CHEMICAL COMMUNICATION, AGGRESSION AND SEXUAL BEHAVIOUR IN THE OWL MONKEY

(Aotus trivirgatus griseimembra)

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by

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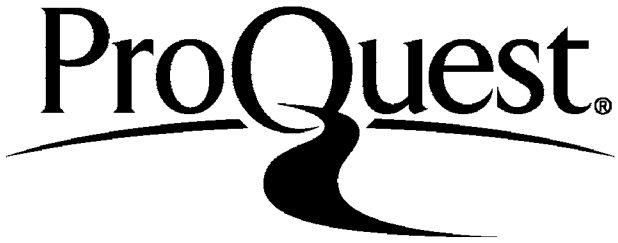

ABSTRACT

This thesis quantified sexual, aggressive and associated behaviours in captive owl monkeys and examined the importance of olfactory cues in mediating these behaviours. Animals of the same sex showed high frequencies of aggressive behaviour but no sexual behaviour. Subordinate animals tended to exhibit lower levels of scent-marking, although individual variability in this behaviour was pronounced. Evidence was obtained which suggested that arching displays (which occur in several Platyrrhine species) primarily subserve an aggressive function.

The effects of partial anosmia upon intermale aggression were investigated. Anosmia was induced by placing plugs containing bismuth-iodoform paste, as near as possible to the cribriform plate. Males fought less readily and showed less contact aggression when anosmic. However, intermale aggression was not abolished and presumably other sensory cues are also involved. Anosmia also had subtle effects on other behaviours, eg, olfactory inspections and proximity. Control experiments indicated that the technique employed produced anosmia to conspecific odours and that its effects were not due simply to discomfort.

The effects of partial anosmia upon sexual behaviour of males paired with familiar females were examined. No consistent effects on sexual behaviour were observed. However, the suggestion that olfactory cues may play a role in sexual attractiveness is not discounted.

The ability of owl monkeys living in family groups to discriminate various odour cues was determined. Breeding males showed the greatest response, in terms of sniffing and scent-marking, to conspecific odours, and subcaudal secretion plus urine elicited a greater response than urine alone. It was impossible to demonstrate discrimination of sex or endocrine status on the basis of odour cues alone. The effect of social factors on responsiveness is discussed.

Histological studies confirmed that patent nasopalatine ducts and vomeronasal organ were present in Aotus and some other primate species. External and histological examinations of the cutaneous glandular complexes in Aotus revealed no sexual dimorphism in these glands, though subspecific differences may exist.

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CHAPTER ONE

INTRODUCTION

This thesis describes a study of olfactory communication, aggression and sexual behaviour in a New World primate, the owl monkey (Aotus trivirgatus).

The aim of this first chapter is to present a brief background to the study of olfactory communication in mammals in general, and in primates in particular, together with some of the problems encountered in such studies. The role played by olfaction in regulating mammalian aggression and sexual behaviour will also be outlined. At the end of the chapter the reasons for supposing that the owl monkey is a good model for studies of primate olfactory communication are presented, together with a description of the behaviour and ecology of the species.

The Study of Olfactory Communication in Mammals

The fact that man regards himself as microsmatic has, perhaps, led him to underestimate the importance of olfaction in the lives of other mammals, although even man can detect odorous substances at concentrations of less than one part per billion (Le Magnen 1964). Yet, in the last 15 years there has been an enormous expansion in the research devoted to mammalian olfactory communication (see contributions in :- Birch 1974; Doty 1976. Muller-Schwarze and Mozell 1977; Muller-Schwarze and Silverstein 1980. Stoddart 1980b). The impetus for this work came from earlier research on insects, and later rodents, which indicated that endocrine changes may be associated with chemosensory stimulation, and from advances in technology

PLATE 1.1

Aotus trivirgatus griseimembra

A family group of Columbian owl monkeys, the infant being carried by the male.

which made the analysis and bioassay of putative 'pheromones' possible. The term 'pheromone' was first introduced by Karlson and Butenant (1959) in the context of insect communication. A pheromone may be defined as a chemical substance which, when released by one animal, influences the behaviour or physiology of another individual.

The pheromone concept was soon applied to mammalian communication although several workers (Beauchamp, Doty, Moulton and Mugford 1976; Bronson 1976; Myktyowycz 1979; Law and Reigner 1971) feel that the term leads to confusion when applied to mammalian chemical communication, as the term usually, either explicitly or implicitly, implies a simple, species-specific substance which elicits an innate stereotyped response. It is unlikely that a pheromone of this nature will ever be found in mammals. Wilson and Bossert (1963) classified pheromones as either 'releasers' (which release specific behaviours), or 'primers' (which elicit a neuroendocrine or developmental change and are, therefore, probably long-term in their action).

Several alternatives to the term pheromone have been proposed for use with mammalian chemical communication (Law and Reigner 1971) but the general term of chemiosignal will be used here (Thiessen 1976). A chemiosignal may be defined as any chemical signal that is generated by one animal, which, when received by another animal (either by ingestion or olfaction) causes, either directly or indirectly, a behavioural or physiological response. Only chemiosignals received by olfaction will be discussed here.

Chemiosignals differ in several ways from visual and auditory signals. The main difference is that they can persist for a long time after the sender has departed, and the freshness of the signal may also allow a temporal component to be transmitted. In theory, an infinitely large amount of information could be transmitted via olfactory cues because

of the large numbers and extensive variability of the compounds present in many mammalian secretions and excretions. However, it appears that most odour cues carry relatively simple information (eg, sexual identity, reproductive state), although many compounds may be responsible for conveying that message effectively.

Olfactory, like auditory, communication is well suited to a nocturnal way of life, where the use of visual cues is limited except under conditions of close proximity. The olfactory sense is also quick to fatigue or habituate, and is therefore, able to respond rapidly to changed stimuli. In mammals, the olfactory sense retains its relatively direct links with the subcortical structures which are involved in the control of sexual, aggressive and other behaviours, and in the regulation of the endocrine system. It is therefore not surprising that olfaction, especially in lower mammals, plays an important role in mediating various social behaviours.

There are many general reviews concerning olfactory communication and scent marking in mammals (Brown 1979; Eisenberg and Kleiman 1972; Johnston 1974; Kleiman 1966; Doty 1976; Ralls 1971; Stoddart 1976, 1980 a and b; Thiessen and Rice 1976; Wemmer and Scow 1977), although the role played by olfaction in social interaction has only been studied thoroughly in a few species. Most of the research carried out into mammalian chemocommunication has been performed on rodents (reviewed by Bronson 1976, 1979; Murphy 1976; Schultz and Tapp 1973). Other non-rodent mammalian species have been studied in depth:- the European rabbit, Oryctolagus cuniculus (Mykytowycz 1965, 1974), the black tailed deer, Odocoileus hemionus columbianus (Muller-Schwarze 1971; Brownlee et al 1969), the red fox, Vulpes vulpes (Henry 1977, 1980; MacDonald 1980; Bailey, Bunyan and Page 1980). Few primate species have been intensively studied in this regard:- the rhesus monkey, Macaca mulatta (Michael and Keverne 1968; Goldfoot et al 1978), the red mantled tamarin Saguinus fuscicollis (Epple 1973, 1978), the ring tail lemur, Lemur catta

(Mertl 1976), the brown lemur, L. fulvus (Harrington 1974, 1976, 1978), the mouse lemur, Microcebus coquereli (Schilling 1980).

Most mammals possess specialized glandular areas, whose structure is surprisingly uniform amongst mammals. These glands consist of either sebaceous or apocrine elements, or a mixture of both types of tissue, and are usually associated with a thickening of the epidermis. These cutaneous glands may be under hormonal control. In many mammals testosterone and other androgens increase the size and activity (in terms of cell proliferation) of the sebaceous glands and these glands may atrophy on castration. Estrogen on the other hand, appears to have an inhibitory effect on sebaceous gland activity, probably by inhibiting intracellular synthesis of sebum (Ebling 1974). The hormonal control of apocrine glands has been less well studied, although studies on the chin gland of the rabbit (an apocrine gland), have shown that testosterone is stimulatory and oestradiol inhibitory, with progesterone having little effect (Wales and Ebling 1971). However, there are species and sex differences in the responses of glands to these hormones. Hormonal control may also be exhibited as a sexual dimorphism in gland size, eg, the chin gland in the rabbit is heavier and more active in the male. Both endocrine and neural mechanisms may be involved in the production and release of secretions from these glands (Adams 1980; Ebling 1974).

The position of these various scent producing glands relates to ecological factors, eg, the possession of sternal glands by many arboreal species and the presence of flank glands in several burrowing rodents. As many as 40 different types of gland can be classified according to position in mammals (Muller-Schwarze 1967). Although glandular secretions may be deposited incidently or accidently, as is the case in reptiles, many mammalian species have developed specialized scent marking behaviours to ensure the effective deposition of their secretion, and scent marking behaviour has been recorded in over 44 species of mammals (Thiessen 1976).

Excretions may also be employed for chemical communication. Urine and faeces are extensively used as marking substances by mammals (Bronson 1974, 1976; Ewer 1968; Kleiman 1966; Bearder and Randall 1978; Franklin 1980). This is not surprising, as they are readily available odorous products which only require the evolution of specialized means of deposition to increase their value as marks. In fact, anogenital rubbing may have evolved from cleaning movements (Ewer 1968). Saliva is another readily available excretion that may serve a communicatory function, eg, hedgehog (Brockie 1976), sugar glider (Schultze Westrum 1965) and the pig (Booth 1980). Vaginal secretions may be yet another source of chemiosignals, eg, in the hamster (Kwan 1978; Singer et al 1976).

Olfactory Communication in Primates

Until comparatively recently little attention had been paid to the study of olfactory communication in primates, compared to studies on olfactory communication in other mammals, even though an extensive literature exists on primate communication in general (eg, Gautier and Gautier 1977; Marler 1965; Oppenheimer 1977; Peters and Ploog 1973). Much of the information concerning scent marking behaviour by primates and the contexts in which olfactory displays occur, has to be extracted from field studies, eg, Jolly (1966), although some reviews exist (Epple 1974, 1976; Keverne 1978; Mai 1972; Michael, Bonsall and Zumpe 1976; Rogel 1978; Schilling 1979). One of the reasons for this de-emphasis of olfaction is that much of the research on primate communication has concerned Catarrhine species in which the visual sense is most highly developed. Primates, of course, do have a reduced olfactory system both peripherally and centrally compared to other mammals (le Gros Clark 1934; Napier 1977; Negus 1956), eg, the snout is reduced and there is a decrease in the size of the olfactory and acessory olfactory bulbs relative to other brain structures (Stephan

and Andy 1969). Within the primates this trend is continued, with a decrease in the importance of olfaction as vision becomes a more important means of sampling the environment. Hence the Prosimian and New World primates possess more specialized scent producing glands and show more scent marking behaviours, than the Old World monkeys and apes.

However, olfaction is an important part of the investigatory responses of non-human primates - the majority of primates show muzzel-muzzel touching as a form of greeting. This probably involves both olfactory and tactile communication (Gautier and Gautier 1977; Oppenheimer 1977; Schilling 1979). Many primates show olfactory and, possibly, gustatory (eg, by licking) investigation of conspecifics, especially in the anogential area (Michael and Zumpe 1971). Many primate species also possess a species characteristic body odour noticeable to the human observer (Hill 1960, 1962 and 1970).

It is highly likely that in primates, whose behaviour is much more flexible than that of other mammals, chemiosignals will have lost much of their rigidity of meaning, and it is therefore especially important to remember that olfactory communication does not occur in a vacuum. The importance of social and environmental context and the interaction between olfaction and the other modalities (vision, touch, hearing) can easily be overlooked. Many mammalian olfactory displays have visual or auditory components (Thiessen 1976) and the primates are no exception, eg, visual and olfactory cues are combined in the 'stink' fights of male Lemur catta, where the conspicous black and white tails are marked with secretions from the brachial and antebrachial glands and then waved in the air (Jolly 1966). Visual cues may also serve to orient a potential receiver towards olfactory cues. Again using L. catta as an example, the spurs on the arm leave marks on the tree trunks, which contain brachial gland secretion.

The scent producing glands in the primates contain the same tissue as those in other mammalian species - the glands consisting of apocrine and/or sebaceous tissue. Both the glands themselves and the scent marking behaviours may be under hormonal control. In the male owl monkey the subcaudal gland does not develop until puberty, when levels of plasma testosterone are elevated (Dixson, Gardiner and Bonney 1980), however, in the laboratory, not all adults mark with the gland (pers. obs.). The circumgenital-suprapubic gland in the red mantled tamarin is not significantly affected by gonadectomy in adulthood in either sex (Epple 1980), although as no histological studies were carried out it is difficult to be sure that the lack of change in the gross appearance of the glands truly reflects a lack of change at the cellular level. Prepubertal castration in the tamarin severely and permanently retarded the development of male scent glands. Frequencies of marking with this gland were unaffected by castration in adulthood, although there was a slight inhibition of marking by prepubertal castration (Epple 1980). The sternal glands in Callithrix argentatus and Callimico goeldii also mature at puberty (Epple and Lorenz 1967). Hormonal control may be manifested by sexual dimorphism in the size of the gland, eg, the sternal gland in Galago crassicaudatus is larger in the male than in the female (Dixson 1976). Hormones can also affect olfactory responses by increasing or decreasing the perceiver's sensitivity to particular stimuli, eg, the olfactory acuity of women varies in a systematic fashion with the phase of the menstrual cycle, being highest at ovulation (Good, Geary and Engen 1976; Mair, Bouffard, Engen and Morton 1978), this being especially marked for musky odours like exaltolide. Little work has been done to investigate such changes in acuity in primates.

As in other mammals, scent glands can be found in many different areas of the body in primate species, and many different forms of scent marking are employed. Glands in the anogenital region mean

that to deposit secretion, the animal either has to squat down and rub from side to side, as in the case of the tamarins and marmosets (Epple 1970; Mack and Kleiman 1978), or it has to pull itself along, rubbing or dragging the anogenital region along the surface, as in the 'pull rubbing' of the suprapubic glands of the tamarin and golden lion marmoset (Mack and Kleiman 1978).

Many primates possess sternal glands and Epple and Lorenz (1967) have distinguished as many as five different types of sternal gland complex in the New World primates. Callitrichids rub the sternal gland directly onto the substrate. Whilst Cebids may do this,they usually rub the gland first with the hand or foot, and this may lead to a mixing of the secretion with other odour sources, eg, urine. In Saimiri seasonally fatted males may urine-wash (see below) and then place the foot, wetted with urine, onto the gland (Baldwin 1968) and Cacajao also mixes urine with the glandular secretion (Fontaine and DuMond 1977). Ateles and Lagothrix drool saliva onto the gland (Epple and Lorenz 1967; Klein and Klein 1974). Some primate species show sternal marking even though the sternal gland is very small, eg, Galago senegalensis (Bearder 1969). Sternal marking has also been reported for the Old World genus Mandrillus (Hill 1944; Jouventin 1975). Aotus and Lagothrix both possess glands in the subcaudal region, although it is much more developed in the former (Hill 1962; pers. obs.).

In the Callitrichidae, scent marking is often accompanied by urination or a few drops of urine are passed (Epple 1970, 1978; Mack and Kleiman 1978). Urine is, in fact, used extensively as a marking substance by Prosimian and New World primates. In the Prosimii, all the Lorisiforms mark with urine, although the situation is more complex in the Lemuriforms, with some species using urine as a marking substance regularly and others not at all (Doyle 1974; Ilse 1955; and excellently summarized by Schilling 1979). Urine marking may be

highly stereotyped, as in rhythmic micturition and urine-washing. Rhythmic micturition occurs almost exclusively in the Prosimii, the hind quarters being lowered and a few drops of urine are released as the animal moves forward (Ilse 1955; Schilling 1980). This is obviously an extremely efficient way of distributing a small quantity of urine over a large area, a function also performed by urine-washing.

In urine-washing a few drops of urine are collected in the palm of the hand and then the ipsilateral palmar and the plantar surfaces are rubbed together, or brought into contact by grasping. Urine can therefore be spread around the animal's environment by locomotion, and grooming will distribute urine onto the bodies of other group members. Urine-washing is of phylogenetic importance as it occurs in almost the same form in Lorisids, Cherogaleus and Cebids (Andrew and Klopman 1974; Hill 1938). Urine-washing has been observed in the following Cebid species:- Aotus trivirgatus grisiemembra, A.t. bolivensis (pers. obs.), Cebus capuchinus (Oppenheimer 1968), C. nigrivatattus (Robinson 1979), C. apella (Hill 1960; pers. obs.) C. albifrons (Andrew and Klopman 1974), Saimiri sciureus (Castell and Maurus 1967, pers. obs.). Urine rubbing has been observed in the mantled howler monkey, Alouatta palliata (Milton 1975). In Cebus, the limbs may be wetted during urine-washing.

Although a chemosensory function for urine-washing has been postulated (Baldwin 1968; Schilling 1979, 1980), a purely homeostatic function has also been proposed. A thermoregulatory function has gained support from both captive and field studies; thus when conditions are dry and hot with relatively low humidity, frequencies of urine-washing increase, presumably to increase heat loss via evaporation (captive Saimiri sciureus - Castell and Maurus 1967; field study on Cebus niggrivitattus - Robinson 1979). Robinson (1979) also suggested that water loss may be reduced by spreading

urine on the hands and feet. Such a function does not seem likely for nocturnal species like Aotus, as their nocturnality confers minimal water loss, although such a function may exist for the diurnal Cebids. The nature of the available substrate and light intensity also affect the frequency of urine-washing (Doyle 1975; Schilling 1979; Seitz 1969) and it seems probable that this behaviour may perform several functions. Urine from the mouse lemur has also been shown to retain its chemosensory potential after evaporation and reconstitution (Schilling 1980).

The use of faeces for marking is rare in the primates, except in the dwarf lemurs (Schilling 1979). Defecation seems to be involved sporadically in the marking behaviour of several other Prosimian species:- Propithecus verreauxi (Pollock 1975; Mertl-Millhollen 1979), Lemur catta (Jolly 1966). In Cercopithecus aethiops faecal odour may serve to mark sleeping trees (Poirier 1970), but no other Catarrhine primate has been reported to use either urine or faeces as a marking agent. It must also be remembered that both urination and defacation can be elicited by fear, and this may lead to errors in interpreting the situations that evoke these behaviours, especially under captive conditions.

It also appears that several other secretions and excretions may be involved in primate olfactory communication. Saliva has already been mentioned and Schwartz and Rosenblum (1980) have reported that nasal secretions expelled by sneezing and accompanied by nasal rubbing on the substrate may also be used for marking purposes. Vaginal secretions may be deposited by rubbing (Epple 1970; Jolly 1966) or appear to have pheromonal activity (Curtis et al 1971 Michael and Bonsall 1977). Rubbing of the cheek has also been reported for Callicebus (Moynihan 1966).

Thus, there does appear to be some evidence for the contention that olfaction plays a role in the communicatory repertoire of primates.

Before reviewing some of the observational and experimental studies which have examined the relationship between olfactory cues and aggressive and sexual behaviour, a brief description of the mammalian olfactory system is presented.

The Structure of the Olfactory System in Mammals

Most mammals are diosmic, that is, they possess two functional olfactory systems - a main olfactory system and a vomeronasal system. The exceptions include the chelonia, cetecea, some bats and the higher primates including man (Cooper and Bhatnagar 1976; Parsons 1958; Roper-Hall 1945). These two systems are distinct from one another anatomically, and they are probably also functionally distinct. Although only these two systems will be described here, it must be pointed out that other nerve supplies exist in the oral and nasal mucosa (eg, the septal organ of Masera) and these may also play a role in olfactory reception (Graziadei 1977). As the morphology of the mammalian olfactory system is dealt with extensively in many reviews (eg, Allison 1953; Moulton and Beidler 1967; Negus 1958; Tucker and Smith 1969; and see Epple and Moulton 1978 for emphasis on non-human primates) only a general description will be given, with slightly more emphasis placed on the vomeronasal system than the main system, to provide a background for the histological studies in Chapter Six.

The Main Olfactory System

In mammals the walls of the nasal cavity are thrown into a complicated series of folds by several series of turbinal bones, the sensory epithelium lying on the ethmoturbinal bone and the cribriform plate in the posterior chamber of the nasal cavity. These convolutions of the turbinal bones expose a large surface area of sensory epithelium to the air, and it has been shown for mammals that the surface area of olfactory epithelium is directly related to olfactory acuity (Ottoson and

[illegible] In the higher primates and man these turbinals are simple scrolls and there is a reduction in the surface area of the sensory epithelium compared to other mammals (Allison 1953).

The olfactory epithelium is composed of receptor cells, support cells and basal cells, and its surface is kept moist by the secretions from the Bowman's glands that lie within it. The receptor cells are bipolar neurones and they bear short cillia at their tips, which may function in olfactory reception (Stoddart 1980a). However, the actual means by which odours are perceived has not yet been conclusively determined, although several theories exist (Davies 1971). One promising approach might be to investigate the reason for the constant turnover of the sensory olfactory epithelium.

The axons of the receptor cells synapse on the mitral cells in the olfactory bulb in the central nervous system. The secondary connections of the main olfactory system may be highly variable between species (Turner and Mishkin 1978). The main projection of the olfactory bulb is ipsilateral to the medial dorsal thalamus via the lateral olfactory tract and prepyriform cortex. From the medial dorsal thalamic nuclei, projections pass to the orbital frontal neocortex. The mitral cells also send fibres to the contralateral olfactory bulb and to the hippocampus. Thus the main olfactory system has fairly direct access to the neocortex.

The Vomeronasal System

The vomeronasal organ was first described fully by Jacobson (1811), although its presence had been noted by Ruysch (1703). Since its discovery the occurrence and structure of the organ has been well documented for many species (Allison 1953; Negus 1956). The vomeronasal organ is a bilaterally symmetrical structure encapsulated by cartilage. Both organs are cigar shaped and open at the

anterior end. The vomeronasal organ lies at the base of the nasal septum and in most mammals it opens onto the nasopalatine canal via the vomeronasal duct. The nasopalatine duct joins the nasal and buccal cavities. In some species, eg, rat, mouse, the vomeronasal duct empties directly into the nasal cavity. In the carnivores, the vomeronasal duct opens into the nasopalatine duct midway between the oral and nasal cavities, whereas in certain ruminates the junction is nearer the oral cavity (Schilling 1970).

The structure of the sensory epithelium is similar to that of the main olfactory system, except that no basal cells or Bowman's glands are present. The receptor cells do not bear cillia, and like the main olfactory cells they have the capacity of regeneration (Graziadei 1977). The organ is present in Strepsrrhine and Platyrrhine adults, but it usually only appears in the foetus of Catarrhine primates and man, although it can persist into adulthood in a very rudimentary form (Eloff 1951; Frets 1912; Johns pers.comm.; Jordan 1972; Roper-Hall 1945; Schilling 1970; Starck 1975). There have also been several reports of patent nasopalatine ducts in human adults (Broome and Seymour 1976; Buchner and Mlinek 1972). A further account of its structure in the primates is given in Chapter Six.

The mechanism by which stimuli reach the vomeronasal organ has not been confirmed. A vascular pumping mechanism was suggested by Hamlin (1926), and recently, elegant experiments by Meredith (1980) have investigated this suggestion further. He suggests that the naso-palatine nerve plays a crucial role in activating this pumping, which, he suggests, is probably activated reflexly following sensory input via the main olfactory system or other sensory systems. It also seems likely that both vapour and liquid can be sampled by, or at least have access to, the vomeronasal organ (Beauchamp et al 1980; Meredith 1980).

The central projections of the main and accessory (vomeronasal) olfactory systems are anatomically distinct (Barber and Raisman 1974).

The axons from the receptor cells in the vomeronasal organ pass (as the vomeronasal nerve) through the cribriform plate to synapse on the mitral cells in the accessory olfactory bulb, which lies on the dorsal, posterior surface of the main bulb. The accessory bulb appears to be absent from those species in which no functional vomeronasal organ is present, although a rudimentary vomeronasal organ may exist when no accessory bulb is present (Cooper and Bhatnagar 1976). The accessory olfactory bulb projects to the cortico-medial amygdala, and from there, via the stria terminalis, to the medial preoptic area, the septal nuclei and the ventromedial hypothalamus (Raisman 1972; Scala and Winans 1976). The accessory olfactory system has fairly direct links therefore with areas involved in the control of sexual and aggressive behaviour and gonadotrophin release. Also, because of its input to the limbic system, stimulation of the vomeronasal system could easily alter the general (non-specific) level of cortical arousal and also affect the expression of a number of behaviours (eg, eating, drinking, sexual and aggressive behaviour) in this way.

It has also been suggested that the two olfactory systems act synergistically - the main olfactory system, with its close neocortical links, initiating sexual behaviour under the appropriate circumstances, whilst the vomeronasal system, acting via the limbic system, ensures the release of the appropriate autonomic and hormonal responses (Keverne 1979).

The Role of Olfaction in Social Interactions

Studies on different species have shown that various characteristics of an individual can be distinguished by odour alone. Some examples from these studies are shown in Table 1.1. The fact that certain mammals can be shown to discriminate, and therefore probably obtain information about, various characteristics of their conspecifics supports the argument that olfaction is involved in social interactions. Olfactory cues have been shown to be important in many different types

TABLE I.I

Characteristics Discriminated by Olfactory Cues -
A Comparison of Experimental Data from Primates and Other Mammalian Species

Mammals Other Than Primates			Equivalent Studies in Primates	
Species	Odour Source	Characteristic Discriminated	Species	Odour Source
Guinea pig (Beauchamp 1973)	Urine	Species	Galago crassicaudatus (Clark 1975) Microcebus coquerli (Schilling 1980)	Complex mark
Mongoose (Gorman 1976)	Anal gland	Individual	Lemur catta (Mertl 1975) Saguinus fuscicollis (Epple 1973)	Brachial gland Complex mark
Beagle (Dunbar 1977)	Urine	Sex	L. fulvus (Harrington 1974) S. fuscicollis (Epple 1979)	Complex mark Complex mark
Mouse (Scott and Pfaff 1970)	Urine	Male's hormonal status	S. fuscicollis (Epple 1979)	Complex mark

/ contd ...

TABLE 1.1 - contd

Rat (Lydell and Doty 1962)	Urine	Stage of the ovarian cycle	Macaca mulatta (Michael and Keverne 1970)	Vaginal origin
Beagle (Doty and Dunbar 1974)	Urine			
Black-tailed deer (Muller-Schwarze 1971)	Metatarsal gland	'Emotional' state (fear/alarm)	Perodicticus potto? (Manley 1974)	Unknown
			Arctocebus calabarensis? (Manley 1974)	Unknown

of social behaviour in primates and other mammals, eg, in mother-infant interactions (Kaplan and Russel 1974; Leon 1978; Wallace, Owen and Thiessen 1973) and trail marking (Schilling 1979), as well as in maturational processes, eg, timing of onset of puberty (Cowley 1980, Vandenberg 1980). However, only the role of chemiosignals in mediating certain aspects of aggressive behaviour and sexual behaviour will be discussed here.

Chemiosignals and Aggression

An animal may be said to have behaved aggressively when it attempts to injure another animal or displays an intention to do so. Aggression is neither a unitary concept nor a unitary phenomenon, and Moyer (1968) has distinguished seven different classes of aggression, eg, predatory, irritable, which he suggests are largely independant of each other and which are possibly mediated by different neural pathways. The topic of aggression has been extensively reviewed (Brain 1979; Collias 1944; Conner 1972; Thiessen 1976, and contributions in Clemente and Lindsley 1967; Garattini and Sigg 1969), and the role of chemiosignals in aggressive behaviour has been reviewed by Thiessen (1976). Here, only two types of intraspecific aggression will be discussed - inter-male (Moyer 1968) and territorial aggression. It must be remembered that, although in many species individuals of the same sex may be highly aggressive to one another, this also applies to females as well as males in many primate species, eg, in the rhesus monkey (Bernstein 1964) and in the talapoin monkey (Scruton and Herbert 1972). Therefore, in discussing inter-male aggression, inter-female aggression will also be mentioned where appropriate.

Primate aggressive behaviour has been well documented, and although in many primate species males are more aggressive than females (Dixson 1980), it does seem that in monogamous, monomorphic primates, it is less likely that any one sex will be more aggressive

than the other, both sexes usually being involved in defense, care of the young, etc. It also seems likely that monogamous primates react more aggressively towards intruders of the same sex (Epple 1980; Kleiman 1977; Mason 1966), although aggression within family groups may be low.

1. Territorial Aggression

A territory is usually described as an area that is actively defended against conspecifics (Hediger 1949). However, once territorial boundaries have been established, active defense in terms of overt threat would be costly in terms of energy. Therefore, it would not be surprising if chemiosignals were employed for boundary demarcation, as they can remain long after the sender has departed. If a relationship existed between territory and olfaction one might expect that animals would mark more in the periphery of their territory than elsewhere. This is the case for some non-primate mammals, eg, mouse (Harrington 1976), gerbil (Thiessen 1973), spotted hyena (Bearder and Randall 1978), badger (Kruuk 1978) and the golden jackal (MacDonald 1980), and also for some ungulates (Grau 1976). However, it is not true for other apparently territorial species, eg, the otter (Gorman 1980). In some animals, such as the rabbit, which are territorial, certain forms of marking occur only within the territory (Mykytowycz 1970) and it must also be remembered that odour may be involved in the spacing behaviour of animals in situations where it is not necessary to invoke the concept of territory.

Marking behaviour may accompany territorial disputes in primates, eg, in Lemur catta (Schilling 1974), and it seems likely that in this context it is functioning as a form of 'reassurance', increasing the animal's 'confidence' (Ewer 1968). In those species where olfactory demarcation of boundaries occurs, territorial aggression should, in fact, be relatively infrequent, as the lack of physical patrolling should

lead to a decrease in the number of intergroup encounters and hence potentially aggressive episodes. This fact may explain the lack of intergroup (or, in the case of semi-solitary species, inter-individual) encounters that have been reported for Prosimian and New World primates (Charles-Dominique 1974,1977; Doyle 1974; Moynihan 1964, 1970 and 1976). In some species it is obvious that vocal means ensure spacing between groups, eg, the howler monkey (Carpenter 1965), but especially in nocturnal species, olfactory demarcation of territorial boundaries may occur. The territorial primate Propithecus verreauxi scent marks at the boundary of its territory far more than in the interior of its territory (Mertl-Millhollen 1979) and there are indications that scent marking functions in intergroup communication and boundary demarcation in the following primate species:- Leontopithecus rosalia rosalia (Mack and Kleiman 1978), Saguinus oedipus (Dawson 1976), Alouatta caraya (Shoemaker 1979), Callithrix jacchus (Epple 1970), Lemur catta (Mertl 1977), Nycticebus coucang (Ilse 1955), Galago alleni (Charles-Dominique 1977). The odours of familiar and unfamiliar conspecifics are also strong stimulators of marking behaviour in C.jacchus and S.fuscicollis (Epple 1970, 1975).

Territorial marking in the rabbit is also dependant on the social status of the animal (Mykytowycz 1968) and marking behaviour may also be under hormonal control, eg, in the gerbil, castration leads to a decrease in territorial marking with the ventral pad, whilst treatment with testosterone (in the males) and oestrogen (in the females) leads to the reinstatement of marking behaviour (Thiessen, Friend and Lindzey 1968). In some non-primate species, territorial aggression is itself dependant upon hormonal factors, eg, red grouse (Watson 1970), although the role played by hormones in the control of territorial aggression in primates has not been investigated.

2. Inter-Individual Encounters

The descriptions of many aggressive encounters between animals of the same species have utilized the concept of 'dominance'. Although many different measures of dominance have been used, eg, access to food, water or sexual partner, such measures often do not correlate well with measures of dominance deriving from direct observations of aggressive behaviour. Therefore, unless otherwise stated, in the experiments which follow, dominance was assessed by measurements of aggressiveness, the dominant individual being the most successful animal in aggressive encounters. There is a large body of evidence that suggests for mammals, dominance, as defined above, and scent marking behaviour are related. In these species, dominance is associated with high marking levels and submissiveness with a reduction in, or total cessation of, scent marking (Desjardins, Maruniak and Bronson 1973; Johnston 1974; Mykytowycz 1965; Ralls 1971; Swanson and Lockley 1978; Thiessen, Owen and Lindzey 1970). In the gerbil and the hamster, subordinates still possess the ability to mark, and will do so if placed in an area where they have not previously experienced defeat, or if the dominant animal is permanently removed.

Similar findings have been reported for primate species. Dominance and scent marking in Prosimians is reviewed by Doyle (1974), and it appears that for Galago senegalensis and G. demidovii, high levels of marking are correlated with high social status. In Lemur catta spur and genital marking are probably concerned with the maintenance of dominance status (Evans and Goy 1968). Similar results have been found for New World primates. In Callithrix jacchus the dominant male and female scent mark more with the circumgenital glands than juveniles or subordinate animals. Only the highest ranking males mark with their sternal glands and then only infrequently, (Epple 1970, 1974). In a field study in Panama, Dare (1977) concluded that in male Ateles geoffroyi overall social dominance (based on affiliation

and power rankings) is also positively correlated with olfactory displays, especially sternal rubbing. In Alouatta palliata dominant animals do not mark more, but muzzel-muzzel sniffing may be involved in the communication of status relations within the group (Jones, pers. comm.) and this may also be true for some higher primates (Gautier and Gautier 1977; Simmonds 1965).

Visual and olfactory displays may be combined, as in the genital displays of Saimiri sciureus and Callithrix jacchus. These displays are always performed by dominant animals towards submissive ones. In S. sciureus urination may accompany the display (Baldwin 1968), and in C. jacchus the recipient of the display may approach the displaying animal and then sniff his or her genitals intensively while giving submissive calls. The displaying animal may then partner mark the recipient (Epple 1970, 1974).

To summarize - it does seem that in the Prosimian and New World primates at least, there is some evidence that social dominance is correlated with high marking levels. However, the relationship between dominance and scent marking is complicated by several factors. Firstly, reproductive condition may depend on the dominance status of an animal, eg, in C. jacchus subordinate females do not ovulate (Abbot and Hearn 1978) and marking is inhibited in these animals. Inhibition of marking could therefore be due to an indirect effect of subordination on reproductive processes.

A second complication is that dominance, as defined here, is based on aggressive interactions. Such aggressive interactions themselves can stimulate marking behaviour, eg, in the hamster (Johnston 1974) and the black tailed deer (Muller-Schwarze 1969), and therefore the correlation between scent marking and dominance per se may be spurious.

Aggressive interactions in Prosimian and New World primates, either between groups of conspecifics or between members of the same group,

are often accompanied by olfactory displays. Scent marking behaviour has been observed during or after intergroup agonistic encounters in the following primate species:- Lemur catta (Budnitz and Davis 1975), L. fulvus (Harrington 1974), Galago crassicaudatus (Andrew and Klopman 1974), Indri indri (Pollock 1975), and Saguinus oedipus (Dawson 1976). Aggressive encounters in captive groups of Callithrix jacchus and S. fuscicollis also stimulate marking behaviour (Epple 1970, 1974). The rubbing of a foot, wetted with urine, onto the sternal gland in male Saimiri sciureus seems to be elicited when there is a potential for aggressive encounters, possibly as an act of self-advertisement (Epple and Mason, unpublished data in Epple 1974), and Dobroruka (1972) reports that in a group of Cebus apella, males and females may mark with their sternal gland in conjunction with a visual threat.

Often it is not possible to distinguish whether the animal is marking because it is highly aroused, as a displacement activity, or whether marking is serving a self-advertising or threatening function. Body odours might also be involved in reducing aggression, as in the mutual patterns of embracing and sniffing of the pectoral region in Ateles (Rondinelli and Klein 1976), which appear to be a form of appeasement behaviour between adult males.

Both dominance and aggressive behaviour may be under hormonal control. This is most readily observed in those species which are seasonal breeders. In many animals the onset of the breeding season is signalled by testicular enlargement, increases in circulating plasma testosterone and increases in aggressive behaviour. This has been shown for the roe deer (Sempere, Garreau and Boisson 1980) and in the seasonally breeding primate, Saimiri sciureus, aggression between males may increase during the breeding season, (Baldwin 1968) although other workers have not found any correlation between testosterone levels and aggressiveness (Mendoza et al 1978).

There have been attempts to correlate dominance with high levels of circulating testosterone (eg, Rose, Holaday and Bernstein 1971) although these results have proved difficult to replicate in further experiments (Gordon, Rose and Bernstein 1976). The relationship between androgens and aggression in primates is reviewed by Dixson (1980) and will not be discussed further here.

Anosmia experiments on intermale aggression have often produced conflicting results, mainly due to the use of different techniques for inducing anosmia. The relative merits of these various techniques will be evaluated in the methodology section (see below). Most of the work on anosmia and aggression has been carried out on rodents. Unfortunately, nearly all experiments which have investigated the effects of anosmia on aggression in the rat, fall outside the scope of the present discussion since they deal with muricide behaviour in rats, rather than with intraspecific aggression (eg, Karli, Vergnes and Didiergeorges 1969).

Edwards, Thimpson and Burge (1972) found that anosmia produced by intranasal zinc sulphate led to increased fight latency between pairs of anosmic male mice, together with a decrease in the number of pairs that fought on the first day of anosmia. Studies on the hamster and gerbil have shown that a reduction in both intermale aggression and territorial marking behaviour occurs after central olfactory blockade (DeVore and Murphy 1973; Macrides, Firl, Schneider, Bartke and Stein 1976; Thiessen, Lindzey and Nyby 1970). There has been no research into the effects of anosmia on aggression in primates, except that Keverne (1978) reported that in male-female pairs of rhesus monkeys which were characterized by aggressive rather than sexual behaviour, anosmia in the male did lead to a reduction in aggression shown by the male towards the female. However, no increases in sexual behaviour were observed.

In conclusion, one can say that there is evidence that olfaction may be important in both territorial and inter-male aggression, although probably to a lesser extent in the Prosimian and New World primates than in other mammals.

Chemiosignals and Sexual Behaviour

The role of chemiosignals in sexual behaviour has been extensively investigated and many reviews exist (Aron 1979; Bronson 1971; Keverne 1978; Schultz and Tapp 1973; Signoret 1976; Wysocki 1979). The 'primer' effects of chemiosignals have also been reviewed (Bronson 1979; Milligan 1980; Parkes and Bruce 1961) and will not be described here. The reason for this is that the existence of primer chemiosignals has only been conclusively proved in rodents, and it is unlikely that chemiosignals will elicit primer effects in primates. Possible exceptions to this are the phenomena of estrous synchrony and seasonal reproduction in some primates, eg, Lemur catta (Evans and Goy 1968), and these will be discussed briefly below.

Two main areas will be discussed :-

1. The role of olfaction in identifying the sex and reproductive status of a potential mate;

2. The importance of olfaction in mediating sexual arousal and copulatory behaviour in the male.

These two areas are not, of course, mutually exclusive.

1. The Role of Olfaction in Identifying Sex and Reproductive Status of a Potential Mate

Evidence for olfactory mediation of reproductive status comes from discrimination studies and from observations of olfactory related behaviours in the context of sexual behaviour. Both the rat and the dog can detect the reproductive state of the female (oestrous versus anoestrous, see Table 1.1). Generally, work on a variety of rodent

and non-rodent species has indicated that the odour from receptive (ie, oestrous) females is preferred by males over the odour from non-receptive anoestrous) females; that any female odour is preferred over any male odour and that both males and females prefer intact male odours over castrate male odours (Drewitt and Spiteri 1979; Kwan 1978; Landauer, Weise and Carr 1977; Landauer, Banks and Carter 1978; Signoret 1976), although exceptions do exist, eg, intact male hamsters prefer the odours of castrate males over those of intact males (Landauer, Banks and Carter 1977). Sexual experience and rearing odours may also play a part in establishing such preferences - a factor which must be taken into account when studying laboratory species (Dizinno, Whitney and Nyby 1978; Doty and Dunbar 1974; Muller-Schwarze and Muller-Schwarze 1971; Nyby et al 1978). From the many experiments that have been performed it does seem that information on sex and reproductive status can be transmitted via chemiosignals in non-primate mammals.

Discrimination studies of this kind have only been performed with a few primate species (eg, Table 1.1) Lemur fulvus and Nycticebus coucang spent more time investigating male odour (complex mark for the lemur and urine for the loris) than female (Harrington 1974; Seitz 1969). The reverse was true for male and female Galago crassicaudatus, who also scent marked female scented perches more (Clark 1975). Epple (1976) found that male and female Saguinus fuscicollis marked male scented perches more than those carrying female odours, although no sniffing preferences existed. Male tamarins sniffed individual samples of odour from intact males more than those from castrate males, but only marked more when pooled samples were presented (Epple 1979). Epple attributes the lack of any female preference for individual samples of intact over castrate male samples to a lack of motivation (although females did sniff intact male samples more when pooled samples were presented).

This is an important point to bear in mind when results from discrimination studies are discussed (see also methodology section).

Thus, evidence from discrimination studies suggests that many mammals including Prosimians and New World primates, are capable of distinguishing sex and reproductive state on the basis of olfactory cues alone. Supportive evidence for a role of olfaction in sexual recognition has come from field and laboratory observations and research using anosmia techniques.

Olfactory investigation by males of females varies with the reproductive condition of the female in many species. In Saimiri sciureus, a seasonal breeder, there was a dramatic increase in the frequency of olfactory inspections of females by males up to and during the months preceding the seasonal mating peak, although marking frequencies did not increase during this period (Hennessy, Coe, Mendoza, Lowe and Levine 1977). Similar results were also obtained for Lemur fulvus in the field (Harrington 1975), and he also found that male marking frequencies did increase at the time of the mating peak. Female L. catta show a peak of genital marking during and just after ovulatory phase of the cycle, applying vaginal secretion and urine as they do so (Evans and Goy 1968; Schilling 1974). Robinson (1979) also suggested that female Cebus nigrivitattus increased marking (in the form of urine-washing) at this time and there was a concommitant increase in male inspections of females.

In the field, olfactory inspections of females by males are common in many primate species, eg, the bonnet macaque during the mating season examines the female's genitalia and frequently inserts his fingers into the vagina sniffing them before mounting (Rahaman and Parthsaray 1971). Similar behaviour has been reported for M. sinica and M. arctoides (Michael and Zumpe 1971). It seems likely that in those species of macaque, eg, M. radiata, M. arctoides where visual cues to reproductive state (eg, sexual swelling) are reduced, olfactory

monitoring may be more important than in other species, eg, M. nemestrina and M. mulatta, where visual cues to reproductive state are present (Dixson, pers. comm).

Similar observations have also been reported for the great apes. Van Lawick-Goodall (1968) observed that male chimpanzees inspect the vagina more frequently during the pre-ovulatory stage of the reproductive cycle, (as indicated by the sexual swelling). Sometimes this simply involved sniffing the vaginal opening, but males were also observed to insert a finger into the opening and then sniff the finger. Captive lowland gorillas at Basel Zoo had a distinctive odour during the ovulatory phase of the cycle and males have been observed to touch the female's genitalia and then sniff their hands, particularly during the pre-ovulatory stage of the cycle. Orogenital contact may be common during the ovulatory phase as a prelude to copulation (Hess 1973). However, in his extensive studies of sexual behaviour in the gorilla, Nadler (1975, 1976) does not emphasize these aspects of olfactory communication.

The role of olfaction in monitoring the reproductive condition of the female has been studied experimentally in an Old World species - the rhesus monkey, Macaca mulatta. Michael and Keverne (1968) used an operant conditioning paradigm, where male rhesus monkeys had to press a lever to gain access to females, which they could see, hear and smell. Each female was ovariectomized and either treated with estrogen or untreated. Males regularly pressed for access to the treated females but rarely responded for access to the untreated females. A reversible anosmia technique was then employed which blocked the main olfactory system by means of gauze plugs, impregnated with bismuth iodoform paste, which were inserted, via the nares, as close as possible to the crib form plate. This was used to determine the importance of olfaction in mediating any change in female attractiveness induced by the estrogen treatment. Anosmia in four

males did not alter their pressing for, or sexual behaviour with, the estrogen treated females, but these males failed to recognize any change in attractiveness in previously untreated females that were now treated with estrogen, a discrimination they could make when not anosmic. The anosmia procedure did not reduce male sexual behaviour with females that had been treated with oestradiol, which affects proceptive behaviour as well as attractiveness (Keverne 1980). The source of the odour mediating attractiveness appeared to be vaginal (Michael and Bonsall 1977), as increasing the red colour of the sexual skin by topical application of estrogen had little effect on the male's sexual behaviour (Michael and Keverne 1970). Therefore, it does seem for the rhesus that olfaction may be involved in the detection of changes in the female's attractiveness.

2. The Importance of Olfaction in Mediating Sexual Arousal and Copulatory Behaviour in the Male

Although this description will focus on effects in the male, anosmia may also affect female copulatory behaviour, eg, olfactory cues are important in initiating the correct receptive ('standing') posture in the sow (Hafez and Signoret 1969). Changes in the female's behaviour may also compensate for (and hence mask) any decreases in sexual motivation in an anosmic male (Keverne 1980 and see below).

Sexual arousal may be heightened by olfactory stimuli, for example, scent marking has been observed prior to, during and after, copulation in several primate species, eg, Lemur fulvus (Chandler 1975), Ateles belzebuth and A. geoffroyi (Klein 1971), Callithrix jacchus (Epple 1970). However, any increase in marking may be due to heightened arousal, rather than the converse.

Most studies that have attempted to investigate the role of olfactory cues in mediating sexual arousal and copulatory behaviour in the male, have employed some form of anosmia technique. Results from these

studies have often been contradictory, mainly due to the different techniques that have been employed. Mating in mammals is seldom eliminated by olfactory impairment, although it may often be seriously impaired (Stoddart 1980a). This is the case for many rodent species, eg, in the rat both peripheral (ie, surgical removal of the olfactory epithelium) and central (ie, lesions in the olfactory peduncle) anosmia techniques affect mating behaviour. Anosmic male rats often mount receptive females and achieve intromission, but rarely ejaculate. For those that do ejaculate, latency to ejaculation is significantly longer than that of controls. Hence different components of mounting behaviour may be affected differentially.

In the golden hamster, intranasal zinc sulphate completely suppressed copulatory behaviour in one study (Lisk, Zeiss and Ciaccio 1972). However, further experimentation with this species (Winnans and Powers 1977) has shown that the vomeronasal system, as well as the main olfactory system, is involved in the initiation of mounting behaviour in the male. Deafferentiation of the vomeronasal system led to a reduction in mating behaviour in 44 percent of male hamsters tested (25 percent of whom failed to exhibit any mounting behaviour). Further deafferentiation of the main olfactory system abolished mating behaviour in the remaining animals.

It is likely that the role of the vomeronasal system in the control of sexual behaviour is a complimentary one, but the vomeronasal system has been directly implicated in the mediation of some of the primer pheromone effects observed in rodents:- in the mediation of oestrous suppression in groups of female mice (Reynolds and Keverne 1979); in the pheromonal induction of delayed implantation in female mice (Bellringer, Pratt and Keverne 1980); in the decrease in oestrous cycle length in naive female rats on exposure to male odour (Sanchez-Criando 1979) and in eliciting reflex ovulation in light-induced oestrous rats (Johns, Feder, Komisaruk and Mayer 1978). It seems probable

that these primer effects are a result of vomeronasal input acting on gonadotrophin release via its connections with the hypothalamus. Further evidence for the involvement of the vomeronasal system in mammalian reproductive processes is provided by Wysocki (1979).

The effect of anosmia on male copulatory behaviour has also been studied in mammals other than rodents. Aronson and Cooper (1974) found that bilateral bulbectomy did not impair the mating performance of male cats. However, this procedure in the domestic sheep did affect the ram's mating behaviour. An intact ram inseminated approximately 97 percent of the ewes in the flock that were in oestrus. This figure dropped to 55 percent when the ram was anosmic (Fletcher and Lindsay 1968). Rouger (1973) found that intranasal zinc sulphate also led to a decrease in mating behaviour in the ram.

Therefore, it seems that the importance of olfaction in mediating copulatory behaviour in the male varies considerably between non-primate mammalian species. Research in this area on primates has also centred on Old World species:- the rhesus monkey, Macaca mulatta and the talapoin monkey, Miopithecus talapoin. Unlike the study by Michael and Keverne (1968), these studies have both looked at the effect of anosmia on sexual behaviour and sexual arousal in the male. Goldfoot et al (1978), using a non-reversible anosmia technique, ie, sectioning of the olfactory nerves, found that anosmia did not affect copulatory behaviour in the male rhesus monkey. This result does not conflict with that of Michael and Keverne (1968) when one considers that the two experiments are asking essentially different questions. Additionally, in Michael and Keverne's experiments (1968) anosmia did not impair copulation (in terms of ejaculations) in those pairings where the female was recognised as attractive by the male (Keverne 1980).

A recent study on the talapoin monkey has examined the effects of anosmia on sexual behaviour in four males of differing social rank,

within a social group of monkeys (Keverne 1980). Male sexual behaviour, in terms of ejaculations and the number of mounting attempts, did not show any consistent changes when the males were anosmic compared to when they were untreated. Although anosmia generally had little effect on the males' sexual behaviour, the females' contribution to sexual interactions, in terms of sexual invitations, increased when the males were made anosmic. This increase in the females' proceptive behaviour together with the fact that the males' behaviour is essentially unchanged, has been interpreted as a "loss in the stimulus value of the female" (Keverne 1980, pg 325), and this does seem the most likely explanation of the results. This result also stresses the importance of looking at both male and female behaviour, even if only the males are made anosmic.

To summarize, it does seem that olfaction is important in mediating certain aspects of primate sexual behaviour. However, it is unlikely that olfactory cues are critically involved in the control of sexual behaviour in many primate species.

Methodology in Olfactory Studies

Descriptive studies are a necessary prelude to experimental studies. Until fairly recently much of the literature on olfactory communication, apart from that on rodents, was purely descriptive. The contexts in which olfactory investigation and scent marking behaviour occurred, for example, during aggressive disputes, were described for many species, both in the lab and in the field, eg, for the wolf (Peters and Mech 1975), for the rabbit (Mykytowcyz 1962), for the fox (Henry 1980) and the ring tail lemur (Jolly 1966). Once such basic knowledge has been obtained, the next stage is experimental, involving the manipulation of environmental and social factors and observing any concomitant changes in olfactory related behaviours. The internal

environment of an animal is easily altered by hormonal manipulations eg, castration and androgen replacement therapy. Such studies have shown that androgens and oestrogens may affect marking frequencies and the development of marking behaviour (Epple 1980; Thiessen, Friend and Lindzey 1968) in several mammalian species. Other studies where the external environment is altered have shown that social factors can strongly influence marking behaviours (Thiessen and Rice 1976). Hormonal and social factors may also act synergistically as in the breeding season of some ungulates (Sempere, Garreau and Boissin 1980).

Another technique that has been used extensively is the elimination of part or all of an animal's olfactory input, either reversibly or permanently, and then observing the subsequent effects on the animal's behaviour. Unfortunately, many different methods have been used to produce anosmia and this often makes it difficult to compare results from different studies. Some of the methods involve removal of central structures, eg, the main olfactory bulbs. Removal of the main olfactory bulbs has been shown to produce effects which are not due to anosmia alone, but can be attributed either to some additional, central non-olfactory action of the bulbs, or to accidental removal of other central nervous tissue, such as the accessory olfactory bulbs (Edwards 1974; Cain 1974). Anosmia produced by bulbectomy cannot therefore be equated with anosmia produced by other central nervous system manipulations, such as sectioning the olfactory nerves, nor with anosmia produced by peripheral methods such as destroying the olfactory epithelium with chemical agents (Sieck and Baumback 1974) and it seems likely that many results which have appeared contraditory may merely result from the use of different techniques. Even peripheral techniques have disadvantages. The olfactory epithelium has the capacity of regeneration and when substances like zinc sulphate are used to destroy the olfactory epithelium, the impairment is only temporary and after a period of several weeks complete acuity may be

restored (Schultz 1960). Zinc sulphate can also cause systemic poisoning which will lead to behavioural changes other than those directly attributable to anosmia (Sieck and Baumback 1974). Different strains of the same species may also be differentially affected, a fact that must be borne in mind, especially when the results from rodent studies are compared (Wysocki 1979). Therefore, care must be taken in such studies that these effects are controlled for and that equivalent concentrations of the anosmic agents are employed.

Peripheral anosmia has also been induced reversibly by means of plugs, either containing an anosmic agent (Keverne 1980, Michael and Keverne 1968) or with no such agent (Verberne 1977), and these techniques have been used to block both the main olfactory system (Michael and Keverne 1968) and the vomeronasal system (Verberne 1977).

The various methods employed to produce anosmia are reviewed and evaluated by Alberts (1974) and by Murphy (1976), and are listed in Table 1.2. It must be borne in mind that in many cases the term partial anosmia should be substituted for the term anosmia, as at least one chemosensory system is usually left intact.

The final experimental approach to be discussed has been to present various conspecific odours to an animal and, by observing the responses of the animal to these odours, determine whether various characteristics of the donor can be discriminated on the basis of odour cues alone. This approach has been used with deer (Broom and Johnston 1980), rodents (Bowers and Alexander 1967, Valenta and Rigby 1968) and several primate species:- Galago crassicaudatus (Clark 1975), Saguinus fuscicollis (Epple 1973), Lemur fulvus (Harrington 1974), Lemur catta (Mertl 1975) and Nycticebus coucang (Seitz 1969). Most of these experiments have involved the habituation of the subject to the odour of one animal and then the

TABLE 1.2

Basic Methodological Approaches to the Study of Mammalian Olfaction

Anosmia Techniques :

- Bulbectomy
- Sectioning of the main olfactory nerve
- Sectioning of the vomeronasal nerve
- Permanent/reversible destruction of the main olfactory epithelium
- Permanent/reversible destruction of the vomeronasal epithelium
- Physical blocking of the input to either system
- Any combination of the above techniques

Other Techniques :

- Purely descriptive studies in the laboratory and in the field
- Responses to manipulations of the physical environment, eg, humidity
- Responses to manipulation of the social environment, eg, group composition
- Responses to novel odours
- Responses to biological odours including bioassay
- Alterations of animals' own odour
- Manipulation of rearing odours

presentation of the odour of another animal. If discrimination has occurred, one would expect an increase in olfactory investigation and possibly scent marking when the unfamiliar odour is presented. Operant conditioning techniques have also been used with other mammals such as the dwarf mongoose (Rasa 1973) and the mongoose (Gorman 1976) and the badger (Gorman 1976).

This is a useful approach but again, there are limitations. The fact that an animal can discriminate, for example, the sex of a donor on the basis of odour alone, in an experimental situation, does not necessarily mean that odour cues alone are used under natural conditions. It is highly probable that higher primates use a combination of sensory cues to distinguish sexual identity in a natural social setting. In some experiments on the rhesus monkey this problem was overcome by presenting the 'test secretions' on a live animal, thereby providing a more natural context in which discrimination could be assessed (Michael and Keverne 1970).

Another problem with this approach is that a lack of differential responding to two stimuli cannot indicate that an animal is not able to discriminate between these two stimuli, even if the testing situation does approximate to natural conditions. The observed response, eg, in terms of scent marking, is often only a fraction of the assimilated information. There is also the possibility that when discrimination does occur the animal might be using (behaviourally) irrelevant stimuli to distinguish between the two odours.

The components of various secretions may be analysed and then assayed for behavioural potency (Muller-Schwartz 1969; Smith, pers. comm., Thiessen et al 1974). Such studies can only be undertaken if there is a definite and easily reproducible response to the secretion in question and require extensive analytic facilities. Therefore, it is unlikely that much work of this nature will ever be carried out with primates, although some work has been attempted (Curtis et al 1971;

Epple 1978, 1979, Michael and Bonsall 1977; Wheeler, Blum and Clark 1977). One problem with this approach is that an animal may respond behaviourally to more than one component in a given odour, or that the effects of the different components may be additive.

A summary of the basic methodology employed to study olfactory communication in mammals is shown in Table 1.2. Many of the studies have of necessity, been performed under highly unnatural laboratory conditions. The work of Calhoun (1962) on the rat in a semi-natural colony situation has shown that the events leading up to copulation may be very complex and the effects of olfactory cues may not be as clear-cut as they are in simple pair tests, although the actual mounting pattern is the same.

The Owl Monkey - Aotus trivirgatus

The owl monkey or dourocouli is a small arboreal cebid monkey, approximately 900-1,000 g in weight. Most of the observations carried out for this thesis were on the Columbian sub-species, *Aotus trivirgatus griseimembra*, as described by phenotype, country of origin and chromosomal analysis. Several Bolivian owl monkeys *Aotus t. bolivensis* and one Brazilian owl monkey *A.t.trivirgatus* were also studied.

Aotus is the only nocturnal anthropoid primate and it has a visual system adapted for this mode of life. The eyes are extremely large and the iris is orange. The eyes lack a fovea centralis and macula lutea (Hill 1960) but both rods and cones are present although the colour sensitivity is weak and abberant, and does not extend into the red end of the spectrum (Jacobs 1977). The presence of cones coupled with the lack of reflective tapetum and the composition of the visual pigment has led to the speculation that the owl monkey is secondarily adapted to this nocturnal mode of life (Jacobs 1977),

and this may be relevant when evaluating the relative importance of the various modes of communication. The ears are small and inconspicuous (Aotes means 'earless') and Beecher (1974, 1976) demonstrated that the auditory range of the owl monkey is almost identical to that of the diurnal squirrel monkey. Therefore it does not appear that the auditory system is specialized for nocturnality. The nostrils are widely separated and point sideways.

The other conspicuous feature of the head is the pattern of black and white markings. These facial markings are highly distinctive between subspecies but show no sexual dimorphism, and individual variability is not always sufficient to allow an unfamiliar observer to recognize individual monkeys on the basis of their facial markings alone. In fact, no sexual dimorphism exists in body weight, size or pelage. This is a feature common in monogamous primates like Aotus, and in nocturnal arboreal mammals in general (Kleiman 1977; Clutton-Brock and Harvey 1977).

Columbian owl monkeys are generally smaller than the Bolivian subspecies, with a duller pelage. The pelage is light grey-brown dorsally, while the ventral fur is a pale yellow colour from the neck to the groin. The fur itself is thick, similar to that found in other nocturnal arboreal animals, eg, slow loris and kinkajou, but its length is variable. The tail is long in relation to body length and darker towards the tip, becoming black in the Columbian subspecies and, although not prehensile, it can be used as a balancing organ or a brake for leaping.

At the ventral tail base there is a relatively large glandular area (Plate 7.1). The hairs in this region are specialized and form a thick triangular mat, which becomes opposed to the perineum when the tail is depressed. Secretions and excretions accumulate on the hairs and are deposited when the gland is rubbed on various substrates. The woolly monkey is the only other cebid to have a gland in this region, although many New World monkeys possess circum-anal or circum-

genital glands (Hill 1960; Wislocki 1936). A sternal gland may also be present (Epple and Lorenz 1967). Glands are present on the palms, soles and digits and also around the alae of the nose (Hanson and Montagna 1962). Unlike many other New World monkeys, Aotus does not have any visible glands on the scrotum (pers. obs.; Hill 1960). In Aotus the genitalia of the male and female are very similar - the penis and clitoris are both very small (unlike some other New World monkeys where the clitoris is hypertrophied (Eisenberg 1978)).

Few accounts have been published on Aotus in captivity and even fewer on Aotus in the wild. The most extensive description of behaviour is contained in a monograph by Moynihan (1964) which deals mainly with captive animals and is a qualitative rather than quantitative study. Other reports are either scanty (Kelly and Liebrecht 1978; Liebrecht and Kelly 1977) or mainly concerned with husbandry (Elliot, Sehgal and Chalifoux 1976; Cicamec and Campbell 1977; Dixson, Martin, Bonney and Fleming 1980; Hunter, Martin, Dixson and Rudder 1979) and only a few contain descriptions of behaviour, eg, Merritt (1976). Some papers have focused on particular aspects of Aotus behaviour, eg, the effect of illumination levels on activity (Kavanau and Peters 1977), or on parental behaviour and puberty (Dixson, Gardiner and Bonney 1980; Dixson and Fleming 1981). Apart from census accounts (Baldwin and Baldwin 1976; Hernandez-Camacho and Cooper 1976), only one paper has been published on Aotus in the wild (Wright 1978).

There would appear to be subspecies differences in Aotus behaviour in terms of general activity and reactivity (pers. obs. Merritt pers. comm.) and the account below refers to the Columbian form.

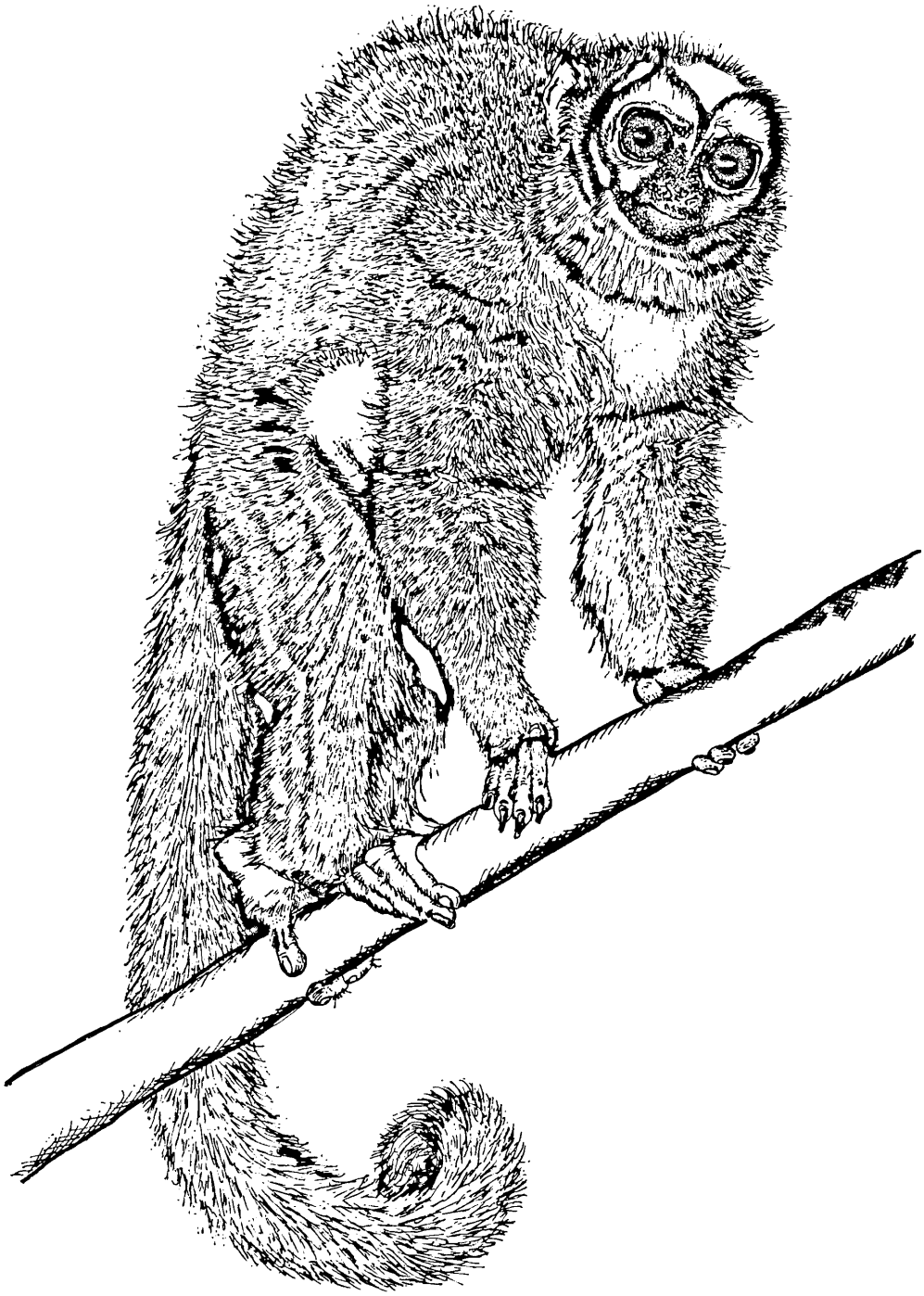
Owl monkeys are monogamous and are found in the wild in what appear to be extended family groups. Nothing is known about group formation and the transfer of individuals between groups. Groups spend the day in sleeping trees and at night they spend most of their time in the lower canopy, never coming lower than 3m above ground (Moynihan

PLATE 1.2

The Stereotyped Arch Posture of the Owl Monkey

The posture is frequently accompanied by piloerection as shown in the drawing.

Drawn by Dr A.F. Dixson



1964; Thorington, Muckenhirn and Montgomery 1976). Wright (1978) found that the home range of one group was about 3.1 hectares, although she did not use radio-tracking and relied on hearing when visibility was poor. Aotus typically become active just after dusk and during the night may become inactive for a brief period, resuming activity in the period preceding dawn.

Owl monkeys are extremely agile from a very early age and are powerful leapers like Callicebus (Moynihan 1964), using both hands and feet to move around. When resting they will sit on a branch in a characteristic hunched posture. Under natural conditions they will eat a great variety of fruit and insects and Hill (1960) says that flies and other insects can be caught on the wing (confirmed by pers. obs.) implying great dexterity and well-adjusted visuo-motor responses.

Owl monkeys have few visual displays, the most obvious being the arch posture. The monkey arches its back, often strongly, but it may be just a brief, small arch. Arching may be accompanied by piloerection depending on the intensity of the display (Plate 1.2). The arch may be maintained for some time and may be accompanied by resonant vocalizations (pers. obs.). Arching is common among New World monkeys, eg, Callicebus (Moynihan 1966), Leontopithecus rosalia (Rathbun 1979) and it seems to function primarily as a threat display (Moynihan 1966). During the present study evidence was obtained which suggests that this display might have other functions.

The black and white facial markings may have some signal value in themselves, but are not intensified in any display. It seems that the owl monkey lacks the extensive repertoire of postures and facial expressions employed in visual communication in other New World primates, eg, Saguinus (Moynihan 1970), Cebus capuchinus (Wiegel 1974), Saimiri (Marriot and Salzen 1978) and Ateles Eisenberg 1976). The owl monkey does, however, employ a range of scent marking displays (Moynihan 1967). Urine-washing (Plate 1.3) has

PLATE I.3

An Adult Owl Monkey Engaged in Urine-Washing

The palmar and plantar surfaces are rubbed together after a few drops of urine have been collected in the palm.

Drawn by Dr A.F. Dixson


DIXSON

been observed in both Columbian and Bolivian subspecies. In tail rubbing the subcaudal gland is rubbed over the bars and branches in the cage (see Plate I.4) and, less frequently, over other group members (pers. obs.). There are other behaviours that could be tentatively described as scent marking, eg, muzzle wiping and sneezing, although Moynihan (1964) considers sneezing to be a displacement activity.

Olfaction also appears to be an important part of the investigatory responses of Aotus, who usually smell food or other objects before handling or mouthing them. Owl monkeys often touch and/or sniff their own or a conspecific's anogenital region (pers. obs.). Another form of sniffing is 'nose-to-nose' sniffing, which is probably a greeting behaviour, as it is in Saguinus geoffroyi (Moynihan 1970).

The owl monkey has an extensive vocal range and observers in the wild have remarked on the power and range of the voice (Hill 1960) which is probably due to the possession of a laryngeal sac. The calls of the owl monkey have been analysed by Moynihan (1964). 'Gruff grunts' and 'resonant grunts' appear to be uttered in aggressive encounters (Wright 1978), whereas moaning calls are mainly heard in situations that are affiliatative or inquisitive. Loud bird-like screams are given when the animal is very frightened and other calls may function as contact calls.

Moynihan (1964) also described mounting behaviour and copulation in Aotus, and says that such behaviour is infrequent under natural conditions. The female is essentially passive. Sexual behaviour in Aotus will be described quantitatively in Chapter 2.

Little quantitative data is available on aggressive behaviour in the owl monkey. Both Moynihan (1964) and Merritt (1977) indicated that Aotus is one of the most aggressive of the New World primates. This aggression is manifested towards animals of the same sex, and in the case of adult pairs, towards other adult pairs. However, within the

PLATE 1.4

An Adult Owl Monkey Engaged in Tail Rubbing

family groups, aggression is infrequent, even when adult offspring are present (Dixson and Flemingin prep). In aggressive encounters, owl monkeys mainly use their hands as weapons, although the teeth are used in highly aggressive encounters.

To summarize - little is known about the behaviour of this species and virtually no experimental work has been performed. Many practical difficulties are associated with research on primates. They are difficult to obtain and handle, and they are expensive to keep. They often require large caging facilities if behavioural measurements are to have any applicability to the wild state. The individual variability in primate behaviour has also deterred research on primate species in the laboratory. It is therefore not surprising that most work on olfactory communication has been carried out on species that are readily available and that show relatively stereotyped responses. However, there is some good anatomical and behavioural evidence for the existence of chemical communication in the Prosimian and New World primates. There were several reasons why it was felt that the owl monkey would be a suitable model for such a study of olfactory communication in primates:-
a relatively large number of animals were available for experimental purposes (all the animals used in the experiments are listed in Table I.3); its nocturnality and lack of visual displays, coupled with the presence of specialized glandular areas and olfactory displays, suggested that chemical cues might be important for this species. Additionally, little was known about the aggressive and sexual behaviour of the owl monkey, and therefore, quantitative data on these behaviours alone, together with the relationship of olfactory communication to them, could be obtained.

A list of all the experimental animals is given in Table I.3.

TABLE 1.3

All experimental animals are shown in this Table, except for the offspring who were present in the family groups during the scent pad discrimination studies, and these are shown in Table 4.1

Individual Data for all the Columbian Owl Monkeys (Aotus trivirgatus griseimembra) Used in Experiments 1 through 5

Clinical Number	Origin	Birthdate	Median Weight (gms)	Caging	Used in Experiment	
(A) Males						
5T	Unknown	Unknown	-	FG	2	D
9T	"	"	1,016	FG	2, 4	
6T	"	"	1,780	FG	4	
13	"	"	1,180	FG	4	
176	"	"	946	FG	4	
186	Wild	"	-	S	1, 2	
192	"	"	1,032	S	1, 2	D
4107	"	"	960	S *	1, 2, 3	D
4287	"	"	836	S	1, 2	D
4288	"	"	832	S	1, 2	D
4367	"	"	992	S	1, 2, 3	D
4368	"	"	1,044	S	1, 2	D
4369	"	"	936	S		D
4370	"	"	1,000	S *	2, 3	D
4371	"	"	1,075	S	1, 2	D
4373	"	"	862	S *	1, 2, 3	D
4451	CZ	28.8.69	990	S *	2, 3	D
4465	CZ	6.10.75	822	S		D
'Foster'	Wild	Unknown	-	S	2	
WLCP2	WLCP	20.9.76	870	S	2	
WLCP3	WLCP	4.11.76	950	S	2	D
WLCP5	WLCP	24.2.77	940	S	2	D
WLCP7	Bristol	24.1.77	1,130	S		D
7093	Unknown	Unknown	-	FG		D

TABLE 1.3 : continued

Clinical Number	Origin	Birthdate	Median Weight (gms)	Caging	Used in Experiment	
(B) Females						
T1	Unknown	Unknown	1,026	S *	5	D
T2	"	"	1,008	FG	4	
T3	"	"	-	FG	4	
T15	"	"	-	FG	4	
81	Wild	"	920	S	3	D
82	"	"	804	S	3	
83	"	"	908	S		D
175	Unknown	"	-	FG	4	
188	Wild	"	902	S	3	D
2455	"	"	1,016	S	1, 3, 5	D
4108	"	"	900	S *	5	
4362	"	"	898	S	1	D
4361	"	"	-	FG	4	
4364	"	"	850	S	1, 3, 5	D
4365	"	"	900	S *	1, 3	
4469	CZ	17.1.74	1,022	S	1, 3, 5	D
4536	Wild	Unknown	876	S	1, 3	D
4537	"	"	948	S	1, 5	D
4811	"	"	-	S	1	
WLCP4	WLCP	19.11.76	875	S		D
WLCP6	Bristol	7.3.77	914	S		D
WLCP23	WLCP	29.7.78	-	FG	5	
WLCP24	WLCP	5.9.78	-	FG	5	
WLCP25	WLCP	9.10.78	-	FG	5	
WLCP29	WLCP	2.5.79	-	FG	5	
7327	Unknown	Unknown	-	FG		D
7329	"	"	-	FG		D

CZ - Born in Zoological Society of London collection

Bristol - Born at Bristol University

WLCP - Born at the Wellcome Laboratories of Comparative Physiology

D - Scent donor for discrimination experiment

FG - Caged in family group

S - Caged alone

* - Previously caged in family group

CHAPTER TWO

PAIRED ENCOUNTER EXPERIMENT : EXPERIMENT 1

2.1 Aims of the Experiment

These pair tests were carried out to quantify any behavioural differences that existed between same and opposite sex pairs of owl monkeys.

2.2 Materials and Methods

Prior to experimentation, all animals were housed in 2 colony rooms. Housing conditions are described in Appendix 1. Eight females and 9 males were tested and 4 of these monkeys (2 males and 2 females) were used previously in the pilot study for this experiment. Data were obtained for 8 resident males and 8 resident females and the clinical numbers of the animals used in this experiment are listed in Table 2.1.

TABLE 2.1 - Pairs of Owl Monkeys Tested in Experiment 1

Resident	Introduced Male	Introduced Female
Males		
192	4288	4469
4287	4367	4536
4368	4107	4362
4288	186	2455
4107	4288	4537
186	4368	4811
4367	4371	4364
4373	4287	4536
Females		
4536	4371	4537
4365	4367	4811
4362	4288	4536
4469	4368	4536
4364	4287	2455
4811	4107	4362
4537	186	4364
2455	4368	4362

Subjects were designated as 'residents' or 'introduced' animals. Introduced animals remained in the main colony room until testing, whereas, one week prior to testing the 'resident' was removed to a clean, double cage (approximately 102 x 110 x 66cm and fitted with branches) situated in an adjacent observation room. Prior to occupation each cage was cleaned with 'Nonidet' disinfectant and detergent, rinsed in water and dried. Residents were allowed one week to become accustomed to their new cage, during which time they were observed twice to habituate them to the extra lighting and to the presence of an observer in the room. All observations were carried out from behind a one-way mirror and no more than 2 residents were present in the observation room at any one time.

Each resident was tested successively with 2 unfamiliar partners, with one week in between tests. The pairings were balanced, such that some animals were tested with a same sex partner first and others with a partner of the opposite sex. Because the number of animals available was restricted, each animal served successively as a resident and as an intruder during different phases of the experiment.

All introductions took place in the resident's cage which was illuminated by 2 additional red light sources (40W bulb). These were switched on an hour before testing to minimise disturbance to the resident. The animal to be introduced was placed in a nest box on the side of the resident's cage and the resident was partitioned off from the box, to minimise prior contact between the 2 animals. After 10 minutes, the boxed animal was released and the box shut. Timing was by means of a clock and stop-watch, and began from the moment of release. Each test lasted 20 minutes unless severe fighting occurred, in which case the test was terminated; at the end of the test the introduced animal was removed.

FIGURE 2.1

Sample Check Sheet Used to Score Tests Between Individuals of the Same Sex

The actual size of the check sheet has been reduced slightly for the purposes of reproduction.

Resident animals were always scored on the left side of the check sheet.

Date:		No:		Home Cage:		Intruder:		Time:									
TIME	PROX	NR	TR	URW	ALLO-GROOM	SNIFFING		ARCH	CA	OTHERS	TR	URW	ALLO-GROOM	SNIFFING		ARCH	CA	OTHERS
						ANG	OTHERS							ANG	OTHERS			
.15																		
.30																		
.45																		
.00																		
.15																		
.30																		
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.15																		
.30																		
.45																		
.00																		

FIGURE 2.2

Sample Check Sheet Used to Score Tests Between Individuals of the Opposite Sex

The actual size of the check sheet has been reduced slightly for the purposes of reproduction.

Date		No.		♂		Plugged/Open		♀		Time							
Time	Prox	NR	♂ TR	URW	Mount	Ang	Sniffs (Other)	Allo-Groom	Agg	Other	♀ TR	URW	Ang	Other Sniff	Allo-Groom	Agg	Other
15																	
30																	
45																	
0																	
15																	
30																	
45																	
0																	
15																	
30																	
45																	
0																	

Scoring Producedure : The checksheets that were used for scoring behavioural events are shown in Figure 2.1 for same sex pairings and in Figure 2.2 for opposite sex pairings. The start of each 15-second unit was signalled by a tone via an earpiece. Major behaviours were scored in the marked columns, but both types of checksheet had spaces for recording other, less frequent, behaviours. The following behaviours were scored - codes for the behavioural categories are given in parentheses :-

Proximity (Prox) - the number of 15-second periods during which the animals remained within 6 inches of each other.

Nose-to-Nose Inspections (NR) - each muzzle-to-muzzle inspection was recorded, irrespective of which animal initiated the inspection, as this was not always easy to determine.

Tail-Rubbing (TR) - each distinct rub was given a score of one.

Urine-Washing (URW) - each urine wash was given a score of one.

Anogenital Inspections (ANG) - each inspection of the anogenital region was recorded, irrespective of duration.

Other Inspections - each time the animal placed its muzzle close to the conspecific as if to sniff, it was recorded as an inspection. Inspection of the following areas was scored :-

H - head (apart from the muzzle)

N - neck

St - Sternum

B - back

Fl - flank

T - tail

Contact Aggression (CA) - each hit, bite or grab received a score of one. The latency to the first onset of contact aggression was also recorded.

Arching (A) - each arch received a score of one. Duration and intensity were not noted.

Mounting (Mt) - the latency to the onset of mounting and the duration of each mount was recorded, as well as the occurrence of pelvic thrusting. The identity of the partner who terminated the mount was also noted.

Allogrooming - every occurrence of allogrooming was recorded.

After each opposite sex pair test the female was caught and a vaginal smear taken to see if spermatozoa could be identified and ejaculation confirmed, as this could not be done behaviourally. Smears were dry-fixed and stained with Greenstein's stain (Appendix 2.1).

2.3 Results

Aggressive Behaviour : Consideration of the aggressive behaviour shown by pairs of owl monkeys revealed that a sex difference existed in aggressive response (as measured by frequencies of contact aggression and arching displays) and that this difference was more pronounced in males. Frequencies of contact aggression in male-male pairs ranged from 0.71/15 seconds to 0/15 seconds (mean = 0.42 ± 0.56/15 seconds) and arching frequencies were also elevated (range 1.26/15 seconds to 0.10/15 seconds; mean = 0.51 ± 0.44). When males were paired with females however, frequencies of these behaviours were very low (contact aggression, mean = 0.02 ± 0.004; arching, mean = 0.26 ± 0.03). As can be seen in Figure 2.3(A), the differences in levels of contact aggression and arching between male-male pairings and male-female pairings are statistically significant (contact aggression, $p < 0.05$; arching $p < 0.01$: 1 tail related t-test). Although resident animals tended to show more aggression towards introduced animals of the same sex, the differences in frequencies of contact aggression and arching are not statistically significant (Figure 2.3(B)). Contact aggression occurred in only 5 out of 8 female-female pairings and

termination of testing before 20 minutes had elapsed only occurred in one test (♀4536-♀4537). However, male-male pairs fought vigorously, fighting occurring in 7 out of 8 male-male pairings and in 4 cases, the test was terminated before 20 minutes had passed (♂192-♂4288, ♂4287-♂4367, ♂4288-♂186, ♂4367-♂4371). In all the tests where fighting occurred between same sex partners, biting was recorded at least once by the attacking partner, however, male-male pairings resulted in more severe wounding than female-female pairings.

Arching (either by the resident or the introduced animal) occurred in all 16 same sex pairings and in 13 opposite sex pairings. There was no significant difference in latency to the first arch display between same and opposite sex pairs (mean latency for same sex pairs (N=16) = 1.68 ± 2.62 min; mean latency for opposite sex pairs (N=13) = 0.87 ± 1.52 mins; data for resident males and females).

In male-male pairings, contact aggression was usually initiated by the resident animal, but in 3 cases (♂192-♂4287, ♂186-♂4368, ♂4373-♂4287) the introduced animal became dominant over the resident. Therefore, it was not possible to predict with certainty whether the resident or introduced male would exhibit the highest frequencies of aggressive behaviour in these tests. Dominance was assessed using the following criteria :- the dominant animals gave more, and received less, contact aggression; they initiated more chases and lunges, and spent more time off the floor on the branches. The submissive animals were designated on the following criteria :- they received more, and initiated less, contact aggression; they consistently fled from the other animal and spent much of the test crouching on the cage floor (often paying a lot of attention to the other animal's movements above). Similar criteria have been used previously to assess dominance and submissiveness in paired interactions in the bushbaby, Galago senegalensis (Bearder and Doyle 1974).

Relationship Between Dominance and the Frequency of Arching Displays : Using the criteria of dominance and submissiveness described above, it was found that in both male-male and female-female pairings in which contact aggression occurred, dominant animals arched significantly more frequently than submissive animals (Figure 2.4). A comparison of arching frequencies both before and after fighting revealed that, although dominant males did not differ in their arching frequencies both before and after fighting, submissive males showed a significant reduction in arching frequency ($p=0.02$: 2 tail related t-test) after fighting had occurred (Figure 2.5). Dominant males and females often made "whup-whup" calls, usually accompanied by several sharp 'clicks'. Such vocalisations were only heard in opposite sex pairs on the rare occasions when contact aggression occurred. Submissive animals made low, moaning or twittering calls, and they often showed visible signs of 'distress' (eg, rapid breathing). The following are excerpts from notes recorded after each test which illustrate the behaviour of dominant and submissive animals during aggressive encounters :-

23.11.78 : ♀2455 and ♀4364

" ..... ♀4364 often came down from the branches, gradually approaching ♀2455, who was on the cage floor. ♀4364 then reached out and hit ♀2455 who fled rapidly and, in this way, she usually managed to avoid ♀4364. If however, in her attempts to escape, she ventured onto the upper branches, ♀4364 immediately pursued and attacked her until she returned to the floor ....."

" ..... ♀2455 paid much attention to ♀4364, but the converse was not true; ♀4364 usually only looked at ♀2455 before an attack, when she would adopt an arch posture and slowly approach ♀2455, maintaining the posture until she had reached the lower branches."

7.3.78 : ♂4288 and ♂186

" ..... the fighting was stopped when ♂4288 continued to attack ♂186, even though the latter remained on the cage floor and fled from these attacks. When they were separated by a grill, ♂186 would not get up off the floor and paid a lot of attention to ♂4288 who continued to arch at him through the grill".

FIGURE 2.3

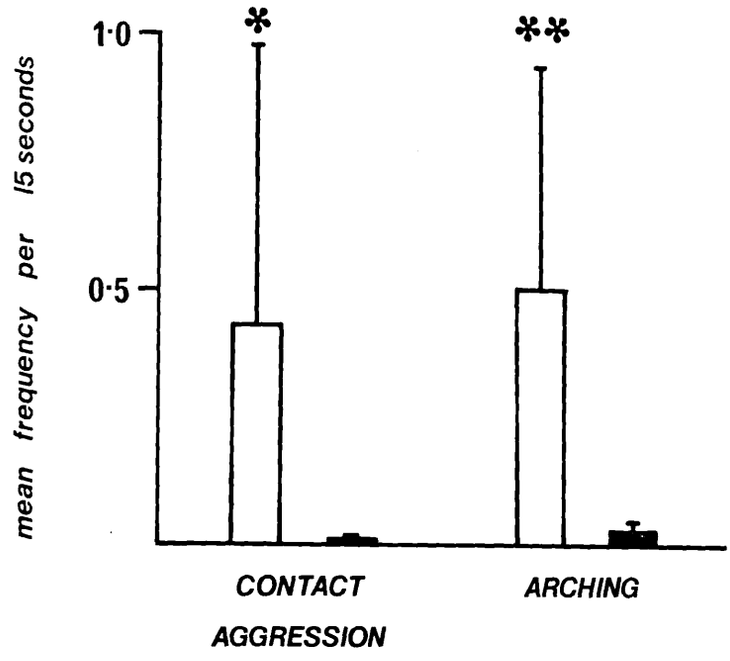
The Mean Frequency Scores for Arching and Contact Aggression for (A) 8 Male Residents and (B) 8 Female Residents Tested with Partners of the Same or Opposite Sex

Frequencies of arching and contact aggression were significantly higher when resident males were paired with males than when they were paired with females (* = $p<0.05$; ** = $p<0.01$; I tail related t-test). However, resident females did not show statistically significant differences in the frequency of these behaviours when tested with same sex partners as opposed to male partners.

With partner of the same sex : □

With partner of the opposite sex : ■

A. *RESIDENT MALES.*



B. *RESIDENT FEMALES.*

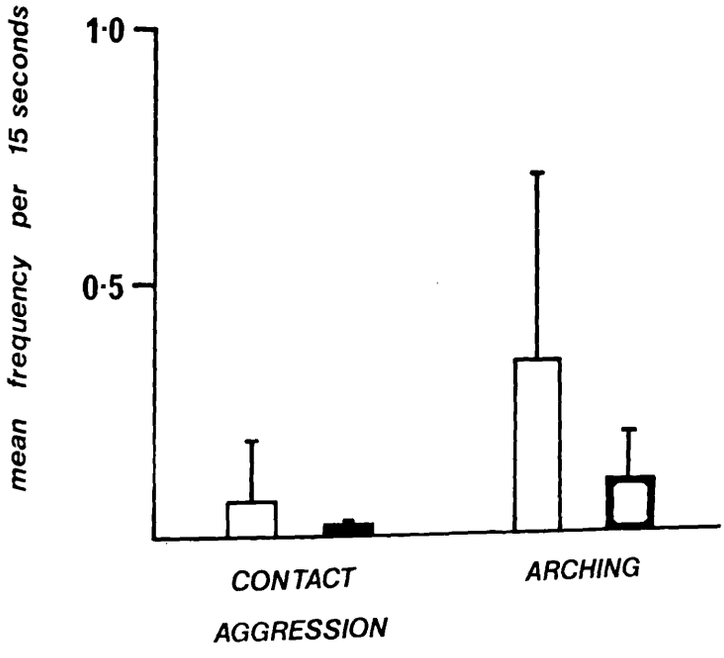


FIGURE 2.4

Mean Frequencies of Arching for the Dominant and Submissive Animals in 7 Male-Male Pairs and 5 Female-Female Pairs where Dominance could be Assessed

Using the criteria to define dominance as described in the text, in both the male-male pairs and the female-female pairs, dominant animals arched significantly more.
(* = $p<0.02$; ** = $p<0.001$: 2 tail unrelated t-test).

Dominant animals : □
Submissive animals : ■

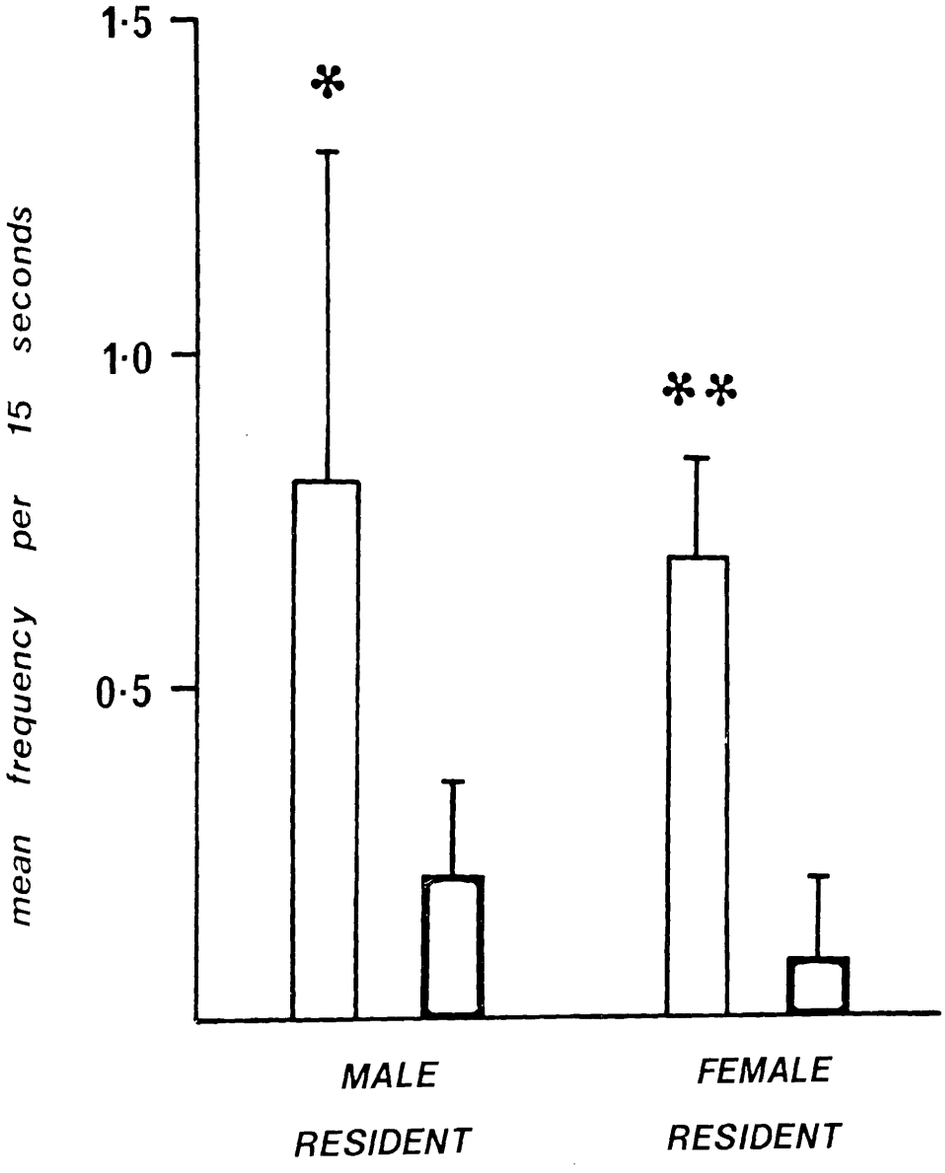
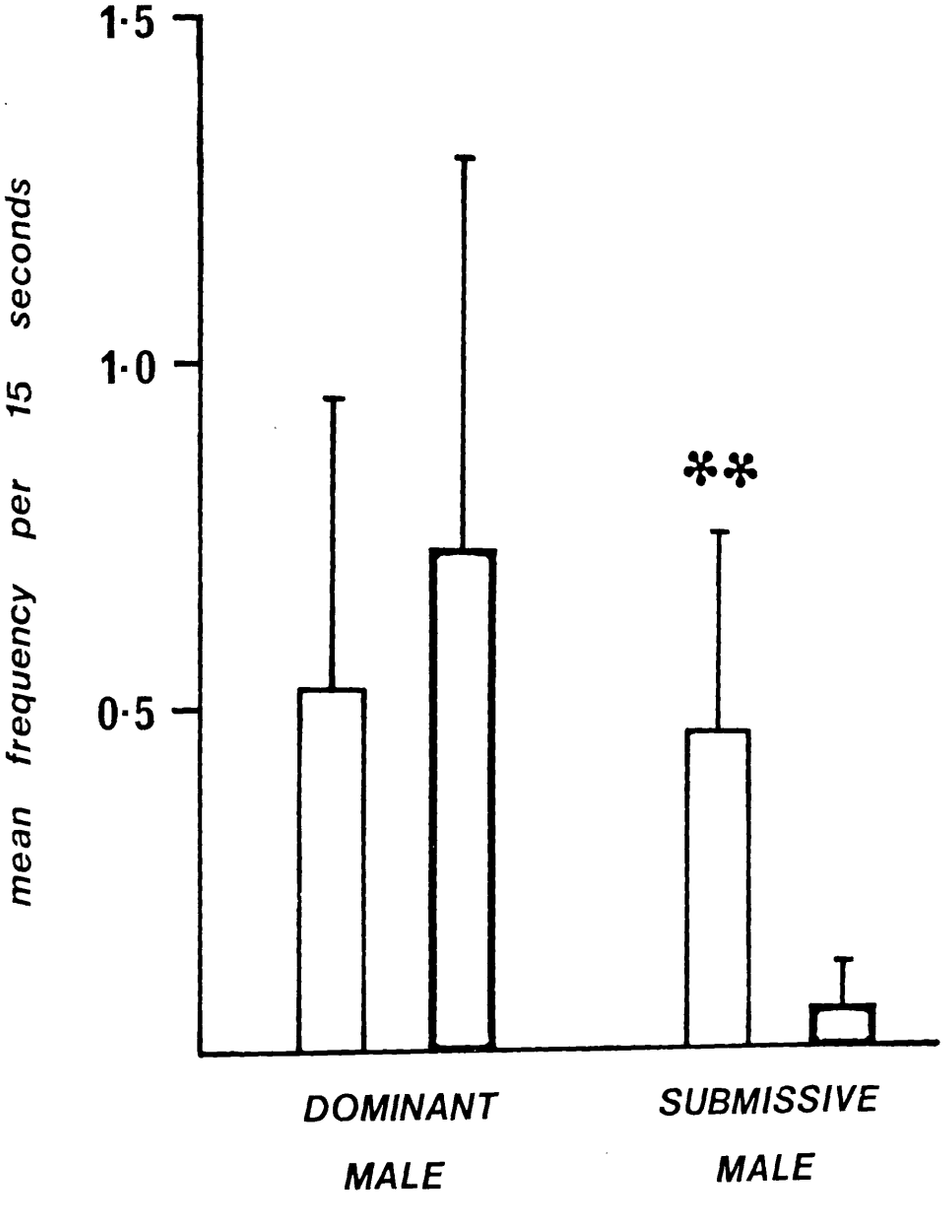

1·5
1·0
0·5
mean frequency per 15 seconds
*
**
MALE RESIDENT
FEMALE RESIDENT

FIGURE 2.5

Mean Frequencies of Arching for Dominant and Submissive Animals in 7 Male-Male Pairs Before and After Fighting had Taken Place

Although there was no difference in the frequencies of arching before and after fighting for the dominant animals, the submissive males showed a significant reduction in arching frequency after fighting had occurred.
(** = $p<0.02$: 2 tail related t-test).

Before fighting : □
After fighting : ■


1·5
1·0
0·5
mean frequency per 15 seconds
**
DOMINANT MALE
SUBMISSIVE MALE

Sexual Behaviour : Males attempted mounting behaviour in 11 out of the 16 opposite sex pairings, whereas no mounting behaviour was observed in same sex pairings. No mounting behaviour by females was observed in any of the 24 tests. The male usually attempts to mount the female from behind, clasping the female around the waist or shoulders, whilst maneuvering his body into a position to insert his penis. The female may sometimes lift her tail away, or the male may push it away slightly with his foot. No definite behavioural signs of intromission or ejaculation during copulation were observed although thrusting was recorded. Thrusting behaviour was usually rapid, although when a male remained mounted for a long period, thrusting only occurred intermittently or in short bursts. Resident males showed a greater tendency to attempt mounting their partners than introduced males. Thus, 7 out of 8 resident males attempted to mount their female partners, whereas only 4 out of 8 introduced males showed this behaviour. Measures of sexual behaviour for the 6 males who acted both as residents and introduced animals are shown in Table 2.2. None of these measures (latency to first mount attempt; duration of first mounting attempt with pelvic thrusting; number of mounting attempts per test) differed depending on whether the male was a resident or introduced animal.

TABLE 2.2 - MEAN VALUES OF VARIOUS INDICES OF SEXUAL BEHAVIOUR FOR 6 MALES WHO ACTED AS BOTH RESIDENT AND INTRUDER

	Male Resident	Male Introduced
Mean Latency to first mount attempt (mins)	11.26 $\pm$ 3.96	5.85 $\pm$ 5.60
Mean duration of first mount with pelvic thrusting (mins)	4.04 $\pm$ 5.64	0.44 $\pm$ 0.02
Mean number of mounting attempts per test	4.00 $\pm$ 5.09	2.83 $\pm$ 4.34

Mounts with pelvic thrusting were usually of short duration, ranging from 23 seconds to one minute 58 seconds (N=7; mean duration = 0.84 $\pm$ 0.58 mins). However, one male resident (♂186) remained mounted for 12 minutes 37 seconds, during which time several bouts of thrusting were observed. 3 males (♂4368 and ♂192 as residents, and ♂186 as an introduced animal) failed to exhibit pelvic thrusting during mounting behaviour.

Mounts were always initiated by the male partner and it was not possible to identify any proceptive behaviour on the part of the female, who remained essentially passive. Females did not often refuse the male mounting attempts or terminate mounts. In 39 mounting attempts, only 8 refusals or terminations by the female were recorded (ie, 20.5%); a refusal or termination consisting of the female walking away from the male. In some cases however, the female was observed to turn her head round, often bringing the arm on the same side round to touch the male. This behaviour immediately preceeded the termination of a mount either by a female (walking away) or by the male (by dismounting).

Because there are no behavioural signs of intromission and ejaculation in Aotus a vaginal smear was taken after each test in which a mounting attempt occurred. None of the vaginal smears taken contained any spermatozoa, although one female did in fact become pregnant (giving birth 133 days after testing); therefore, ejaculation must have occurred but no evidence of spermatozoa had been found in the smears taken after this test. This is not surprising in view of the low spermatozoa count in Aotus (Dixson, Martin, Bonney and Fleming 1980; Hunt, Chalifoux, King and Trum 1975).

Olfactory Inspection and Scent Marking Behaviour : Olfactory inspections occurred frequently during pair tests, irrespective of the sexes of the participants. Thus, nose-to-nose inspections occurred in 93% of same sex pairings and anogenital inspections in 93% of these tests. In opposite sex pairs, nose-to-nose inspections occurred in 93%, and anogenital inspections in 81% of these tests. When an animal was introduced into the observation cage the usual response of both monkeys was to approach one another and engage in nose-to-nose investigations, often accompanied by mutual arching displays.

Anogenital inspections then occurred and sometimes animals stood nose-to-tail and circled round in this position. Often it appeared that each monkey was attempting to sniff the anogenital region of its partner, whilst attempting to avoid receiving such inspections. Contact aggression between same sex partners was always preceeded by some form of olfactory investigation (either by the resident or the intruder). Sexual behaviour rarely occurred without any prior olfactory inspection. In the 11 tests where mounting behaviour was attempted, in only one did the male not inspect the female before attempting to mount her.

There were no statistically significant differences in the frequencies of olfactory investigation (nose-to-nose; anogenital or other inspections) between same and opposite sex pairings or between male and female residents (Figure 2.7). Frequencies of anogenital inspections by resident males did decrease after mounting (opposite sex pairs, N=7, from 0.59 $\pm$ 0.48/15 secs to 0.16 $\pm$ 0.13/15 secs), or fighting (same sex pairs, N=7, from 0.46 $\pm$ 0.32/15 secs to 0.05 $\pm$ 0.07/15 secs; $p < 0.02$: 2 tail related t-test). Males also investigated females anogenitally significantly less when they were residents than when they were introduced to the females (N=6; mean = 0.22 $\pm$ 0.11/15 secs when resident versus mean = 0.09 $\pm$ 0.11/15 secs when intruders; $p < 0.02$: 2 tail related t-test). Frequencies of nose-to-nose inspections decreased after fighting in same sex pairs (N=7; mean = 0.85 $\pm$ 0.67/15 secs to mean = 0.34 $\pm$ 0.30/15 secs : $p < 0.05$: 2 tail related t-test). But, there was a slight increase in nose-to-nose inspections after the first mount in opposite sex pairs (before mounting mean = 0.15 $\pm$ 0.12/15 secs, after mounting mean = 0.33 $\pm$ 0.29/15 secs).

Frequencies of tail rubbing and urine-washing were very low in these experiments and showed great individual variability (Table 2.3 and Figure 2.8). There was no statistical difference in the frequencies of these behaviours when either males or females were paired with partners of the same or opposite sex. Introduced animals did not mark significantly more or less than resident animals. However, there was a tendency (not statistically significant) for dominant animals to urine-wash more often than their submissive partners. In fact, none of the submissive males urine-washed although 5 out of the 7 dominant males did so

FIGURE 2.6

Mean Proximity Scores in Minutes for 8 Male Residents and 8 Female Residents Tested in Same Sex and Opposite Sex Pairings

Male residents spent significantly more time in close proximity with an opposite sex partner than with a same sex partner (** = $p<0.02$: 1 tail related t-test). This was not the case for the resident females.

With partner of the same sex : ☐

With partner of the opposite sex : ■

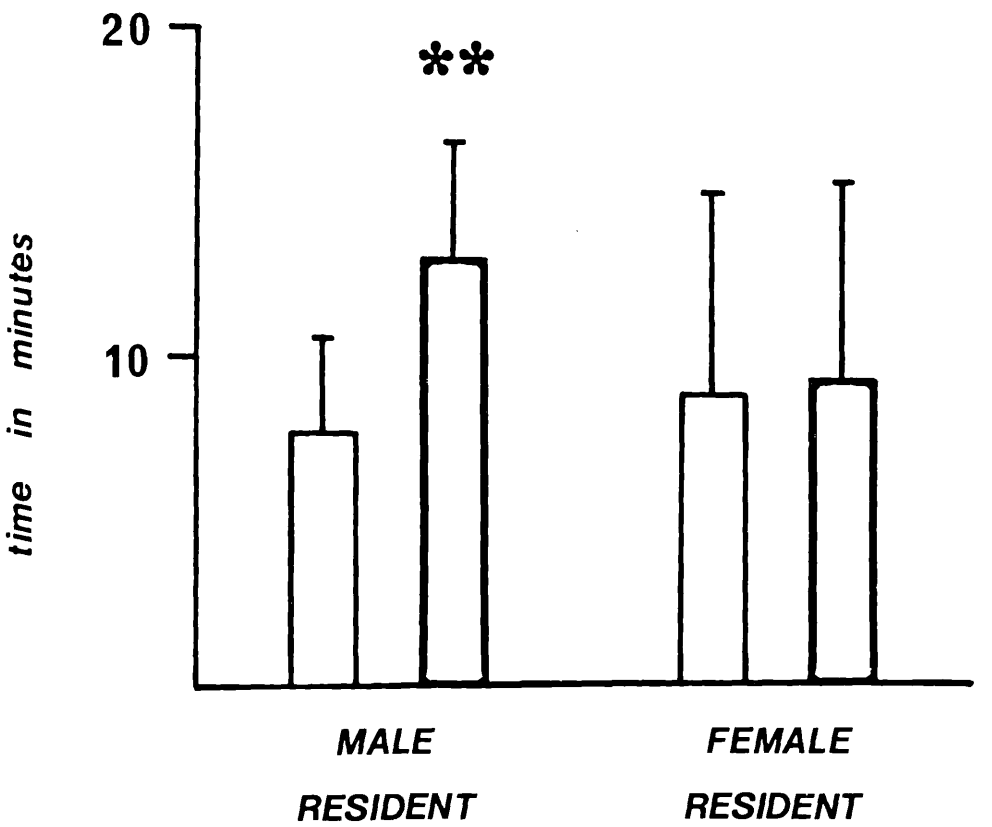

20
10
**
time in minutes
MALE
RESIDENT
FEMALE
RESIDENT

FIGURE 2.7

Mean Scores for Various Types of Inspection Behaviour for 8 Male Residents and 8 Female Residents Tested in Same or Opposite Sex Pairs

None of the measures of olfactory inspection used (nose-to-nose inspections, anogenital inspections and inspections directed towards other areas of the body) showed any significant differences between same sex and opposite sex pairings.

With partner of the same sex : □
With partner of the opposite sex : ■

MR - Male Resident
FR - Female Resident

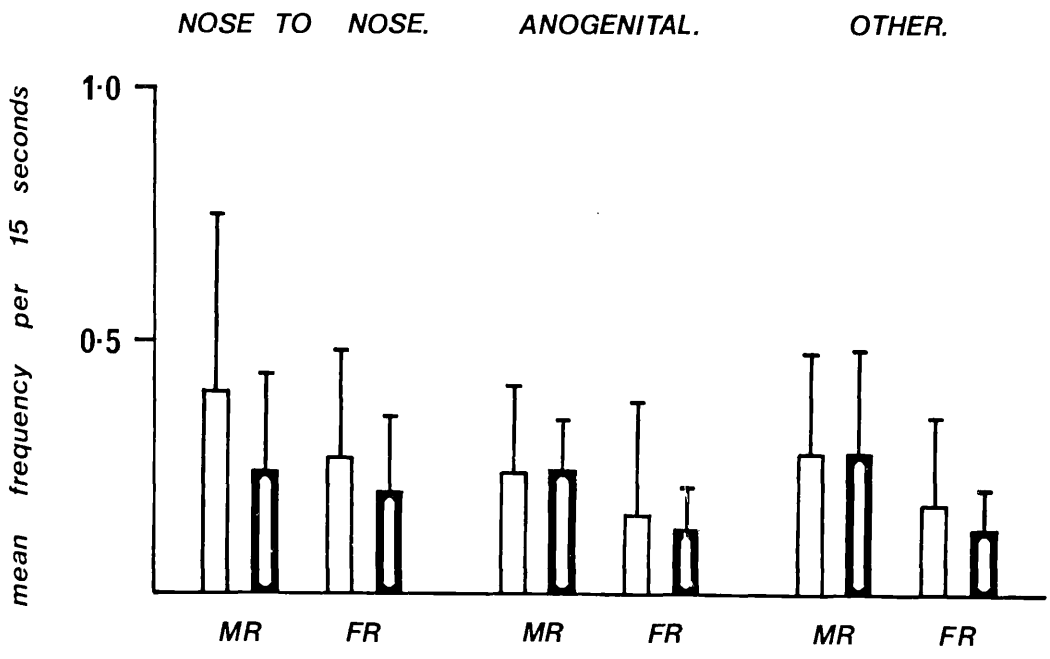

NOSE TO NOSE.
ANOGENITAL.
OTHER.
mean frequency per 15 seconds
1·0
0·5
MR
FR
MR
FR
MR
FR

FIGURE 2.8

Frequencies of Urine-Washing (A and C) and Tail Rubbing (B and D) for the Dominant and Submissive Partners in 7 Male-Male Pairings (A and B) and 5 Female-Female Pairings (C and D)

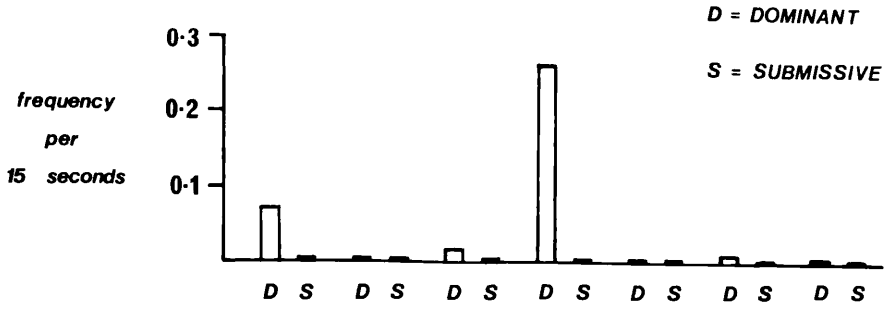
Pairs where no fighting occurred (ie, those where dominance could not be assessed) were omitted.

Dominant males and females did not urine-wash or tail rub significantly more than submissive animals.

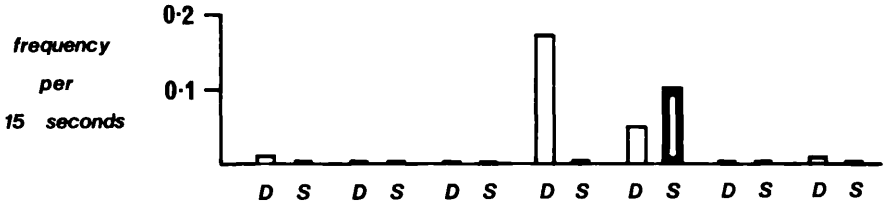
Dominant : ☐

Submissive : ■

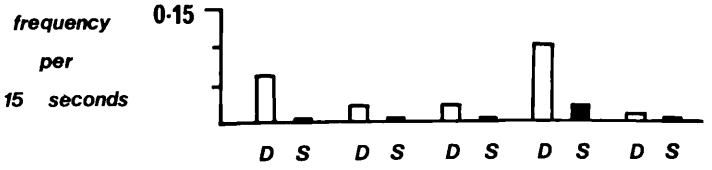
A. *URINE WASHING — MALES*



B. *TAIL RUBBING — MALES*



C. *URINE WASHING — FEMALES*



D. *TAIL RUBBING — FEMALES*

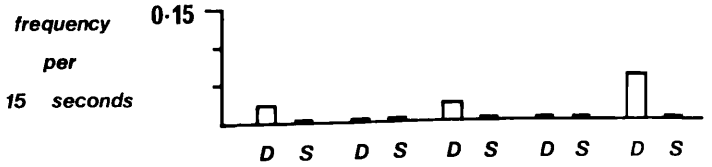


TABLE 2.3

Frequencies of Urine-Washing, Tail Rubbing and Allogrooming for 8 Resident Males and 8 Resident Females when Paired with Same or Opposite Sex Partners

Behaviour Scored	Urine-Washing		Tail Rubbing		Allogrooming	
Sex of Partner	Same	Opposite	Same	Opposite	Same	Opposite
Male Residents						
186	0	0.28	0	0	0	0.50
4107	0.26	0.02	0.17	0.70	0.02	0
4367	0.01	0.07	0.01	0.08	0	0
4288	0.03	0	0	0.46	0	0.03
4368	0	0	0.05	0	0	0
4373	0	0	0	0	0.01	0
4287	0	0.02	0	0	0	0
192	0	0.05	0	0	0	0.36
mean	0.03	0.05	0.02	0.15	0.003	0.11
S.D.	0.09	0.09	0.05	0.27	0.0	0.20
Female Residents						
4536	0	0	0	0.02	0	0
4365	0.02	0.05	0	0	0.01	0
4362	0.05	0	0.05	0	0.05	0
4469	0	0	0.01	0	0	0
4364	0.02	0	0.02	0	0	0
4811	0.02	0	0	0	0	0
4537	0	0.02	0	0.03	0	0
2455	0	0	0.13	0.43	0.01	0
mean	0.01	0.008	0.02	0.06	0.008	0
S.D.	0.01	0.01	0.04	0.14	0.01	0

All scores are expressed as frequencies/15 seconds

on at least one occasion (Figure 2.8). In 2 cases the dominant male was observed for 10 minutes after the test was terminated and the submissive male removed from the room. Both these dominant animals showed higher frequencies of urine-washing in this period than during the tests (♂4288 during the test, frequency = 0.03/15 secs; post-test frequency = 0.12/15 secs. ♂4287 during the test, frequency = 0/15 secs; post-tests frequency = 0.07/15 secs).

Measures of Proximity and Grooming Interactions : Resident males spent significantly more time in close proximity with partners of the opposite sex than with partners of the same sex ($p<0.02$: 1 tail related t-test) but this finding did not apply to resident females. Not unexpectedly, it was found that males in the male-male pairings spent less time in close proximity once contact aggression had been initiated (precontact proximity score, mean per test = 3.82 ± 3.38 mins; postcontact, mean per test = 1.39 ± 1.83 mins; $p<0.01$: 1 tail related t-test).

Allogrooming was either manual or a combination of manual and oral grooming. Frequencies of allogrooming were very low in these experiments, except in the case of males 192 and 186 when they were paired with females (see Table 2.3). Allogrooming occurred in 8 out of the 16 opposite sex pairings and in 6 of the 16 same sex pairings. The frequencies of allogrooming behaviour did not differ in any statistically significant fashion between same or opposite sex pairings, for either male or female residents, or depending on whether the animal was introduced or resident. Neither was allogrooming found to be related in any sequential fashion to the act of copulation.

2.4 Summary and Conclusions

Male residents showed significantly higher frequencies of contact aggression and arching behaviour towards introduced males than towards introduced females. Male-male pairs also fought vigorously, whereas fighting was observed less frequently in female-female pairs. In same sex pairs the

resident animal was not neccessarily the dominant animal of the pair, and it also appeared from these tests that dominance tended to be associated with higher levels of arching.

Mounting behaviour was only observed in opposite sex pairs and resident males were more likely to attempt mounting than the introduced males. However, other indices of mounting behaviour, eg, duration of first mount with pelvic thrusting, did not differ depending on whether the male was a resident or intruder. No proceptive behaviour on the part of the females could be discerned, and females rarely refused a male's mounting attempts. Occasionally, mounting occurred without any prior olfactory inspection, but olfactory inspections occurred frequently in both same and opposite sex pairings.

Scent marking levels varied considerably between individuals and it appeared that urine-washing was suppressed in submissive animals. The only other significant result was that resident males spent more time in close proximity with a partner of the opposite sex than with a partner of the same sex.

It therefore seems that the main behavioural differences that exist between same and opposite sex pairs of owl monkeys relate to aggressive and sexual behaviour, with aggressive behaviour occurring more frequently in same sex pairs and sexual behaviour only occurring in opposite sex pairs.

CHAPTER THREE

THE EFFECTS OF PARTIAL ANOSMIA ON SEXUAL BEHAVIOUR AND INTER-MALE AGGRESSION

3.1 Aims of the Experiments

Two experiments were performed to investigate the effects of partial anosmia on sexual and aggressive behaviour. Section 3.2 describes the means by which partial anosmia was achieved and is followed (3.3) by a description of the experiment which investigated the effects of partial anosmia on aggression. It was decided to use males for this experiment because the results from Experiment 1 (2.3) indicated that males showed more predictable aggressive responses in same sex pair tests. Section 3.4 describes the study of partial anosmia and sexual behaviour in males. The partial anosmia technique employed was reversible, so that each animal could serve as his own control.

3.2 The Partial Anosmia Technique

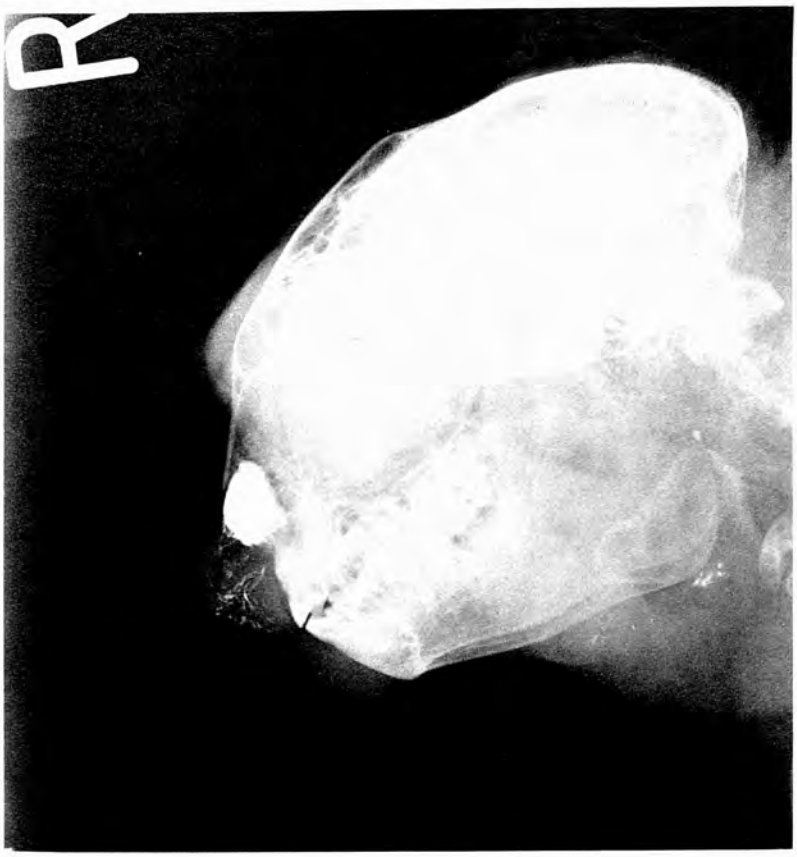
The method employed was similar to that used previously with Old World primates (Keverne 1980; Michael and Keverne 1968). Small plugs made from optical gauze were impregnated with a busmuth iodoform paste, an anosmic agent. One plug was inserted up each nostril via the nares and placed as near as possible to the cribiform plate. The naso-pharynx therefore remained unblocked so that the animal could breathe normally. The bismuth iodoform paste also allowed the position of the plugs to be checked by radiography (Plate 3.1) and this was done both after insertion and before removal. During these procedures the animal was tranquillized by i.m. injection of 10mg ketamine HCl ('Vetelar', Parke Davis).

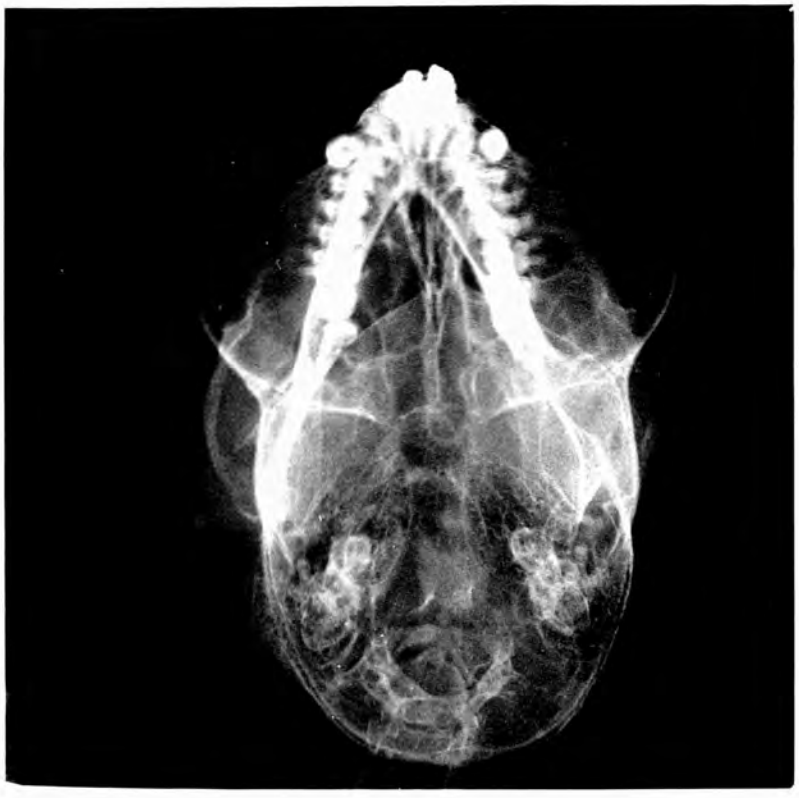
In the experiment investigating the effects of partial anosmia on aggression, further tests were carried out to control for any effects due to discomfort caused by the presence of the plugs alone. In these control tests each

PLATE 3.I

To Illustrate the Use of Radiography to Check the Position of the Nose Plugs Used in Experiments 2 and 3

The nose plugs show up well as 2 dense masses in the lower, dorsal view, and an X-ray taken from the side allows further checks to be made on the position of the plugs.


R



animal received one gauze plug (placed in the right nostril) which contained distilled water only. Therefore, radiography could not be used to verify the position of the plugs and it was assumed for the purposes of the experiment that, if the plug could not be extracted after testing, the animal had removed it.

Although the technique employed only causes partial anosmia as it only affects the main olfactory system, for the sake of brevity the term 'anosmia' will be used in the description and discussion of the materials and methods and the results for both partial anosmia experiments.

3.3 The Effect of Anosmia on Inter-Male Aggression : Experiment 2

3.3.1 Materials and Methods : All the 16 males used in this experiment are listed in Table 3.1. Animals were again designated as residents or introduced animals. Resident animals were placed in the observation room 2 weeks before testing, but caging and observation conditions were as described previously (2.2.).

Seven resident males were each paired successively with 2 unfamiliar male partners (Table 3.1) with a two-week gap in between tests. Pairs were either untreated or both animals were rendered anosmic by the method described above. Both animals were treated because pilot tests and the results from Experiment 1 indicated that either the resident or the introduced animal may be responsible for initiating aggression. Therefore, making only the resident anosmic might swamp any effects due to anosmia. The animals were treated 2 days before testing, the plugs being removed as soon as possible after testing in the anosmic condition. The order of testing was balanced such that some males were tested first in the anosmic condition, and others when untreated.

Animals were not fed before testing, which took place between 14.00 and 16.00 hours, ie, in the dark phase of the light cycle. The procedure was the same as described in Section 2.2, with each test lasting 20 minutes unless severe fighting occurred.

TABLE 3.1

The Male Pairings for Experiment 2 to Investigate the Effects of Reversible Anosmia on Inter-Male Aggression

Resident Male	Introduced Male	Condition
4367	192	Open
	WLCP3	Plugs present
4107	WLCP5	Plugs present
	9T	Open
4368	4367	Open
	4107	Plugs present *
4287	4371	Plugs present
4288	WLCP5	Open
	5T	Plugs present
4370	4107	Open
	5T	Plugs present
4451	4288	Plugs present
	4107	Open

Pairings are shown in the order of testing and all pairings were between intact males, ie, no castrate males were used in this experiment.

* This test was discarded because ♂4107's right plug was found, on X-ray after testing, to have been removed.

The check sheets used were the same as have previously been described for scoring same sex interactions (Figure 2.1) and scoring procedures were the same as in Section 2.2. Data were obtained for 7 resident males.

The control tests were performed after the anosmia tests described above. Each resident animal was removed to the observation room as previously described and allowed 2 weeks to settle down. The male to be introduced was placed in a single cage in the observation room one week before testing. Two days before testing each animal was caught, tranquillised and one plug inserted as described in Section 3.2. Results were obtained for 2 residents in this condition, ♂4288 and ♂4367.

3.3.2 Results : Data from this experiment are presented for 5 resident males who underwent both treated and untreated conditions, together with results for another 2 resident males (♂4368 and ♂4287) who, for different reasons, were not able to be tested in both conditions. ♂4287 was tested first in the anosmic condition and after this test it was found that the left-hand side plug could not be removed (although its presence was confirmed by radiography). Therefore, this male could not be tested in the untreated condition. ♂4368 was tested in the untreated condition and then in the treated condition. After testing in the anosmic condition it was found that, although ♂4368 still had both plugs in place, the introduced male had lost his right plug and the test was therefore invalid. Subsequently, it was discovered that ♂4368's left plug could not be removed and so it was impossible to repeat any tests with this male at a later date. Males 4287 and 4368 are therefore considered as an unmatched pair. Data for the 2 control experiments are presented at the end of the Results section.

Aggressive Behaviour : It was hypothesised that blocking the main olfactory system would remove olfactory cues to the sexual identity of the anosmic partner, and therefore, in view of the results obtained in Experiment 1, presumably lead to a decrease in aggressive response. Aggressive response was measured by latency to the first onset of contact aggression and by the actual amount of contact aggression that occurred. Arching was also included as a measure of aggressive response, as this display had been shown in Experiment 1 to be associated with dominance and high levels of contact aggression.

Latencies to the onset of contact aggression were increased in the treated (anosmic) condition in 4 out of the 5 matched pairs and 5 out of the 6 pairs, when the one unmatched pair was included. This increase in the latency to onset of contact aggression approached significance when the results for the 5 matched pairs were considered (Figure 3.1 mean = 1.09 ± 1.71 min (untreated) versus 9.14 ± 7.95 min (anosmic). If the sixth unmatched pair was included in the analysis the observed increased latencies to first contact

TABLE 3.2

Individual Scores and Mean Values for Each Condition for the 7 Resident Males Tested in Experiment 2

Male No.	Latency (Mins)		Contact Aggression		Arching		Proximity (Mins)		Nose-to Nose Inspections		Anogenital Inspections		Other Inspections		Tail Rub		Urine-Wash	
	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A
4107	0.26	14.96	0.66	0.08	0.16	0.42	0	2.25	0.33	0.28	0	0.41	0	0.17	0	0.06	0	0.03
4367	0.93	2.23	0.82	0.32	0.88	0.58	0	1.50	0.64	0.64	0	0	0.11	0.87	0	0	0	0
4288	0.2	5.91	0.16	0.02	0.91	0.37	0	5.25	0.16	0.56	0	0.15	0.01	0.38	0	0	0.01	0
4370	0	*20.0	0.10	0	0.63	0.01	0.75	0	0.42	0.36	0	0.01	0.05	0	0	0	0	0
4451	4.10	2.58	0.07	0.01	0.35	0.28	1.00	3.00	0.35	0.57	0	0.03	0.12	0.15	0	0	0	0
4368	0.11	-	0.33	-	0.35	-	0	-	0.10	-	0	-	0	-	0.25	-	0.01	-
4287	-	*20.0	-	0	-	0.17	-	0	-	0	-	0	-	0	-	0.05	-	0.02
Mean	0.93	10.94	0.35	0.07	0.54	0.30	0.29	2.00	0.33	0.40	0	0.12	0.04	0.26	0.04	0.01	0.003	0.008
S.D.	1.58	8.38	0.31	0.12	0.30	0.19	0.45	1.90	0.19	0.24	0	0.17	0.05	0.32	0.10	0.02	0.005	0.01

All scores are expressed as frequencies per 15 seconds unless otherwise stated.

* indicates that in this test no fight occurred so the maximum possible latency was awarded for statistical purposes.

The following tests were terminated before 20 minutes had passed : ♂4107 (untreated) at 1 min 30 seconds
♂4367 (untreated) at 4 mins 15 seconds
♂4367 (anosmic) at 7 mins 45 seconds

A = anosmic
O = untreated

TABLE 3.3

Individual Scores and Mean Values for Each Condition for the Introduced Animals Tested with Each Resident Male in Experiment 2

Introduced to Resident Male	Contact Aggression		Arching		Anogenital Inspections		Other Inspections (Excluding Nose-to-Nose)		Tail Rub		Urine-Wash	
	O	A	O	A	O	A	O	A	O	A	O	A
♂4107	0.16	0.02	0.16	0.15	0	0.02	0	0.01	0	0	0	0
♂4367	0.05	0	0	0.03	0	0	0.10	0.16	0	0	0	0
♂4288	0	0.02	0.17	0.05	0	0.05	0.01	0.38	0	0	0	0
♂4370	0.21	0	0.47	0.50	0	0	0	0	0.11	0	0.02	0.02
♂4451	0	0	0.05	0.21	0.07	0.02	0.02	0.11	0	0	0	0
♂4368	0.28	-	0.07	-	0	-	0	-	0	-	0	-
♂4287	-	0	-	0	-	0	-	0.02	-	0	-	0
Mean	0.11	0.003	0.15	0.13	0.01	0.01	0.02	0.11	0.01	0	0.003	0.003
S.D.	0.11	0.01	0.16	0.18	0.02	0.01	0.03	0.14	0.04	0	0.008	0.008

All these scores are for the introduced animals and scores are expressed as frequencies per 15 seconds unless otherwise stated.

A = anosmic
O = untreated

aggression reached statistical significance (mean = 0.93 ± 1.57 min (untreated) versus 9.96 ± 4.36 min (anosmic); $p < 0.05$: 1 tail unrelated t-test).

Latencies to first onset of contact aggression in the untreated condition were generally lower than those found in male-male pairs in the first experiment (Experiment 1 (N=8) mean = 6.98 ± 6.58 min; Experiment 2 (N=6 untreated) mean = 0.93 ± 1.58 min). In 2 cases in the anosmic condition, no fighting occurred and a maximum latency of 20 minutes was awarded for the purposes of statistical analysis. Three tests were stopped before the full 20 minutes had passed - for resident ♂4367 in both anosmic and untreated conditions and for resident ♂4107 in the untreated condition.

Frequencies of aggressive contact were significantly lower between anosmic partners (Figure 3.1) averaging 0.08/15 seconds as compared to 0.36/15 seconds between untreated partners (N=5) $p < 0.05$: 1 tail related t-test). This is also true if the sixth unmatched pair is included in the analysis (Table 3.2) with frequencies of contact aggression averaging 0.07/15 seconds between anosmic partners compared with 0.35/15 seconds for untreated pairs ($p < 0.05$: 1 tail related t-test). Frequencies of contact aggression in the untreated condition were slightly lower than frequencies between male-male pairs in Experiment 1 (mean frequency = 0.42 ± 0.56 (Experiment 1 N=8); mean frequency = 0.35 ± 0.31 (untreated Experiment 2 N=6)).

Arching frequency did not show any significant difference between anosmic and untreated pairs. This was true for both the 5 matched pairs (untreated, mean frequency/15 seconds = 0.58 ± 0.32; anosmic, mean frequency/15 seconds = 0.38 ± 0.21) and for the 6 unmatched pairs (Table 3.2 and Figure 3.2). However, as in Experiment 1, arching was found to be related to dominance. Consideration of the 12 pairings, irrespective of condition, showed that in 6 of these pairs the dominant and submissive animals could clearly be delineated, using the same criteria as in Experiment 1 (in 4 tests it was not possible to assign dominance with certainty using these criteria, and in 2 other pairings no fighting occurred). The 6 dominant animals were all resident males (♂4367, ♂4288, ♂4451 and ♂4368 in the untreated condition, and ♂4367 and ♂4107 in the anosmic condition). These dominant

animals did arch more than their submissive counterparts (mean frequency for dominant animals = 0.61 ± 0.23/15 seconds compared with a mean frequency of 0.05 ± 0.06/15 seconds for the submissive animals : $p<0.005$: 1 tail unrelated t-test).

Frequencies of arching for the resident males did not alter significantly after fighting had occurred, irrespective of condition (mean frequency before fighting = 0.47 ± 0.41; mean frequency after fighting = 0.46 ± 0.41). This result is not unexpected in view of the data obtained for dominant males in Experiment 1 (ie, frequencies of arching remained unchanged for dominant animals before and after fighting had occurred) given the fact that, where dominance could be assessed, the resident males, not the intruders, were dominant. There was a decrease in frequency of arching for introduced males, when scores before and after fighting were compared, however, this difference was not significant (frequency before fighting, mean = 0.20 ± 0.28/15 seconds; frequency after fighting, mean = 0.10 ± 0.15/15 seconds).

Sexual Behaviour : No mounting behaviour was observed between untreated males in this experiment; however, in one test in the anosmic condition, the resident male (♂4288) was observed to mount the introduced male (♂5T). This brief mounting attempt which occurred after 4 minutes 40 seconds, was not accompanied by any obvious thrusting behaviour. The male dismounted and one minute 15 seconds later, attacked the introduced male. This test where mounting occurred was also the only test in Experiment 2 where allogrooming occurred, the resident grooming the introduced male once prior to mounting.

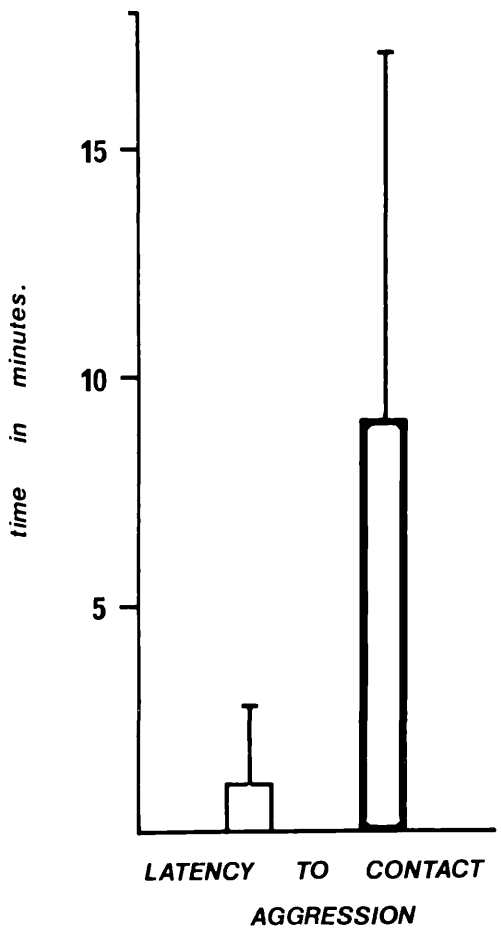
Proximity : Anosmic males remained in close proximity for longer periods than untreated pairs, the difference being small but consistent ($p<0.05$ for 5 matched pairs 1 tailed related t-test and see also Figure 3.2). This is not surprising when the results from the first experiment are considered, where resident males spent more time in close proximity with members of

FIGURE 3.1

The Mean Latency to the Onset of Contact Aggression and the Mean Frequency of Contact Aggression for the Resident Males in the 5 Matched Pairs of Male Owl Monkeys

Significantly less contact aggression occurred when the residents were tested in the anosmic condition than when they were tested with an untreated partner.
(** = $p<0.05$: 1 tail related t-test)

Untreated : □
Anosmic : ■


time in minutes.
15
10
5
LATENCY TO CONTACT AGGRESSION

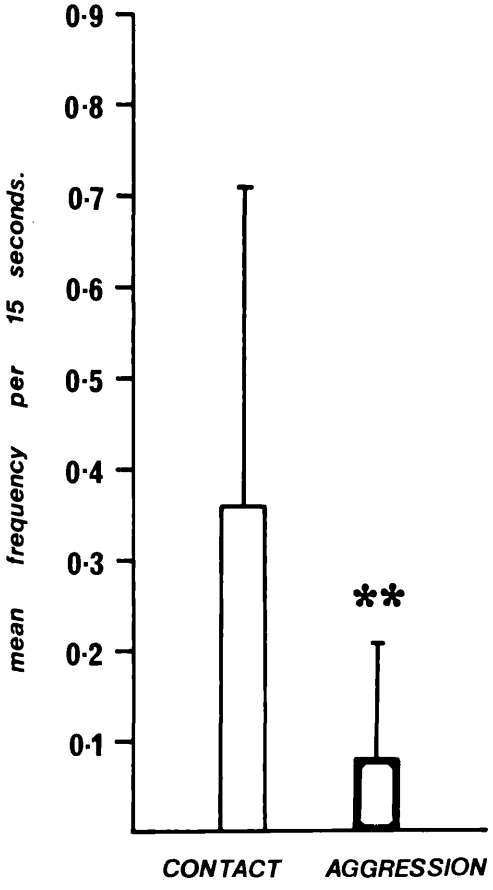

mean frequency per 15 seconds.
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
**
CONTACT
AGGRESSION

FIGURE 3.2

The Mean Frequency of Arching and the Mean Time Spent in Close Proximity for the 5 Matched Pairs of Male Owl Monkey

Frequencies of arching for the resident males were not significantly different between the 2 conditions, but anosmic animals spent more time in close proximity than untreated pairs. (** = $p<0.05$: 1 tail related t-test)

Untreated : □

Anosmic : ■

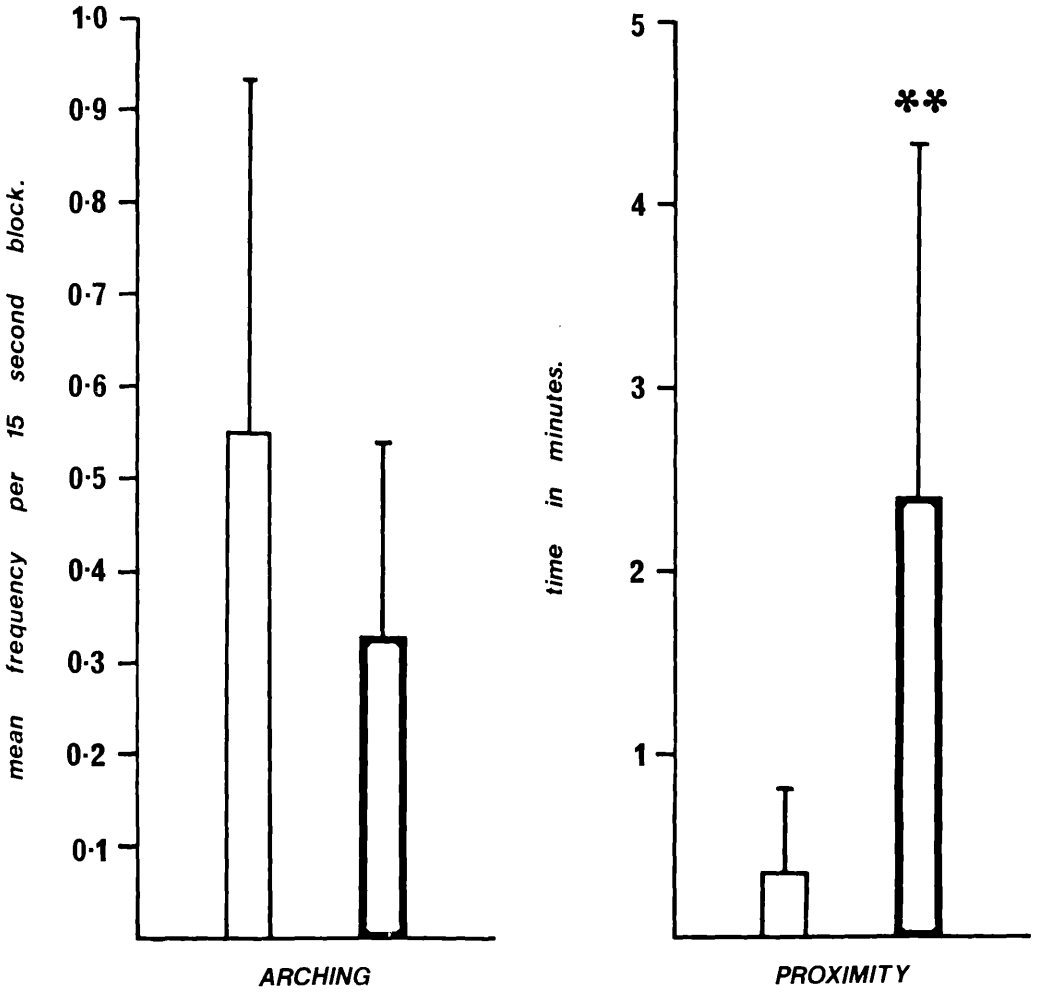

mean frequency per 15 second block.
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
ARCHING
time in minutes.
5
4
3
2
1
**
PROXIMITY

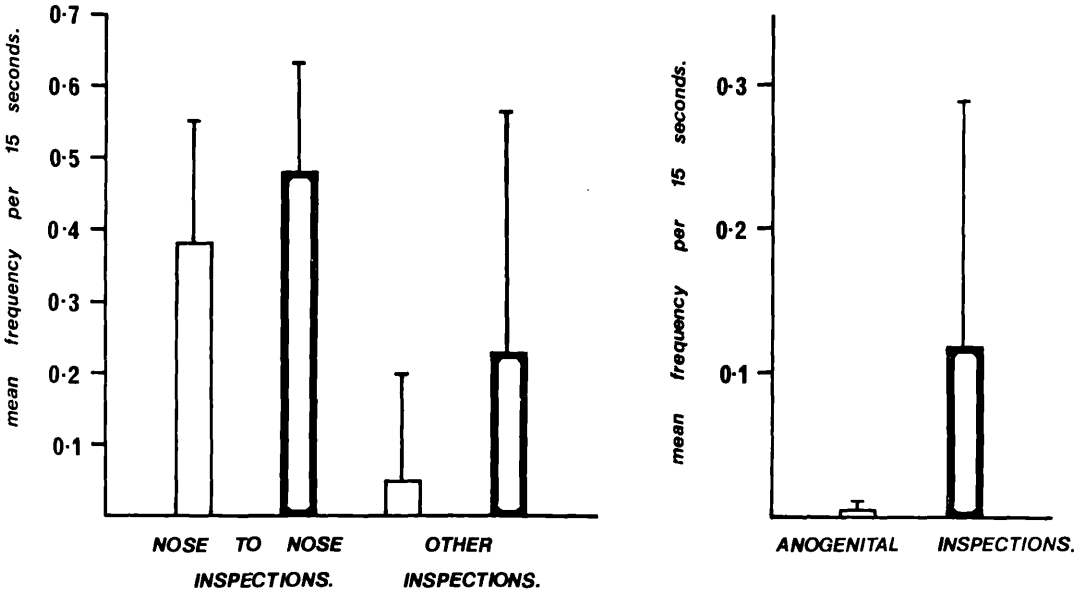
FIGURE 3.3

The Mean Frequency of Various Olfactory Inspections Performed by the Male Residents in the 5 Matched Pairs of Male Owl Monkeys

None of the 3 measures of olfactory inspection used (nose-to-nose, anogenital and inspections directed towards other areas of the body) differed significantly between the 2 conditions.

Untreated : □

Anosmic : ■


mean frequency per 15 seconds.
0·7
0·6
0·5
0·4
0·3
0·2
0·1
NOSE TO NOSE INSPECTIONS.
OTHER INSPECTIONS.
mean frequency per 15 seconds.
0·3
0·2
0·1
ANOGENITAL INSPECTIONS.

the opposite sex than with members of the same sex. However, unlike the first experiment, proximity scores did not decrease significantly after fighting had begun. This result may reflect the fact that proximity scores were quite low in this experiment, eg, untreated mean proximity score (before) = 0.20 $\pm$ 0.44 minutes versus mean (after) = 0.15 $\pm$ 0.33 minutes. The respective means for before and after fighting for the anosmic condition are 1.20 $\pm$ 1.47 minutes and 1.20 $\pm$ 1.30 minutes.

Olfactory Investigation and Scent Marking Behaviours : Frequencies of nose-to-nose inspections, anogenital inspections and inspections directed towards other areas of the body showed no significant difference between the anosmic and untreated conditions (Table 3.2 and 3.3 and Figure 3.3) for either resident or introduced males. However, if all the main forms of olfactory investigation are summed together, and the mean frequencies analysed for the 5 matched pairs, a significant difference between the 2 conditions is apparent (mean frequency untreated = 0.45 $\pm$ 0.20/15 seconds versus mean frequency anosmic = 0.93 $\pm$ 0.41/15 seconds; $p<0.05$ 1 tail related t-test).

In 3 cases in the untreated condition, no inspections of any sort at all occurred before fighting (50% of tests), whereas in the anosmic condition every fight was preceded by some form of olfactory inspection. It was hoped to clarify the relative importance of these various forms of olfactory investigation in determining the sex of the partner by looking at the relative frequencies of these behaviours before and after fighting had occurred (ie, before and after the sex of partner had, presumably, been definitely determined). Unlike the first experiment, none of these various indices of olfactory inspection (nose-to-nose; anogenital; other) showed any statistically significant differences when frequencies before and after fighting were compared, irrespective of whether these behaviours were considered individually or summed together, and irrespective of condition (Table 3.4). There was, however, a tendency for frequencies of olfactory inspection to decrease after fighting had occurred, eg, considering all forms

of inspection summed together the mean frequencies in the untreated condition were 1.08 $\pm$ 1.23/15 seconds (before) and 0.58 $\pm$ 0.39 (after). These results may possibly be affected by the fact that latencies to first onset of contact aggression were generally lower than in the first experiment, and also levels of inspections generally appeared to be much lower than in the first experiment, in both the untreated and anosmic conditions.

Anogenital inspections were only observed in 5 out of the 12 tests, and 4 of these tests where anogenital sniffing occurred were in the anosmic condition. In these 4 anosmic tests where anogenital inspections were observed, frequencies of inspection were higher before fighting than after in all 4 tests. However, when all 5 anosmic pairings were analysed together this difference did not reach statistical significance (mean before fighting = 0.13 $\pm$ 0.15/15 seconds; mean after fighting = 0.03 $\pm$ 0.005/15 seconds).

Scent marking levels were extremely low and marking only occurred in 6 out of the 12 pairings (Tables 3.2 and 3.3). Anosmia did not alter the marking levels of resident or introduced males in any statistically significant fashion, and as so many animals did not show any marking behaviour it was not pertinent to analyse the results further with respect to dominance.

Control Tests : Results were obtained for 2 resident males in the control condition, male 4288 and male 4367. For male 4288 in this control condition, the latency to the onset of contact aggression was 14 seconds, as compared to previous values of 12 seconds (untreated) and 355 seconds (anosmic). For male 4367 the corresponding value was 2 seconds, as compared with values of 56 seconds (untreated) and 134 seconds (anosmic). These 2 males also fought vigorously in this control condition and both tests were terminated before the full 20 minutes had passed (after 45 seconds for male 4367's test and male 4288's test was terminated after 6 minutes). Frequencies of contact aggression were high for both males, with a mean frequency of 0.29/15 seconds for male 4288 and 2.0/15 seconds

for male 4367. The previous values for contact aggression were 0.16/15 seconds (untreated) and 0.02/15 seconds (anosmic) for male 4288, and 0.82/15 seconds (untreated) and 0.32/15 seconds (anosmic) for male 4367. Male 4367 did not arch during this control test, although this probably reflects the fact that he chased and attacked his opponent vigorously. However, male 4288 arched frequently (mean = 0.66/15 seconds) during his test in the control condition (see Table 3.2 for arching frequencies in the untreated and anosmic conditions). Male 4288 also urine-washed once during this control test (mean frequency = 0.04/15 seconds), no other scent marking occurred during these 2 control tests.

Continued experimentation on this point was limited because of a lack of naive subjects, as repeated testing itself can lead to increased variability in the aggressive response. Another reason is that the turbinate system is much more complex in New World primates than in Old World primates (see Chapter Six) and considerable difficulty was experienced in removing the plugs from some animals as was the case with male 4287 and male 4368.

3.3.3 Summary and Conclusions : Increased latencies to the onset of contact aggression were observed in the anosmic males as compared to untreated males. Once fighting had begun, frequencies of aggressive contact between anosmic partners were lower than frequencies of aggressive contact between untreated partners, and in two pairs in the anosmic condition, no contact aggression occurred during the test. Frequencies of arching, however, did not differ between the two conditions, although this behaviour was still related to dominance as in the first experiment. In a control experiment the presence of a single plug did not affect male aggressive behaviour.

In one test in the anosmic condition male-male mounting followed shortly by fighting was observed. Mounts were never observed between untreated male partners. Anosmic partners spent more time in close proximity than untreated partners. Resident males performed more olfactory inspections

when anosmic than when they were tested in the untreated condition, although levels of inspections were generally lower than in the first experiment, irrespective of condition. Scent marking only occurred infrequently in these tests.

It seems therefore, that blocking input via the main olfactory pathway leads to a reduction in inter-male aggression in the owl monkey. The anosmia technique employed also appeared to have other, more subtle, effects on proximity and the frequency with which olfactory inspections occurred.

3.4 The Effect of Partial Anosmia on Sexual Behaviour : Experiment 3

3.4.1. Materials and Methods : Five resident males and 5 females were used in this experiment, together with another 2 females in the preliminary tests. It had been intended to test each male with several different females, but due to the variability in the behaviour of each male with different females, it was decided to pair the same male with the same female in each condition. The female chosen was one with which the male consistently showed mounting behaviour during preliminary pair tests.
All the animals used are shown in Table 3.4. Each male was placed in a cage in the observation room 2 weeks before testing began. Caging and observation conditions are as described previously (2.2). Females were either caged next to males in the observation room (but separated by 2 solid metal dividers) or they were introduced by the method used in previous tests (2.2).

TABLE 3.4

Male and Female Owl Monkeys Used in Experiment 3 (to study the effects of anosmia on sexual behaviour)

Male	Female Tested With for Sexual Behaviour	Eventual Female Partner
4370	4365	4365
4107	82, 81	81
4451	2455	2455
4367	188, 4365, 4469	4469
4373 *	188, 4364	4364

* ♂4373 discarded from the experiment as on X-ray after the 8 anosmic tests it was found that his right plug was missing.

Each pair was tested for compatibility for 15 minutes on 4 consecutive days. The criterion to judge for compatibility was that the full mating pattern (mounts and thrusting) occurred in 3 out of the 4 tests. One week after the completion of the initial tests, each pair was tested once a day for 15 minutes on 8 consecutive days. This was the untreated condition. After 2 weeks, the males were made anosmic by the method described in Section 3.2 and then 2 days later tested on 8 consecutive days with the same female. The anosmic male's health was observed each day and abnormal amounts of sneezing or obvious breathing troubles were recorded. The floor of the cage was left free of sawdust, and was checked every day for signs that the plugs had been removed. After the last test in the anosmic condition, the plugs were removed. Two weeks later the same male and female pairs were tested for a further 8 consecutive days. This was to control for the effects of repeatedly pairing the male with the same female. The hormonal status of the female was not monitored daily as it has been shown that in Aotus, the female's behaviour does not vary with stage of the cycle, and that the male continues mounting throughout the cycle (Dixson, Bonney and Fleming 1980). At the end of each 8 day block, urine was collected from each female and subjected to the Subhuman Primate Pregnancy Test (developed by N.I.H. in the USA).

The behavioural testing procedures were the same as described in Section 2.2 except that each test lasted 15 minutes and took place between 14.00 and 17.00 hours. The checksheets and scoring methods have been described previously (2.2) using the checksheets for scoring opposite sex interactions (Figure 2.2), except that 'approaches' and 'walk-aways' were also scored. Each time one animal approached the other to within 6 inches, this was scored as one 'approach' (APP); each time an animal walked away from the other animal this was scored as one 'walk-away' (WA). Abbreviations for these behaviours are given in parentheses. Data were obtained for 4 resident males.

3.4.2. Results : Data are presented for 4 resident males - ♂4451, ♂4107, ♂4367 and ♂4370. On radiography after the last test in the anosmic condition, it was discovered that the right side plug in male 4373's nose was missing. Therefore, data on this male were excluded from the analysis. Scores are not expressed as frequencies per 15 seconds as all tests were of equal duration (15 minutes) and therefore direct comparisons were possible. Results were analysed using a two-way analysis of variance and then further compared by means of 2-tail protected t-tests (Welkowitz, Ewen and Cohen 1976). When a homogeneity of variance test revealed that the data were not suitable for such analysis an unrelated t-test was used where appropriate to compare scores for individual animals between conditions.

Sexual Behaviour : None of the 4 measures of sexual behaviour used (mean number of mounts per test; mean latency to first mount attempt; mean duration of first mount with thrusting and percentage of mounts terminated by the male) showed any consistent variation over the 3 conditions (Figure 3.4 and Table 3.5). However, considerable variation in the scores existed between males.

All males, except ♂4367, mounted at least once in every test. In 4 tests ♂4367 did not attempt to mount the female - 3 of these were in the anosmic condition and he did not attempt to mount in the first test in the control condition. An analysis of variance on mounting frequency revealed that overall there was no significant difference between the 3 conditions, although it did indicate a significant subject effect and that a subject x condition interaction existed. Comparison by 2-tail protected t-tests revealed some statistically significant effects. Male 4107, who mounted more frequently per test than any other male (mean = 4.5 ± 1.5, $p < 0.001$), showed significantly higher rates of mounting in the anosmic ($p < 0.001$) and control ($p < 0.05$) conditions than in the untreated condition. Male 4451 and male 4367, on the other hand, showed a significant decrease in the number of mounts per test in the anosmic condition compared to the untreated and control conditions ($p < 0.001$). Male 4367 also showed a significantly lower

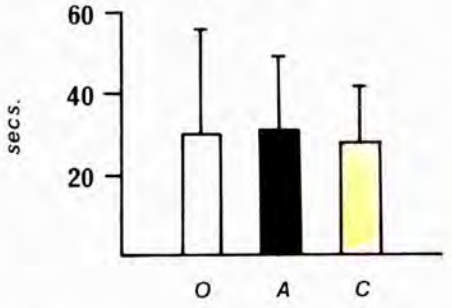
FIGURE 3.4

The Mean Scores of Various Indices of Sexual Behaviour Together with the Mean Number of Anogenital Inspections for all 4 Males in Each of the 3 Conditions

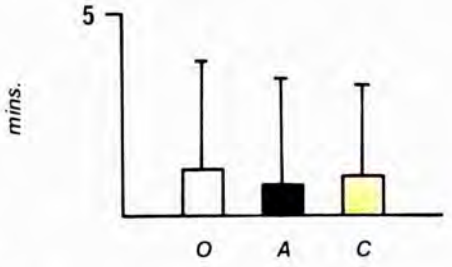
None of the 3 indices of sexual behaviour presented in the figure showed any statistically significant variation with respect to condition. There was however, a significant decrease in the number of anogential inspections performed by the males in the anosmic as compared to the untreated condition (* = $p<0.001$: 2 tail protected t-test).

Untreated : □
Plugs present : ■
Plugs removed : ■

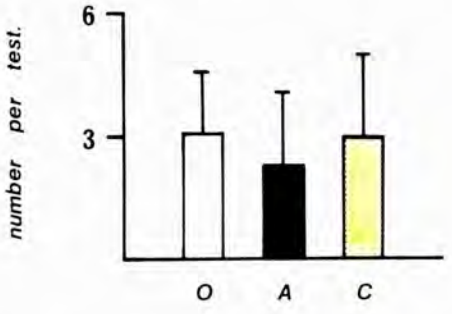
A. *MEAN DURATION OF FIRST MOUNT.*



B. *MEAN LATENCY TO FIRST MOUNT.*



C. *MEAN NUMBER OF MOUNTING ATTEMPTS.*



D. *MEAN NUMBER OF ANOGENITAL INSPECTIONS.*

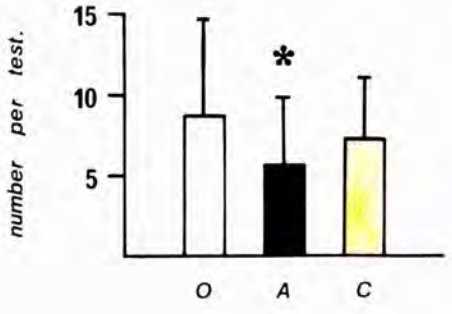


TABLE 3.5

Data for 4 Resident Males to Show the Effects of Anosmia on Mounting Behaviour

	Male No.	Untreated	Plugs Present	Plugs Removed
Mean latency to first mount attempt (secs)	4107	20.0 ± 9.4	20.3 ± 11.5	14.6 ± 5.5
	4367	230.2 ± 297.4	194.0 ± 394.1*	219.2 ± 231.6**
	4451	24.1 ± 10.7	15.7 ± 1.7	23.5 ± 10.9
	4370	16.7 ± 7.4	14.5 ± 13.7	6.3 ± 1.3
Overall Mean		72.4 ± 166.4	47.4 ± 161.2	61.0 ± 133.3
Mean number of mounts per test	4107	4.0 ± 1.1	4.7 ± 1.7	4.5 ± 2.3
	4367	2.5 ± 1.7	0.7 ± 0.8	1.6 ± 0.9
	4451	4.2 ± 1.1	2.5 ± 1.0	4.3 ± 1.5
	4370	1.7 ± 0.7	1.3 ± 0.7	1.3 ± 0.5
Overall Mean		3.1 ± 1.5	2.3 ± 1.8	3.0 ± 2.0
Mean duration of first mount with thrusting (secs)	4107	40.2 ± 17.3	27.1 ± 9.7	21.8 ± 15.1
	4367	16.6 ± 8.3	19.6 ± 15.8	23.8 ± 12.9
	4451	27.1 ± 0.6	23.2 ± 15.6	41.0 ± 14.0
	4370	38.5 ± 22.3	44.0 ± 21.7	26.6 ± 10.7
Overall Mean		30.6± 20.6	31.1 ± 18.3	28.4 ± 14.5
% of mounts terminated by the male (per block of 8 tests)	4107	100%	68%	73%
	4367	75%	100%	61%
	4451	100%	100%	100%
	4370	71%	61%	36%

All males mounted in every test except ♂4367 (* = did not mount in 3 tests; ** = did not mount in one test).

number of mounts in the control condition than in the untreated condition ($p<0.001$). Male 4370 showed no significant changes in mounting frequency over the conditions.

Latencies to the first mount with thrusting did not differ significantly between the 3 conditions nor was there a significant subject x condition interaction. Male 4367 did have significantly longer latencies to the first mount attempt than the other 3 males ($p<0.001$: 2-tail protected t-test, excluding those tests where no mount attempts occurred). No other male had a latency longer than 55 seconds, whereas, in 8 tests, male 4367 had latencies in excess of 178 seconds. Thus the mean latency to first mount over all 3 conditions was 217.3 ± 279.8 seconds for male 4367, compared to 18.3 ± 8.9 (♂4107); 21.2 ± 9.0 (♂4451); 12.1 ± 9.3 (♂4370).

The duration of first mount with thrusting did not show this large individual variation (see Table 3.5), nor did it alter significantly over the 3 conditions.

No qualitative changes in mounting behaviour were observed, although as in Experiment 1, ejaculation and intromission could not be confirmed behaviourally.

Generally, males terminated at least 60% of the mounts in each condition (Table 3.5) and male 4451 terminated all mounts. The data for male 4370 in the control condition provides an interesting exception to this general rule. In the control condition his female partner, ♀4365, terminated 64% of the mounts. Female 4365 was also the only female to show positive results on the Subhuman Primate Pregnancy Test. Positive results were only obtained after the tests in the control condition, and it is therefore likely that she became pregnant during the tests in the untreated condition. However, the foetus aborted and it was not possible to estimate its age and hence determine the approximate date of conception.

No female was ever observed to mount her male partner in any of the 96 tests.

Aggressive Behaviour : Male 4370 and male 4451 were never aggressive towards their female partners. Males 4367 and 4107 never showed any

contact aggression towards their female partners in the untreated and control conditions. However, in the last test in the anosmic condition, ♂4107 bit ♀81 as she tried to pass in front of him, and in 3 tests in the anosmic condition, ♂4367 showed contact aggression towards ♀4469. Male 4367 frequently displaced female 4469, especially if she was sitting by the cage bars or in a corner, although no contact aggression was shown in such situations. However, in 3 tests in the anosmic condition, displacement was achieved by means of contact aggression, the male grabbing the female and pushing her off the branch, causing her to fall. No other incidents of contact aggression were observed.

Male arching behaviour did not show any consistent variation with condition (see Table 3.6). The large variance in the overall mean for the anosmic condition can be mainly attributed to male 4367, with a range of 0 to 15 arches per test in the anosmic condition. Other males showed very low levels of arching behaviour (see Table 3.6).

Levels of arching in the females were slightly higher overall than those for the males (see Table 3.8) although, as in the males, there was no consistent variation across the 3 conditions. Female 4469, male 4367's partner, exhibited the highest levels of arching behaviour of any animal, with an overall mean score of 6.7 ± 5.6 per test irrespective of condition.

Olfactory Inspection and Scent-Marking Behaviour : Levels of nose-to-nose inspections did not differ in a statistically significant fashion between the 3 conditions. More nose-to-nose inspections occurred in tests between ♂4367 and ♀4469 than in other pairs ($p<0.002$: 2-tail related t-test). There were no interaction effects between individual pairs and the 3 test conditions. In the tests between ♂4107 and ♀81, low vocalizations often accompanied nose-to-nose inspections and such inspections usually seemed to be initiated by the female.

Anogenital inspections by the males decreased in the anosmic condition (Figure 3.4 and Table 3.7) and this difference was statistically

significant when the scores in the anosmic condition were compared with those in the untreated condition ($p<0.001$: 2-tail protected t-test). The only individual difference that existed was that male 4367 inspected the anogenital region of his female partner more frequently than the other 3 males (overall mean for male 4367 = 11.5 ± 5.0 : $p<0.001$: 2-tail protected t-test). Levels of anogenital inspections by females were generally lower than male levels, except for female 2455 (Table 3.8).

Males directed significantly less inspections to other areas of the body in the anosmic condition than in the untreated condition ($p<0.01$: 2-tail protected t-test). Consideration of the males individually revealed that ♂4367 showed consistently higher levels of these inspections (mean = 11.3 ± 4.9) than either ♂4107 (mean = 5.8 ± 4.0) or ♂4370 (mean = 6.7 ± 3.5) ($p<0.001$: 2-tail protected t-test). The levels of inspections towards other areas of the body were remarkably similar for all the females (Table 3.8) and there were no significant differences between either conditions or individuals.

Olfactory inspections occurred immediately before mounting attempts in 70% of cases for ♂4367; 55% of cases for ♂4370; 53% of cases for ♂4107 and 45% of cases for ♂4451, and there was no consistent difference in this measure across treatments.

Levels of scent marking in males showed considerable individual variability. Male 4451 never urine-washed and only tail rubbed 4 times in these tests and male 4370 never tail rubbed and only urine-washed in the control condition (mean = 1.3 ± 1.2). Therefore, only the scent marking scores of male 4367 and male 4107 will be discussed further (Figure 3.5 A and B).

Figure 3.5 shows that for each male a similar pattern existed for both forms of marking across the 3 conditions. Male 4107 showed a decrease in both tail rubbing and urine-washing in the anosmic condition compared to the control and untreated conditions. Male 4367 on the other hand, showed a progressive increase in both types of scent marking across the 3 conditions.

Female marking scores are shown in Table 3.9. Levels of urine-washing were generally very low, except for female 4365 (overall mean, irrespective of condition, = 2.7 $\pm$ 1.7 per test). However, all females tail rubbed at least twice in each condition (Table 3.9). Female 2455 showed consistently high levels of tail rubbing across the 3 conditions, whilst female 4469 progressively increased her levels of tail rubbing over the 3 conditions (in one test in the control condition, this female tail-rubbed 127 times). Female 4469 tail rubbed significantly less in the untreated condition than in either the anosmic or control conditions ($p<0.02$: 2-tail unrelated t-test).

Allogrooming and Proximity : Allogrooming by males (Table 3.6) occurred in the following percentage of tests for each male :-
50% (♂4107); 71% (♂4370); 75% (♂4367); 91% (♂4451).
Both male 4367 and male 4451 showed a significant increase in the amount of allogrooming in the control condition compared to the anosmic condition (♂4367, $p<0.05$; ♂4451, $p<0.02$; 2-tail unrelated t-tests). Levels of allogrooming exhibited by females were generally lower than those for males (see Table 3.8) and in neither case did they show any consistent variation across the 3 conditions.

Proximity scores between test partners did not vary in any statistically significant fashion across the 3 conditions (Table 3.6). Male 4367 and female 4469 spent less time in close proximity than the other 3 pairs (overall mean = 5.1 $\pm$ 5.4 minutes per test, irrespective of condition, $p<0.05$: 2-tail protected t-test).

Approach Behaviour : Figure 3.6 (A) illustrates the fact that the number of times a male approached his female partner did not vary in a consistent fashion across the 3 conditions. Figure 3.6 (B) shows the equivalent data for the female partners. It is clear from this figure that changes in the male's behaviour are not due to any changes in the female partner's approach behaviour.

TABLE 3.6

Data for 4 Resident Males to Show the Effects of Anosmia on Arching and Allogrooming Behaviour Together with the Mean Proximity Scores for Each Pair

	Male No.	Untreated	Plugs Present	Plugs Removed
Mean Amount of time spent in close proximity (mins per test)	4107	6.9 ± 2.2	9.0 ± 2.1	5.8 ± 1.7
	4367	5.7 ± 1.5	2.1 ± 1.1	2.0 ± 1.0
	4451	7.1 ± 1.6	10.3 ± 2.5	11.9 ± 2.0
	4370	7.9 ± 2.0	10.0 ± 1.9	10.1 ± 0.9
Overall Mean		7.0 ± 1.9	8.0 ± 3.8	7.4 ± 4.1
Mean number of Allo-grooms (per test)	4107	1.1 ± 2.4	1.2 ± 1.7	1.5 ± 1.0
	4367	2.5 ± 2.2	0.8 ± 1.1	2.8 ± 1.9
	4451	3.3 ± 1.3	1.5 ± 1.1	10.6 ± 6.6
	4370	1.2 ± 1.4	2.5 ± 2.5	2.1 ± 1.5
Overall Mean		2.0 ± 2.0	1.5 ± 1.7	4.2 ± 5.0
Mean number of arches (per test)	4107	3.1 ± 2.1	1.2 ± 1.3	1.8 ± 1.1
	4367	1.7 ± 1.0	2.5 ± 2.0	1.7 ± 2.1
	4451	0.2 ± 0.4	0	0.5 ± 0.5
	4370	1.3 ± 1.0	0.3 ± 0.7	1.8 ± 1.8
Overall Mean		1.6 ± 1.61	1.5 ± 3.1	1.50 ± 1.5

TABLE 3.7

Data for 4 Resident Males to Show the Effects of Anosmia on Various Olfactory Inspections

	Male No.	Untreated	Plugs Present	Plugs Removed
Mean number of nose-to-nose inspections (per test)	4107	9.7 ± 3.4	7.7 ± 3.1	6.7 ± 1.5
	4367	15.2 ± 4.9	14.2 ± 4.7	10.8 ± 2.1
	4451	7.2 ± 4.3	7.8 ± 3.3	7.6 ± 3.7
	4370	7.1 ± 2.9	7.0 ± 2.8	7.7 ± 1.9
Overall Mean		10.0 ± 5.0	9.2 ± 4.4	8.2 ± 2.7
Mean number of anogenital inspections (per test)	4107	8.6 ± 4.5	7.2 ± 2.6	9.7 ± 3.4
	4367	16.6 ± 2.3	8.6 ± 5.2	9.3 ± 3.1
	4451	4.6 ± 1.7	6.6 ± 2.7	7.3 ± 2.4
	4370	5.2 ± 2.9	0.6 ± 1.4	2.3 ± 1.4
Overall Mean		8.7 ± 5.6	5.7 ± 4.3	7.2 ± 3.8
Mean number of inspections directed to other body areas (per test)	4107	6.6 ± 2.6	6.5 ± 5.6	4.5 ± 3.8
	4367	13.0 ± 7.8	10.3 ± 3.5	10.6 ± 2.6
	4451	9.6 ± 2.8	4.8 ± 2.1	10.3 ± 4.9
	4370	9.2 ± 3.3	4.0 ± 3.1	7.0 ± 2.2
Overall Mean		9.6 ± 4.9	6.4 ± 4.3	8.1 ± 4.2

FIGURE 3.5

The Mean Scores for (A) Tail Rubbing and (B) Urine-Washing for Each Individual Male in the 3 Conditions

(A) Tail Rubbing :

Male 4107 tail rubbed significantly less in the anosmic condition as compared to both untreated and control conditions (* = $p<0.02$: 2-tail related t-test). Male 4367 tail rubbed significantly more in the control condition than in the untreated condition (** = $p<0.05$: 2-tail unrelated t-test).

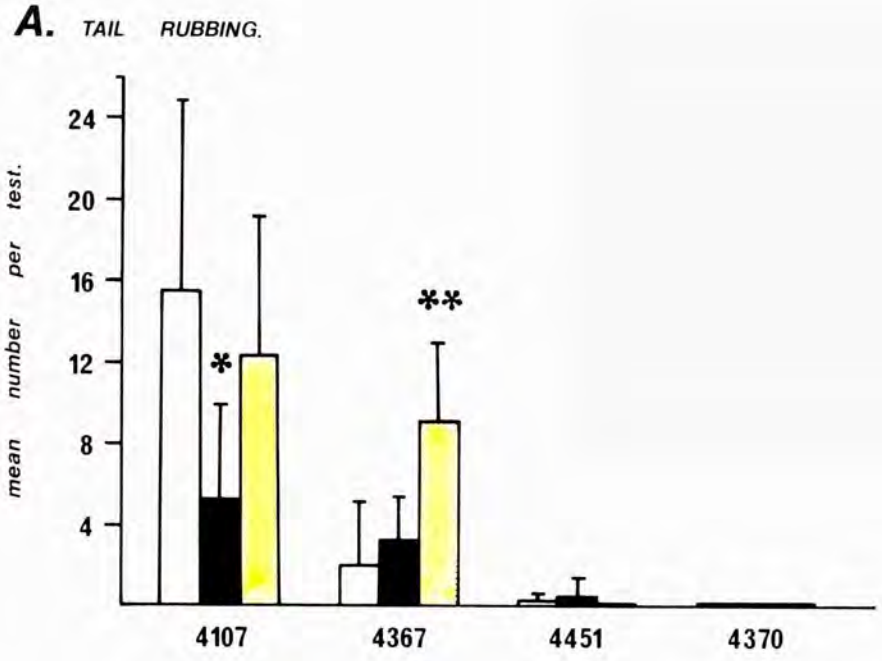
(B) Urine-Washing :

Male 4107 urine-washed significantly less in the anosmic condition as compared in the control condition (* = $p<0.02$: 2-tail related t-test). Male 4367 showed a progressive increase in urine-washing across the 3 conditions, with levels in the untreated condition being significantly lower than those in the control condition (** = $p<0.002$: 2-tail related t-test).

Untreated : □

Plugs present : ■

Plugs removed : □


A. TAIL RUBBING.
mean number per test.
24
20
16
12
8
4
*
**
4107
4367
4451
4370

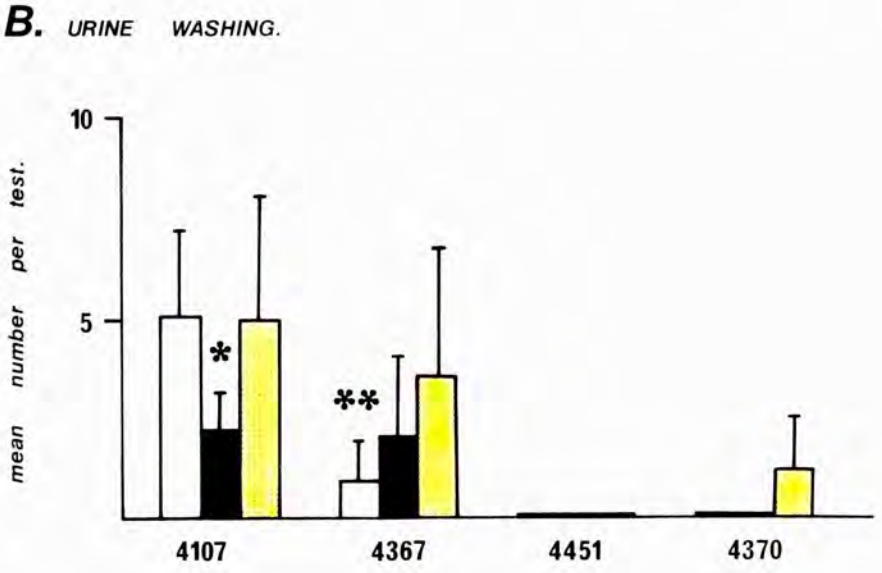

B. URINE WASHING.
mean number per test.
10
5
*
**
4107
4367
4451
4370

TABLE 3.8

Data for the 4 Female Partners for Arching and Allogrooming Behaviour and Olfactory Inspections

	Female No.	Untreated	Plugs Present	Plugs Removed
Mean number of arches (per test)	81	1.5 ± 1.9	1.0 ± 0.9	0.6 ± 0.9
	4469	5.2 ± 2.4	6.7 ± 5.5	8.3 ± 8.1
	2455	0	0.1 ± 0.3	0
	4365	3.5 ± 2.7	0.5 ± 0.7	1.5 ± 1.6
Overall Mean		2.5 ± 2.7	2.0 ± 3.7	2.6 ± 5.1
Mean number of anogenital inspections (per test)	81	1.1 ± 0.9	0.1 ± 0.3	0.2 ± 0.4
	4469	0.7 ± 0.8	0.8 ± 1.1	0
	2455	1.8 ± 1.9	5.3 ± 2.2	2.2 ± 2.1
	4365	0.5 ± 0.5	0.7 ± 0.5	0.3 ± 0.1
Overall Mean		1.8 ± 1.8	5.3 ± 2.1	2.2 ± 2.0
Mean number of inspections to other body areas (per test)	81	3.8 ± 1.8	2.3 ± 2.4	3.1 ± 1.8
	4469	2.8 ± 1.4	4.1 ± 1.1	2.3 ± 1.5
	2455	3.6 ± 2.1	3.8 ± 1.7	2.1 ± 1.2
	4365	3.3 ± 1.1	2.6 ± 1.5	3.8 ± 2.5
Overall Mean		3.4 ± 1.6	3.3 ± 1.8	2.8 ± 1.8
Mean number of allogrooms (per test)	81	0.2 ± 0.4	0	0.5 ± 1.0
	4469	0.3 ± 1.0	0.6 ± 1.0	0
	2455	0.1 ± 0.3	0.6 ± 1.7	1.2 ± 2.1
	4365	3.6 ± 3.7	1.2 ± 2.4	0.6 ± 0.9
Overall Mean		1.0 ± 2.3	0.6 ± 1.5	0.5 ± 1.2

TABLE 3.9

Data for the 4 Female Partners on Scent Marking Behaviour

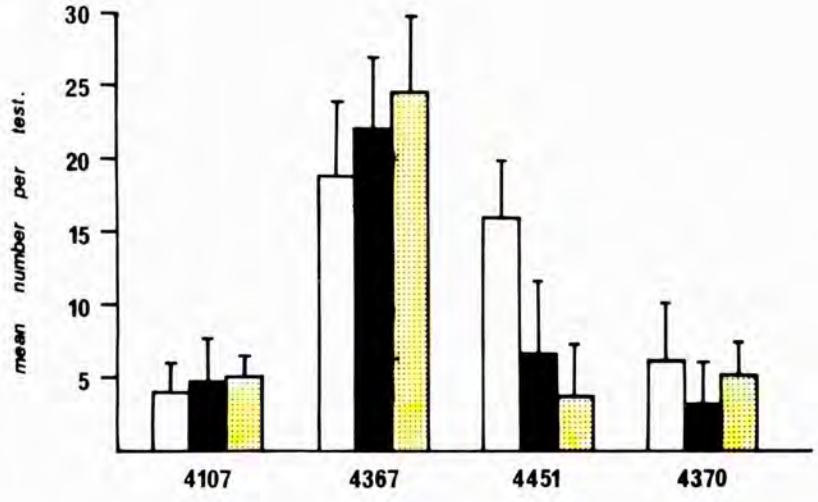
	Female No.	Untreated	Plugs Present in Male	Plugs Removed From Male
Mean number of tail rubs (per test)	81	1.6 ± 1.5	0.8 ± 0.9	0.2 ± 0.4
	4469	22.7 ± 18.9	66.6 ± 13.4	90.7 ± 33.3
	2455	13.1 ± 5.1	12.3 ± 8.4	13.8 ± 13.5
	4365	1.7 ± 1.9	0.7 ± 0.7	0.5 ± 0.5
Overall Mean		9.8 ± 12.7	20.1 ± 28.2	26.3 ± 41.1
Mean number of urine-washes (per test)	81	0.8 ± 1.2	0.1 ± 0.3	0
	4469	0.1 ± 0.3	0	0
	2455	0.1 ± 0.3	0	0.1 ± 0.3
	4365	3.5 ± 2.5	2.1 ± 1.2	2.7 ± 0.8
Overall Mean		1.1 ± 1.9	0.5 ± 1.0	0.7 ± 1.2

FIGURE 3.6

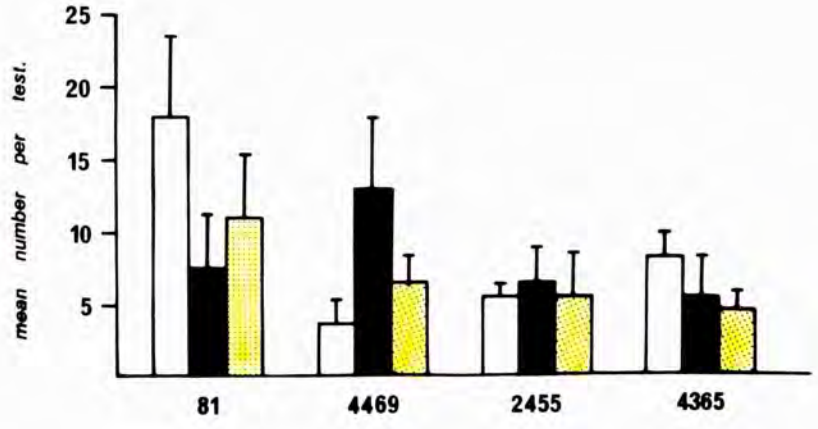
The Mean Number of Approaches per Test made by (A) Males and (B) Females

Untreated : □
Plugs present : ■
Plugs removed : ■

A. *MALES.*



B. *FEMALES.*



3.4.3. Summary and Conclusions : Although there existed subtle individual effects of anosmia on various indices of mounting behaviour in certain males, eg, male 4367 did not mount his female partner in 3 tests in the anosmic condition, there did not appear to be any consistent effects of partial anosmia on the mounting behaviour of male owl monkeys. In these tests, males terminated nearly all mounting attempts and in only one pair did the female terminate more than 60% of the mounts. This occurred in the control condition and may possibly be correlated with the fact that this female became pregnant sometime during the tests in the first 2 conditions.

Levels of aggressive behaviour were low and arching behaviour by either males or females did not vary in any consistent fashion with condition, although females generally arched more than males. The pair in which the most contact aggression was observed also showed the highest levels of arching behaviour.

Apart from nose-to-nose inspections, levels of inspections directed by males decreased in the anosmic as compared to the untreated condition. Scent marking was only performed regularly by 2 out of the 4 males. In contrast, all females tail rubbed and urine-washed although these behaviours were performed more frequently by some females than others.

The amount of time spent in close proximity was not affected in any consistent fashion by the partial anosmia technique, and this was also true for both allogrooming and approach behaviour by both males and females.

CHAPTER FOUR

SCENT DISCRIMINATION STUDIES : EXPERIMENT 4

4.1 Aims of the Experiment

Discrimination experiments have shown that both Prosimians and New World primates can discriminate between individuals on the basis of odour cues alone (Epple 1973, 1976; Harrington 1976 and, see also Chapter One). However, all these tests have been performed with animals isolated from their natural social group. The present studies concern the responses of family groups of Aotus to various conspecific odour cues. In the first series (A), only one scent source was presented in each test to clarify group members' responses to that particular odour. In the other series (B) and (C), 2 odour sources were presented simultaneously to see if discrimination on the basis of preference could be demonstrated.

Finally, it was decided to make 2 males partially anosmic by the technique described in 3.2 to see whether this technique did affect an animal's responsiveness (in terms of olfactory inspection and scent marking) to conspecific odours. It was hoped to verify that an animal treated in this way is anosmic with respect to biologically relevant odours.

4.2 Materials and Methods

Five family groups of owl monkeys served as experimental subjects. Groups were composed of an adult breeding pair and their offspring, the exact composition of each group being shown in Table 4.1. A list of all donor animals is given in Table 4.2. No experimental group member served as a donor.

TABLE 4.1

The Composition of the 5 Family Groups of *Aotus* Used in Experiment 4

Group Number	Adult Parents	Offspring Present	Birth Date of Offspring
1	♂ T9 ♀ T3	♂ 7 (a) ♀ 19 ♂ 27	24. 1. 77 24. 2. 78 26. 11. 78
2	♂ 176 ♀ 175	♂ 13 ♂ 22 ♂ 28	11. 7. 77 13. 7. 78 7. 1. 79
3	♂ T6 ♀ T3	♀ 9 (b) ♂ 17 ♀ 24	28. 7. 77 25. 12. 77 5. 9. 78
4	♂ 13 ♀ 15	♀ 8 (b) ♂ 18 ♀ 25	21. 2. 77 25. 12. 77 9. 10. 78
5	♂ Foster ♀ 4361	♂ 12 * ♂ 26	12. 6. 77 23. 11. 78

(a) All offspring born at Wellcome Laboratories of Comparative Physiology, except for male WLCP7.

(b) Removed from the group after series B.

* WLCP ♂12 had received a subcutaneous implant of testosterone propionate at the age of 4 months for the purposes of an earlier, unrelated experiment.

TABLE 4.2

Donors Used in Experiment 4 (Series A B and C)

	Urine Only	Subcaudal Secretion and Urine
A. Intact Males		
5T	x	-
192	x	x
4107	x	x
4287	x	-
4288	x	-
4367	x	x
4368	x	-
4370	x	-
4371	x	-
4451	x	x
WLCP3	x	-
WLCP5	x	-
WLCP7	x	x
7093	-	x
B. Intact Females		
81	-	x
83	x	x
188	x	-
2455	x	-
4364	x	-
4469	x	-
4536	x	x
4537	x	-
WLCP4	x	-
WLCP6	x	-
7327	-	x
7329	-	x
C. Castrate Males		
4287 (7.11.78)	x	x
4368 (7.11.78)	x	x
4369 (29.3.77)	x	x

A 'x' indicates that the urine or urine and subcaudal secretion from that donor was used at least once.

Dates in parenthesis are the dates of castration.

Urine was collected by fitting the cage base with a removable tray, sloping towards a funnel at the base to allow collection of 24-hour urine samples. Trays were cleaned thoroughly between samples. 5 mls of test solution (24-hour urine sample or saline) were pipetted onto a gauze pad approximately 3cm square. This test pad was then attached to the front grill of the cage with a clip.

Subcaudal gland samples were collected from each tranquillized animal (10mg ketamine HCl 'Vetelar', Parke Davis) and a 5ml quantity of urine from the same animal was then pipetted on to a gauze pad and both sides of the pad wiped 3 or 4 times over the gland. The scented pad was then placed in a clean glass jar and kept at room temperature (approximately 18^{o}C) for about 3 hours prior to testing. Gauze pads were more practical than the branches or pieces of wood used by other workers (Epple 1973; Clark 1975) given the design of the cages.

All tests took place during the dark phase of the light cycle, between 14.15 and 17.00 hours. Two 40 watt red lamps were used to aid observation, and these were always switched on 5 minutes before testing. The test pad was clipped on to the middle of the grill or, if 2 pads were to be used, one was clipped to the right side and the other to the left side (about 50cm apart). Each test lasted 10 minutes and scoring was carried out in full view of the subjects. Each group had been observed in a similar fashion for 2 years previously and was habituated to the presence of an observer. Check sheets were used for scoring and samples are shown in Figures 4.A (single pad) and 4.B (2 pads). Part of each checksheet was divided into 10 second intervals and these were signalled through an earpiece.

Behaviours were scored for the 2 parents and the 2 oldest offspring of each group. The number of inspections that each animal directed to the pad(s) was scored. In addition, to overcome any bias due to single, but lengthy, inspections, the 10-second divisions were used to score this behaviour for the 2 breeding animals. If a sniff lasted into

FIGURE 4.A

Sample Check Sheet used to Score Tests
Where a Single Pad was Presented

Date:		Group:		Time:		ND:	Scent Used: 116		
MALE		OTHERS		FEMALE		INFANT	INFANT.	OCCURRENCE OF SNIFF	
URW	TR	♂	♀	URW	TR			♂	♀
							1		
							2		
							3		
							4		
							5		
							6		
							7		
							8		
							9		
							10		

FIGURE 4.B

Sample Check Sheet used to Score Tests
Where Two Pads were Presented

Date:	Grp:	Test:	Left:	Right: 117

URW	TR	♂	♀	URW	TR	Infant	Infant	♂ L	♂ R	♀ L	♀ R

the next 10-second period, this was indicated and a score of one allotted for each extra 10-second period entered. Urine-washing (URW) and tail rubbing (TR) were also recorded - in marked columns for the adult pair and in shorthand in the 2 respective columns for the offspring. Other behaviours of interest were also scored in shorthand in the columns ear-marked for each animal, eg, any muzzle wiping on branches, etc.

The protocol for each series of tests is given in Table 4.3. In series A a different donor was used on each day. In series B and C different donors were used for each 5-day block of tests, but within each block of tests the same 2 donors were always compared in each test, although fresh samples were always used. This was due to a shortage of donors, and it was felt that as these tests were preference tests between individuals, habituation would not confound the results for olfactory inspections. Subcaudal secretion alone was not used, as it was impractical to collect subcaudal secretion uncontaminated by some urine. Therefore, it seemed to be preferable to combine the 2 potential odour sources in the last series in this experiment.

Data are presented for 5 groups for series A and B, and for 4 groups for series C, and analysis was by means of an analysis of variance by ranks (Meddis 1980).

Six months after the last series of discrimination tests (series C) the experiment to investigate the effects of partial anosmia on responsiveity to conspecific odours was performed. Two males were used in these tests - male T6 and male T9. These males were selected on the basis of results from the discrimination tests which indicated that these 2 males showed high levels of marking behaviour in the presence of conspecific odours. The discrimination tests also indicated that subcaudal secretion plus urine was a more potent stimulus than urine alone, and therefore, subcaudal secretion plus urine was the odour source presented in these tests. The methods of scent collection, presentation and observation were the same as those previously described above for the discrimination tests.

Erratum: Page 138 should follow after
Page 118

TABLE 4.3

Testing Regime for the Discrimination Tests

Number of Days of Testing (one test per day)		5	2	5	2	5	2	5	2	5	Family Groups Tested
Series A											
One pad only		Saline	No test	Saline	No test	Male* urine	No test	Saline	No test	Female* urine	1, 2, 3, 4, 5.
Series B											
2 pads :	Pad 1	Saline	No test	Male urine	No test	Male urine	No test	Saline	No test	Male urine	1, 2, 3, 4, 5.
	Pad 2	Saline	No test	Saline	No test	Castrate male urine	No test	Saline	No test	Female urine	
Series C											
2 pads :	Pad 1	Saline	No test	Male urine and tail gland	No test	Male urine and tail gland	No test	Male urine and tail gland	No test		1, 2, 3, 4.
	Pad 2	Saline	No test	Female urine & tail gland	No test	Female urine & tail gland	No test	Castrate male urine & tail gland	No test		

For tests with 2 pads, the position of the 2 scented pads (right or left) was balanced to correct for any bias due to side preference.

* = different donor on each day.

4.3 Results

In the following description of the results, the term 'breeding male' will be used to denote the adult male parent in each group and the term 'breeding female' to denote the adult female parent in each group. The term 'offspring' refers to both the mature and immature offspring present in each group. Data are presented for the oldest (between one year 10 months to 2 years 8 months) and the second oldest (between 5 months and one year 6 months) offspring only, irrespective of how many offspring were in fact present. In the results for each series of tests, the data for the adult breeding pair will be presented first, followed by the data for the offspring. Olfactory inspections are termed 'sniffs' for the sake of brevity.

SERIES A

Adult Pair : Breeding males directed significantly more sniffs towards pads containing urine than towards pads containing saline (X^2 = 17.7 : Z=3.7, $p<0.001$: 1 tail). Although there was no statistically significant difference for breeding females there was a tendency for breeding females to direct more sniffs towards pads containing urine than towards pads containing saline (X^2 = 5.90), as can be seen in Figure 4.1.

There were large individual variations in the number of sniffs directed towards the pad, irrespective of condition. Male 'Foster' and male 6 rarely sniffed the pad more than twice per test, although there were exceptions to this when urine was presented, (mean number of sniffs/test 1.3 $\pm$ 1.2 (♂6) and 1.3 $\pm$ 1.0 (♂Foster). Males 9 and 13, on the other hand, showed high levels of sniffing behaviour, especially when the pad contained urine (mean number of sniffs/test 6.0 $\pm$ 4.4 (♂9) and 8.6 $\pm$ 3.3 (♂13). Although individual differences did exist between females with respect to the amount of sniffs directed towards the pads, they were much less marked than in the males and, overall, females sniffed the pad slightly less than the males irrespective of condition (overall mean

number/test for males = 3.8 $\pm$ 4.4 overall, mean number/test for females = 2.0 $\pm$ 2.2).

Higher levels of scent marking behaviour were also exhibited by breeding males as compared to breeding females (see Figure 4.2). Breeding males urine-washed significantly more in tests where urine was presented than in tests where saline was presented (X^2 = 16.2 : Z = 3.3, $p<0.001$: 1 tail. See Figure 4.2.B). Breeding females, on the other hand, did not urine-wash more in tests where urine was presented (X^2 = 2.1).

Levels of tail rubbing by females were too low to merit further analysis (Figure 4.2.A) as this behaviour only occurred in 7 tests. By contrast, breeding males tail rubbed much more frequently, although there were large individual differences in this behaviour. Male 176 for example, was never observed to scent mark in this way, and male Foster only tail rubbed 3 times. Despite these large individual variations, there was a statistically significant increase in tail rubbing by breeding males in those tests where urine was presented as compared to those tests where saline was presented (X^2 = 20.9 : Z = 3.9, $p<0.001$: 1 tail, See Figure 4.2.A).

Offspring : Both the oldest and the second oldest offspring directed more sniffs towards pads containing urine than towards pads containing saline alone, as shown in Table 4.4 (oldest offspring - X^2 = 19.9 : Z = 2.6, $p<0.004$: 1 tail; second oldest offspring - X^2 = 9.7 : Z = 2.4, $p<0.006$: 1 tail). As with the breeding females, although individual differences did exist, these were not marked.

Levels of scent marking, however, did show great individual variability. Tail rubbing rarely occurred and was only performed by 2 offspring WLCP 12 and WLCP 8. Males WLCP 7 and WLCP 13 never tail rubbed and rarely urine-washed. The other 8 offspring all urine-washed regularly, although levels of urine-washing for these 8 animals were not as high as the levels of breeding males and females (see Table 4.4). There was no significant increase in the occurrence of scent marking by offspring, either urine-washing or tail rubbing, in those tests where urine was present as compared to those tests involving only saline.

FIGURE 4.1

Series A : The Mean Number per Test of Inspections Directed by Breeding Males and Breeding Females to Pads Containing either Saline or Urine

Breeding males directed significantly more inspections towards pads containing urine than towards the pads containing saline (* = $p < 0.001$: 1 tail).

Breeding males : ■

Breeding females : □

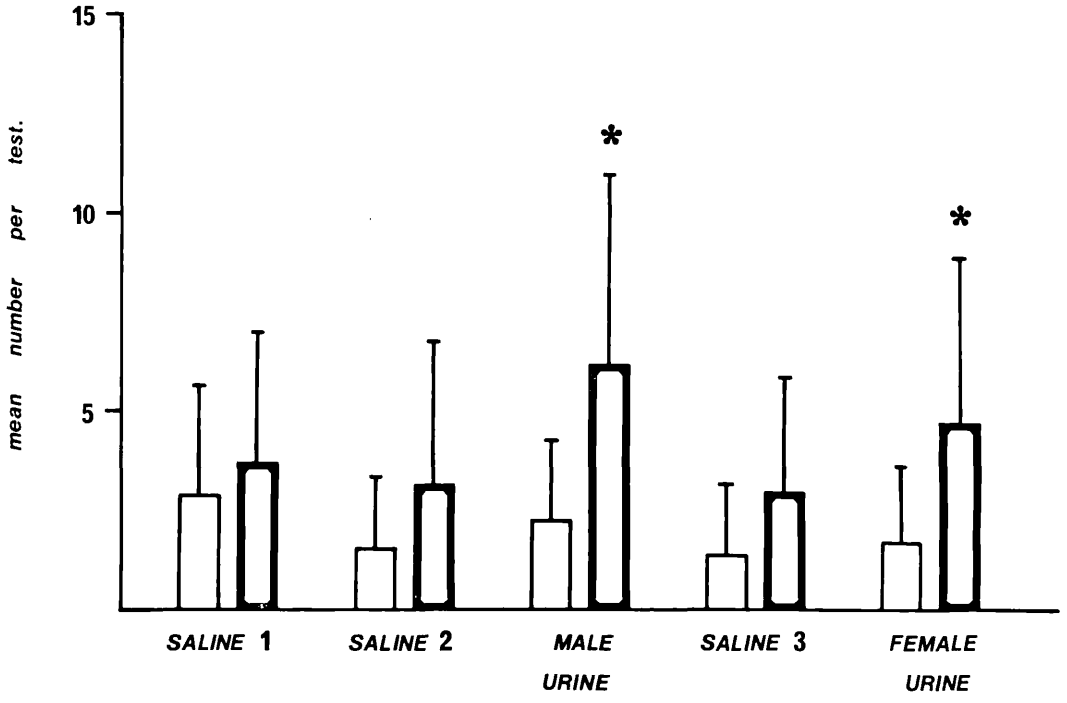

15
10
5
mean number per test.
*
*
SALINE 1
SALINE 2
MALE URINE
SALINE 3
FEMALE URINE

FIGURE 4.2

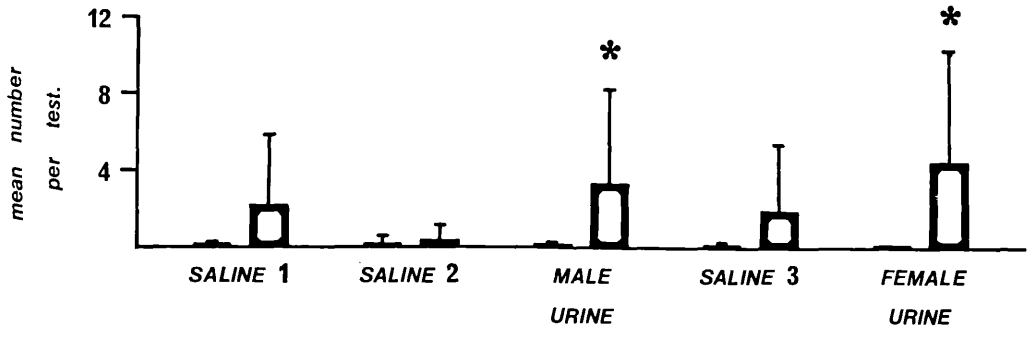
Series A : The Mean Number per Test of (A) Tail Rubs and (B) Urine-Washes Performed by Breeding Males and Breeding Females Presented with Pads Containing either Saline or Urine

Breeding males urine-washed and tail rubbed significantly more in those tests where urine was present compared to those tests where only saline was present (* = $p < 0.001$: 1 tail).

Breeding males : ■

Breeding females : □

A. *TAIL RUBS.*



B. *URINE WASHES.*

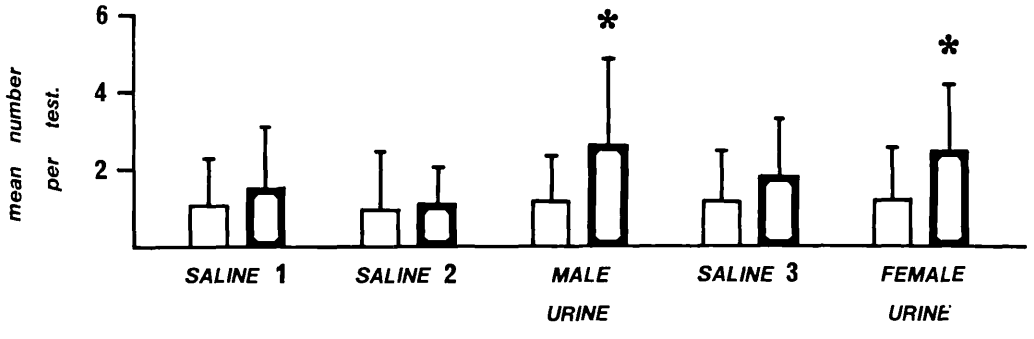


TABLE 4.4

Series A : The Mean Number per Test of (A) Scent Marking Behaviours and (B) Olfactory Inspections for the 2 Oldest Offspring in all 5 Family Groups

(A) Scent Marking Behaviours		Saline 1	Saline 2	♂ Urine	Saline 3	♀ Urine
Oldest Offspring (N = 5)	Urine-Washes	0.6 ± 1.0	0.3 ± 0.6	0.4 ± 0.8	0.6 ± 0.9	0.6 ± 0.7
	Tail Rubs	0	0.1 ± 0.5	0	0	0.1 ± 0.6
Second Oldest Offspring (N = 4)	Urine-Washes	0.2 ± 0.5	0.5 ± 0.6	0.5 ± 0.7	0.9 ± 1.0	1.3 ± 1.4
	Tail Rubs	0	0	0	0	0

(B) Inspections Directed Towards the Pad	To Saline 1	To Saline 2	To ♂ Urine	To Saline 3	To ♀ Urine
Oldest Offspring (N = 5)	6.5 ± 4.9	3.8 ± 3.2	5.1 ± 4.4	1.8 ± 1.6	3.8 ± 3.8
Second Oldest Offspring (N = 4)	3.1 ± 3.2	1.6 ± 1.4	3.9 ± 3.0	2.1 ± 1.6	2.7 ± 2.7

All scores are expressed as means per test

SERIES B

In this series of tests 2 pads were presented simultaneously. It was therefore possible to examine whether one type of olfactory cue elicited more inspection than another. In the first block of tests both pads contained saline and the data on olfactory inspections for breeding males and females was examined to see if a side preference existed. Analysis revealed that some individuals usually did sniff a pad presented on one side of the cage (left or right) more than the pad presented simultaneously on the other side. However, there was no consistent side bias across the 5 groups. Because of this and because the position of presentation of the pads was balanced, (as described in section 4.2) it was not felt necessary to correct the results for any side bias before they were analysed statistically.

Adult Pair : As in series A, breeding males sniffed the pads more frequently, irrespective of condition, than the breeding females (overall mean = 4.7 ± 4.2 (males) and 2.8 ± 2.6 (females). In the second block of tests breeding males directed more sniffs towards the pads containing male urine than towards the pads containing saline (Figure 4.3.A, $Z = 1.8$ $p<0.03$: 1 tail). The breeding females, however, did not inspect pads containing male urine more than those that only contained saline (Figure 4.3.B. $Z = 0.05$). Breeding males did not inspect pads containing intact male urine more than those containing castrate male urine ($Z = 0.3$), nor did they inspect pads containing male urine more than those containing female urine ($Z = 1.0$). Breeding females also showed no increase in the number of inspections directed towards intact male urine as compared to castrate male urine ($Z = 0.3$), although there was a tendency for females to direct more sniffs towards pads containing male urine than towards pads containing female urine ($Z = 1.5$).

The breeding males in these family groups urine-washed significantly more in those tests where urine was present than in those tests where saline only was presented ($X^2 = 12.2$: $Z = 2.9$, $p<0.002$: 1 tail - see Figure 4.4.B).

Breeding females generally exhibited lower levels of urine-washing than males, irrespective of condition (overall mean for males 1.9 $\pm$ 1.7: overall mean for females = 0.9 $\pm$ 1.0). Levels of urine-washing by females were not significantly higher in those tests where urine was presented (X^2 = 5.2; Figure 4.4.B).

As in the first series, levels of tail rubbing by breeding females were extremely low (see Figure 4.4.A) and did not merit further analysis. Most breeding males on the other hand, did exhibit this behaviour, although again, there were great individual differences in the frequency with which it occurred. Male 'Foster' never tail rubbed during these tests and male 176 was observed to tail rub only twice. The other 3 males showed higher levels of tail rubbing, for example, male 9 tail-rubbed 20 times during one test. Unlike urine-washing, tail rubbing by breeding males did not occur more frequently in those tests where urine was present as compared to those tests where saline alone was present (X^2 = 7.4. See Figure 4.4.A).

Offspring : The mean scores per test for both the oldest and second oldest offspring in all 5 groups are shown in Table 4.5. The mean number of sniffs directed towards either pad tended to be higher for both the eldest and the second eldest offspring than for the breeding males. However, the only significant difference that emerged from the statistical analysis was that the oldest offspring inspected pads containing male urine more than pads containing saline ($Z = 2.66$, $p<0.01$: 1 tail). This was not the case for the second oldest offspring and neither the oldest or the second oldest offspring inspected intact male urine more than castrate male urine, or intact male urine more than intact female urine.

Scent marking levels were generally low (see Table 4.5) and were comparable to the levels of marking exhibited by the breeding females, with no tail rubbing being exhibited by any offspring in these tests. Levels of urine-washing were also low and did not increase in a statistically significant fashion in those tests where urine was presented as compared to those tests where saline alone was present.

FIGURE 4.3

Series B : The Mean Number of Inspections per Test Devoted to Each Pad for (A) Breeding Males and (B) Breeding Females

(A) Breeding males inspected pads containing male urine more than pads containing saline (* = p = 0.03 : I tail). They did not inspect pads containing intact male urine more than those containing female urine or more than those containing castrate male urine.

(B) Breeding females did not show any statistically significant preference in any of these comparisons.

Breeding males : ■

Breeding females : □

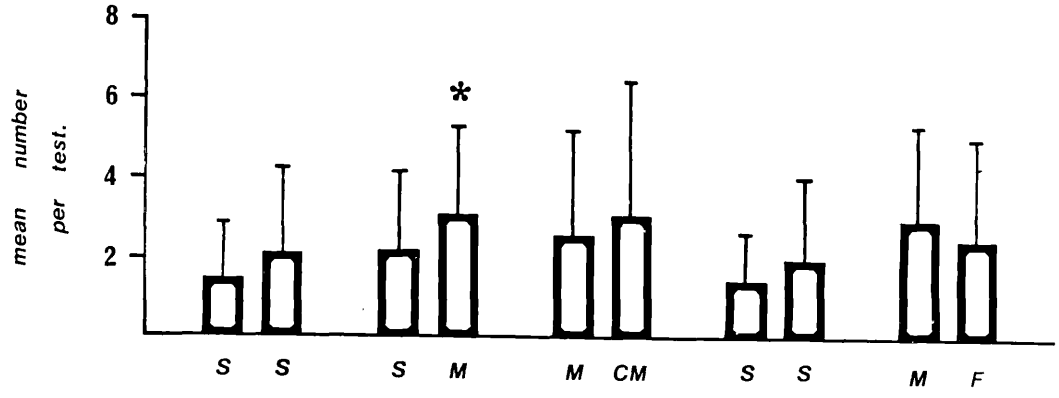
S = Saline

M = Male urine

CM = Castrate male urine

F = Female urine

A. *MALES.*



B. *FEMALES.*

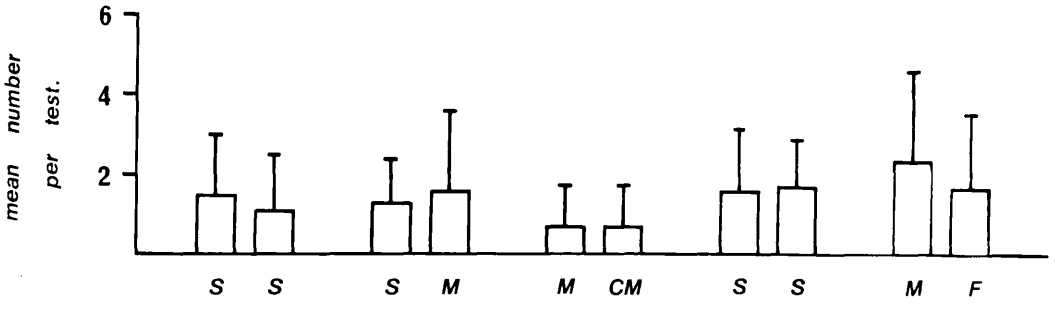


FIGURE 4.4

Series B : The Mean Number per Test of (A) Tail Rubs and (B) Urine-Washes Performed by Breeding Males and Breeding Females

Breeding males urine-washed significantly more in those tests where urine was presented as compared to those tests where saline alone was presented (* = $p < 0.002$: 1 tail).

Breeding Males : ■

Breeding Females : □

S	=	Saline
MU	=	Male Urine
IM	=	Intact Male Urine
CMU	=	Castrate Male Urine
FU	=	Female Urine

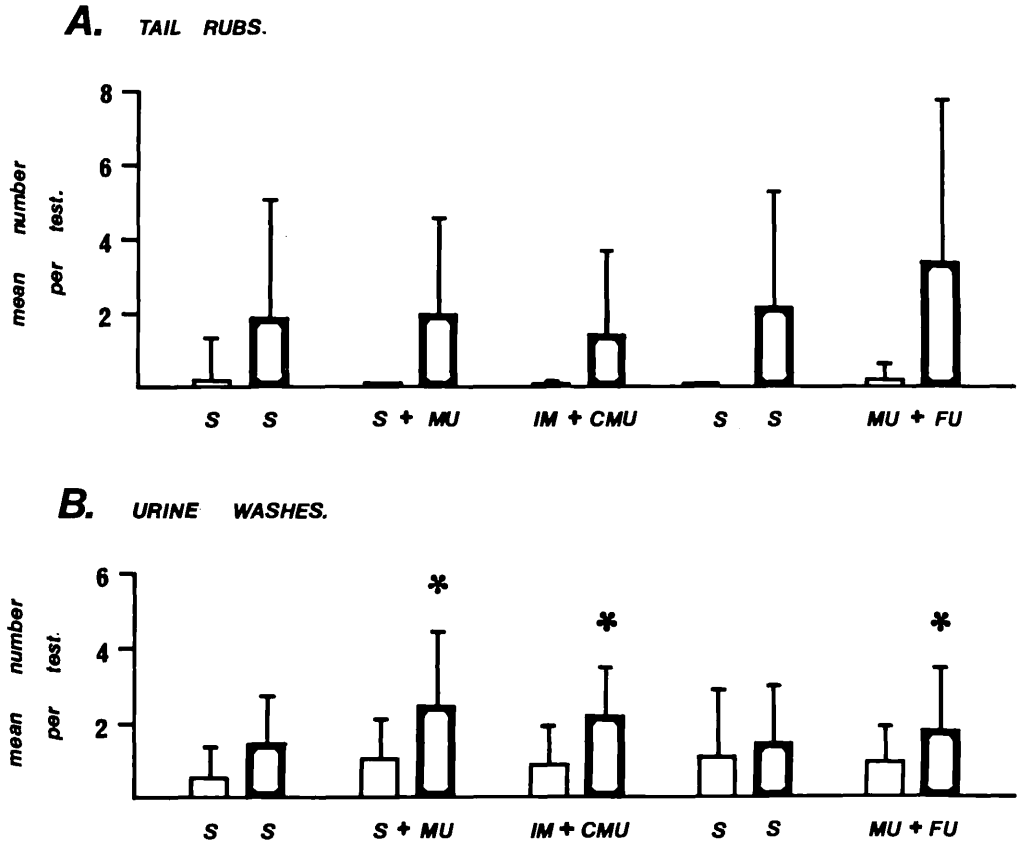

A. TAIL RUBS.
mean number per test.
8
6
4
2
S S
S + MU
IM + CMU
S S
MU + FU
B. URINE WASHES.
mean number per test.
6
4
2
*
*
*
S S
S + MU
IM + CMU
S S
MU + FU

TABLE 4.5

Series B : The Mean Number per Test of (A) Scent-Marking Behaviours and (B) Olfactory Inspections for the 2 Oldest Offspring Present in all 5 Family Groups

(A) Scent-Marking Behaviours		Saline	♂ Urine & Saline	♂ Urine & ♂ Urine	Saline	♂ Urine & ♀ Urine
Oldest Offspring (N = 5)	Urine-Washes	0.05 ± 0.21	0.5 ± 0.7	0.6 ± 0.8	0.2 ± 0.5	0.5 ± 0.7
	Tail Rubs	0	0	0	0	0
Second Oldest Offspring (N = 5)	Urine-Washes	0.2 ± 0.6	0.4 ± 0.7	0.9 ± 0.9	0.1 ± 0.8	0.4 ± 0.6
	Tail Rubs	0	0	0	0	0

(B) Inspections Directed Towards Each Pad	To Saline	To ♂ Urine	To Intact ♂	To Castrate ♂	To ♂	To ♀
Oldest Offspring (N = 5)	2.4 ± 2.3	3.9 ± 3.2	3.5 ± 2.1	2.7 ± 2.1	3.0 ± 2.2	2.8 ± 1.6
Second Oldest Offspring (N = 5)	2.5 ± 1.9	3.5 ± 2.6	3.9 ± 2.6	2.9 ± 1.9	2.3 ± 1.9	2.6 ± 1.3

All scores are expressed as means per test

SERIES C

Adult Pair : In the first discrimination between both male and female subcaudal secretion plus urine, breeding males directed more sniffs towards the pad containing male subcaudal secretion and urine than towards the pad containing female subcaudal secretion plus urine ($Z = 3.04$: $p<0.001$: 1 tail). However, this result was not repeated when the data from the second discrimination between male and female subcaudal secretion plus urine were analysed (Figure 4.5.A). Breeding males also showed no statistically significant difference in the number of sniffs directed towards intact male subcaudal secretion plus urine as compared to the number of sniffs directed towards pads containing castrate male subcaudal secretion and urine (Figure 4.5.A).

Although breeding females showed a tendency to direct more sniffs towards pads containing male subcaudal secretion plus urine than towards pads containing female subcaudal secretion plus urine, this difference was not statistically significant ($Z = 1.39$). In the second discrimination between male and female subcaudal secretion plus urine, as with the males, this result was not repeated, with neither male scent nor female scent eliciting more olfactory investigation than the other. Breeding females also showed little difference in the number of sniffs they directed towards intact male and castrate male subcaudal secretion plus urine (see Figure 4.5.B).

Breeding males urine-washed significantly more in those tests where urine plus subcaudal gland secretion was presented than in those tests where saline alone was presented ($X^2 = 10.14$: $Z = 1.73$; $p = 0.03$: 1 tail). As in the other 2 series of tests (A and B), levels of urine-washing by females were lower overall than those for males (see Figure 4.6.B) and they did not increase significantly in those tests where urine plus subcaudal secretion was presented as compared to those tests where saline alone was presented ($X = 5.34$).

Consideration of the data for tail rubbing reveals some interesting effects. Male 176 was only observed to tail rub once during this series of tests. Levels of tail rubbing for the other 3 males were relatively high, male 6, for example, tail rubbed 33 times in one test and analysis of the data showed that the breeding males performed significantly more tail rubs in those tests where subcaudal secretion and urine was present than in those tests where saline alone was presented ($X^2 = 8.05$: $Z = 2.65$, $p<0.004$: 1 tail and Figure 4.6A). The scent-marking scores for these 4 males for the 5 tests where male and female urine was presented (series B) were compared to the scent marking scores for the first 5 tests where urine and subcaudal secretion from a male and a female were presented (series C). It was felt that a comparison would be meaningful, as both series had been preceded by a saline control period of 5 tests. There was no statistically significant difference between the urine-washing scores in the 2 conditions. There was, however, a statistically significant increase in tail rubbing scores in those tests where urine plus subcaudal secretion was presented as opposed to those tests where urine alone was presented ($Z = 3.14$, $p<0.002$: 2 tail).

Tail rubbing scores for 3 breeding females were low. Female 3 only tail rubbed once, female 2 only twice, and female 15 tail rubbed 7 times. Female 175 presents a slightly different picture; she never tail rubbed during the first block of tests where saline alone was presented, but during the next block of tests, she tail rubbed 9 times, and during the third and fourth blocks, she tail rubbed 20 and 28 times respectively. Her tail rubbing score therefore progressively increased with each block of tests where urine plus subcaudal secretion was presented. It is interesting that this female's partner was male 176, the male who only tail rubbed once in this series of tests. Female 3 on the other hand, who was the female who tail rubbed the least in these tests, was paired with male 9, who performed more tail rubs than any other male during the tests where urine and subcaudal gland were presented. Therefore, it

seems possible that, within the group, social factors may affect the response, in terms of scent marking, to some types of olfactory stimuli. These results are represented graphically in Figure 4.7.

Offspring : In none of the 3 blocks of tests where subcaudal gland secretion and urine were presented did either the oldest or the second oldest offspring sniff one type of scent statistically significantly more than another. The results for the offspring are presented in Table 4.6. There is a slight tendency for more sniffs to be directed towards the pads containing female subcaudal secretion plus urine, rather than to the pads containing male subcaudal secretion plus urine, although the differences are very small.

Levels of urine-washing by both the eldest offspring and the second eldest offspring, did not increase in those tests where urine and subcaudal secretion were present as compared to those tests where saline alone was presented (Table 4.6). The same was also true for tail rubbing, although there were great individual differences in both behaviours. If we consider the eledest offspring first, analysis of the individual data reveals that males WLCP 17 and 18 tail rubbed and urine-washed relatively frequently, although the situation is complicated by the fact that these 2 males were not the oldest offspring present in their groups in the previous 2 series of tests. Their older siblings were removed after series B and therefore, these 2 males who had previously been the second oldest offspring in their groups, were now the oldest offspring present. This was not the case for WLCP 7 and WLCP13, who remained in their groups throughout the course of the experiment. As in the previous 2 series of tests, these 2 males hardly ever scent-marked in series C. Male WLCP 7 only urine-washed in 3 tests and never tail rubbed, whereas male WLCP13 tail rubbed twice but was never observed to urine-wash. As WLCP 7 was the oldest offspring tested it seems unlikely that maturational factors are responsible for the observed individual differences, especially as these differences are consistent across the 3 series of tests.

FIGURE 4.5

Series C : The Mean Number of Inspections per Test Devoted to Each Pad for (A) Breeding Males and (B) Breeding Females

(A) In one block of tests breeding males inspected pads containing male odour more frequently than pads containing female odour (* = $p < 0.001$: 1 tail). However, no other consistent discriminations were shown.

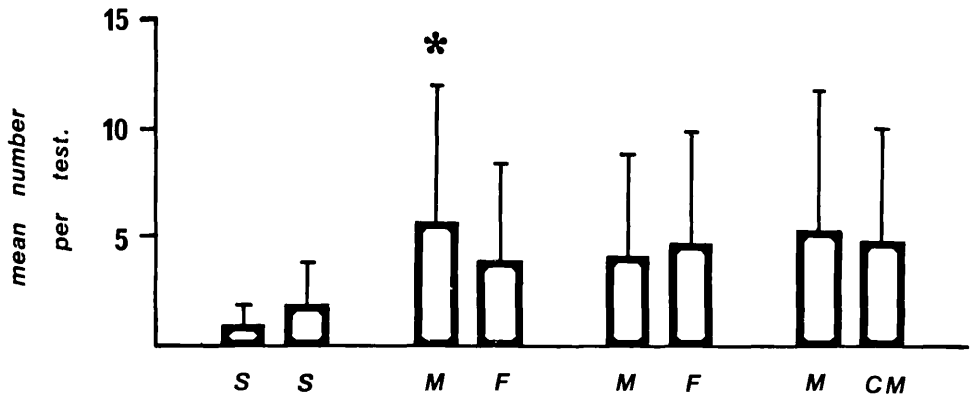
(B) Breeding females did not show any statistically significant preference in any of these comparisons.

Breeding Males : ■

Breeding Females : □

S	=	Saline
M	=	Male subcaudal secretion plus urine
F	=	Female subcaudal secretion plus urine
CM	=	Castrate male subcaudal secretion plus urine

A. *MALES.*



B. *FEMALES.*

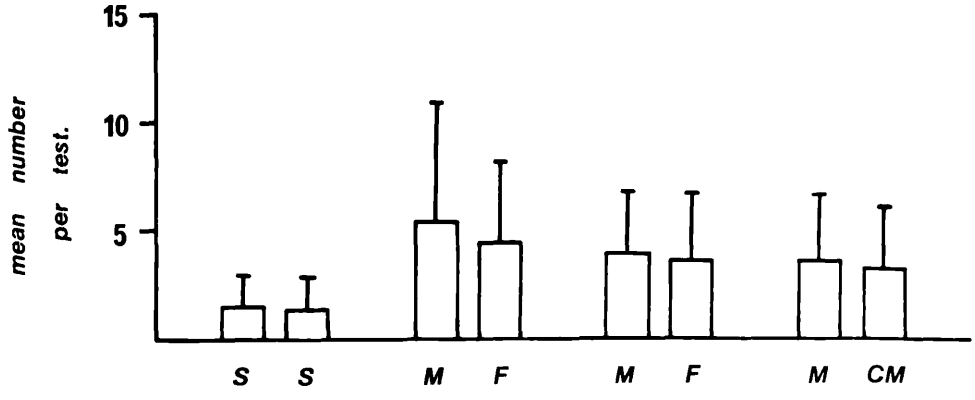


FIGURE 4.6

Series C : The Mean Number per Test of (A) Tail Rubs and (B) Urine-Washes Performed by Breeding Males and Breeding Females

In this series the responses of animals to saline or subcaudal secretion plus urine were examined.

Breeding males urine-washed and tail rubbed significantly less in those tests where saline was present compared to those tests where subcaudal secretion plus urine was present.

* = $p = 0.03$; 1 tail : ** = $p < 0.002$; 1 tail

Breeding Males : ■

Breeding Females : □

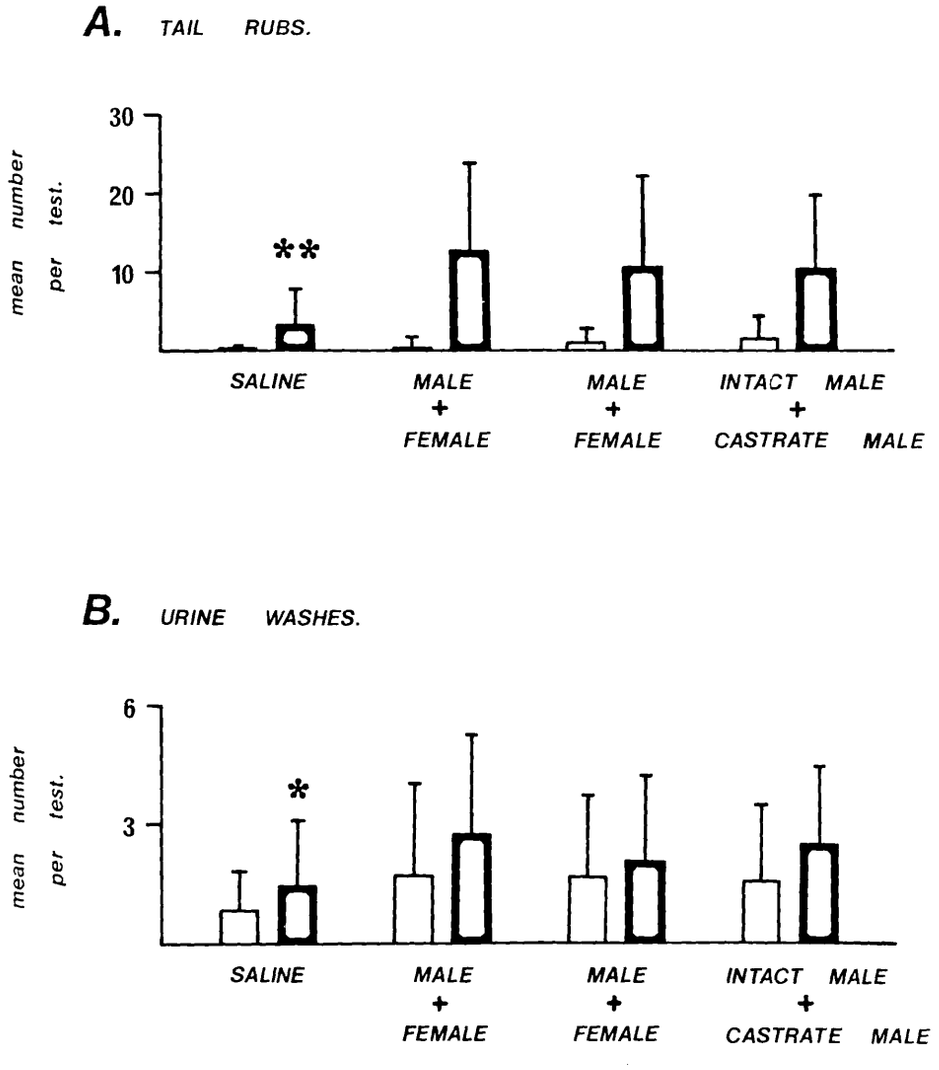

A. TAIL RUBS.
mean number per test.
30
20
10
**
SALINE
MALE + FEMALE
MALE + FEMALE
INTACT MALE + CASTRATE
MALE
B. URINE WASHES.
mean number per test.
6
3
*
SALINE
MALE + FEMALE
MALE + FEMALE
INTACT MALE + CASTRATE
MALE

FIGURE 4.7

The Effect of Social Factors on
Responsiveness to Conspecific Odours

The mean tail rubbing scores per test for the breeding males and females from 2 family groups are shown.

In Group A, where the breeding male showed high levels of tail rubbing to conspecific odours, female responsiveness was low.

In Group B, where the male rarely tail rubbed, the female showed elevated tail rubbing levels when a potent odour source was presented.

Male and Female Urine Presented : ☐

Male and Female Subcaudal Gland Secretion plus Urine Presented : ☐

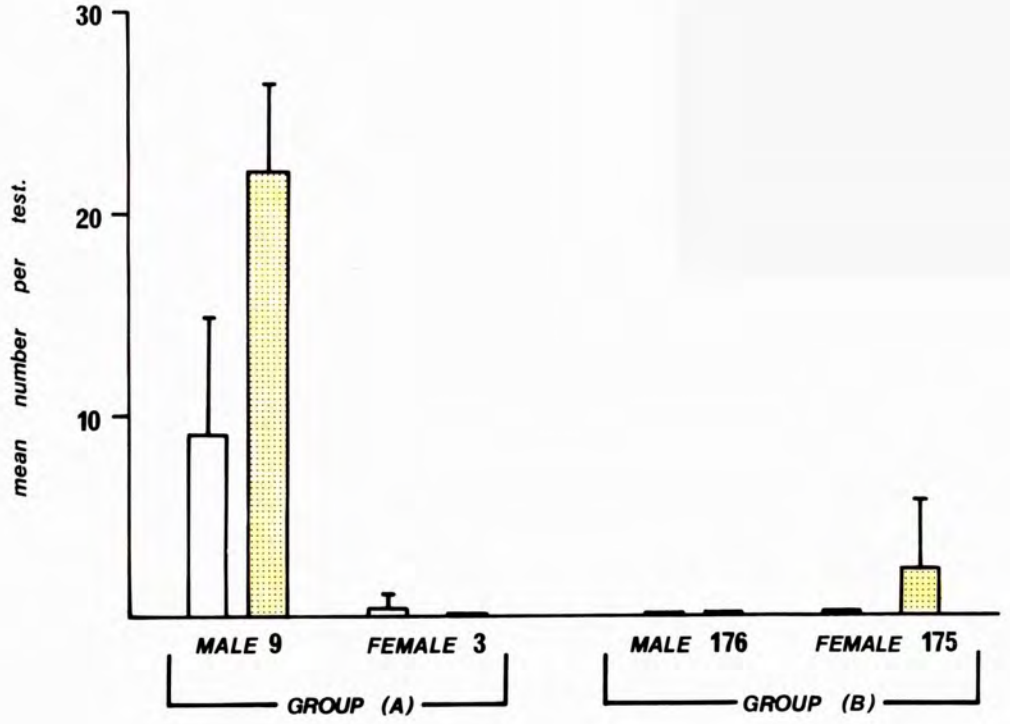

30
20
10
mean number per test.
MALE 9
FEMALE 3
MALE 176
FEMALE 175
GROUP (A)
GROUP (B)

TABLE 4.6

Series C : The Mean Number per Test of (A) Scent-Marking Behaviours and (B) Olfactory Inspections for the 2 Oldest Offspring Present in all 4 Family Groups

(A) Scent Marking Behaviours		Saline	♂ + ♀ TG U	♂ + ♀ TG and U	♂ + ♂ TG and U
Oldest Offspring (N = 4)	Urine-Washes	0.7 ± 1.0	1.3 ± 1.8	0.9 ± 1.2	0.6 ± 1.0
	Tail Rubs	0.5 ± 1.2	0.6 ± 1.1	0.8 ± 1.2	0.5 ± 0.8
Second Oldest Offspring (N = 4)	Urine-Washes	0.9 ± 1.0	0.1 ± 0.3	0.4 ± 0.5	1.0 ± 1.2
	Tail Rubs	0	0.1 ± 0.4	0.3 ± 0.7	0.1 ± 0.4

(B) Inspections Directed Towards Each Pad	To ♂	To ♀	To ♂	To ♀	To Intact ♂	To Castrate ♂
Oldest Offspring (N = 4)	4.2 ± 2.2	5.0 ± 3.3	4.0 ± 2.4	4.2 ± 2.1	2.6 ± 1.3	2.6 ± 1.6
Second Oldest Offspring (N = 4)	3.7 ± 2.3	4.2 ± 2.8	3.0 ± 2.1	3.6 ± 2.3	2.5 ± 1.9	2.6 ± 1.9

Such marked individual variation was not apparent when the scores for the second oldest offspring were considered. Urine-washing levels were comparable with those of the oldest offspring (see Table 4.6), but tail rubbing occurred less frequently. Tail rubbing by the second oldest offspring was only seen in 7 tests, whereas tail rubbing by the oldest offspring occurred in 28 tests.

The Effects of Partial Anosmia on the Responses to Conspecific Odours :

Because only 2 males were tested in this partially anosmic condition, a different way of analysing the results was adopted, and the results will be described in a qualitative, rather than a statistical manner. The scores for each male in the first 2 blocks of tests in series C represented the untreated condition, and those from the 2 blocks of tests when the males were partially anosmic represented the treated condition. The scores were expressed as percentages of the total score, thus if the scores for male 9 for urine-washing in the untreated condition are examined :-
3 urine-washes occurred in the saline tests and 15 occurred in the tests where conspecific odour was presented, expressed as percentages these would be 17% (saline) and 83% (odour).

The results for both males for sniffing, tail rubbing and urine-washing are shown in Figure 4.8. In the untreated condition both males show higher percentages of sniffs, tail rubs and urine-washes in the block of tests where conspecific odour was presented, and from this, one can infer that these animals can discriminate odour from saline. In the treated condition this pattern is not repeated, and the males failed to show any discriminatory response. In male 9's case the frequency of occurrence of all three behaviours actually showed a decrease when odour was presented as compared to the saline control.

Male 9 and male 6 were removed from their groups, tranquillized (10mg Ketamine HCl, 'Vetelar' Parke Davis) and made partially anosmic by the technique described in section 3.2. The position of the plugs was verified by radiography, and then the 2 males were returned to their respective groups and allowed 2 days to recover from the anaesthesia. The protocol for testing these males was the same as that employed for the first 2 blocks of tests in series C, ie, 5 days of saline alone, 2 days rest, 5 days with one pad containing male subcaudal secretion plus urine and the other pad containing female subcaudal secretion plus urine. The rational for this was that if, as actually happened, it was impossible to remove both plugs from each animal, then the results from series C could serve as a meaningful, untreated comparison.

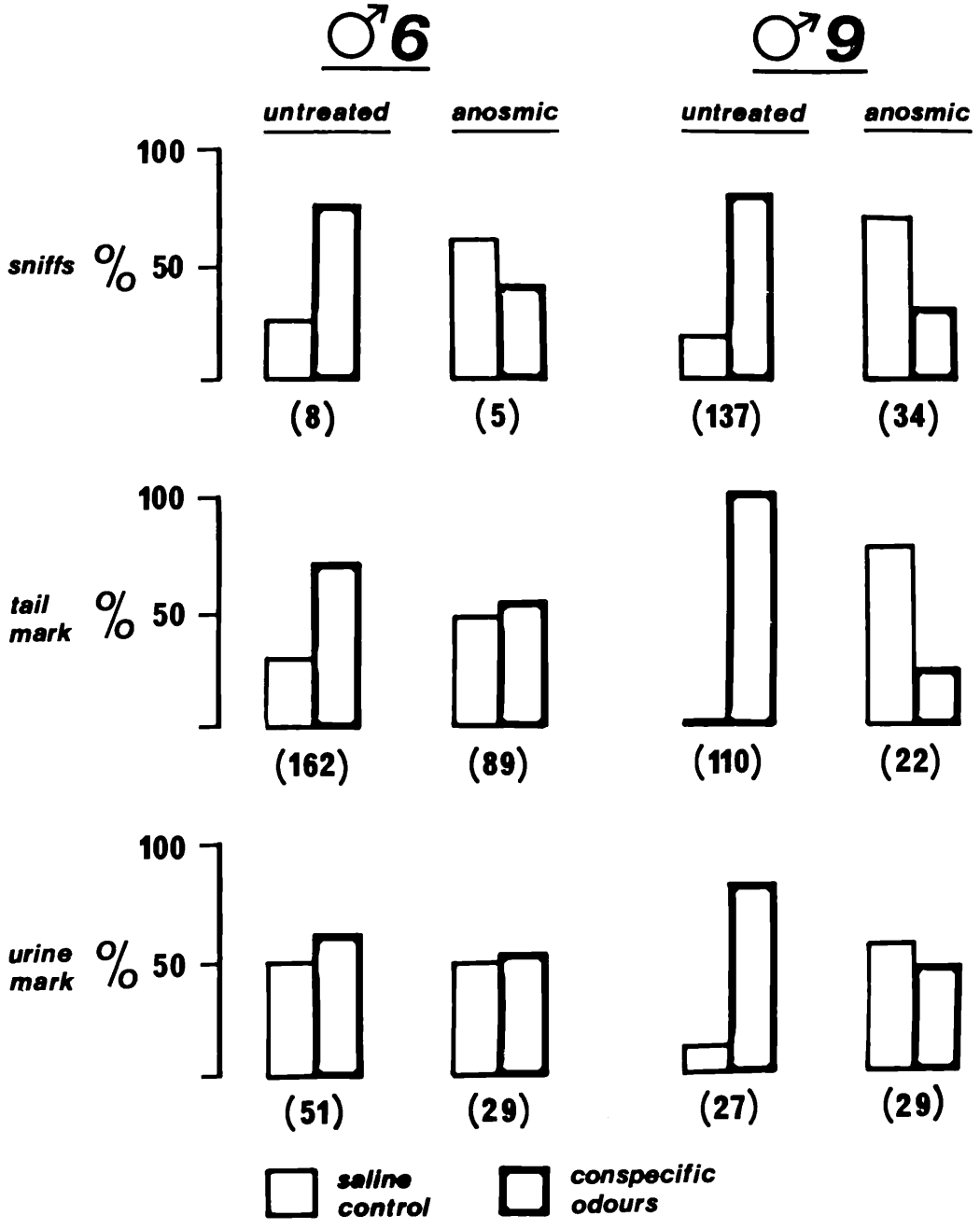
After the last test (subcaudal secretion plus urine) both males were again removed from the group, tranquillized as before and the presence of the plugs verified by radiography. The plugs were then removed, although it was not possible to remove the right plug from male 6.

FIGURE 4.8

Percentage Scores for Two Males Presented with Pads Containing Saline or Conspecific Odours in Both Untreated and Anosmic Conditions

Each score is expressed as a percentage of the total scores in each condition. The numbers in parenthesis are the totals for 5 tests in each condition.

When untreated, both males directed a higher percentage of sniffs towards pads containing conspecific odours (male and female subcaudal secretion plus urine) than towards pads containing saline. This result was reversed when the males were made anosmic.


♂6
♂9
untreated
anosmic
untreated
anosmic
100
sniffs % 50
(8)
(5)
(137)
(34)
100
tail mark % 50
(162)
(89)
(110)
(22)
100
urine mark % 50
(51)
(29)
(27)
(29)
saline control
conspecific odours

4.4 Summary and Conclusions

In general, breeding males respond more to conspecific stimuli than the breeding females or offspring. This was true for both sniffing behaviour and scent-marking. Males also showed great individual variability with respect to these behaviours, and these differences were consistent across the 3 series of tests. The same individual variability was also found in the marking behaviour of the offspring, although levels of scent-marking by offspring were lower than those of breeding adults.

Series A : Breeding males and offspring sniffed pads containing urine more than pads containing saline. Breeding males also tail rubbed and urine-washed more when urine was present than when saline only was present. This was not true for breeding females or offspring.

Series B : Breeding males and oldest offspring sniffed pads containing urine significantly more than pads containing saline in a choice situation. No age-sex class showed a significant preference for male over female urine, or intact over castrate male urine. Breeding males urine-washed significantly more when urine was present than saline alone.

Series C : Breeding males investigated male odour more than female odour in the first block of tests. No age-sex class showed a significant preference for male over female odour in the second block, or for intact over castrate odour. Breeding males urine-washed and tail rubbed more when odour (subcaudal secretion plus urine) was present than when saline alone was present, and this complex odour elicited more tail rubbing than urine alone.

In 2 males partial anosmia abolished the increase in sniffing and scent-marking which occurred when subcaudal secretion was present as compared to saline alone.

CHAPTER FIVE

EXPERIMENT 5 : TO INVESTIGATE THE EFFECT OF FEMALE ODOUR CUES ON ADULT FEMALE AGGRESSIVE BEHAVIOUR

5.1 Aims of the Experiment

To investigate whether chemical cues from one adult female can influence the aggressive response of another adult female, it was decided to place these cues on an immature animal which would normally receive little or no aggression from an adult (Dixson and Fleming, in prep; pers obs). It was hypothesised that adult female scent might contain aggression promoting cues and that if this was the case, then the aggressive response of an adult female towards an immature female treated with adult scent, would be enhanced.

5.2 Materials and Methods

All the females used in this experiment are listed in Table 5.1. Adult female residents were placed in the observation room one week before testing. Caging and observation conditions were the same as described previously (2.2). Infants were removed from their family groups for 2 weeks and placed in the observation room in single cages (102 x 55 x 66cm). Only one resident and one infant were caged in the observation room at any one time and all pairings were between unfamiliar animals.

TABLE 5.1

Resident Females and Infant Females Pair Tested in Experiment 5

Resident (Adult) Female	Infant Female	Condition *
2455	WLCP 23	Control
	WLCP 24	Test solution (♀4364)
4108	WLCP 25	Test solution (♀4537)
	WLCP 29	Control
4537	WLCP 23	Control
	WLCP 25	Test solution (♀4108)
4469	WLCP 29	Test solution (♀TI)

* clinical numbers of the donor females are given in parentheses.

Each infant, except WLCP 25, met one resident in a control condition (infant sprayed with distilled water), and another resident in a treated condition (infant sprayed with scent from another adult female), with one week between tests and the order of testing was balanced. Each resident female met an infant in the control condition and a different infant in the treated condition - except ♀4469 who only met an infant in the treated condition this was due to a lack of suitably aged female infants.

Collection and Application of Odour Sources : The female odour cue used was a mixture of tail gland secretion and urine, which was collected from a female that was unfamiliar to the adult female with which the infant was to be tested. The female donor was tranquillized with 10mg Ketamine

HCl ('Vetelar', Parke Davis). The hairs from half her subcaudal gland were cut as close as possible to the skin and placed in a glass flask. A small piece of gauze was wiped over the shorn area of the gland and this was placed in the flask together with a 24-hour urine sample from the same female. The mixture was left for 4 hours at room temperature ($\pm$ 18°C). It was then filtered to remove the hairs and gauze and the volume of filtrate measured. The filtrate was then placed in a plastic spray gun.

Half an hour before behavioural testing the solution (either odour cue or distilled water) was sprayed finely onto the infant taking care to avoid the eyes. The amount of solution sprayed onto the infant was estimated by measuring the residue left in the spray gun and subtracting this amount from the original volume. The mean amount sprayed was 14.9ml of liquid, although not all of this would necessarily fall directly on to the infant.

The testing procedure was the same as described previously (2.2) using the checksheets designed to score same sex interations (Figure 2.1). All testing took place between 15.00 hours and 16.00 hours and each test lasted 20 minutes apart from one, which was stopped after 2 minutes due to the severity of the adult's attacks on the infant.

5.3 Results

Aggressive Behaviour : Contact aggression was only observed in 2 out of the 7 tests. One incident of contact aggression was observed in the test between ♀2455 and I23 (control) at 13 minutes 19 seconds. ♀2455 pushed I23, dislodging her from the branch on which she had been sitting. I23 immediately returned to ♀2455's side and no further incidents of contact aggression were observed in this test. In the other test where contact aggression occurred, ♀4537 was tested with I23 (treated). In this test, ♀4537 repeatedly chased I23 and attacked her so intensely that the test was terminated after 2 minutes. It was subsequently found that I23 had

TABLE 5.2

Individual Scores for the 4 Adult Females Used in Experiment 5

	Contact Aggression		Arching		Proximity (Mins)		Nose-to-Nose Insp.		Anogenital Inspection		Other Inspections		Number of Approaches		Number of Walk-Aways	
	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U
♀2455	0.01	0	0.01	0	1.50	0	0.40	0.15	0.31	0.01	0.30	0.06	9	12	4	1
♀4108	0	0	0.01	0.43	10.0	0	0.35	0	0.05	0	0.16	0	2	0	16	0
♀4537	0	*0.50	0.15	1.25	0.75	0	0.33	0	0	0	0.11	0	8	7	8	0
♀4467	-	0	-	0	-	13.0	-	0.3	-	0.05	-	0.11	-	0	-	3
Mean Score	0.003	0.12	0.05	0.42	4.08	3.25	0.36	0.11	0.12	0.01	0.19	0.04	6.33	4.75	9.33	1.0
SD	0.004	0.21	0.06	0.51	4.19	5.62	0.02	0.12	0.13	0.02	0.08	0.04	3.09	5.06	4.98	1.22

All scores are expressed as frequencies per 15 seconds unless otherwise stated.

* indicates that this test was stopped after 2 minutes.

H_2O = control condition
TG+U = treated condition

TABLE 5.3

Individual Scores for the 4 Female Infants Used in Experiment 5

	Contact Aggression		Arching		Anogenital Inspections		Other Inspections		Number of Approaches		Number of Walk-Aways	
	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U	H_2O	TG+U
I ♀23	0	*0	0	0	0.01	0	0.03	0	39	0	39	8
I ♀24	-	0	-	0	-	0	-	0	-	3	-	13
I ♀25	0	0	0	0	0	0	0	0	1	0	2	0
I ♀29	0	0	0.03	0.10	0.06	0.01	0.01	0.01	17	4	0	0
Mean Score	0	0	0.01	0.02	0.02	0.002	0.01	0.002	19	1.75	13.66	5.25
SD	0	0	0.01	0.04	0.02	0.004	0.01	0.004	15.5	1.78	17.93	5.53

All scores are expressed as frequencies per 15 seconds unless otherwise stated.

* indicates that this test was stopped after 2 minutes.

H_2O = control condition
TG+U = treated condition

been severely bitten on the tail. Contact aggression was initiated after 17 seconds of the test had passed, although chasing of the infant by the female started almost instantly. This female, ♀4537, did not show any contact aggression when tested with an infant in the control condition.

No consistent effects were observed on arching behaviour, but in 2 individual cases (♀4537 and ♀4108) frequencies of arching were considerably higher for these females when they were tested with an infant in the treated condition, than when they were tested with an infant in the control condition (♀4537 : arching frequencies were 1.25/15 seconds (treated infant) versus 0.15/15 seconds (control infant); ♀4108 : arching frequencies were 0.43/15 seconds versus 0.01/15 seconds respectively). The higher frequency of arching by female 4108 was also accompanied by strong piloerection and vocalizations ('whup-whups' and 'clicks') and female 4108 spent the whole test on the upper branches whilst I25 crouched on the cage floor.

Female 4537's arching behaviour was interesting - when tested with an infant in the control condition she initially arched frequently, (frequency of arching before nose-to-nose inspections had occurred 2.0/15 seconds). Once nose-to-nose inspections had occurred, 4537 arched infrequently and paid little attention to the infant (frequency of arching after nose-to-nose inspections had occurred 0.06/15 seconds). The infant spent much of the time on the cage floor, but she did not adopt a typically 'submissive' crouching posture or vocalize and she appeared to pay little attention to female 4537.

Female 2455 only arched once, and this occurred just before the incident of contact aggression with I23 as described above. Neither female 2455 nor female 4469 arched when tested with an infant treated with subcaudal secretion and urine. Contact aggression by infant females towards their adult female partners was never observed, and only one infant, I29, showed any arching behaviour (see Table 5.3).

Olfactory Inspections and Scent Marking Behaviours : Tail rubbing by either infant or adult was never observed. Urine-washing was only observed in one test, where female 4537 urine-washed once when tested with I25 (control condition).

In 2 tests, no olfactory inspections of any kind occurred (♀4108 with I25 (treated) and ♀4537 with I23 (treated)).

Levels of anogenital inspections by adult females were generally low, except for female 2455, when she was tested with I23 (see Table 5.2).

Consideration of the results for the 3 adult females who were tested with infants in both experimental conditions (♀2455, ♀4108, ♀4537) revealed that the frequency of nose-to-nose inspections was greater in tests with a control- treated infant partner, than in tests where these females were paired with an infant treated with conspecific scent (mean frequency of nose-to-nose inspections = 0.36 ± 0.02/15 seconds (control) versus 0.05 ± 0.07/15 seconds (treated)). Inspections directed towards other body areas by adult females were also greater when the female was tested with an infant treated with water (mean = 0.19 ± 0.08/15 seconds) than when they were tested with an infant treated with conspecific scent (mean = 0.02 ± 0.02/15 seconds). In one test, the infant (I24 - treated with conspecific scent) avoided any approach or inspection by the adult female, female 2455. This female would often proceed to inspect the area that the female infant had just vacated, a behaviour that had not been seen in this female's previous test with an infant in the control condition.

Levels of olfactory inspection by infants were too low for any further analysis to be meaningful (see Table 5.3).

Allogrooming and Proximity : Adult females were never observed to groom their infant female partners. In one test infant 23 groomed female 2455 briefly, after approaching female 2455 and touching muzzles with her. Grooming occurred before the one incident of contact aggression described above in this test was recorded. No other grooming of adult females by infants was seen.

For the 3 females who were tested with infants in both experimental conditions, proximity scores were higher when they were paired with infants in the control condition (mean = 4.08 $\pm$ 4.19 minutes) than when they were tested with infants treated with conspecific scent (mean = 0 minutes). Female 4469, who was only tested with an infant in the scent-treated condition, spent 13 minutes in close proximity with the infant (see Table 5.2), although the infant (129) was responsible for the maintenance of close proximity, ie, during the test the infant performed all the approaches, while the adult female was responsible for all the 'walk-aways'. From the results in Tables 5.2 and 5.3 it does appear that whether the adult or the infant is responsible for the maintenance of close proximity depends on the individuals involved, rather than on the test condition.

5.4 Summary and Conclusions

The experiment examined the effects of treating juvenile females with urine and subcaudal gland secretions from adult females upon behavioural interactions with adult female partners. A brief incident of contact aggression was observed in one test in the control condition. Contact aggression also occurred in one test in the treated condition, the attacks being so severe that the test was stopped after 2 minutes. This female did not attack an infant in the control condition. Arching behaviour by adults did not differ consistently between the 2 conditions and only one infant showed any arching behaviour. Scent marking was only observed once.

Levels of olfactory inspections by adults and proximity scores were generally higher when the adults were tested with an infant in the control condition, as compared to tests in the treated condition, although the numbers used were too small to be meaningfully analysed.

To conclude, it appears that in one case only did the presence of adult

female odour cues lead to an increase in the aggressive response. Treatment of the infant with adult female subcaudal secretion and urine also tended to lead to a decrease in proximity and the frequency of adult olfactory inspections.

CHAPTER SIX

The Structure of the Vomeronasal Organ and Nasopalatine Ducts in Aotus and Some Other Primates

6.1 Aims : To verify the existence of a vomeronasal organ and patent nasopalatine ducts in the owl monkey and several other primate species.

6.2 Materials and Methods : The palate and rhinarium of one specimen of each of the following species were examined externally:-

Aotus trivirgatus griseimembra; A.t.bolivensis; Saguinus fuscicollis; Callithrix jacchus and Ateles geoffroyi;

All specimens examined were from adult animals.
Histological studies were carried out on a total of 5 owl monkeys - one specimen from each of the following primate species was also examined for comparative purposes:-

Saguinus fuscicollis; Ateles geoffroyi and Arctocebus calabarensis (angwantibo).

Specimens had been preserved in 10% buffered formol saline. From each head the frontal portion of the upper jaw, anterior to the orbits was removed, including the palate and the nasal fossa as far as the cribiform plate. Attached skin and muscle tissue was removed, apart from the skin around the upper lip, which was left untouched. The canines were cut away as much as possible to enable decalcification to proceed quickly. Sections were then decalcified for periods of between 3 and 5 months, depending on the weight of the tissue. The decalcifying solution is described in Appendix 2.2. Initially, each piece of tissue was X-rayed and weighed so that the progress of

decalcification could be followed. When radiography and the rate of weight loss indicated that decalcification was well advanced, the tissue was cut down into smaller pieces for embedding. A double embedding technique was used, and this and the mounting medium for sections are described in Appendix 2.3. 10μ or 15μ sample sections were obtained, depending on the ease of sectioning, for, in some places, the tissue remained hard, eg, at the roots of the canines. At the cut faces hard tissue was softened using Baker's solution (Appendix 2.4).

Specimens were either stained with a trichromate stain, Martius-Scarlet - Blue (MSB) or with Luxol Fast Blue - Cresyl Fast Violet stain (LFB - CV). The formulae for these stains are given in Appendix 2.5. and Appendix 2.6.

For one owl monkey, the vomeronasal organ and its associated cartilages were dissected out. They were then embedded, mounted and sectioned in the same way as described above.

6.3 Results

External Examinations : The rhinarium was smooth in all specimens examined, there being no median cleft or furrow present as in the Strepsrrhine condition. However, in the specimen of C. jacchus examined, a short, median and distinctly narrow furrow was found in the external surface of the upper lip (arrowed in Plate 6.1). The furrow does not split the upper lip as it disappears when it reaches the glaborous margin of the upper lip. Therefore, no furrow, or sulcus, exists to join the rhinarium to the sulcus papillae palatinae, as exists for the prosimian primates (pers. obs.; Hoffer 1977; Schilling 1970). The upper lip in all the specimens examined was not tethered to the gum, as it is in the Prosimian primates and thereby the upper lip in these species examined appears to be free to be fully involved in facial expression.

The structure of the palatine ridges in the primates is reviewed by Schultz (1949) and none of the specimens examined showed any significant variation from the results he described. On, or just above, the first palatal ridge, a pair of incisive ducts or foramen, open into the oral cavity (Plate 6.1). The shape of these ducts differs between species but appears to be fairly constant between individuals. In the 2 subspecies of Aotus, the separation of the foramen was approximately the same, although their shape was slightly different. The papilla palatina were also similar in structure. The openings of the ducts were approximately 3mm apart in the specimen of Ateles that was examined, and they appeared more elongated and slit than those of the other species examined. The papilla palatina of the C.jacchus were very distinctive, overhanging the incisive openings slightly (see Plate 6.1D).

Histological Examinations

Aotus :

Transverse sections were taken from 2 animals. The papilla palatina do not have any specialized cartilage associated with them, as has been previously reported for some other species (Whorrmann-Reppening 1978). In these frontal sections the lamina transversalis anterior is well-developed and joins, but does not fuse with, the septum nasi. The nasopalatine ducts are kidney shaped in T.S. and are curved outwards. The ducts are patent, ie, they join the nasal and oral cavities with no occlusion along their length. However, they do not appear to travel directly upwards towards the nasal cavity, but at first bend backwards slightly, and then they run upwards to join the nasal cavity. The ductus vomeronasalis joins the nasopalatine canal just below its point of fusion with the nasal cavity (see Plate 6.3). The ductus vomeronasalis is very short and it connects the vomeronasal organ with

PLATE 6.I

The Palatal Opening of the Nasopalatine Ducts in Aotus, Saguinus, Callithrix and Ateles.

A = Aotus trivirgatus

B = Ateles geoffroyi

C = Saguinus fuscicollis

D = Callithrix jacchus

Each picture is not photographed to the same scale.

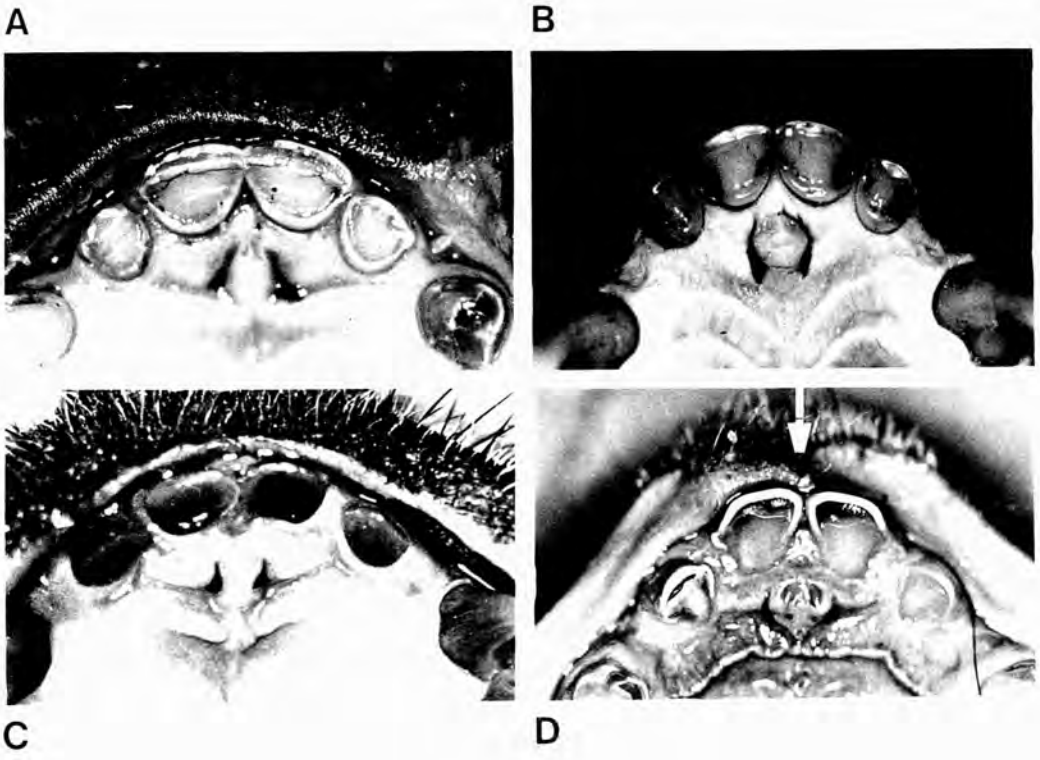

A
B
C
D

PLATE 6.2

The Vomeronasal Organ of the Owl Monkey and its Associated Cartilage

This plate shows a saggital section of an Aotus vomeronasal organ which was dissected out from the animal with its associated cartilage prior to sectioning.

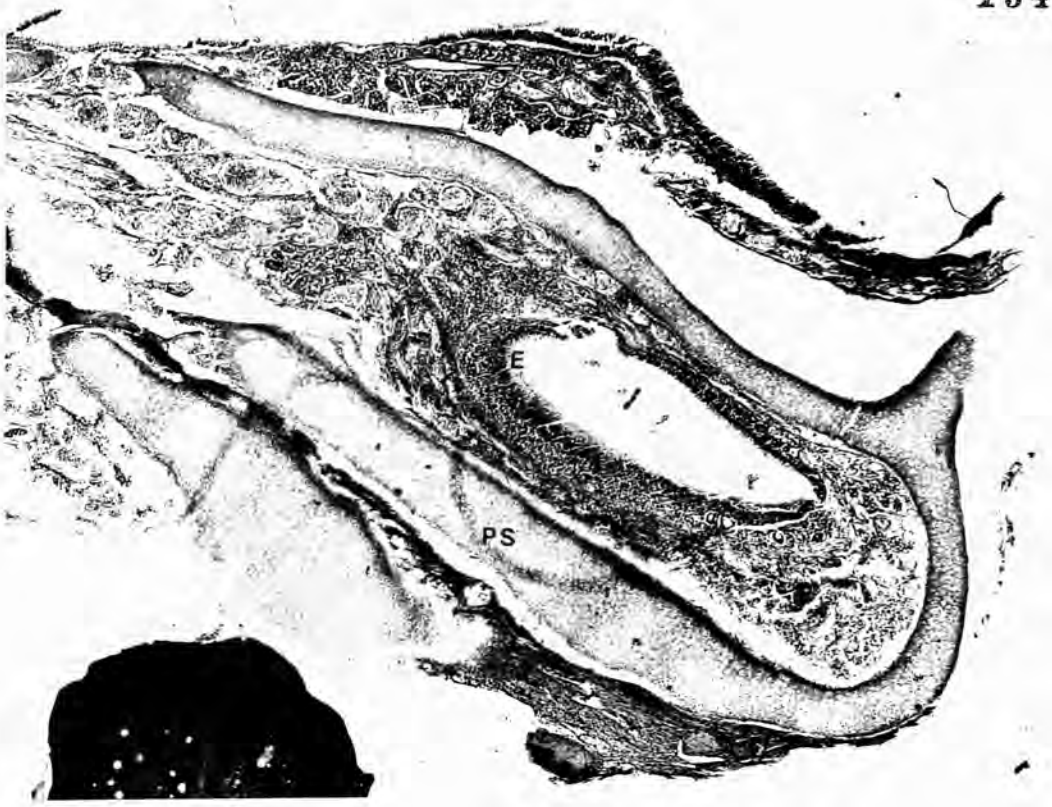
E	=	Vomeronasal epithelium
PS	=	Paraseptal cartilage

PLATE 6.3

Fusion of the Vomeronasal Duct and Nasopalatine Duct in Aotus

On the left side of the picture the organ is separated from the nasopalatine duct, which has opened into the nasal cavity. On the right side of the picture the vomeronasal duct joins the vomeronasal organ and the nasopalatine duct, and the latter is about to open into the nasal cavity.

S	=	Septum
N	=	Nasal Cavity
NPD	=	Nasopalatine duct
V	=	Vomeronasal organ
DV	=	Vomeronasal duct


E
PS

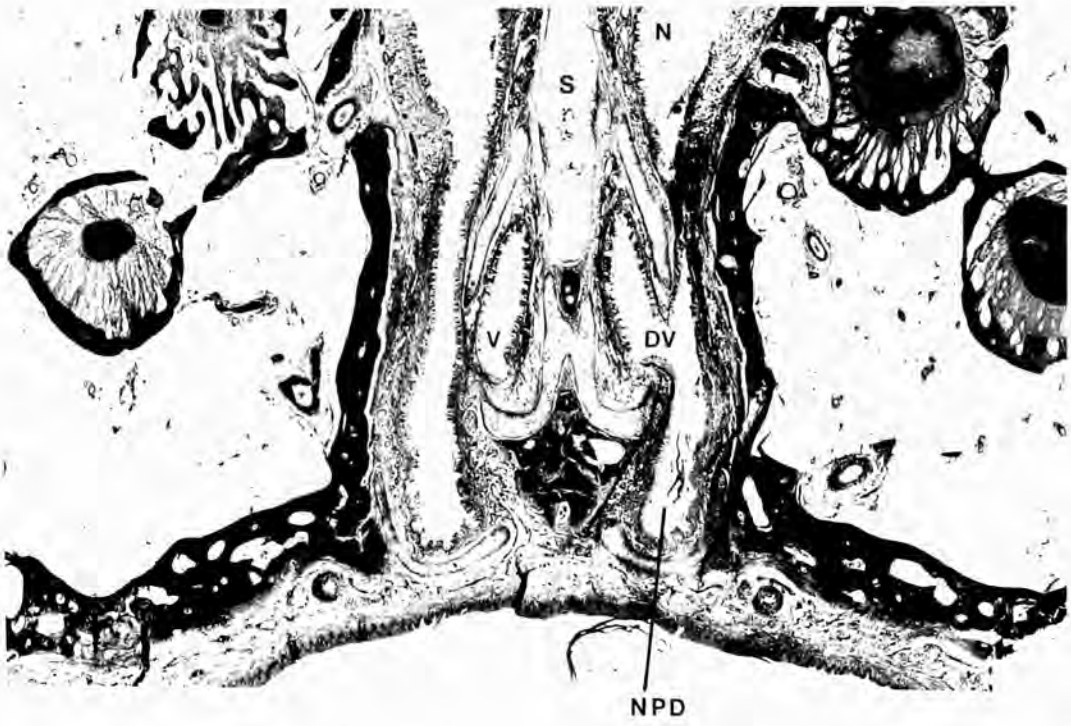

N
S
V
DV
NPD

PLATE 6.4

A Longitudinal Section of the Vomeronasal Organ in Aotus

The tissue is stained with MSB stain.

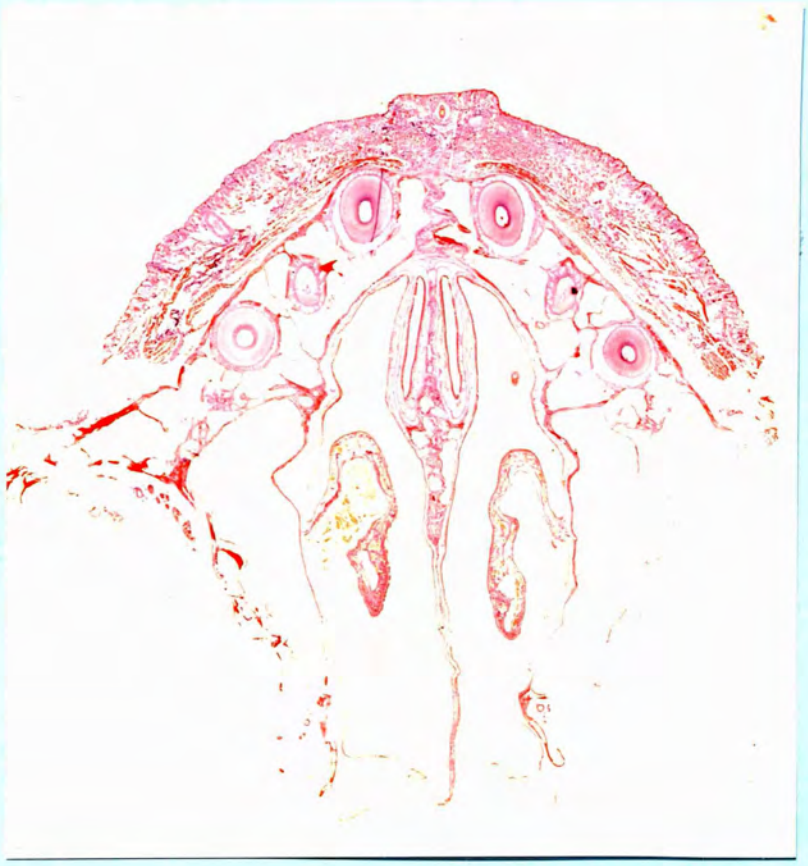


PLATE 6.5

Transverse Sections of the Vomeronasal Organs of Aotus, Saguinus and Ateles

A. Aotus trivirgatus

This section lies posterior to the entry of the nasopalatine ducts into the nasal cavity.

B. Saguinus fuscicollis

The organ is essentially similar in structure to that of Aotus, although in T.S. it has a more rounded appearance.

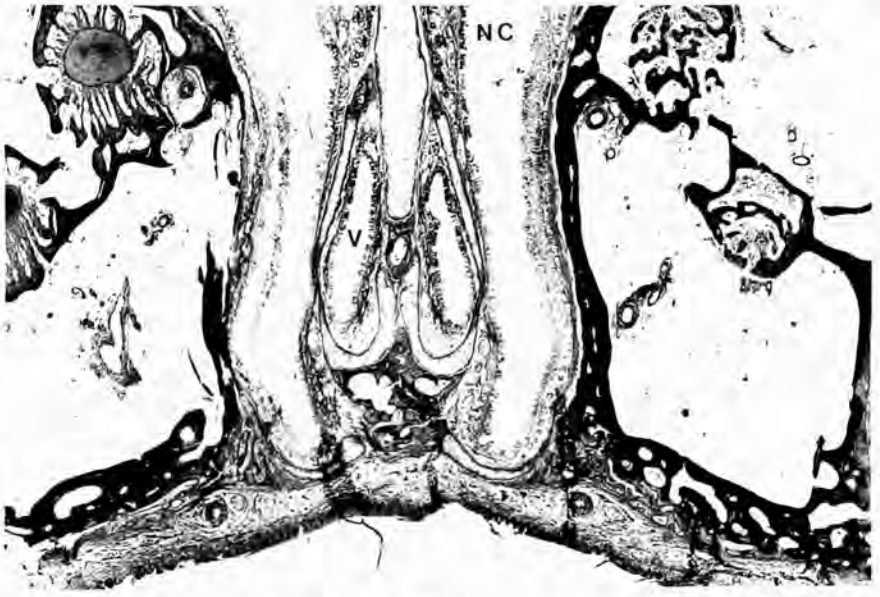
C. Ateles geoffroyi

The organ is extremely small in T.S. and appears to be essentially a lumen with no specialized epithelial lining.

In all 3 sections the paraseptal cartilage encapsulating the organ can clearly be seen.

NC = Nasal cavity
V = Lumen of the vomeronasal organ

A



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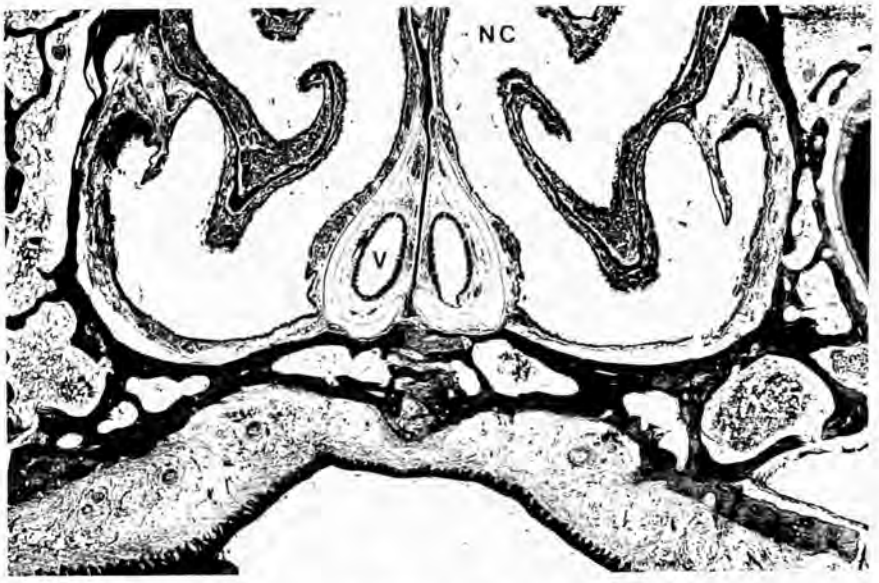
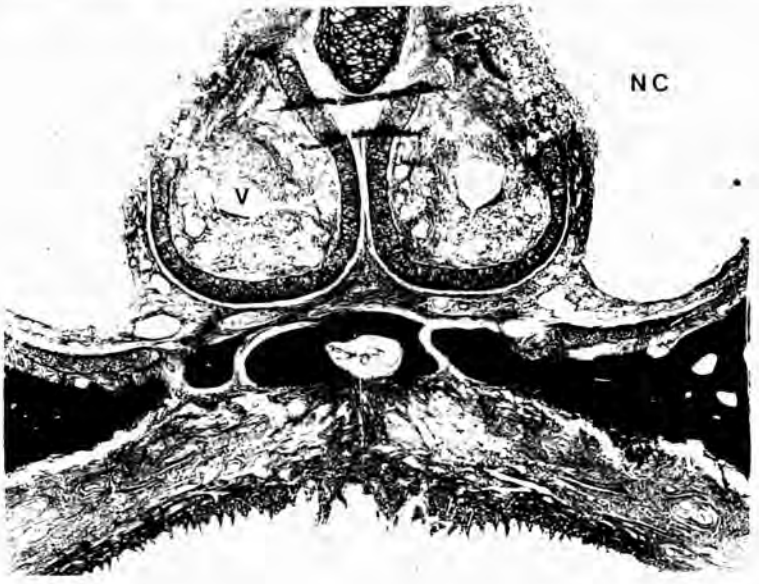


C



the nasopalatine canal, thereby allowing access to both oral and nasal cavities. The vomeronasal organ lies just beside the margin of the setum nasi and at the base of the nasal cavity. It is almost completely enclosed by cartilage - the paraseptal (or vomeronasal) cartilage. In Plate 6.3 the 2 anterior paraseptal cartilages are fused together ventrally whilst the dorsal segments are separate and neither cartilage is joined to the septum nasi. The ductus vomeronasalis passes between these 2 parts of the paraseptal cartilage on either side. These dorsal and ventral cartilages eventually fuse so that the organ is almost completely encased in cartilage. In Plate 6.3 a large vein is visible just below the septum and the organ itself is well vascularized. The premaxillary bone and the cartilago palatina are also visible in this Plate.

The organ is oval in shape in cross-section, and decreases in size at the posterior end. The paraseptal cartilage also begins to disappear, although it terminates a little way beyond the posterior margin of the vomeronasal organ. The vomer bone also becomes visible towards the posterior region of the vomeronasal organ, approaching the paraseptal cartilage but not joining it.

A longitudinal section through the organ is shown in Plate 6.4. Two owl monkey nasal regions were sectioned in this way. In these sections a small amount of cartilage was associated with the nasopalatine canals and alar cartilage in the anterior nasal region was also visible. The nasopalatine canals appear roughly triangular in shape and the paraseptal cartilage gradually appears at the apex of the duct. Soon after the appearance of the cartilage in the ductus vomeronasalis joins the nasopalatine duct. The vomeronasal organ can clearly be seen to be almost completely surrounded by cartilage (Plate 6.4). Blood vessels are visible (the corpuscles are stained yellow by MSB stain) and what appears to be nervous tissue lies between the organ and the cartilage. Attempts were made to

selective stain the nervous tissue by staining with Luxol Fast Blue and Cresyl Fast Violet. However, no additional information was obtained.

The organ itself is cigar-shaped and its size appears to vary considerably between individuals - the mean lengths for 3 animals were approximately 3.3mm, 3.3mm and 1.7mm, and the respective widths were 0.33mm, 0.28mm and 0.25mm. The animal with the smallest vomeronasal organ was a female who had apparently died of old age. The other 2 organs measured were from an adult male and an adult female. All measurements were made on the right organ in each animal, although the left organ never showed any significant difference in size from the right. To clarify the situation further measurements were taken of the organs from 2 more female owl monkeys. In these 2 specimens the organs were much shorter in length being 1.6mm and 2.0mm approximately. Unfortunately, there were no more specimens from males available for examination to investigate the possibility that sex differences existed in the size of the organ.

No sections were prepared for electron microscopy but examination of the vomeronasal epithelium revealed that it was similar in appearance to the sensory epithelium found in the nasal cavity. The epithelium was columnar but it was more closely packed and elongated than the mucais epithelium lining the nasopalatine ducts. A detailed examination of the sensory epithelium was not possible as the sections taken were too thick. Therefore, the exact structure of the vomeronasal epithelium Aotus awaits further investigation.

Other Species Examined :

In all the species examined (Arctocebus; Saguinus and Ateles) the nasopalatine ducts were patent. In Saguinus and Arctocebus the structure of the vomeronasal organ and associated cartilages was similar to that found in Aotus (see Plate 6.5). In both species the

vomeronasal duct joined the nasopalatine just below its point of fusion with the nasal cavity. An extremely elaborate turbinate system is present in Arctocebus compared to the other New World primates examined. As only transverse sections were taken no accurate measurement of length could be obtained. The width of the organ in Saguinus was 0.33mm which is equivalent to that of the owl monkey, although if body size and weight is taken into account, the width of the organ is relatively greater in Saguinus. The width of the organ at its widest point in the one male specimen Ateles examined was 0.66mm. The organ was partially surrounded by paraseptal cartilage along its length (see Plate 6.5). The epithelium lining the organ is similar in appearance to that found lining the nasopalatine ducts and appeared less thick and close-packed than that found in the 3 other species examined.

6.4 Summary and Conclusions

Incisive papillae and patent nasopalatine ducts were found in all species examined. The structure of the vomeronasal organ was essentially similar in Aotus, Saguinus and Arctocebus, although it differed somewhat from that in Ateles.

CHAPTER SEVEN

THE STRUCTURE OF THE SUBCAUDAL AND STERNAL GLANDS IN AOTUS

7.1 Subcaudal Gland Measurements

The subcaudal gland was measured externally in live animals and histologically in preserved specimens to quantify the size and structural components of the gland. The possibility of sex differences in these 2 parameters was investigated.

7.1.1. Materials and Methods

External measurements were taken from 24 Columbian Aotus - 10 intact males, 3 (post-pubertally) castrated males and 11 intact females. Four Bolivian animals were also examined - 2 intact males and 2 intact females (see Table 7.1). The width and length of the gland were measured with calipers fitted with a vernier scale. Each measurement was repeated 3 times and a mean was calculated. The animal's weight was also noted, together with a brief description of the gland. The gland can also be distinguished by virtue of its thick specialised hairs (see Plate 7.1) and the secretion from this gland is often visible on branches in the cage.

Histological measurements were made on sections taken from 8 adult males and 7 adult females (see Table 7.2). One juvenile male was also examined (aged 5 months). Tissue was removed from the proximal end of the gland and 2 samples were taken from each animal. In one female, samples were taken from the whole length of the gland to see if the density of glandular tissue varied with position along the gland. Tissues were fixed in 10% buffered formol saline and later dehydrated, embedded and sectioned at 10 μm. Sample sections were then mounted

PLATE 7.1

(A) Scent Marked Branch from an Owl Monkey Cage

This was taken from a cage containing a single owl monkey. The dark, sticky mark consists of subcaudal secretion deposited during tail rubbing. On the right-hand side of the picture, one can see that hairs have become attached to the secretion on the branch.

(B) The Subcaudal Gland of an Adult Male Owl Monkey

The hairs in this region are darker and thicker than hairs elsewhere on the tail. Secretions and excretions accumulate on these glandular hairs.

A

B

TABLE 7.1

A List of the Male and Female Owl Monkeys Whose Subcaudal and Sternal Glands were Examined Externally, Together with the Measurements Taken.

	Weight gms	Mean Length mm	Mean Width mm
INTACT MALES			
Columbian			
WLCP7	1,130	640.6 ± 32.5	145.6 ± 3.2
9T	1,016	518.9 ± 35.1	134.3 ± 8.1
* 176	1,062	783.3 ± 13.8	164.6 ± 2.0
192	1,031	643.3 ± 15.6	124.9 ± 19.0
* 4107	1,010	725.3 ± 20.0	247.6 ± 2.0
* 4367	1,016	800.6 ± 15.0	106.6 ± 5.8
4371	1,116	729.6 ± 14.5	138.3 ± 18.9
* 4373	860	637.6 ± 16.2	143.9 ± 12.1
* 4451	950	535.9 ± 13.8	155.6 ± 7.7
* Foster	not weighed	551.6 ± 12.5	123.9 ± 11.5
Bolivian			
* 4928	980	536.3 ± 10.2	144.0 ± 3.2
* 4937	1,020	364.6 ± 4.1	87.3 ± 5.7
Mean	1017.3± 74.0	622.3 ± 127.1	143.0 ± 39.0
CASTRATE MALES			
Columbian			
4287	854	860.9 ± 14.9	100.0 ± 16.3
4368	1,046	707.3 ± 13.0	103.3 ± 17.5
4369	978	583.3 ± 23.6	128.3 ± 16.5
Mean	959.3 ± 97.3	717.1 ± 139.0	110.5 ± 15.4

* known breeder

Measurements were taken of the length and width of the subcaudal gland. All animals measured were adults.

TABLE 7.1 : continued

	Weight gms	Mean Length mm	Mean Width mm
INTACT FEMALES			
Columbian			
WLCP9	1,226	229.3 ± 20.5	104.0 ± 3.2
WLCP8	898	354.0 ± 14.7	87.1 ± 0.8
81	1,022	804.3 ± 6.6	108.6 ± 7.5
82	902	378.3 ± 17.1	131.6 ± 3.2
83	908	468.6 ± 9.4	208.3 ± 12.4
84	804	521.6 ± 26.0	91.3 ± 3.2
* IT	1,020	692.6 ± 10.9	109.0 ± 12.1
* 175	1,148	550.6 ± 24.1	78.3 ± 2.8
188	902	523.6 ± 22.8	123.0 ± 4.1
4469	1,022	478.3 ± 13.2	153.6 ± 16.4
4537	1,024	819.0 ± 11.9	158.6 ± 16.4
Bolivian			
* 4931	1,259	373.0 ± 4.1	100.0 ± 8.1
* 4939	1,359	411.0 ± 21.2	73.0 ± 2.4
Mean	1038.0 ± 165.4	508.0 ± 175.9	117.4 ± 37.8

* known breeder

Measurements were taken of the length and width of the subcaudal gland. All animals measured were adults.

with egg albumen on glass slides and stained with haematoxylin and eosin. These sections were examined by light microscopy and the sections that contained the best developed tissue from each animal were used for further measurements.

TABLE 7.2

Relevant Information Concerning the 16 Deceased Animals Whose Subcaudal Glands were Examined Histologically

Assigned Number	Subspecies	Age at Death	Cause of Death
FEMALES			
1	Columbian	10yrs 4 months	Haemorrhaging after birth.
2	Columbian	Adult	Paralysis of legs
3	Columbian	Adult	Unknown
4	Columbian	Adult	Senility
5	Columbian	Adult	Unknown
6	Bolivian	Adult	Euthanized *
7	Bolivian	Adult	Euthanized *
MALES			
8	Columbian	Adult	Died under routine anaesthesia.
9	Columbian	Adult	Unknown
10	Columbian	Adult	Unknown
11	Columbian	Adult	Unknown
12	Columbian	Adult	Unknown
13	Columbian	2 yrs (adult)	Unknown
14	Columbian	5 months	Leg injury
15	Bolivian	Adult	Euthanized *
16	Bolivian	Adult	Euthanized *

* these were healthy animals euthanized by Dr Zeki U.C. London, after experiments on the visual cortex.

In cases where the cause of death is unknown routine examination had revealed no superficial detriments in the reproductive and endocrine systems of these animals.

The depth of sebaceous tissue was measured using an eyepiece micrometer and 20 readings were taken along each section. This method had previously been used elsewhere to demonstrate a difference in the size of the sternal gland in the greater galago, Galago crassicaudatus (Dixson 1980). The sections were next examined with an image analyser ("Optomax", Micromeasurements Limited). This allowed the measurement of the area of secretory tissue in each section within a frame of known dimensions and several scans were taken to determine accurately the area of sebaceous and apocrine tissue within a given frame size. (The use of the image analyser and its reliability are described in Appendix 2.7). The resulting values in picture points were transformed into square millimeters and analysed statistically by means of unrelated t-tests. The external measurements were analysed by means of a Spearman Rank Correlation and unrelated t-tests.

7.1.2 Results

(A) External Measurements

Table 7.1 shows the data obtained from 28 animals. A Spearman Rank correlation was first performed to see if the size of the subcaudal gland was proportional to body weight. Neither the length of the gland ($r_s = -0.06$) nor the maximum width ($r_s = -0.33$) were significantly correlated with body weight, although the rs for width approached statistical significance, ie, there was a tendency for smaller maximum width to be correlated with greater body weight. In view of this, it was not felt necessary to correct for body weight when comparing individual measurements. Considering the means for all intact males and females, it transpires that the means are lower for females for both length (mean = 508.0 $\pm$ 175.9mm compared to mean = 622.3 $\pm$ 127.1mm) and width (mean = 117.4 $\pm$ 37.8mm compared to mean = 143 $\pm$ 39.0mm). Consideration of the Bolivian and Columbian animals separately reveals that there is no apparent sex difference in the 4 Bolivian animals examined in either width or length. Columbian females generally, had shorter and narrower subcaudal glands than males (mean length = 529.1 $\pm$ 183.3mm (females) versus 656.1 $\pm$ 96.1mm (males); mean width = 123.0 $\pm$ 38.2mm (females) versus 148.5 $\pm$ 38.5mm (males), but there was no statistically significant sex difference in either length or width.

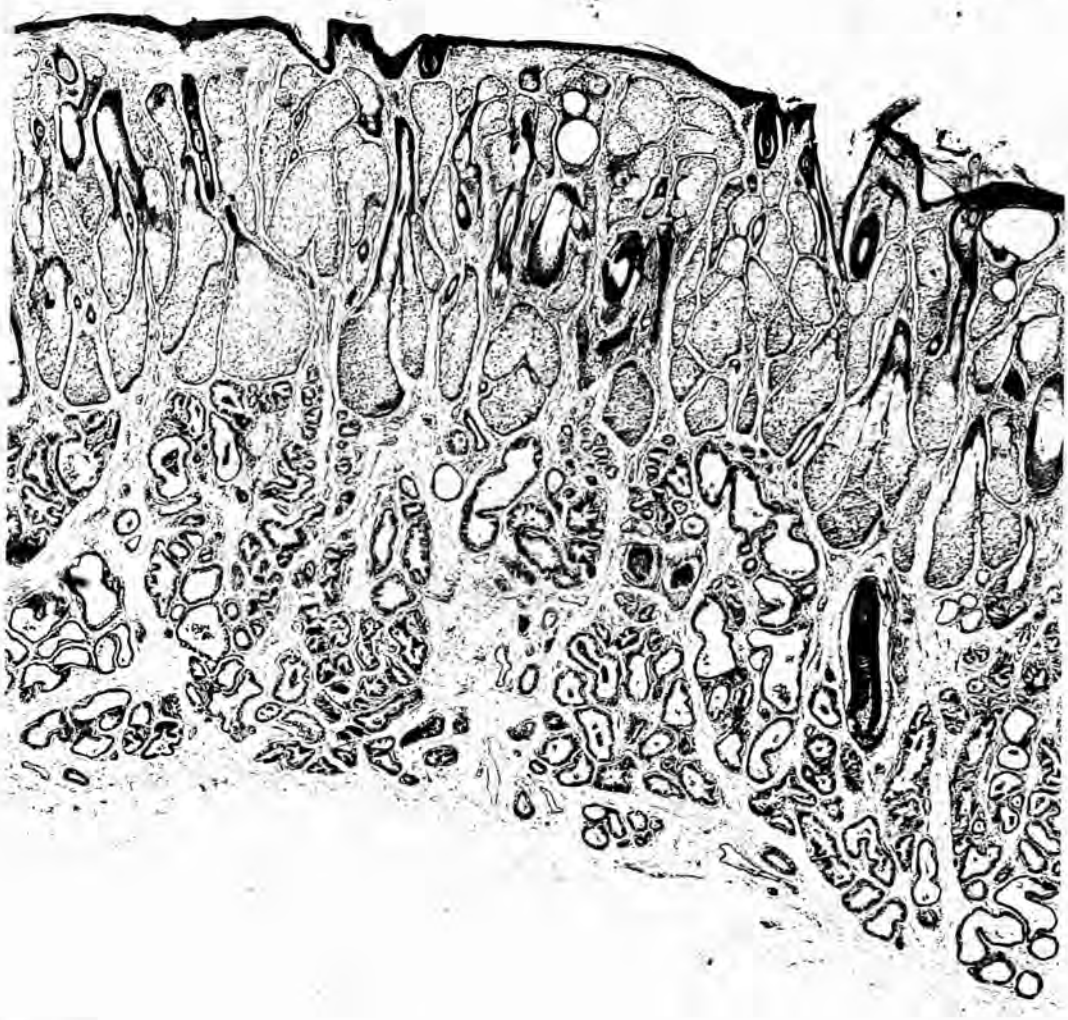
No correlation was evident between the width of the gland and the length, ie, the longest glands are not necessarily the widest ones ($r_s = 0.06$). The actual shape of the gland appears to vary - some glands appear triangular, whilst others are more oblong. The actual amount of secretion and excretion present on the glandular surface and hairs also varies from animal to animal. Some glands are dry and appear relatively clean, whilst others are matted and sticky. The hairs, even on clean glands, may still have some secretion attached, for cutting them off and placing the cut ends in alcohol leads to a significant paling of the colour of the hairs. Brown granules may also be present on the surface of the skin in the subcaudal region, around the perineum and in other areas of the tail.

PLATE 7.2

Transverse Sections of the Subcaudal Glands from :

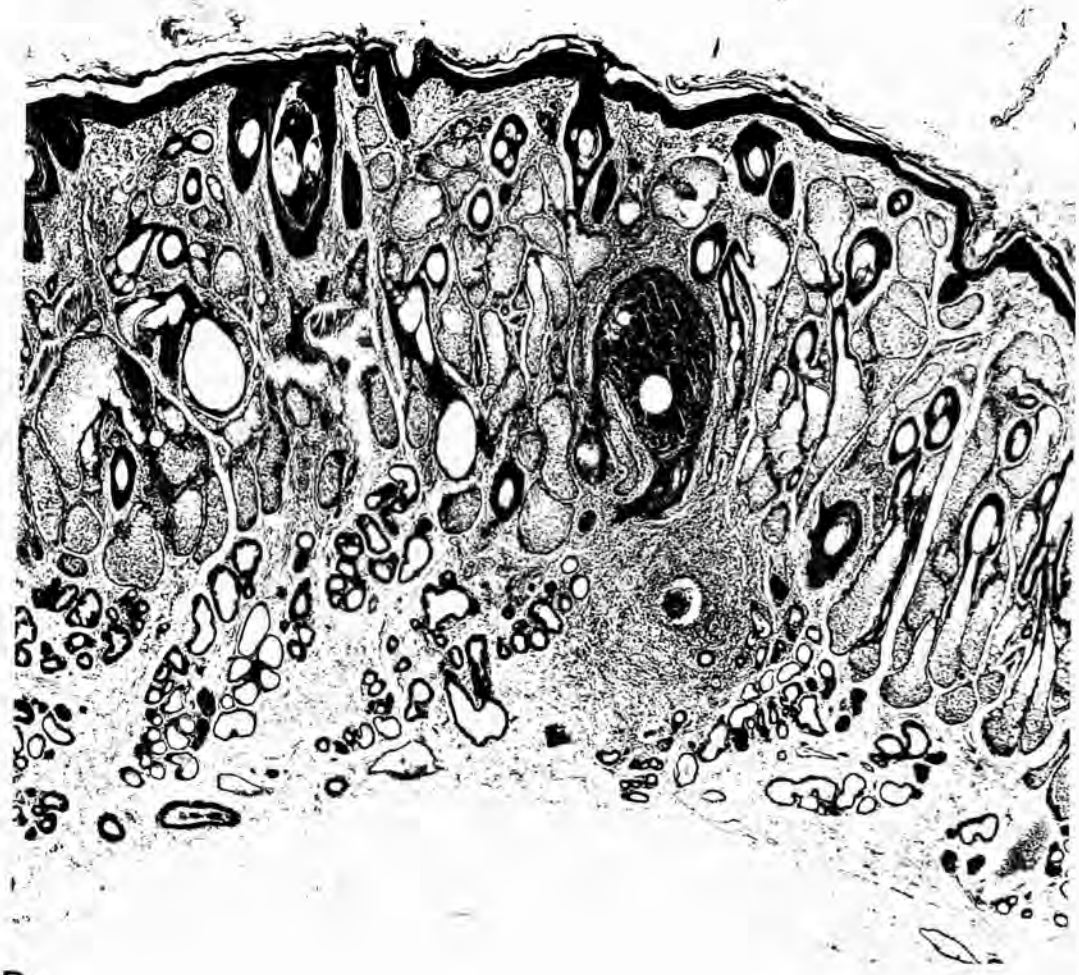
(A) An Adult Male
(B) A Juvenile Male
(C) An Adult Female
(D) A Female who Died Shortly after Giving Birth

A

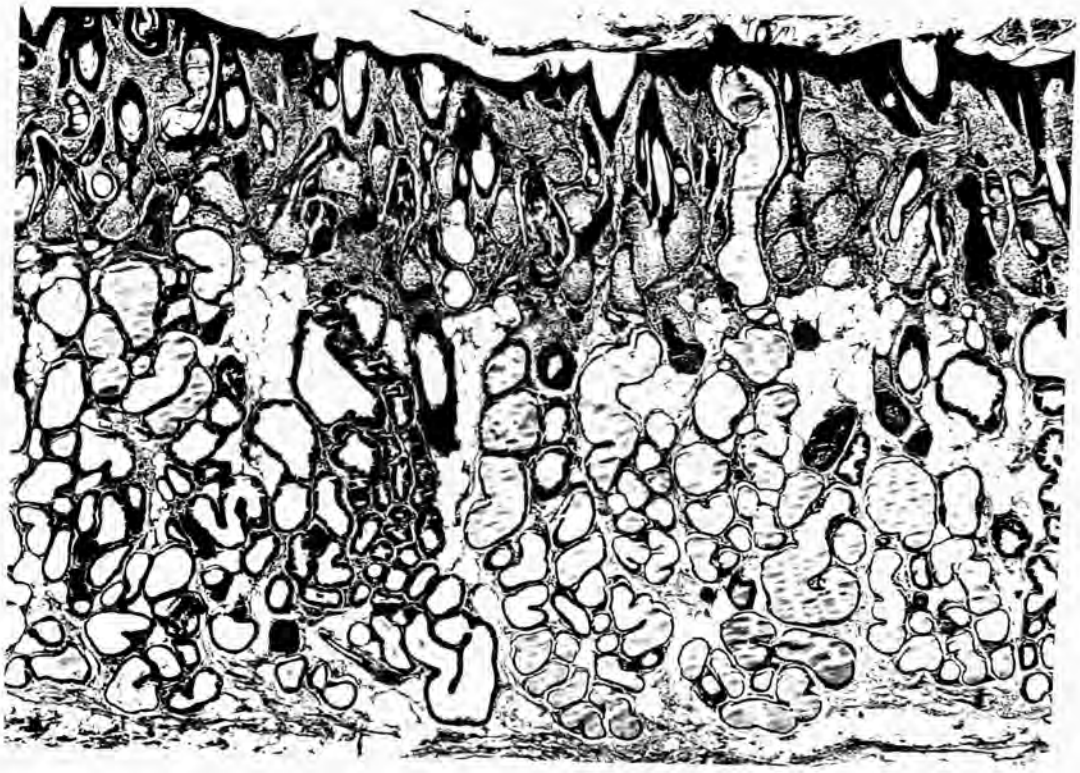


B

C



D



(B) Histological Measurements

The subcaudal gland in the owl monkey is composed of both sebaceous and apocrine elements (Plate 7.2). The apocrine ducts appear to open separately onto the surface (see Plate 7.2.D) and it has been suggested that these glands may actually be intermediates between eccrine and apocrine glands (Hanson and Montagna 1962). The hairs from the subcaudal region have been examined thoroughly (Hill, Appleyard and Auber 1959) and were found to be specialized in several ways - they are thicker than hairs from other areas of the body and the distal end of each hair is fragmented into a number of fine filaments. These filaments intermesh with others from neighbouring hairs and are partly responsible for the matted appearance of the gland.

There was no obvious difference in the depth of sebaceous tissue between the sexes. Although the female mean depth ($98.4 \pm 26.4 \mu m$) was lower than that for the males ($115.4 \pm 28.5 \mu m$), this difference was not statistically significant (see Figure 7.1). In fact, the animal that had the greatest depth of sebaceous tissue overall was a female (mean = $149.0 \pm 31.0 \mu m$).

The mean area of sebaceous tissue and apocrine tissue was measured within a given frame on the image analyser (area of the frame = $2.514 mm^2$). First, 3 scans were taken where sebaceous tissue only was measured. Then 3 scans were taken where apocrine tissue only was measured. The individual means for the 3 scans for each tissue are shown in Figure 7.3 (apocrine) and Figure 7.2 (sebaceous).

The most obvious feature of Figure 7.3 is the large amount of apocrine tissue per frame for animal No.1, a female. A section of the subcaudal gland from this female is shown in Plate 7.2.D for comparison with that from a normal female (Plate 7.2.C). This female (animal No.1) died 5 weeks after aborting and it seems likely that the large size of the aprocrine tubules is due to hormonal factors operating during pregnancy. The increased activity in the apocrine cells is shown by the large amounts of

colloid within these tubules compared to the tubules of a normal female (Plate 7.2.C and D). This female (No.1) was therefore excluded from any statistical analysis for either apocrine or sebaceous tissue.

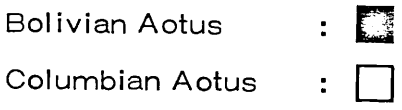
The area of apocrine tissue per frame did not differ statistically between the 4 female and 6 male Columbian owl monkeys, although the mean area of apocrine tissue for females (N = 4, mean = 0.25 ± 0.07mm^2) was lower than that for males (N = 6, mean = 0.40 ± 0.14mm^2). If the 4 Bolivian animals are included in the analysis the results are similar, with the mean area of apocrine tissue for the female (N = 6, mean = 0.21 ± 0.08mm^2) still lower than that for the males (N = 8, mean = 0.34 ± 0.15mm^2) although, again, this difference was not statistically significant.

Consideration of the mean area of sebaceous tissue within the frame also failed to reveal any statistically significant differences between the sexes (see Figure 7.2). Animal No.1 did not show any abnormal enlargement of the sebaceous tissue, but it was felt that it would be prudent to exclude her from the analysis in case there had been any (positive or negative) hormonal effects due to pregnancy on the sebaceous tissue. For the Columbian animals the mean area of sebaceous tissue within the frame did not differ in any statistically significant fashion between the 2 sexes (N = 4, mean for females = 0.37 ± 0.11mm^2; N = 6, mean for males = 0.39 ± 0.24mm^2). If the Bolivian animals are included in the analysis, the mean area of sebaceous tissue per frame is actually greater for females (N = 6, mean = 0.43 ± 0.12mm^2) than for males (N = 8, mean = 0.36 ± 0.22mm^2). As can be seen in Figure 7.2, the Bolivian females have much larger areas of sebaceous tissue than their male counterparts.

Data on the subcaudal gland from the juvenile male (No.14)were not included in the statistical analysis, but will be mentioned for comparative purposes. As Plate 7.2.B shows, both sebaceous and apocrine elements are present in the juvenile subcaudal gland, but both types of tissue are very under-developed compared to the adult glandular tissue (Plate 7.2.A).

FIGURE 7.1

To Show the Mean Depth of Sebaceous Tissue in Individual Sections of the Subcaudal Glands of Male and Female Owl Monkeys



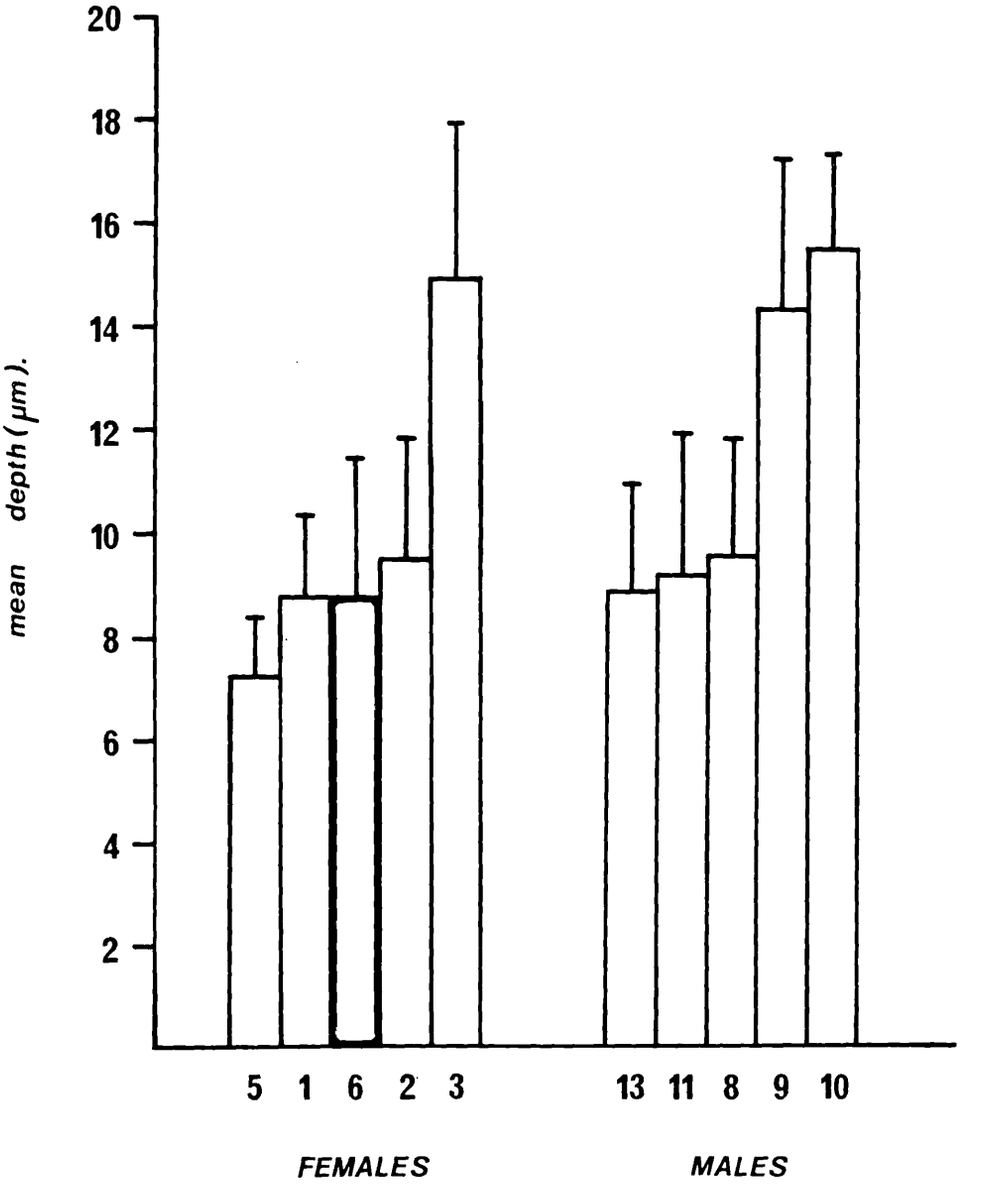

20
18
16
14
12
10
8
6
4
2
mean depth (μm).
5 1 6 2 3
13 11 8 9 10
FEMALES
MALES

FIGURE 7.2

To Show the Mean Area of Sebaceous Tissue Contained per Frame for each Individual Sample Examined

Measurements were taken on one section from each animal.

Bolivian Aotus : ■

Columbian Aotus : □

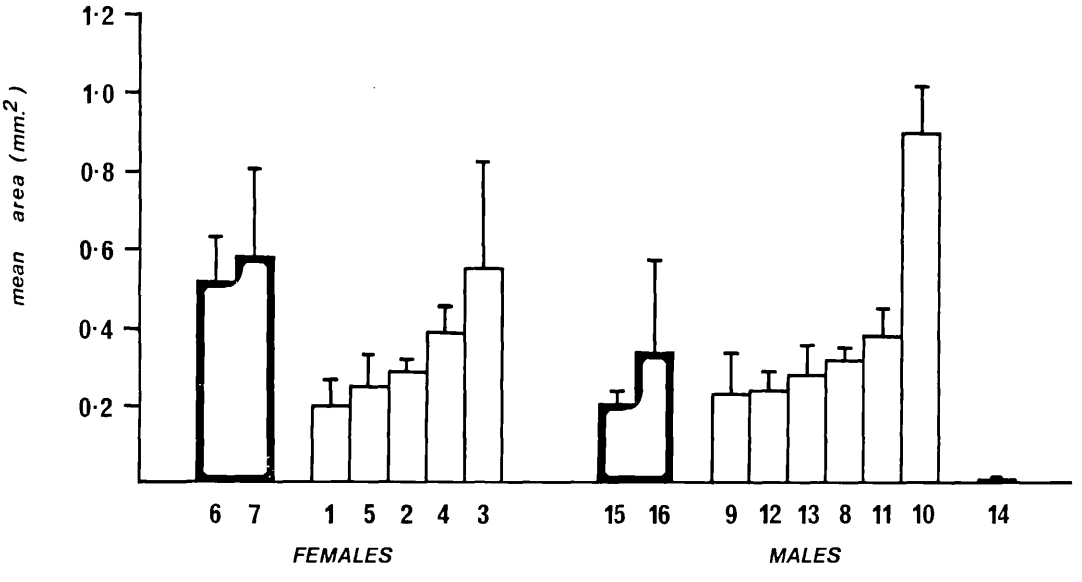

mean area (mm.²)
1·2
1·0
0·8
0·6
0·4
0·2
6 7 1 5 2 4 3 15 16 9 12 13 8 11 10 14
FEMALES
MALES

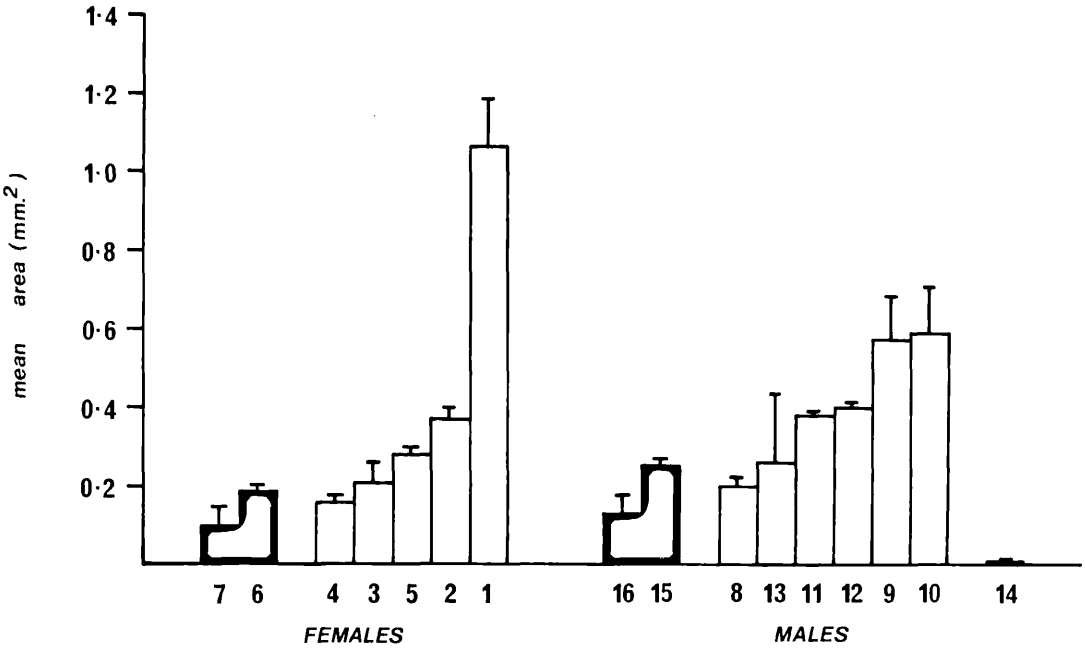
FIGURE 7.3

To Show the Mean Area of Apocrine Tissue Contained per Frame for each Section Examined

Measurements were taken on one section from each animal.

Bolivian Aotus : ■

Columbian Aotus : □


1·4
1·2
1·0
0·8
0·6
0·4
0·2
mean area (mm.²)
7 6 4 3 5 2 1
16 15 8 13 11 12 9 10 14
FEMALES
MALES

Finally, the subcaudal gland of one Bolivian female was examined at 6 points along its length to see if the density of sebaceous and apocrine tissue within the frame varied along the length of the gland, even though externally, there did not appear to be any difference. The subcaudal gland was divided into 6 segements approximately I cm apart and sample sections were taken from each segment. The results are shown below in Table 7.3 :-

TABLE 7.3

Variation in Density of Glandular Tissue Along the Length of the Subcaudal Gland of One Female Aotus

Proximal End	Length Along Gland					Distal End
Section	6	5	4	3	2	I
Apocrine :						
Mean per frame mm^2	0.19± 0.01	0.11± 0.01	0.04± 0.02	0.04± 0.02	0.03± 0.02	0.03± 0.002
Sebaceous :						
Mean per frame mm^2	0.58± 0.23	0.41± 0.06	0.34± 0.18	0.35± 0.12	0.31± 0.1	0.28± 0.001

This table shows that the density of both apocrine and sebaceous tissue varies with position along the gland, being greatest at the proximal end. Although these data concern only one animal, they suggest that samples should be taken from the same area for comparative purposes.

7.1.3 Summary and Conclusions

The subcaudal gland of the owl monkey appears externally to be a well differentiated structure. Measurements taken externally indicated that no correlation existed between the size of the gland and the animal's body weight, or between the length of the gland and the width of the gland. Both the amount of secretion present on the gland and the shape of the gland varied between individuals. There were no statistically significant differences between the sexes in the size of the gland, although females did tend to have shorter and narrower glands.

Histological examination confirmed previous findings that the gland was composed of both sebaceous and apocrine elements. One female had comparatively large apocrine tubules and it seemed likely that the increase in tubule size was related to hormonal factors in pregnancy. Neither the depth of sebaceous tissue nor the mean area of either sebaceous or apocrine tissue showed any statistically significant differences between the sexes. The subcaudal gland from one juvenile Aotus was also examined. The gland from this animal contained small amounts of both types of secretory tissue although the tissue elements were poorly developed compared to those in the adult.

Measurement of the density of apocrine and sebaceous tissue along the length of the subcaudal gland of one female showed that the density of both types of tissue varied with position along the gland.

7.2 Sternal Gland Measurements

The sternal gland was examined in live animals and in preserved specimens. It was hoped to quantify any subspecific or sexual differences in the structure of the gland.

7.2.1 Materials and Methods

External examinations were made on 24 living adult Columbian Aotus (3 castrate males, 10 intact males and 11 intact females), 6 living adult Bolivian Aotus (3 males and 3 females) and on the one Brazilian male (an adult) in our colony. The presence or absence of an externally visible gland was recorded with a brief description of the gland if present. The skins of 56 specimens of Aotus held at the British Museum were also examined and the subspecies of each specimen was determined on the basis of place of origin and pelage characteristics.

Biopsies of the sternal gland were taken from 4 of the Bolivian animals that were examined externally (2 males and 2 females) and from the Brazilian male. These were fixed in formol saline and then embedded and sectioned serially at 10 μ. These sections were then mounted with egg albumen on glass slides and stained with haematoxylin and eosin. Skin from the sternal area of one Columbian Aotus (which had not been examined externally) was also prepared in this way. Stained sections were then examined by light microscopy and the image analyser (as described in Appendix 2.6), to determine the structure of the gland and the density of secretory tissue. The resulting values in picture points were transformed into square millimeters.

7.2.2. Results

(A) External Examinations

Out of the 24 living Columbian owl monkeys examined, 2 females and 4 males possessed a small, visible glandular patch in the sternal region. Two other males examined had dark tips to the normally pale, long hairs in this region, but no evidence of glandular tissue could be found. In the Columbian animals, the external appearance of the sternal gland varied from just a very small bare patch of skin, slightly pinker than the surrounding skin (♀ 81) to a larger, deeply tinged area with short, stiff subble-like hairs. Males WLCP7 and 176 had few of these hairs, but did have a definite reddish patch of skin, whilst the other 2 males (Foster and 4367) possessed many more of these stiff hairs. However, in all the Columbian owl monkeys the gland was very small and difficult to locate.

Sternal glands were present in all 6 Bolivian Aotus (A.t. bolivensis) One male and one female had sternal glands that were similar in appearance to the Columbian sternal glands, being very small and difficult to see, and on shaving, the area of pink tissue was approximately 2.5mm^2 . The other 4 animals had more obvious sternal glands. Shaving revealed a dark pink patch about 10mm by 5mm, and the skin in this region was tough and hard to cut (for biopsy purposes). Many short, stiff hairs were also present.

However, the largest and best developed sternal gland was found in the one Brazilian male (A.t. trivirgatus). The short, stiff hairs were darker and more closely packed than in the other 2 sub-species. When the gland was palpated, a clear viscous fluid was obtained. On shaving this region, a triangular patch of dark pink skin was revealed measuring about 10mm by 7mm at its widest point. In none of the animals examined were the hairs in this region matted and encrusted with secretion as has previously been reported (Hanson and Montagna 1962).

TABLE 7.4

Showing the Occurrence of Sternal Glands in Preserved Specimens of Different Subspecies of Aotus Monkey

Country of Origin	Pelage Characteristics	Presumed Subspecies	Age	Gland Present	Gland Absent
Brazil	Dark orange ventrally. Silver and grey dorsally with central brown stripe. Prominant black and white facial markings.	Aotus trivirgatus	Adult	7	0
			Sub-Adult	1	0
Peru	(a) As above	A.t.trivirgatus	Adult	7	0
	(b) Lighter - no brown stripe Intermediate between Brazilian and Bolivian.	A.t.miconax	Adult	10	2
Bolivia	Medium orange ventrally. Less vivid face markings than Brazilian and no stripe.	A.t.bolivensis	Adult	6	1
Ecuador	Pale pelage ventrally Brownish dorsally	A.t.grisiemembra	Adult	3	4
			Sub-Adult	0	2
Columbia	Pale pelage ventrally Brownish dorsally	A.t.grisiemembra	Adult	2	4
			Sub-Adult	0	1
Venezuela	Pale pelage ventrally Brownish dorsally	A.t.grisiemembra	Adult	0	2
			Sub-Adult	0	1

The data obtained from animals in our colony does not suggest that a marked sex difference is present in the occurrence of the sternal gland as has been suggested (Hanson and Montagna 1962; Epple and Lorenz 1967). This was also true for the specimens examined from the British Museum, although in some cases the sex of the animals was not always discernable.

Table 7.4 shows the occurrence of sternal glands in 56 preserved specimens of owl monkeys in the collections of the British Museum. All the animals from Brazil had fairly large sternal glands and this was also true for the 7 Peruvian animals, which resembled the Brazilian form closely. These animals were assigned to the A.t. trivirgatus subspecies because of their pelage and the fact that they were caught in the Amazonian/Ucayali region of Peru near the Brazilian border. The other Peruvian specimens were collected in the Andean foothills and had thicker, browner fur, and appeared in other pelage characteristics (tail colour, facial markings) to be intermediate between the Bolivian and Brazilian forms. These animals were all considered separately as the subspecies A.t. miconax. Sternal glands were absent in 2 adult specimens and medium to small size sternal glands were present in the other 10 adults and 3 subadults.

The 5 Bolivian animals in which sternal glands were present were caught in the Andean foothills (Cochobamba) but the specific location of origin of the single Bolivian animal with no sternal gland was not stated. All these Bolivian animals were very similar in pelage colouration to those in our colony and were assigned to the subspecies A.t.bolivensis.

The animals from Ecuador, Venezuela and Columbia were all very similar with a pale or very pale ventral pelage, a light brown dorsal pelage and the facial markings were not particularly vivid. The animals from Ecuador and Venezuela were caught at regions near the Columbian border in all but one case. These animals were all tenatatively assigned to the subspecies A.t. griseimembra. Only 5 of the 14 animals from these countries possessed a sternal gland (see Table 7.4).

(B) Histological Measurements

From the biopsies and sections of sternal tissue examined, it appears that the sternal gland in the owl monkey, unlike the subcaudal gland, consists primarily of apocrine tissue, with the subaceous glands resembling those found over the general body surface in both size and structure. The apocrine tubules did not appear to open directly onto the surface. The values obtained from the image analyser measurements are shown in Table 7.5 :-

TABLE 7.5

A Comparison of the Mean Area of Apocrine Tissue per Frame in the Sternal Gland of 3 Subspecies of Aotus Monkey

Columbian	:	♀ unknown	0.002 ± 0.001
Bolivian	:	♀ 4938	0.01 ± 0.005
		♀ 4939	0.05 ± 0.03
		♂ 4994	0.04 ± 0.01
		♂ 4937	0.02 ± 0.01
Brazilian	:	♂ 4289	0.26 ± 0.08

All values are shown in square millimeters.

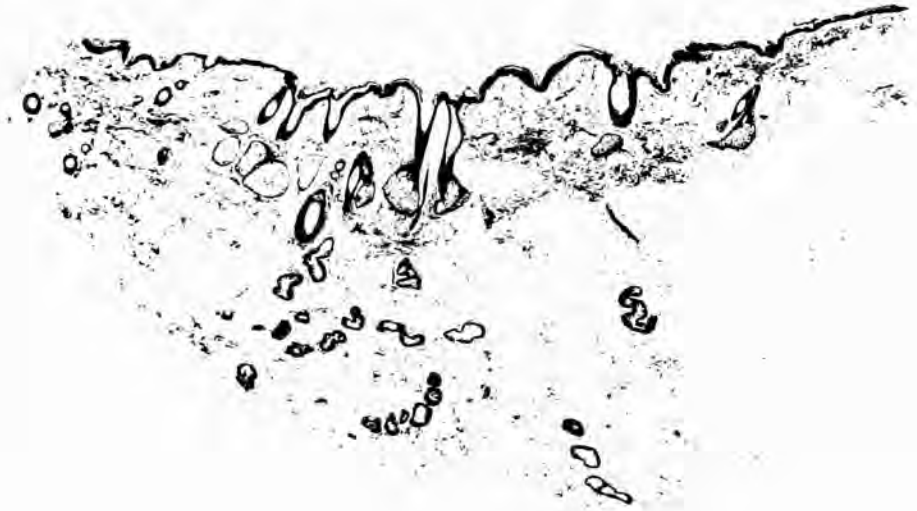
This Table confirms to a limited extent the results from the external examinations. The Columbian female had a minute amount of apocrine tissue with tiny tubules and hardly any visible lumen. The Bolivian animals all had more apocrine tissue in this region then the Columbian female (Plate 7.3.A) and those animals which possessed the smallest glands externally (♂4937 and ♀4938) also possessed the smallest amounts of apocrine tissue as measured by the image analyser. The sternal gland from the Brazilian male, which was the best developed gland externally, also had the greatest amounts of apocrine tissue as measured by the image analyser, with relatively large tubules and well-developed lumens, often filled with colloid (see Plate 7.3.B).

PLATE 7.3

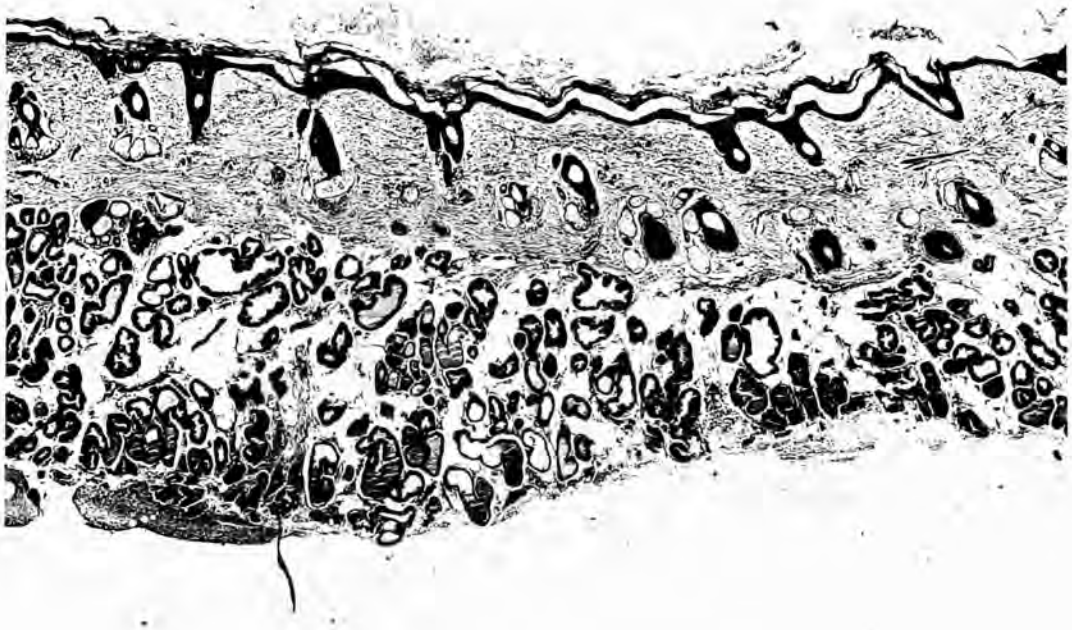
Transverse Sections of the Sternal Gland from :

(A) Aotus trivirgatus bolivensis
(B) A.t. trivirgatus

A



B



7.2.3. Summary and Conclusions

Examinations of the sternal region in 31 animals in our colony suggested that there might be subspecific differences in the occurrence of the gland, as a sternal gland was present in all 7 Bolivian and Brazilian animals examined, but was only present in 6 out of the 24 Columbian animals. No sex differences were apparent in the size of occurrence of the gland. Similar results were obtained when the 56 preserved specimens from the British Museum were examined.

Histological examination revealed that the sternal gland, unlike the sub-caudal gland, consists primarily of apocrine tissue. The Brazilian and Bolivian animals all had relatively large amounts of apocrine tissue in the sternal gland, whilst the one Columbian female examined had virtually no apocrine tissue in this region. Of the 5 animals biopsied, the 2 which had the smallest glands externally also had the smallest amount of apocrine tissue.

CHAPTER EIGHT

Discussion

Before discussing the results in detail, some general criticisms of methodology should be answered.

A major criticism which could be levelled is the lack of interobserver reliability. This was unavoidable due to lack of available personnel and space. However, the relatively short observation periods employed (10-20 minutes), coupled with the fact that few animals were under observation at any one time, meant it was unlikely that observer error would affect the results. It was decided that continuous recording for shorter periods of time would provide more accurate results than any time-sampling techniques, especially where behaviours of brief duration, ie, scent-marking and olfactory inspections, were involved. In the case of Experiments 1, 2, 3 and 5, only two animals were tested together, thus negating the need for focal sampling as both animals were always in view. In Experiment 4, where a maximum of four animals were observed at the same time, focal sampling was not appropriate to the testing situation as the number of responses could have decreased over time. Check sheets were considered to be the best scoring method available, as other methods, eg, tape recording or event recording, were either too noisy or did not allow enough data to be collected.

The second methodological criticism is that the method of introducing animals to each other was highly artificial and that, because of this and the limitations of cage area, the occurrence of various behaviours (eg, aggression and scent-marking) was heightened. It is possible that increases in the frequency of these behaviours did occur and, indeed, the probability that aggression would occur between same sex animals was maximised. This was desirable for experimental

purposes and these experiments should provide a useful complement to field studies and suggest possible avenues for future field research. However, the results are discussed with the above limitations in mind.

Aggressive behaviour and sexual behaviour will be discussed separately, together with the relation of both of them to olfaction. The results from Experiment 4 will be considered separately, as will those from Chapters Six and Seven, except where data are applicable to the general discussion.

Aggressive Behaviour

The aggressive behaviour of owl monkeys in these experiments was similar to that described by Moynihan (1964), ie, mainly hitting with biting occurring in most disputes. However, unlike Moynihan (1964), no evidence of 'spitting' during aggressive encounters was observed. Same sex pairs of owl monkeys were more aggressive than opposite sex pairs. A similar observation has also been made for other monogamous New World primates, eg, Callithrix jacchus (Epple 1970) and Saguinus fuscicollis (Epple 1980) as well as for semi-solitary primates, eg, Galago senegalensis (Bearder 1969) Galago alleni (Charles-Dominique 1977) and for primates which live in groups, eg, Miopithecus talapoin (Scruton and Herbert 1972); Macaca fuscata (Kawai 1960) and M. mulatta (Bernstein 1964, but see also Bernstein, Gordon and Rose 1974; Southwick 1967). Non-monogamous New World primates do not show this difference in aggressive response to introduced animals of the same sex, eg, Cebus apella (Becker and Berkson 1979) and Ateles geoffroyi (Klein 1974).

In view of the data from Experiment 1, it seems likely that in Aotus, both males and females may play a role in group defence, although the males may be more aggressive than the females as the male-male pairs fought more vigorously than the female-female pairs.

Dawson (1976) found that, in the wild, male Saguinus oedipus also tended to be more aggressive in situations involving contact aggression than females, but Epple (1980), in a laboratory study, observed that in another species of tamarin, S. fuscicollis, the female members of an adult male-female pair appeared to be more aggressive than the male to strangers of the same sex. The participation of both members of the adult pair in group defence is obviously advantageous in a species where the male plays an important role in caring for offspring.

With repeated testing the aggressive response in the owl monkey becomes progressively more variable. Males that were tested in both Experiments 1 and 2 generally initiated fights more rapidly in the second experiment than experimentally naive males, irrespective of condition. In the few cases where an animal had been severely attacked in a previous test, it was impossible to use that animal for any testing for some time afterwards, as he or she would run blindly around the cage until exhausted if introduced to another animal. This made continued experimentation, for example, in Experiment 2, impossible as there was a shortage of experimentally naive males.

Invariably in the tests between pairs of owl monkeys of the same sex, dominance could be readily assigned to one of the pair, on the basis of the criteria defined in the materials and methods (Section 2.2). It is interesting that in the first experiment one could not predict that the resident would automatically become the dominant animal, although in Experiment 2, where the residents spent much longer in their home cage before each introduction, they were dominant in the six cases where dominance could be assessed. Bearder (1969) also found that the resident animal was not always dominant when pairs of female Galago senegalensis were tested, although in male-male pairs, the introduced male was always

submissive to the resident. The freezing/crouching posture of the submissive owl monkey, which usually remains on the cage floor, has been described for other primate species in a submissive context, eg, Erythrocebus patas (Hall et al 1965); Saguinus oedipus geoffroyi (Moynihan 1970) and Lemur catta (Evans and Goy 1968), although submissive L.catta avert their gaze from the dominant animal whereas a submissive Aotus pays a lot of attention to the dominant animal (as is the case in a group situation in talapoin monkeys (Keverne et al 1978)). It must be remembered however, that the submissive animal could not escape in these tests and such submissive postures may not be seen in the wild, where an animal can easily flee from the aggressor.

The severity of most of the male-male encounters suggests that Moynihan (1964) is correct in stating that owl monkeys are extremely aggressive, and it is possible that aggression might be one of the main factors maintaining the separation of groups of Aotus in the wild. However, Wright (1978) observed a high proportion of encounters between Aotus groups in the wild, but she did not see any actual contact aggression. This suggests that displays of some description (eg, arching displays) might be acting to keep potentially damaging aggression to a minimum, and indeed, Wright observed visual, vocal and scent-marking displays during each intergroup encounter. Ninety-seven percent of the encounters she observed took place on moonlit nights, when presumably, visual signals would be most effective.

The relationship of arching behaviour to aggression is an interesting one. Initially the arch display in the owl monkey was considered to be a pure threat posture (Moynihan 1964; Wright 1978). There is some evidence from the present study to support this interpretation of arching behaviour :-

1. Arching frequencies were elevated in same sex encounters as compared to opposite sex ones in Experiment 1.

2. In Experiments 1 and 2, arching was performed more frequently by dominant (defined in terms of aggressive behaviour) animals and appeared to be suppressed in submissive animals. A similar relationship between dominance and arching behaviour was found by Rathbun (1979) in the golden lion tamarin. There is a difference in the arching behaviour of the two species, in that arching in the tamarin was invariably directed away from other animals, whereas the converse is true for the owl monkey.

3. The male-female pairing in Experiment 3 which showed the most aggressive behaviour (although the overall frequency was very low compared to male-male pairings) also showed the most arching behaviour.

These facts suggest that one of the functions of arching behaviour is to signal aggressive intent. A similar function for arching behaviour has been postulated for several other New World species, eg, Callicebus moloch (Moynihan 1976); Ateles fusciceps (Eisenberg 1976); Saguinus fuscicollis (Epple pers.comm. cited in Rathbun 1979); Callithrix jacchus and C. leucocephalia (Epple 1967; Moynihan 1970).

The occurrence of the arch posture or modifications of it in many New World genera, suggest that the ancestors of the Platyrrhinii also possessed this display. In Aotus the display is fairly stereotyped, varying only in the strength of the arch and the degree of gross piloerection and these subtle variations were not scored in this study. Vocalizations ('whup-whups, clicks and gruff-grunts') often accompanied arching in an aggressive context in these experiments, and similar vocalizations were noted by Wright (1978) to accompany

arching during intergroup encounters in the wild. These vocalizations were not observed in other contexts where arching occurred. In diurnal New World primates, vocalizations infrequently accompany the display, but the display may show further, visual elaborations, and it may act to accentuate various pelage characteristics (Rathbun 1979). The fact that the converse is true for the owl monkey probably reflects its nocturnal mode of life.

It does appear from the present study that arching by Aotus may occur in situations which are not purely aggressive, eg, arching occurred in all but three opposite sex encounters in Experiment 1, and, in both same sex and opposite sex pairings, arching was often mutual, being performed whilst the animals were nose-to-nose sniffing/touching. It seems in this context that arching may be elicited as the result of conflict between a tendency to approach and investigate a strange conspecific and a tendency to avoid an unfamiliar animal. In Galago senegalensis, for example, the motivation to sniff a dominant animal is high, even if it results in antagonism (Bearder and Doyle 1974). Arching could also be functioning in this context as a defensive threat, rather than a purely hostile posture. A similar arching posture is found in several mammalian species, eg, domestic cat (Darwin 1873), where it acts as a defensive threat posture. Consideration of the untreated trials in Experiment 3 (ie, before any anosmic treatment was performed), revealed that arching still occurred in the male-female pairs, even after they had been tested several times. Arching occurred at least once per test on average for both male and female partners in three out of four pairs tested. Additionally, no incidents of contact aggression were observed during these untreated tests, so it seems unlikely that arching is subserving a purely aggressive function. More precise measurements of the degree of piloerection accompanying the arch may clarify the situation, as piloerection is associated with

threat postures in many mammalian species (Ewer 1968), and may increase the aggressive or threatening component of the arch display. It is interesting to note that in Experiment 3, the females arched slightly more than the males in this experiment, which may reflect the fact that interactions always took place in the male's cage.

It is unlikely that arching in the owl monkey functions as a displacement activity, as all the observed arches were always directed towards a conspecific, even if it was only towards the animal's own reflection. It does seem likely that in the owl monkey arching does not function purely as a threat posture. Similar results have been reported for the golden lion tamarin, Leontopithecus rosalia rosalia, where arching may be important in maintaining the pair-bond (Rathbun 1979).

The Relationship Between Olfaction and Aggression in the Owl Monkey

From the results of this study it does appear that olfaction is involved in the mediation and maintenance of aggression in Aotus.

In Experiment 1, contact aggression between same sex partners was always immediately preceded by some form of olfactory inspection (by either partner). Olfactory cues may aid intraspecific recognition and would therefore be involved in the mediation of aggression in as much as they would allow conspecifics of the same sex to recognise each other; presumably as potential aggressors. The results from Experiment 4 suggest that males at least may gain information about the sex of a conspecific from olfactory cues alone. A similar function for olfaction has been discussed by Bearder and Boyle (1974) for Galago senegalensis. The introduction of a strange male bushbaby into a group leads to an increase in sniffing among group members, as if to compare their own odour with that of the introduced animal (Bearder, pers. comm.).

Another indication that olfactory cues are involved in the mediation of the aggressive response of the owl monkey can be found in Experiment 5. Here two adult females showed higher frequencies of arching behaviour when tested with an infant partner treated with conspecific odour compared to an untreated infant partner, and a treated infant was severely attacked. Infants normally receive little aggression from adults (Dixson pers.comm.; pers.obs.) and they present very different visual and vocal stimuli from those of an adult animal. It therefore seems likely that the aggression shown by these two females (in terms of arching and contact aggression) was influenced by the adult odour cues present on the treated infants.

For the other two adult females tested, the olfactory stimulus was obviously not strong enough to overcome the visual and auditory cues provided by the infant. It is interesting that Keverne (1976) found that in intact male - ovariectomized female pairs of rhesus monkeys which were characterized by aggressive tendencies, the application of vaginal secretions onto the female partner led to a reduction in the number of aggressive interactions (although such secretions did not stimulate sexual behaviour). Therefore it is possible that odour cues applied to an individual can act to reduce or increase aggression in some primate species, depending on the context in which they are used and the availability of information from other sensory systems. Similar experiments have been performed with rodents, eg, Lee and Brake (1971); Mackintosh and Grant (1966). Nose-to-nose inspections are frequently associated with mutual arching in pairs of owl monkeys, irrespective of the sex of the participants. It may be that nose-to-nose sniffing functions in aggressive or conflict situations as an aggression reducing display, although the male-female pair in Experiment 3 that showed the highest levels of arching behaviour also showed the highest levels of nose-to-nose sniffing. Nose-to-nose inspections are often observed in family groups of owl monkeys after low intensity disputes between two animals, and occur

when two animals are placed together, either for the first time or after a period of separation. As well as functioning as an aggression reducing display, nose-to-nose inspections may also be involved in maintaining the pair-bond.

Another way of examining the relationship between scent-marking and aggression is to look at the relationship between scent-marking and aggressive behaviour. Under natural conditions it is extremely unlikely that separate groups of Aotus are able to get sufficiently close to allow the mutual inspections described above to occur (Wright 1978) and scent-marking displays may replace olfactory inspections as an aid to intraspecific recognition. Indeed, Wright (1978) did observe tail rubbing (called by her, perineal rubbing) in association with high intensity displays between groups of wild Aotus, although no actual fighting was ever observed between these groups. Dawson (1976), during a field study of Saguinus oedipus, noted that scent-marking both preceded and followed aggressive confrontations, and marking also appeared to be more frequent in those parts of the home range which overlapped the home ranges of other groups, although he does not give any quantitative data regarding this point.

Any interpretation of observations of scent-marking behaviour in the present study was complicated by the fact that large variations existed between individuals in the frequency with which scent-marking occurred. Urine-washing was performed by both Columbian and Bolivian owl monkeys. Some authors, eg, Moynihan (1964) and Merritt (pers.comm.) have not observed this behaviour in their captive Aotus, whilst others, eg, Hill (1938) and Andrew and Klopman (1974) observed urine-washing in several primate species, including Aotus. In the present study some animals were seen to mark frequently, whilst others never marked in a variety of social situations. This individual variation was especially pronounced with regard to tail rubbing. Epple (pers. comm.) has also noted large individual differences in scent-marking frequencies in the

tamarin, Saguinus fuscicollis. When the individual variation in scent-marking by Aotus is coupled with the relatively small number of animals tested, the general applicability of the results from the present study is obviously limited. However, the results can be discussed bearing in mind these constraints.

In Experiment 1, same sex pairs did not show higher frequencies of marking than opposite sex pairs. This contrasts with results from studies on two other New World species - Saguinus fuscicollis and Callithrix jacchus (Epple 1970; 1980) where scent-marking by group members (as opposed to pairs) was stimulated by aggressive encounters with conspecifics of the same sex. However, no sexual behaviour was recorded in Epple's experiments, whereas sexual behaviour was usually observed in opposite sex interactions in Experiment 1. Sexual, like aggressive, behaviour may stimulate marking behaviour (see introduction) and this may account for the similarities in scent-marking frequencies of same and opposite sex pairs of Aotus in the first Experiment. An alternative explanation for this similarity in marking frequency is that attacks in same sex pairings were often so intense that little time was available for scent-marking, especially in those tests which were terminated prematurely. This explanation gains support from observations carried out on two dominant males after testing. Both males showed an increase in their scent-marking frequencies during the period immediately after testing compared with the period of the test. In her studies on S.fuscicollis Epple (1980) overcame this problem by separating the introduced animal from the adult pair by means of a wire mesh partition. Observations on male and female resident Aotus made during the week prior to testing in Experiment 1, indicated that marking levels were elevated when a conspecific was introduced, irrespective of the sex of the introduced animal. It seems likely from the experimental results, and from Wright's (1978) observations, that social interactions, whether aggressive or sexual, can stimulate scent-marking in the owl monkey.

In the present study, dominance was assessed in terms of aggressive behaviour. One might therefore expect that, if aggression and scent-marking were positively related, a dominant monkey (ie, the more aggressive monkey) might have scent-marked more frequently than his or her submissive partner. The results from the first experiment did indicate that such a relationship might exist. There was a tendency for scent-marking to be suppressed in subordinate animals, and this trend was most pronounced for urine-washing. However, it was not possible to predict an animal's dominance status on the basis of its scent-marking frequencies. Such predictions are possible with S.fuscicollis where high markers are usually dominant, but marking frequencies in these experiments were measured over a long period of time (Epple and Cerny 1979). In contrast, although scent-marking is suppressed in subordinate owl monkeys, 'low' markers are not necessarily subordinate. Suppression of scent-marking activity in subordinate animals has also been described for several other species, both primate and non-primate (Bearder and Doyle 1974; Doyle 1975; Schilling 1979; Swanson and Lockley 1978; Thiessen 1976).

Unfortunately, the relationship between dominance and scent-marking could not be clarified further in Experiment 2, as marking levels were too low for further analysis. The reason for this decrease is not certain, although it is unlikely to be due to the partial anosmia treatment per se as in this experiment, scent-marking frequencies were not significantly lower in the partially anosmic, compared to the untreated, condition. Additionally, in Experiment 3, partial anosmia only produced a decrease in marking frequencies in one of the two males who showed high levels of scent-marking in the untreated condition.

Although partial anosmia (henceforward called 'anosmia' for brevity) did not produce any consistent effects on scent-marking behaviour, anosmia did affect the expression of aggressive behaviour in male owl monkeys. Previous studies have not investigated the effects of anosmia

on inter-male aggression in primates, although some studies have been carried out on rodents (reviewed in Brown 1979). Partial anosmia increased the latency to the onset of contact aggression in pairs of male Aotus. This supports the suggestion that olfactory cues aid intraspecific recognition. A similar increase in latency was found by Edwards, Thimpson and Burge (1972) using pairs of male mice. The fact that in the present study four out of the six anosmic male pairs did fight, suggests that other cues (visual, auditory or tactile) can provide the stimuli necessary for the initiation of contact aggression. This contrasts with results from some rodent species where anosmia may abolish inter-male aggression, eg, in the gerbil (unpublished data cited in Wechkin and Cramer 1971). It is interesting that anosmia also produced a decrease in the actual amount of contact aggression observed in pairs of owl monkeys. This suggests that olfactory input is also important for the maintenance of contact aggression as well as for its initiation. Aggressive intent may still be high as arching frequencies did not show a significant decrease in the anosmic condition.

The two males studied in the control experiment provided evidence that it was not merely any discomfort or stress caused by the presence of the plugs alone that was responsible for the effects on aggression observed. Keverne (1980) measured plasma prolactin and cortisol levels during the course of an experiment on anosmia and sexual behaviour in the talapoin monkey, employing the same technique as the present study. None of the four males he studied showed significant increases in prolactin levels, and only one had elevated cortisol levels. It therefore seems likely that the effects observed on aggressive behaviour in the owl monkey are due to a decrease in olfactory input, rather than to any stress caused by the anosmia procedure.

To summarize: Observations on scent marking behaviour in aggressive contexts provide some evidence to link scent-marking with aggression, although the relationship is not simple. It is possible that aggression

may affect one type of scent-marking behaviour and not another, in a way not revealed by the experimental procedures used. Urine-washing for example, may be elicited during aggressive encounters as a result of non-specific arousal or because the animal is frightened, rather than acting as a threatening olfactory signal. Urine-washing in Aotus can be elicited by several different, though arousing, stimuli and can occur when the animal appears to be frightened.

It seems probable that olfactory cues play some role in sexual recognition in Aotus, and thus in determining whether or not aggression will occur between unfamiliar conspecifics. Anosmia does not abolish intermale aggression however, and other cues (visual, auditory or tactile) must also be involved, although the exact degree of involvement remains to be determined. 'Dominance', as assessed by measures of aggression is linked to scent-marking behaviour in as much as subordinate owl monkeys tend to mark less than their dominant partners. The data on scent-marking frequency and aggressive behaviour are consistent with observations on other New World species.

Sexual Behaviour and its Relation to the Ovarian Cycle

In monogamous primate species there is less dimorphism in sociosexual behaviour than in non-monogamous primates (Kleiman 1977). It is also true that Old World primates, eg, the rhesus monkey and various baboon species, show great physical and behavioural dimorphism (Bramblett 1976; Mitchell 1979). The behaviour of male and female owl monkeys is consistent with the reduction in dimorphism shown by monogamous New World primates compared to non-monogamous Old World species, although all sexual behaviour appears to be initiated by the male. Females were never observed to show any proceptive behaviour. Precopulatory displays by either sex are absent in Aotus. In family groups of Aotus mating behaviour was rarely observed (Dixson,

Bonney and Fleming 1980; pers.obs.) but during pair tests in the present study, copulation occurred at least once per test. Daily pair tests have also elicited regular mounting behaviour in Aotus (Dixson and Fleming 1980) and in another monogamous species Saguinus oedipus oedipus (Brand in prep.). It is possible that in monogamous primate species sexual activity occurs more frequently during the formation of the pair bond, but is relatively infrequent thereafter.

Sexual behaviour of male owl monkeys does not appear to vary in any consistent fashion during the ovarian cycle of the female (Dixson, Bonney and Fleming 1980). Therefore, in the present studies the stage of the female's ovarian cycle was not recorded or controlled for. There are indications that some Callithricid species do show cycle variations in sexual behaviour (Kleiman 1978), although few experimental studies have been performed to investigate the relationship between the ovarian cycle and sexual behaviour in New Workd primates. Epple (pers.comm.) found that pairs of S.fuscicollis did not show any regular cyclical fluctuations in male sexual behaviour with the stage of the ovarian cycle. Similar results were obtained for S.oedipus oedipus (Brand in prep.) These findings do not apply to other New World species, eg, Saimiri sciureus, which has an eight-day cycle, mating appears to be restricted to the day of ovulation (Wilson 1977). Field studies of other cebids have suggested that most sexual activity occurs around the time of ovulation (Carpenter 1935 ; 1965). It is important to bear in mind that accurate studies can only be done in the laboratory where hormone levels can be monitored. Such experiments as those described above for Saguinus fuscicollis and S.oedipus oedipus involve the use of regular pair tests with the animals separated between tests. It is possible that in those species where sexual behaviour occurs more frequently in pair tests than in the family group, any cyclic changes in sexual behaviour are obscured by the testing situation, and therefore, the possibility that such variations may occur in family groups cannot be ruled out. Additionally, changes in male sexual behaviour in terms

of intromissions and ejaculations could have occurred during the ovarian cycle of the female, as in the present study it was not possible to confirm that intromission and ejaculation had taken place by behavioural means. Smear tests also failed to confirm ejaculation. Unlike Moynihan (1964), we were unable to observe any final, quivering thrust which could be interpreted as confirming the occurrence of ejaculation.

Aotus females do not show any variation in receptivity with the stage of their ovarian cycle (Dixson, Bonney and Fleming 1980), although the only measure of female rejection employed was the number of times the female walked away from a mount. In the present study it was also found that females rarely rejected the male's mounting attempts by walking away. However, females were observed to turn their heads around to face the male, and this behaviour often preceded the termination of the mount. This stereotyped head turning of the female has been observed in other primate species, eg, Saguinus oedipus geoffroyi (Moynihan 1970), Saguinus fuscicollis (Epple pers.comm.), and Saguinus oedipus oedipus (Brand pers.comm.). In the Callithricids it is unlikely that this behaviour is involved in the rejection of male mounting behaviour as much tongue flicking and licking accompanies this display in the tamarins (Epple pers.comm.) and it is possible that head turning may function as a copulatory display in the tamarins. Tongue flicking was not observed in the owl monkey.

It is possible that reproductive inhibition of the offspring occurs in family groups of Aotus, as no sexual behaviour has been observed between group members other than the breeding pair, although the offspring are capable of reproducing once removed from the group (Dixson and Fleming in prep; pers.obs.). Similar reproductive inhibition within the group has been reported for other New World primates, eg, Callithrix jacchus (Abbot and Hearn 1978). The mechanism by which reproductive inhibition is maintained in Aotus and other New World primates is not known. It may be appropriate to mention the fact that mechanisms which

repress the expression of sexual behaviour between close relatives (eg, parent-offspring or brother-sister matings) may exist - such observations have been made for some primate species, eg, Macaca mulatta (Sade 1968). The possibility that olfaction may play some role in this inhibition of reproduction has not been investigated in primates, although evidence from research on rodents suggests that olfactory cues can produce reproductive inhibition and retard sexual development (Brown 1979; Swanson and Lockley 1978).

The Relationship Between Sexual Behaviour and Olfaction

In the present study, sexual behaviour was usually directly preceded by some form of olfactory inspection, and, less frequently, olfactory inspections also occurred after dismounting. Similar results have been reported for other primate species in the field and under semi-natural conditions:- Cacajao rubicundus (Fontaine and DuMond 1977); Ateles belzebuth and A.geoffroyi (Klein 1971); and Indri indri (Pollock 1975). In a laboratory group of Saimiri sciureus male olfactory inspections of the females increased significantly during the mating season compared to observations made outside the breeding season (Hennessy et al 1977). Olfactory inspections do not increase at or just before mid-cycle in owl monkeys (Dixson pers.comm.). However, olfactory inspections of the female may function within the family group to indicate ovulation and hence mediate female attractiveness.

Although male partners do initiate mounts, they do so extremely infrequently (Dixson pers.comm.). It is possible that in groups males respond to subtle changes in female sexual attractiveness, which fail to operate as determinants of copulatory frequency in pair tests where the females were (relatively) unfamiliar. Olfaction has also been implicated in the control of oestrous synchrony in seasonally breeding species, eg, Saimiri sciureus (Baldwin 1968) and Lemur catta (Evans

and Goy 1968). However, Aotus does not appear to be a seasonal breeder in either the laboratory (Hunter, Martin, Dixson and Rudder 1979) or in the field (Rathbun and Gauche 1980).

In pair tests the frequency of male anogenital inspections of females decreased after the first mount and introduced males, which were less likely to show sexual behaviour, also inspected the anogenital region of females less frequently than resident males. This supports the suggestion that cues from the anogenital region might be important for initiating sexual behaviour. In the rhesus monkeys olfactory cues from the vagina can stimulate sexual behaviour (Michael and Keverne 1970; Curtis et al 1971) and in several primate species, routine inspections of the vagina or anogential area of the female occur under natural conditions, eg, Erythrocebus patas (Hall 1965); Pan troglodytes (van Lawick-Goodall 1968). In Aotus anogenital inspections will also involve inspections of the adjacent subcaudal gland and therefore chemical cues from both the vagina and the subcaudal gland might be utilized. The presence of two potentially different sources of chemical cues implies that several different types of information, eg, sex and reproductive condition, could be provided by inspections of this area.

Nose-to-nose sniffing was not related in any sequential fashion to the act of copulation, but it may well function to maintain the pair bond. In Experiment 1 frequencies of nose-to-nose sniffing were higher after mounting had first occurred, and in Experiment 3, irrespective of condition, levels of nose-to-nose sniffing remained quite high throughout the period the experiment. In family groups nose-to-nose sniffing was performed by all group members, including the adult pair, and it may well be that nose-to-nose sniffing also maintains the integrity of the group, possibly by acting as an aggression reducing display. Muzzel touching has been implicated in the maintenance of the pair bond in several other primate species, eg, Callithrix jacchus (Abbot and Hearn 1978).

In the Callithricidae it appears that scent-marking and olfactory investigation of the partner's scent marks are regular components of courtship and copulatory behaviour (Epple 1970; 1975). However, this is not the case for Aotus, where no clear relationship between scent-marking and sexual behaviour is evident. Both tail rubbing and urine-washing occurred in most male-female pairings, and tail rubbing was performed by both sexes, contrary to Moynihan's (1964) observations that this behaviour was only performed by males. Unfortunately, in the vast majority of pair tests copulation occurred at least once and it is, therefore, not possible to investigate whether scent-marking scores were higher in those tests where copulation did not occur compared to those where it did occur. As previously mentioned, tail rubbing is highly variable between individuals, with some animals consistently showing high levels of tail rubbing behaviour (eg, ♀2455) in experiments, whilst others rarely marked. Moynihan (1964) suggested that tail rubbing was produced by a combination of sexual and aggressive tendencies, and although some evidence from the present study does support this theory (see above discussion on scent-marking and aggression), the large individual variation in the occurrence of this behaviour makes any single interpretation difficult.

It has been suggested that partner marking in Saguinus fuscicollis may be involved in maintenance of the pair bond (Epple 1975), and in Lemur fulvus males scent mark females more frequently during the breeding season (Harrington 1974; 1975). In Aotus, partner marking was occasionally observed in both family groups and in pair tests, with the male passing over the female and rubbing his subcaudal gland on her in an unmistakable fashion. Females were never observed to mark males in this way. However, this behaviour occurred so infrequently that it is not possible to relate it to any particular behavioural context, and it may even be an artefact of captivity (Moynihan 1970).

Overmarking of a partner's scent marks was observed but, again, this behaviour was infrequent. Olfactory inspections of an animal's own

marks or those of its partner also occurred, but none of these behaviours appeared to be related in any way to copulation. These results suggest that, in the laboratory, scent-marking does not play an important part in the mediation of sexual behaviour or sexual arousal in the owl monkey, although such a role has been postulated for scent-marking in other primate species, eg, Lemur fulvus (Harrington 1975). This does not mean that scent-marking is not involved in courtship and sexual behaviour of Aotus under natural conditions, eg, scent-marking may be involved in the maintenance of the pair bond in ways not reflected in the present study. It is also possible that scent-marking may be important in the establishment of new pairs in the wild, as nothing is known about group formation in Aotus under natural conditions.

Blocking the main olfactory system did not produce any consistent changes in the sexual behaviour of male owl monkeys, although individual differences did occur. There were no changes in the receptive behaviour of the females during this experiment, and because of this and the lack of any proceptive behaviour in female owl monkeys, it is unlikely that the female partners were compensating for (and thereby masking) any deficits in the male's sexual behaviour (cf. Keverne 1980). Therefore it seems that olfactory cues are not critically involved in the mediation of copulatory behaviour in male owl monkeys, unlike the results reported for some rodent species. Results similar to those from the present study have also been reported for the rhesus monkey and the talapoin monkey (Keverne 1980; Michael and Keverne 1968) using a similar technique to induce anosmia. In both species anosmia did not impair the copulatory performance of the male with those females with whom he was copulating before anosmia was induced. However, as pointed out above, ejaculations and intromissions could not be confirmed in the present study, and therefore the possibility that qualitative changes in mounting behaviour may have occurred in the present study cannot be ruled out.

In the present study, pairs of owl monkeys which showed sexual behaviour were tested, as male owl monkeys do not show sexual behaviour with

every female with which they are paired. Presumably, females differ in their 'attractiveness' and to control for this variation in female attractiveness, each male was tested repeatedly with the same female in Experiment 3. It may be that the attractiveness of the female is determined in part by olfactory cues. In the rhesus monkey, olfactory impairment removes the ability of males to recognise changes in the attractiveness of the female (Keverne 1976). In the present study the male whose mounting behaviour was most affected by the anosmia procedure (in terms of number of mounting attempts and latency to first mounting attempt), was also the male who apparently found the female partner least attractive, as he showed longer latencies to first mount than the other males, and the pair spent less time in close proximity. His overall number of mounting attempts was also low. It seems probable that in the owl monkey, female attractiveness is mediated by a combination of sensory components, the exact nature of which still remains to be determined. It may be that when the stimulus value of the female is low (ie, low attractiveness), a decrease in the olfactory input of the male may lead to a decrement in sexual behaviour. When the stimulus value of the female is high, reduced olfactory input does not decrease the stimulus value to a level at which sexual behaviour is impaired.

The fact that olfactory inspections decreased in the anosmic condition is not easy to account for. All olfactory inspections apart from nose-to-nose, decreased in the anosmic, compared to the control, condition. A possible explanation is that as anosmic males receivedlittle or no information when they sniff their female partners, they decreased their inspections, and concentrated on cues from the other senses, eg, visual. The fact that the males were familiar with their female partners may also be important. Unfortunately, the other studies which have investigated the effects of anosmia on sexual behaviour (Goldfoot et al 1978 Keverne 1980; Michael and Keverne 1968) have not measured olfactory inspections of females by males.

Discrimination Studies

The results from these studies do not permit positive statements to be made about the ability of owl monkeys to discriminate olfactory cues. However, some interesting findings did emerge concerning differences in responsiveness within the family group and differential effects on the two forms of scent-marking behaviour. When discussing scent-marking it must be borne in mind that the conditions in the test rooms were theoretically those which would increase the liklihood that urine-washing would occur, ie, hot and dry (Castell and Maurus 1967; Robinson 1969). It must also be remembered that urine-washing and tail rubbing could serve the same purpose in different contexts, eg, urine-washing could be employed when conditions are dry, and tail rubbing when conditions are wet.

Consistent individual differences in responsivity, in terms of scent-marking and sniffing behaviour, did exist and this obviously affected the results, eg, three males were high markers and two males showed low levels of marking. Similar individual differences have also been found in Saguinus fuscicollis (Epple pers.comm.). Breeding females did not show such great individual variation in their responses and this may reflect the fact that the females generally showed low levels of responsivity and breeding males were more responsive than either breeding females or offspring. Epple (1970) also found that the breeding (ie, dominant) male in a group of Callithrix jacchus was more responsive than other group members, in terms of scent-marking, to conspecific odour cues. In contrast, in S.fuscicollis both members of the adult pair may show increases in scent-marking and sniffing behaviour in response to conspecific odours (Epple 1978a, 1979). It is unlikely that the sexual dimorphism in response in Aotus reflected an inability on the part of the females to discriminate odour cues but rather reflected a lack of sufficient stimulation to respond. This is supported by the fact that when a potent stimulus (urine plus subcaudal gland secretion) was

presented to a group where the breeding male did not respond, the breeding female was capable of responding to the stimulus.

Other factors which were not controlled for in the present study could also have affected the results, eg, whether the breeding male was carrying an infant, and the reproductive state of the female. Although no quantitative data were obtained, the male did not appear to be more or less responsive when he was carrying the infant compared to when he was not. Several females became pregnant during the study period and there did not appear to be any changes in female responsiveness concommitant with changes in reproductive condition. However, in Leontopithecus rosalia rosalia infant carrying by the male and pregnancy in the female both appear to affect scent-marking frequencies (Kleiman and Mack 1980) and similar results have been found for Callithrix jacchus (Box 1978). Therefore, the possibility that these two factors may have affected responsivity of Aotus monkeys cannot be ruled out and requires further investigation. Additionally, in the present study the stage of the ovarian cycle of the donor females was not ascertained, although none of the donor females used were pregnant at the time of testing. In several mammalian species the odours from estrous females are highly attractive to males, eg, beagle (Doty and Dunbar 1974) and hamster (Landauer, Weise and Carr 1977), although in both these species, experiential factors are important in determining whether or not discrimination will occur. Evidence from primate species on this point is inconclusive, although it seems likely that some prosimian species may be able to detect changes in the females ovarian cycle by olfactory cues, eg, Lemur catta (Bailey pers.comm.).

In the choice situation employed,discrimination could only be inferred on the basis of increased sniffing behaviour, as no marking of individual gauze pads was observed. However, it is possible to compare marking behaviour between those trials where a conspecific odour was presented and those trials where only saline was presented. This comparison

revealed that breeding males were the only group members to show an increase in both types of scent-marking in the presence of conspecific ocour - either urine in Series A, or subcaudal secretion plus urine in Series C. In Series B, although breeding males showed elevated levels of urine-washing when urine was present, there was no significant change in tail rubbing behaviour. This dichotomy is hard to explain in view of the results from Series A. It seems most likely that tail rubbing habituated more quickly than urine-washing within each block of tests in this series (where the same donors were compared within each block), rather than a gradual decrease in tail rubbing behaviour over the period of testing. Consideration of the data within each block lends support to this idea.

The first two series of tests did not demonstrate that owl monkeys could discriminate either sex or hormonal status on the basis of urinary cues alone. Other workers have found that urinary cues did not elicit any response at all, eg, in Lemur catta (Bailey pers.comm.) and in Galago crassicaudatus (Clark pers.comm.), although urine may be an important source of information for some primates, eg, Nycticebus coucang (Seitz 1969), Galago alleni (Charles-Dominique 1977) and Microcebus coquereli (Schilling 1980). Urinary cues may be of some importance to the owl monkey, but further experimentation will be required to determine exactly what its stimulus value is. Possibly, the means of presentation or the context in which the urine was presented were inappropriate for discrimination to occur in the present study. In Aotus it is unlikely that urine contains much subcaudal secretion, as during urination, the tail is lifted clear of the urine stream and the urine passes well away from the branch on which the animal is sitting, although urine may contain vaginal secretion and traces of faecal material. These contaminants may also be a source of olfactory information.

It is possible that Aotus can distinguish sex on the basis of odour cues from the subcaudal gland, as the combined odour (sub-caudal secretion plus urine) may contain more information than urine alone. The results from the present study are equivocal. In one block

of tests a consistent discrimination by breeding males of the sex of the donor was demonstrated but this result was not repeated for the second block of tests. The combined odours were also a more potent stimulator of tail rubbing behaviour than urine alone, although this was not the case for urine-washing. The reason for this dichotomy is not known although it is interesting that urine appears to stimulate urine-washing more than tail rubbing (in Series B), whilst the converse is true for the combined odour. Epple (1976) also found that urine was a less potent stimulus than the complex mark in S.fuscicollis, but concluded that urine alone "probably carried at least some of the information communicating sex" (p. 262).

The offspring in the groups exhibited much lower levels of scent-marking than the breeding males and levels were generally lower than those of the breeding females. However, offspring were slightly more responsive than the breeding females in terms of olfactory investigation. Individual differences accounted for much of the variability in the scent-marking data, although tail rubbing occurred relatively infrequently. This behaviour developed much later in ontogeny than urine-washing (Dixson and Fleming 1981) but it did appear that tail rubbing was suppressed in post-pubertal offspring. It is possible that the factors governing tail rubbing are more complex than those determining urine-washing. Suppression of scent-marking in offspring and non-breeding adults has been noted for some other New World primates:- Callithrix jacchus (Box 1978) and Leontopithecus r.rosalia (Kleiman and Mack 1980).

There did not appear to be any sexual dimorphism in responsiveness in the offspring, and therefore, the sex of the offspring was not taken into account when the results were analysed. In Leontopithecus r.rosalia, the sex of the offspring did affect the development of marking behaviour, and this was also affected by the presence of younger siblings. In the present study it did not appear that offspring showed any discrimination of sex or hormonal status on the basis of odour cues alone, although they inspected the pads frequently.

Epple (1970) reported that juvenile male Callithrix jacchus scent-marked more frequently when a clean perch was placed into their cage than when no perch was present. However, a perch containing conspecific odour did not elicit more scent-marking than a clean perch. No data were given concerning olfactory investigations. Studies on non-primate mammals have indicated that age or experience may be important determinants of the response to conspecific odours (Nyby, Whitney, Schmitz and Dizinno 1978). Further studies are needed to determine whether age and experience are important in establishing the signal value of conspecific odours in the owl monkey.

To summarize, it seems that many factors affect the marking behaviour of owl monkeys in response to conspecific odours. Few studies have investigated the responses of family groups, instead of isolated individuals, to conspecific odours, although the results from the present study suggest this would be a worthwhile approach.

The combination of the discrimination and anosmia technique is a unique one, in as much as no work has previously been done with anosmia and the discrimination of biologically relevant odours in primates. This overcomes a major methodological criticism of most of the anosmia studies in primates. Goldfoot et al (1979) attempted to induce permanent anosmia in the rhesus monkey by ablating the olfactory epithelium with formalin (zinc sulphate having proved ineffective). They checked the effectiveness of this technique by testing its effect on the retrieval of buried anise-scented biscuits, and they were criticized for not using biologically relevant odours to demonstrate anosmia (Hennessy 1979; Slotnik 1979). In his studies on the talapoin monkey Keverne (pers. comm) utilized the same reversible technique as the present study, and he also used the retrieval of buried food, or rather the lack of it, as a test for the effectiveness of the anosmia procedure. On the basis of the scores from the two males tested in the present study, it seems that the reversible anosmia technique does produce anosmia to biologically

relevant odours. This result, coupled with the results from the control experiment performed on two males after the anosmia and aggression experiment, indicates that the reversible technique used in the present study is a valid one for producing partial anosmia in primates.

Anatomical Studies

a. Cutaneous Glands : The hormonal control of odour producing glands has been reviewed by several authors (eg, Adams 1980; Ebling 1977 and Thiessen 1976). In a large number of species sebaceous and apocrine glands may show sexual dimorphism, being more pronounced in males, eg, Galago crassicaudatus (Dixson 1976). However, in the subcaudal gland of the owl monkey, no sexual dimorphism is evident, either in external measurements or histologically, although individual differences were apparent in the quantity of secretion visible on the external surface of the gland, and a similar result has been reported for Saguinus fuscicollis (Epple and Cerny 1979). This contrasts with reports for Prosimian species, eg, Lemur catta (Andrimiandra and Rumpler 1968) and G. crassicaudatus (Dixson 1976) although Epple (1980) found that prepubertal castration severely retarded the development of the suprapubic-circumgenital glands in the tamarin, S.fuscicollis, but she did not carry out any histological examinations. Prepubertal castration in S.fuscicollis also caused slight inhibition of scent-marking compared to sham castration, whereas castration in adulthood did not affect scent-marking behaviour.

It is likely that gonadectomy before puberty would affect the structure of the gland in Aotus, as the development of the gland is under hormonal control, not reaching adult size until after puberty (Dixson, Gardiner and Bonney 1980). The poorly differentiated appearance of the gland in the juvenile animal was paralleled by poorly developed secretory elements when the juvenile gland was examined histologically. Marking levels in

castrated animals may still be high (pers.obs.) and, as Epple (1980) concluded for the tamarin, it seems likely that in Aotus social, rather than hormonal, factors will play an important part in determining the tail rubbing activity of a given individual.

The enormous enlargement of the apocrine glands in the female who died shortly after giving birth is probably the result of elevated hormone levels during pregnancy. Whether this enlargement is caused by the action of estrogens, progesterone or a synergistic action of the two types of steriod remains to be determined. Progesterone increased the size of apocrine glands in the shrew, but estrogen had no effect (Dryden and Conway 1967), whilst in the male rabbit estrogen had an inhibitory effect on the apocrine submandibular gland, but progesterone had no effect (Mykytowycz 1965). In the gerbil parous females have larger ventral scent glands than non-parous females (Swanson and Lockley 1978) and in Saguinus oedipus the pudendal pad in multiparous females is larger than that in nulliparous females (Dawson 1976), although it could be that the nulliparous females were not yet mature (cf. Abbot and Hearn 1978). Epple (1975) also reports that pregnant S.fuscicollis show increased glandular activity, visible externally by increased secretion, especially when they are close to term. It therefore seems possible that the one Aotus female which possessed enlarged apocrine tissue is not an isolated case but represents a real phenomenon. Unfortunately, it was not possible to investigate whether multiparous females have larger glands externally than nulliparous females, as the reproductive histories of many of the females who were not caged in groups were unknown. The two female offspring caged alone did have shorter glands than the other females who were examined, but this could still be the result of physiological suppression due to caging with the family group.

The fact that some individual Aotus show almost no morphological differentiation of the sternal area, whilst others possess a comparatively well-developed gland, has also been observed in Saguinus fuscicollis

(Epple pers.comm.). This difference does not appear to be related to the sex of the individual in Aotus. Apparently the sternal gland in Aotus is morphologically similar to that of most Callithricids, but disimilar to that of most Cebids (Epple and Lorenz 1967; Epple pers. comm.). However, no animal in our colony was ever observed to rub with the sternal gland, unlike the marmosets and tamarins, where sternal rubbing often occurs (Epple and Lorenz 1967; Kleiman and Mack 1980), or other cebids where the gland is also rubbed (Fontaine and DuMond 1977; Oppenheimer 1977). Sometimes individual Aotus occasionally lie prone on the branches thereby bringing the gland and the substrate into contact, but no rubbing has ever been observed in this position. In view of the extremely small size of the gland in the Columbian subspecies, coupled with the large individual variation in its occurrence, it is unlikely that this gland plays a significant role in the communicatory reportoire of this subspecies. It may seem paradoxical that in a nocturnal primate an additional glandular field may be regressing. It is possible that some of the functions served by sternal marking in other species have been replaced in Aotus by the specialized subcaudal gland and tail rubbing display. Owl monkeys do sniff the sternal regions of their conspecifics and the gland may therefore still have some communicatory function, perhaps when animals are in close proximity (eg, the sternal gland in Ateles geoffroyi is thought to function to reduce inter-individual antagonism during the pectoral sniffing embrace (Rondelli and Klein 1976)). However, it must be borne in mind that some subspecies of Aotus (eg, Brazilian) have a more pronounced sternal gland and it is difficult to account for these subspecific differences.

b. The Vomeronasal Organ : The structure of the vomeronasal organ in Aotus is similar to that described for other primate species, eg, Cebus capuchinus (Jordan 1972), although no electron microscopy was carried out to determine the fine structure of the epithelium, as has been previously done with the vomeronasal epithelium from the mouse

lemur Microcebus murinus (Schilling 1970). The epithelium in the vomeronasal organ of the tamarin and owl monkey was not atrophic and appeared functional, although electron microscopy would be needed to confirm this. In the spider monkey the epithelium appeared quite different - it seemed essentially similar to the mucosal epithelium lining the nasopalatine duct. As only one specimen was examined it is possible that this may be an isolated case, or that the epithelium was distorted during the prolonged decalcification needed for the spider monkey tissue (because of its size).

In all the specimens examined (Aotus, Saguinus, Ateles and Arctocebus) patent nasopalatine ducts were present. Martin (1973) has hypothesised that only the strepsirrhine primates possessed patent nasopalatine ducts and a functional vomeronasal organ. However, other studies have shown that patent nasopalatine ducts and a vomeronasal organ are present in Platyrrhine primates, eg, Cebus capuchinus (Jordan 1975); Callicebus, Saimiri and Alouatta (Starck 1975); Callithrix jacchus, Saguinus fuscicollis illigeri and S.f.nigrifrons (Wysocki and Epple; unpublished data cited in Wysocki 1979). The results of the present study confirm some of these observations and enlarge upon them.

Until relatively recently many of the histological investigations of the vomeronasal organ in primates were carried out on foetal material (eg, Frets 1912), which obviously leads to developmental complications when the results from such studies are interpreted. In the present study all the specimens were adults, so this complication does not arise. In three specimens from Aotus, the vomeronasal organ was sectioned longitudinally, thus allowing fairly accurate measurements of the length of the organ to be taken, although tissue shrinkage cannot be ruled out. In these three animals the vomeronasal organ ranged in length from 1.6mm to 3.3mm. This variation of over 100% is too large to be accounted for simply by difference in body dimensions. In Microcebus murinus (which is approximately one-fifth of the weight of an owl monkey) the vomeronasal

organ is approximately 3mm long (Schilling 1970 and pers.comm.). Compared to this, the size of the organ in Aotus is small. The large individual variation in the size of the organ coupled with its relatively small size, make it unlikely that the vomeronasal organ plays a crucial role in olfactory communication in the owl monkey.

The structure of the vomeronasal organ in Aotus, Saguinus and Arctocebus was similar, and incidental observations on the nasal fossa confirmed that the turbinal bones in the New World species were less elaborate than in those of the Prosimian.

Some speculation has existed as to the possible role of the vomeronasal organ in mediating reproductive processes in primates. The organ may be absent in Old World monkeys and appears to be vestigial in man. If a reduction of olfaction is a characteristic of more highly evolved primates (Napier 1977), then it might be expected that in Ateles the vomeronasal organ would be less well-developed than in other Platyrrhines. The spider monkey is a highly specialized animal and exhibits other modifications, eg, reduction of the thumb and absence of the penile bone (Dixson pers.comm.). It is therefore, not surprising that the male spider monkey examined did not possess a vomeronasal organ which appeared functional. This observation strengthens the suggestion that the organ does not play a crucial role in behaviour or neuroendocrine processes, especially as suggestions for such a role have centred around the spider monkey (Klein 1971). Against this must be set the fact that several New World species possess accessory olfactory bulbs (Stephan and Andy 1965) and that absence of the accessory olfactory bulb does not necessarily indicate the absence of a vomeronasal organ (Cooper and Bhatnagar 1976). Additionally, many Callithricids possess licking and tongue-flicking displays which regularly preceed copulation (Abbot and Hearn 1978; Epple pers.comm.; Moynihan 1970). These displays may serve to bring chemical substances into communication with the organ.

The occurrence of 'Flehmen' in primates has been reported for several species, eg, Lemur catta (Bailey 1978; Evans and Goy 1968) and Saguinus fuscicollis (Epple, pers.comm.). In Aotus a behaviour reminiscent of Flehmen was occasionally observed during the discrimination tests and, rarely, during the pair tests. However, without photographic analysis, it cannot be stated that the expression was indeed a 'Flehmen' face. The occurrence of Flehmen has been linked to vomeronasal function (Estes 1972), but the evidence is not conclusive (Dagg and Taub 1970; Verberne 1976).

In summary, it seems likely that, with the possible exception of the prosimians, the vomeronasal organ does not mediate reproductive processes in primates.

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APPENDIX 1

General Housing Conditions for the Aotus Colony

All animals were housed under conditions of controlled temperature (68-75F) and lighting with 12 hours of artificial white light (01.00-13.00 hours) and 12 hours of dim red light (13.00-01.00 hours). Animals were either housed individually in cages separated from each other by solid or mesh dividers (cages approximately 102 x 55 x 66cm in dimension), or in family groups in cages that were double the size of the single cages (approximately 102 x 110 x 66cm). Each cage was fitted with a nest box and this was used to catch the monkeys up, either for transportation or tranquillization.
The humidity in the rooms was also kept constant, between 30 and 50mm of mercury.

The animals were fed daily with pelleted diet (Mazuri), cereal (Farex), fruit (apple, orange, grape, banana and dates), vegetables (lettuce, cabbage) and seeds (sunflower and groundnut). Locusts, a meat preparation (ZF6) and mealworms were provided regularly, and water was available ad libitum.

Each cage was branched and the floor covered with sawdust and wood-chips, unless urine was being collected, in which case, the normal tray was removed and the cage base was fitted with a removable sloping tray with a funnel at the base for collecting the urine.

APPENDIX 2

Histological Methods and Staining Techniques

2.1 Fixing and Staining Vaginal Smears : The smears were dry-fixed. The following solution was used :-

Carbo-wax (1500) : Polyethylene glycol	1 gm
Distilled water	2 ml
Ethyl alcohol	100 ml
Glacial acetic acid	10 drops

The carbo-wax was dissolved in the water by gentle heating. The acetic acid was then added with the alcohol. The slide with the smear on it was then flooded with this dry fix and left to air dry.

Greenstein's stain (1964) was then used to stain the smears. The schedule was as follows :-

1. Tap water for 10 minutes
2. Greenstein's stain solution A for 4 minutes
3. Tap water for 4 minutes
4. Greenstein's stain solution B for 2 minutes
5. Rinsed in distilled water
6. Rinsed in 50% Ethyl alcohol
7. Rinsed in 70% Ethyl alcohol
8. Rinsed in 95% Ethyl alcohol
9. 100% Ethyl alcohol for 2 minutes

The slides were then cleared in xylene baths 1 and 2 and mounted in DPX. Each slide was then examined for evidence of spermatozoa under a light microscope.

2.2 Decalcifying Solution

This particular solution was chosen as it is very gentle to the tissue :

10 ml NaH_2PO_4 (500 mM)

40 ml Na_2HPO_4 (500 mM)

This mixture was then diluted to 500ml with distilled water. 5-10% E.D.T.A. was then added and dissolved using heat as necessary. 100ml of solution was used per gram of tissue. The solution was replaced every week until decalcification was complete.

2.3 Embedding Schedule for Decalcified Material

Place tissue in 70% alcohol for one day.

Day 1 : all day in 90% alcohol; pm overnight in absolute ethyl alcohol I.

Day 2 : am in absolute alcohol II; pm overnight in absolute ethyl alcohol III.

Day 3 : am place in an absolute alcohol : ether mixture (50:50) all day and overnight.

Day 4 : am in 1% celloidin in absolute alcohol and ether (50:50) I.
pm in 1% celloidin in absolute alcohol and ether (50:50) II overnight.

Days 5-7 : pm in chloroform.

Day 8 : wax bath x 3 all day and embed in the evening.

Cut and stain as normal paraffin, although mount using a chrome gelatin adhesive.

Chrome gelatin adhesive : 1% potassium dichromate and 1% gelatin in 1% phenol. Add 2ml per litre to distilled water bath and use fresh each day.

2.4 Baker's Solution (for hard tissue)

60% alcohol - 9 parts
Glycerine - 1 part

2.5 Martius-Scarlet-Blue Method (MSB)

The main solutions were made up as follows :-

Martius Yellow :	Martius yellow	0.5gm
	Phosphotungstic acid	2.0gm
	95% ethyl alcohol	100ml
Brilliant Crystal Scarlet SR :	Brilliant crystal scarlet	1 gm
	Glacial acetic acid	2.5ml
	Distilled water	97.5ml
	1% Phosphotungstic acid	
Aniline Blue :	Soluble (aniline) blue	0.5gm
	Glacial acetic acid	1.0ml
	Distilled water	99ml

Method :-

1. Bring sections to water
2. Stain with haematoxylin for 5 minutes
3. Wash in tap water 3-5 minutes
4. Differentiate in 0.25% acid alcohol
5. Wash in tap water 5-10 minutes
6. Rinse in 95% ethyl alcohol
7. Stain in Martius yellow for 2 minutes
8. Rinse in tap water
9. Stain with Brilliant crystal scarlet for 10 minutes
10. Rinse in tap water
11. Treat with phosphotungstic acid for 5 minutes
12. Rinse in tap water
13. Stain with analine blue for 10 minutes
14. Rinse in water, dehydrate, clear and mount

Nuclei are stained black, fibrin is stained red, collagen, blue and red blood corpuscles are stained yellow.

2.6 Luxol Fast Blue and Cresyl Fast Violet Stains

The main staining solutions were made up as follows :-

0.1% Luxol Fast Blue :	Luxol fast blue	1 gm
	95% Ethyl alcohol	1000ml
	10% acetic acid	5ml

This solution should be filtered before use.

Cresyl Fast Violet :	Cresyl fast violet	0.5gm
	Double distilled water	100ml
Cresyl Fast Violet Differentiation :	95% Ethyl alcohol	90ml
	Chloroform	10ml
	Glacial acetic acid	3 drops

Staining procedure :-

1. Dewax in xylene. Wash in 100% alcohol
2. Wash in 95% ethyl alcohol for 3 minutes
3. Stain in luxol fast blue at 56C overnight
4. Wash in 95% Ethyl alcohol for 3 minutes
5. Wash in double distilled water
6. Differentiate for a few seconds in 0.5% Lithium carbonate
7. Transfer to 70% Ethyl alcohol and check for colour
8. Transfer to distilled water x 2 and leave in the water for several minutes to check for colour loss
9. Stain in cresyl fast violet for 6-10 minutes
10. Wash in distilled water x 2 for 3 minutes
11. Differentiate for 1-2 minutes
12. Rinse in 95% alcohol, 100% alcohol and finally xylene
13. Transfer to fresh xylene and mount

APPENDIX 2.7

The Use of the Image Analyser

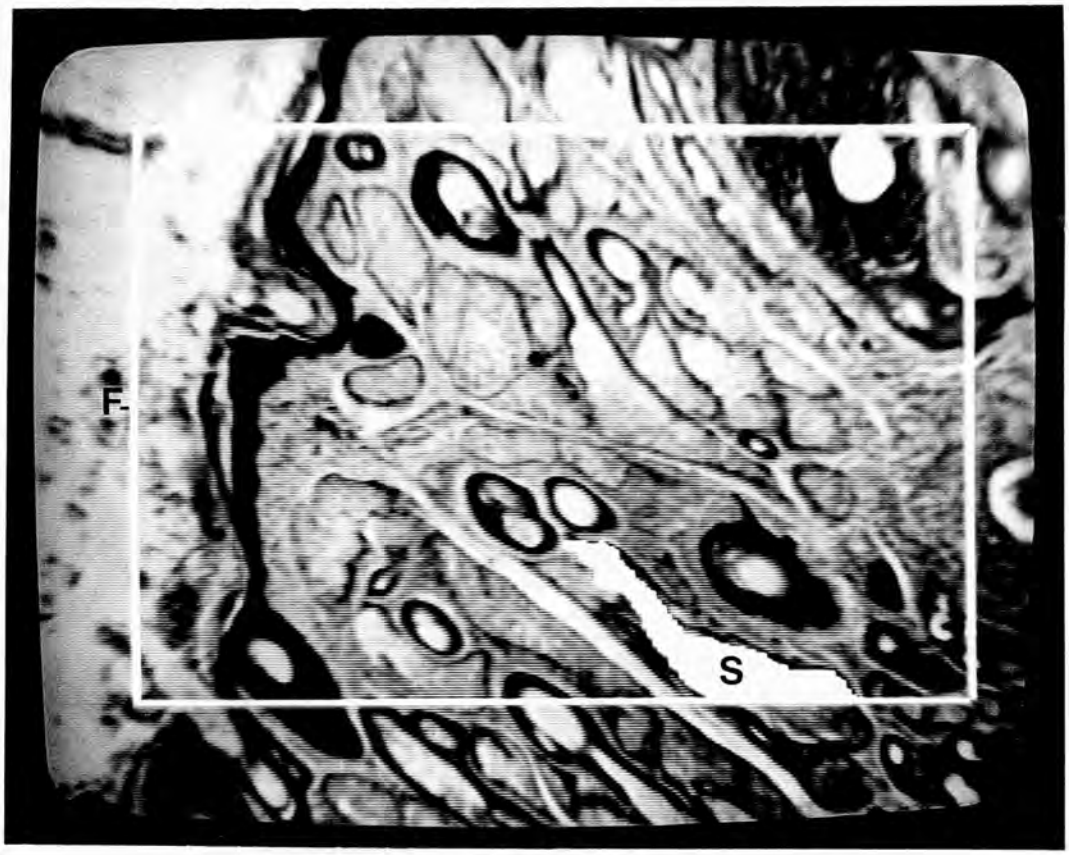
The "Optomax" Image Analyser used was made by Micromeasurements, Cambridge. The image from the microscope was projected onto a television camera (lens : 15mm, F 1.3) whose output then passed to a closed circuit television monitor to provide a television image (see Plate A.1). The output from the camera also passed to a detector unit where the signals from the features to be measured were discriminated and selected from the rest of the signal. The output from the detector was fed into a computer where the area measurements were calculated. All measurements were made within a detection frame ((F) - Plate A.1). The Flexidraw facility allowed the area whose measurement was required to be enclosed. This area was then measured in terms of square picture points. Using a micrometer scale the values in terms of square picture points could be converted to square microns.

For each section of tissue to be measured, 3 scans of the area of sebaceous or apocrine elements within the frame were taken. The position of the frame was altered between scans by automatically moving it a constant distance. This negated any selection bias by the experimenter.

PLATE A.I

A Section of Tissue Projected onto the Screen of the Image Analyser

This plate shows a section of tissue , taken from the subcaudal gland of an owl monkey, projected onto the television screen of the "Optomax" image analyser. The frame (F) is kept a constant size for each scan of the tissue. The tissue whose area measurement is required is enclosed and 'filled in' as shows (S). The machine then computes the area enclosed in picture points which can be converted to square microns.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