches a recently [3-20 minutes old] laid human track at right-angles it spends 3-5 seconds sniffing intensively at 2-5 footprints and then begins to track rapidly in the direction in which the trail layer moved (Thesen *et al.*, 1993). This necessitates detecting a difference in scent between footprints made 1-4 seconds apart, 3-20 minutes previously.

The care devoted to sniffing scent marks and the enormous olfactory acuity of dogs suggests that much information is potentially available but its precise nature is still uncertain. Considering the

close relationship between dog and man, this lack of information is surprising. It emphasises the way our poor sense of smell limits our intellectual curiosity about olfactory matters.

Unlike dogs, cats use scent to mark home ranges, particularly the paths they use and also a smaller area of territory within the home range which they may defend against intruders. Urine is sprayed strategically by both sexes and projecting objects at head height are marked with secretion from facial glands (Leyhausen, 1979). Male cats, neutered or intact, mark ranges about 10 times the area of females and these encompass several female ranges. The female ranges tend to only overlap common resources such as feeding stations and in urban populations of housecats they typically occupy the home garden (Tabor, 1983). Defaecation is commonly used to mark territorial boundaries. The significance of burying the faeces may be to stop them drying out and extend the life of the semiochemicals. A cat transplanted to a strange environment, particularly if it smells of a strange cat, will be uneasy until it has thoroughly scent-marked the place. A synthetic spray of marking pheromones is now available which seem to reassure the cat and reduce its need to urine mark.

Pheromones modifying aggression.

Mice and rats are socially aggressive and a urine pheromone in dominant mature males promotes inter-male fighting (Mugford, 1973). The testosterone dependant mixture of a brevicomin and a toliudine compound together with another unidentified urinary component, induce male aggression as well as affecting female reproduction (Novotny *et al*, 1985). There is some evidence that the secretion of aggression pheromone is increased by agonistic encounters. Free living colonies of mice in which the olfactory nerves or bulbs have been sectioned are always more peaceful than colonies of intact animals (Slotnick, personal communication). Male laboratory rodents can be caged in same-sex groups, particularly if carefully matched with congenial cage mates, but there is a tendency for serious aggression to occur immediately after cage cleaning. Mouse aggression is worse if the cage itself is not cleaned or the old environmental enrichment objects are returned to the cage (Gray and Hurst, 1995). Aggression in male mice is reduced if cages are thoroughly cleaned, bedding renewed and objects used to enrich the environment are clean and novel (Ambrose and Morton, 1997). The

basis of these results seems to be that cleaning disrupts the group's stability and the dominant mouse becomes more aggressive if there is a remnant of its own odour in the cage.

Pigs are aggressive within hours of birth and, although rarely killing one another, they do inflict serious injuries. In stable social groups, fighting is minimal and good husbandry depends upon understanding the causes of aggression in order to minimise it. Experiments have shown how pigs relate to each other in group-housed systems. Strange pigs meeting for the first time sniff each others' muzzles intensely and, if fairly matched in size and dominance, the encounter will escalate into a fight. Blindfolding the animals has little effect (Ewbank *et al.*, 1974) but sectioning the olfactory bulbs prevents fighting (Meese and Baldwin, 1975).

In a stable group of pigs, the glucocorticoid levels tend to be highest in those which frequently but unsuccessfully challenge the dominant pigs. Glucocorticoid levels are usually not so high in the most dominant pigs or in those which avoid aggressive encounters (Mendl *et al.*, 1992). There are at least three pheromones exerting a subtle control over aggressive encounters. Like the rat, one is produced by dominant males and other pigs when they fight. The pheromone is in the urine and plasma and its effect is to suppress fighting among other pigs of any class. Another pheromone found in the urine is stimulated by general stress, for instance handling, so it is probably cortisol dependent and increases the level of general aggression in other pigs (McGlone *et al.*, 1987). Yet a third pheromone identified in behavioural tests is produced in the urine of the loser of a fight and signals submission with consequent de-escalation. It has a two-fold action; firstly, of signalling the submission of the producer and, secondly, of inducing submissive behaviour in other pigs (McGlone, 1988). The chemical identity of these volatiles is not yet known but they could be described as releaser pheromones and the response to them indicates perceptual awareness.

Androstenone also suppresses aggression among prepubertal pigs but has no effect on adult pigs of either sex (McGlone, 1988). This response in young pigs may be a learned olfactory association leading to unprovocative behaviour in the presence of a mature male pig and as such would be an example of cognition awareness. In the wild pig, aggressive encounters between boars are more common and the victor is the largest dominant boar which produces the most copious flow of saliva with the highest androstenone content. Slavering is provoked by any aggressive interaction with another wild boar or with men (Booth and Baldwin, 1980; Pearce *et al.*, 1988). This last observation

is interesting because male armpit sweat contains androstenone and the level is higher than in women's sweat (Gower and Booth, 1986).

Fear Pheromones.

Alarm pheromones signalling danger are used extensively in shoaling fish and herding mammals. In fish, the alarm substance is produced by damaged skin and rapidly causes the shoal to disperse. In artiodactyls, alarm pheromones are secreted by skin glands on the rump, tail or hind leg and alert conspecifics to a nearby predator. Experiments with mice and rats have shown that some volatile signal emitted by a frightened animal will induce fear in conspecifics in adjacent cages or when they walk across the place where an animal has recently received an electric shock (Mackay-Sim and Laing, 1981; Fanselow, 1985). The chemical identity of these mammalian pheromones is unknown but alarm pheromones have been well investigated in many insects. They are often not species-specific, for instance, β -farnesine is a common aphid alarm pheromone. The volatile is only detected by aphids feeding within a few centimetres of each other and all are genetically identical to the emitter. Thus, the sacrifice of one individual to save the group is a sound survival strategy and a similar potential advantage applies to a group of grazing deer or antelope.

Although hard evidence for mammalian alarm and fear pheromones is limited, they may be universally employed in gregarious species. It is probable that such secretions are glucocorticoid dependent and possible that stress related changes in metabolism will influence body odour in ways that might be detected by any species. This may be the explanation for the anecdotal "smell of fear" in humans and also account for the way a diffident or nervous person will cause dogs to attack them or horses to panic. These contrasting responses could be the appropriate ones for a carnivore living in a social hierarchy and a herbivore threatened with predation.

Fear, of course, is a major factor in domestic animal suffering. It can induce long term immunosuppression so it is sound husbandry to minimise fear. Experienced calm handlers can have a beneficial effect on animal management at all stages of pig production (Hemsworth *et al.*, 1993). Sources of aggression should be controlled and any animal which has to be handled for therapeutic procedures should be gently isolated and only returned to the group when calm. Making sure ventilation systems remove the odours produced by frightened animals from incoming conspecifics

will improve animal welfare in slaughter houses (Grandin, 1993). Similarly, thoroughly cleaning buildings and transporters between successive batches of animals may help to reduce fear.

DISCUSSION AND CONCLUSIONS

Apart from photoperiodicity, olfaction is the major sensory pathway for ordering the reproductive physiology of vertebrates. It is generally used together with sight and hearing for conspecific communication and environmental interaction and is likely to be the major source of sensory information in many mammals.

The sense of smell is profoundly important for mammalian reproduction but the animals cannot be said to be 'aware' of the smell of a primer pheromone although their behaviour eventually changes as a result of its effects. The animal is certainly aware of other pheromones, such as releaser pheromones, and artificial interference with the normal behaviour associated with these, could cause distress. For instance, an animal in reproductive condition must feel some frustration if deprived of a mate and this frustration will be more intense if it is exposed to releaser pheromones from the opposite sex. For example, does a sow perceive an artificial inseminator assisted by a can of "Boarmate" as a satisfactory substitute for a good boar? Almost certainly not but this does not seem to be a serious infringement of good welfare.

Artificial interference at the level of recognition awareness can undoubtedly cause suffering. Good mothering depends upon good bonding and some failure in early contact between mother and offspring may account for poor mothering in sheep, pigs and zoo animals. This causes great distress to the young as they attempt to bond with their mother. The common farm practice of removing calves soon after birth can greatly distress cow and calf. However, the distress is worse if the separation occurs 4-5 days later. Research into the details of mother-offspring olfactory bonding in other species than the sheep is overdue and could lead to improved management.

Rats and mice have complex social behaviour patterns heavily dependent on pheromones to mark living areas and control dominance aggression. Conventional laboratory management frustrates their natural life styles. Non-breeding laboratory mice attempt to build nests and prefer certain sorts of

nesting materials, for example paper towels rather than wood shavings (Sherwin, 1997). They should not be housed singly nor put in transparent empty cages which are frequently but incompletely cleaned and lack environmental enrichment. When cleaning it is important that all traces of marking odour are removed since the predominant marks will be those of the dominant animal and these will encourage its aggressive behaviour after physical disturbance of the group. Young rats can be paired up by carefully selecting compatible partners of the same sex and these will remain on amicable terms for life (personal observation). Rodents should be supplied with a darkened, litter-filled nesting compartment (Broom and Manser, 1996).

Pheromonal aggression control in pigs is complex and the possibility that similar systems operate in other social mammals should not be overlooked. An interesting exercise would be to identify and synthesise the submissive pheromone with a view to artificially reducing aggression levels in group housed pigs. Should it prove effective in humans, one would have a valuable instrument for crowd control. Meanwhile, it is scarcely practicable to decommission the olfactory system of all the pigs in a production unit and so management should be designed to maintain a peaceful colony. Olfactory contact with a boar will have a salutary effect on the in-fighting of young pigs and the level of fertility of the herd. New pigs should be introduced behind bars for a few days or their odours introduced first. Frequent gentle human contact will accustom the pigs to handling.

Transport and bad handling are a major stressors so the current trend to fewer and larger abattoirs is detrimental to good animal welfare and its effects should be ameliorated where ever possible.

It is crucial to understand the olfactory interactions of animals in order to optimise humane management for food production and research. Humans are one of the least olfactorily aware animals and so we may seriously misjudge the priorities of other species. We must ever bear in mind this limitation when legislating about animal welfare.

REFERENCES

- Al-Merestani, M.R., Bruckner, G.1992. Influence of hormonal secretion and fertility in merino mutton sheep by exogenous pheromone application during the breeding season. Beitr. Trop. Landwirtschaft. Veterinärmed. 30, 397-406.
- Albone,E.S., 1984, Mammalian Semiochemistry: The investigation of chemical signals between mammals. Wiley, New York.
- Albone, E.S., Gronneberg,T.O. 1977. Lipids of the anal sac secretion of the red fox, *Vulpes vulpes*, and of the lion, *Panthera leo*. *J. Lipid Res.* 18, 474-479.
- Ambrose, M., Morton, D.B. 1997. The effects of environmental enrichment on cage-cleaning aggression in male laboratory mice. B & K Science Now 6 1, 1-3.
- Banks, G.R., Buglas, A.J., Waterhouse, J.S. 1992. Amines in the marking fluid and anal sac secretion of the Tiger. *Panthera tigris*. *Z. Naturforsch.* 47c, 618-620.
- Belcher, A., Epple, G., Kuderling, I., Smith, A.B.1988. Volatile components of scent material from cotton-top tamarin (*Saguinus o. oedipus*): a chemical and behavioral study. *J. Chem Ecol.* 14, 1367-1384.
- Bland, K.P., Jubilan, B.M., Lang, C.W., Nizamlioglu, M. 1992. Failure to detect a putative oestrus-indicating pheromone in the urine or vaginal secretions of female sheep. *Acta. Vet. Hung.* 40, 17-25.
- Bland, K.P., 1979. Tom-cat odour and other pheromones in feline reproduction. *Vet. Sci. Commun.* 3, 125-136.
- Booth, W.D. 1975. Changes with age in the occurrence of C19 steroids in the testes and submaxillary gland of the boar. *J. Reprod. Fertil.* 42, 459-472.
- Booth, W.D., Baldwin, B.A.1980. Lack of effect on sexual behaviour or the development of testicular function after removal of olfactory bulbs in prepubertal boars. *J. Reprod. Fertil.* 58, 173-182.
- Broom, D.M., Johnson, E. 1980. Responsiveness of hand-reared roe deer to odours from skin glands. *J.Nat.Hist.* 14, 41-47.
- Broom, D.M. 1996. Animal welfare defined in terms of attempts to cope with the environment. *Acta Agric. Scand., Anim. Sci.Suppl.*, 27: 22-28.
- Broom, D.M. (in press). Welfare, stress and the evolution of feelings. *Adv.Stud. Behav.*
- Broom, D.M., Manser, C.E. 1996. Housing and welfare in rats. In Proc. 30th Int. Cong. Int. Soc. Appl. Ethol., ed. I.J.H. Duncan, T.M. Widowski and D.B. Haley, Guelph: Centre for Study of Animal Welfare, pp. 8.
- Brown, O.P. 1874. *The Complete Herbalist*. O. Phelps Brown, London.

- Brown, R.E. 1985. The rodents,1: effects of odours on reproductive physiology. in *Social Odours in Mammals*, vol. 1. ed. R.E.Brown and D.W.Macdonald, Clarendon Press: Oxford, pp. 245-344.
- Bruce, H.M. 1960. A block to pregnancy in mice caused by the proximity of strange males. *J. Reprod. Fertility* 1, 96-103.
- Claus, R., Over, R., Dehnhard, M. 1990. The effect of male odour on LH secretion and the induction of ovulation in seasonally anoestrous goats. *Anim. Reprod. Sci.* 22, 27-38.
- Cohen-Tannoudji , J., Einhorn, J., Signoret, J.P. 1994. Ram sexual pheromone: first approach of chemical identification. *Physiol. Behav.* 56, 955-961.
- Crowell-Davis, S.L., Houpt, K.A. 1985. Coprophagy by foals: effect of age and possible functions. *Equine Vet. J.* 17, 17-19.
- Dawkins, M. 1993. *Through Our Eyes Only*. Oxford: W.H. Freeman.
- Dorries , K.M., Adkins-Regan, E., Halpern, B.P. 1995. Olfactory sensitivity to the pheromone, androstenone, is sexually dimorphic in the pig. *Physiol. Behav.* 57(2), 255-259.
- Doty, R. L., Snyder, P., Huggins, G., Lowry, L. D. 1981. Endocrine, cardiovascular and psychological correlates of olfactory sensitivity changes during the human menstrual cycle. *J. Comp. Physiol. Psychol.* 95, 45-60.
- Epple, G. 1978. Reproductive and social behaviour of marmosets with special reference to captive breeding. In: N. Gengozian and F. Deinhardt (Eds). *Marmosets in Experimental Medicine*, Basle: Karger, pp.50-62.
- Epple, G., Golob, N. F., Smith, A. B. 1979. Odour communication in the tamarin *Saguinus fuscicollis* (Callitrichidae): behavioural and chemical studies. In: F.J.Ritter (Ed.). *Chemical Ecology, odour communication in animals*. Amsterdam: Elsevier, pp. 117-130.
- Ewbank , R., Meese, G.B., Cox, J.L. 1974. Individual recognition and the dominance hierarchy in the domestic pig. The role of sight. *Anim. Behav.* 22, 473.
- Fanselow, M. 1985. Stressed rat odour effect in unstressed rats. *Behav. Neurosci.* 99, 589.
- Fraser, A.F., Broom, D.M. 1990. *Farm Animal Behaviour and Welfare*. Wallingford: C.A.B. International.
- Friend, T.H., Knabe, D.A., Tanksley. T.D.Jr. 1983 Behaviour and performance of pigs grouped by three different methods at weaning. *J. Anim.Sci.* 57, 1406-1411.
- Gower, D.B., Booth, W,D, 1986. Salivary pheromones in the pig and human in relation to sexual status and age. In *Ontogeny of Olfaction*, W.Breipohl (Ed.). Springer-Verlag, Berlin, pp.255-264.
- Grandin, T. 1993. Handling and welfare of livestock in slaughter plants. In *Livestock Handling and Transport*, T. Grandin (Ed.). Wallingford, C.A.B. International, pp. 289-306.
- Gray, S., Hurst, J.L. 1995. The effects of cage cleaning on aggression in groups of laboratory mice. *Anim. Behav.* 49, 816-821.

- Griffin, D.R. 1981. *The Question of Animal Awareness*, 2nd edn. New York: Rockefeller University Press.
- Hawk, H.W., Conley, H.H., Kiddy, C.A. 1984. Oestrus-related odours in milk detected by trained dogs. *J. Dairy Sci.* 67, 392-397.
- Hemsworth, P.H. 1992. Behavioural problems. In *Diseases of Swine*, A.D. Leman et al (Eds). Iowa University Press, Ames, Iowa, pp.653-659.
- Hemsworth, P.H., Barnett, J.L. 1990. Behavioural responses affecting gilt and sow reproduction. *J. Reprod. Fertil., Suppl.* 40, 343-354.
- Hemsworth, P.H., Barnett, J.L., Coleman, G.J., 1993. The human-animal relationship in agriculture and its consequences for the animal. *Anim. Welf.* 2, 33-51.
- Hendriks, W.H., Moughan, P.J., Tartelin, M.F., Woolhouse, A.D. 1995. Feline: a urinary amino acid of Felidae. *Comp. Biochem. Physiol. B. Biochem Mol. Biol.* 112(4), 581-588.
- Hepper, P.G. 1986. Kin recognition: functions and mechanisms. A review. *Biol. Rev.* 61, 63-93.
- Hepper, P.G. 1988. The discrimination of human odour by the dog. *Perception.* 17(4), 459-554.
- Hepper, P., 1992. The quest for the developmental origins of behaviour. *Quart. J. Exper. Psych.* 44B, 161-163.
- Herscher, L., Richmond, J.B. Moore, A.U. 1963. Maternal behaviour in sheep and goats. In *Maternal Behaviour in Mammals*. H.L. Rheingold, (Ed.). New York: Wiley, pp. 203-232.
- Hudson, R., Distel, 1986 Olfactory guidance of nipple-search behaviour in newborn rabbits. In *Ontogeny of Olfaction*. W. Breipohl (Ed.). Berlin: Springer-Verlag, pp.243-254.
- Hurst, J.L., Fang, J., Barnard, C.J. 1993. The role of substrate odours in maintaining social tolerance between male house mice (*Mus musculus domesticus*). *Anim. Behav.* 45, 997-1006.
- Hurst, J.L., Nevison, C.M. 1994. Do female house mice, *Mus domesticus*, regulate their exposure to reproductive priming pheromones? *Anim. Behav.* 48, 945-959.
- Jackson B., Reed, A., 1969. Catnip and the alteration of consciousness. *J. Amer. Med. Ass.* 207, 1349-1350.
- Jemiola, B., Alberts, J., Schohiniski-Wiggins, S., Harvey, S., Novotney, N., 1985. Behavioural and endocrine responses of female mice to synthetic analogues of volatile compounds in male urine. *Anim. Behav.* 33, 1114-1118.
- Jeppeson, L.E., 1982. Teat-order in groups of piglets reared on an artificial sow. II Maintenance of teat order with some evidence for the use of odour cues. *Appl. Anim. Ethol.* 8, 347-355.
- Kirkwood, R.N., Hughes, P.E. 1979. The influence of age at first boar contact on puberty attainment in the gilt. *Anim. Prod.* 29, 231-238.

Kalmus, H. 1955. The discrimination by the nose of the dog of individual human odours and in particular of the odour of twins. *Br. J. Anim. Behav.* 3, 25-31.

Kennedy, M.J., Broom 1994. A method of mixing gilts and sows which reduces aggression experienced by gilts. *Proc. 45th Meeting Eur. Ass. Anim. Prod.*, Edinburgh: E.A.A.P, pp. 333.

Kennedy, M.J., Broom, D.M. 1996. Factors modulating aggression received by pigs mixed individually into groups. In *Proc. 30th Int.Cong.Int.Soc.Appl.Ethol.*, ed. I.J.H. Duncan, T.M. Widowski and D.B. Haley. Guelph : Centre for Study of Animal Welfare, pp.52.

Larson, M.A., Stein, B.E. 1984. The use of tactile and olfactory cues in neonatal orientation and localisation of the nipple. *Dev. Psychobiol.* 17, 423-436.

Leyhausen, P. 1975. *Verhaltensstudien an Katzen*. 4th edit. Berlin: Paul Parey.

Lindsay, D. R. 1965. The importance of olfactory stimuli in the mating behaviour of rams. *Anim. Behav.*, 20: 452-456.

Macdonald, D.W.1985. The carnivores: order Carnivora. In *Social Odours in Mammals*, vol. 1. ed. R.E.Brown and D.W.Macdonald. Clarendon Press. Oxford, pp. 619-82.

Mackay-Sim, A., Laing, D.G. 1981. Rats' responses to blood and body odours of stressed and non-stressed conspecifics. *Physiol. Behav.* 27, 503-510.

McDonnell, S.M., Diehl, N.K., Garcia, M.C., Kenney, R.M. 1989. Gonadotrophin releasing hormone (GnRH) affects precopulatory behavior in testosterone-treated geldings. *Physiol. Behav.* 45, 1, 145-149.

McGlone, J.J., Stansbury, W.F. and Tribble, L.F. 1987. Effects of heat and social stressors and within-pen weight variation on young pig performance and agonistic behaviour. *J. Anim. Sci.*, 63: 456-462.

McGlone, J.J. 1988. Olfactory signals that modulate pig aggression and submissive behavior. in *Social Stress in Domestic Animals*. R. Zayan and R. Dantzer (Eds) 86-109. Dordrecht: Kluwer, pp.619-82.

Meese, G.B., Baldwin, B.A. 1975. The effects of the ablation of the olfactory bulbs on aggressive behaviour in pigs. *Appl. Anim. Ethol.* 1, 251-262.

Melese-D'Hospital, P.Y. and Hart, B. 1985. Vomeronasal organ canulation in male goats: evidence for transport of fluid from oral cavity to vomeronasal organ during flehmen. *Physiol. Behav.* 35: 941-944.

Mendl, M., Zanella, A.J., Broom, D.M. 1992. Physiological and reproductive correlates of behavioural strategies in female domestic pigs. *Anim. Behav.* 44, 1107-1121.

Meredith, M., Fernandez-Fewell, G. 1994. Vomeronasal system, LHRH and sex behaviour. *Psychoneural Endocrinology* 19, 657-672.

Michael, R.P. 1973. The effects of hormones on sexual behaviour in the female cat and rhesus monkey. In: *Handbook of Physiology*, American Physiological Society. Section 7(2), pp.187-221.

- Morrow-Tesch, J., McGlone, J.J. 1990. Sensory systems and nipple attachment behaviour in neonatal pigs. *Physiol. Behav.* 47, 1-4.
- Mugford, R. G. 1973. Intermale fighting affected by home cage odours of male and female mice. *J. Compar. & Physiolog. Psychol.* 84, 2, 289-295.
- Müller-Schwarze, D., Müller-Schwarze, C. 1975. Subspecies specificity of response to a mammalian social odour. *J. Chem. Ecol.* 1, 125-131.
- Novotny, M., Harvey, S., Jemiola, B., Alberts, J., 1985. Synthetic pheromones that promote intermale aggression in mice. *Proc. Natl. Acad. Sci. USA* 82, 2059-2061.
- Papi, F., Wallraff, H.G. 1992. Birds. In *Animal Homing* ed. F. Papi. London: Chapman and Hall, pp. 263-319.
- Patterson, R.L.S. 1968. Identification of 3-hydroxy-5-androst-16-ene as the musk odour component of boar submaxillary gland and its relationship to the sex odour taint in pork meat. *J. Sci. Food Agric.* 19, 434-438.
- Peacock, A.J. and Hughes, P.E. 1995. The effects of daily exposure to oestrous and anoestrous gilts and sows on the attainment of puberty in the gilt. *Anim. Reprod. Sci.*
- Pearce, G.P., Hughes, P.E., Booth, W.D. 1988. The involvement of boar submaxillary salivary gland secretion in boar induced precocial puberty attainment in the gilt. *Anim. Reprod. Sci.* 6, 125-134.
- Pearce, G.P. and Pearce, A.N. 1992. Contact with a sow in oestrus or a mature boar stimulates the onset of oestrus in weaned sows. *Vet. Rec.* 130, 5-9.
- Perry, G.C., Patterson, R.L.S., Stinson, C.G. 1972. Submaxillary salivary gland involvement in porcine mating behaviour. 7th International Congress of Animal Reproduction and Artificial Insemination. Munich, pp.395-399.
- Petchey, A.M., English, P.R. 1980. A note on the effect of boar presence on the performance of sows and their litters when penned as groups in late lactation. *Anim. Prod.* 31, 107-109.
- Rubenstein, D.I. 1981. Behavioural ecology of island feral horses. *Equine Vet.J.* 13, 27-34.
- Schinckel, P.G. 1954. The effect of the ram on the incidence and occurrence of oestrus in ewes. *Austr. Vet. J.* 30, 189-195.
- Schinckel, P.G. 1954. The effect of the presence of the ram on the ovarian activity of the ewe. *Austr. J. Agric. Res.* 5, 465-469.
- Schoon, G.A.A., de Bruin, J.C. 1994. The ability of dogs to recognise and cross-match human odours. *Forensic Sci. Int.* 69, 111-118.
- Semke, E., Distel, H., Hudson, R. 1995. Specific enhancement of olfactory receptor sensitivity associated with fetal learning of food odors in the rabbit. *Naturwissenschaften* 82, 148-149.

- Settle, R.H., Sommerville, B.A., McCormick, J.P., Broom, D.M. 1994. Human scent matching using specially trained dogs. *Anim. Behav.* 48, 1443-1448.
- Signoret, J.P. 1970. Reproductive behaviour of pigs. *J. Reprod.Fertil., Suppl.* 11, 105-117.
- Sokolov, V.E., Karavaeva, E.A., Belaia, Z.A., Zinkevich, E.P. 1995. Interspecies effect of the boar sex pheromone: effect on the status of the female cattle sex cycle. *Dokl. Akad. Nauk.* 341, 140-142.
- Sommerville, B.A., Green, M.A., Gee, D.J. 1990. Using chromatography and a dog to identify some of the compounds in human sweat which are under genetic influence. In: *Chemical Signals in Vertebrates 5* Ed. by D.W.Macdonald, D.Müller-Schwarze & S.E.Natynczuk (Editors), Oxford, Oxford University Press, pp.634-639.
- Sommerville, B.A., Wobst, B., McCormick, J.P., Eggert, F., Zavazava, N., Broom, D.M. 1995. Volatile identity signals in human axillary sweat: the possible influence of MHC class I genes. *Chemical Signals in Vertebrates 7*, R. Apfelback, D. Müller-Schwarze, K. Reutter, and E. Weiler (Editors), *Adv. Biosci.*, 93: Oxford: Pergamon, pp.539-542.
- Stahlbaum, C.C. Houpt, K.A. 1989. The role of the flehmen response in the behavioral repertoire of the stallion. *Physiol. Behav.* 45, 1207-1214.
- Sugiyama, T., Sasada, H., Masaki, F., Yamashita, K. 1981. Unusual fatty acids with specific odour for mature male goats. *Agric. Biol. Chem.* 45, 2655-2658.
- Tabor, R. 1983. *The Wildlife of the Domestic Cat.* Arrow Books Ltd., London.
- Todd, N. B. 1963. Behaviour and genetics of the domestic cat. *Cornell Vet.* 53, 99-107.
- Thesen, A., Steen, J.B., Doving, K.B. 1993. Behaviour of dogs during olfactory tracking. *J. Exp. Biol.* 180, 247-251.
- Van Toller, S., Kendal-Reed, M., 1995. A possible protocognitive role for odour in human infant development. *Brain and Cognition* 29, 275-293.
- Vandenbergh, J.G. 1973. Acceleration and inhibition of puberty in female mice by pheromones. *J. Reprod. Fertil. Suppl.* 19, 411-419.
- Vince, M.A. 1993. Newborn lambs and their dams: the interaction that leads to sucking. *Adv.Stud. Behav.* 22, 239-268.
- Whitten, W.K. 1958. Modification of the oestrous cycle of the mouse by external stimuli associated with the male. Changes in the oestrous cycle determined by vaginal smears. *J. Endocrinol.* 17, 307-313.
- Whitten, W.K. 1959. Occurrence of anoestrus in mice in caged groups. *J. Endocrinol.* 18, 102-107.