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CHEMICAL COMMUNICATION IN *GALAGO CRASSICAUDATUS*

Zohar Katsir

A Dissertation Submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, for the Degree of Master of Science.

Johannesburg 1979

I hereby declare that this dissertation
is my own work and has not been submitted
to any other university.

Z. KATSIR

ABSTRACT

The social structure of Galago crassicaudatus was studied in the field, in order to establish a natural basis for analysing communication by scent marking. Chest rubbing behaviour was chosen for closer investigation. The chest gland secretion was collected, chemically analysed and three components were identified. Artificial scents were prepared using these components and tested under natural conditions. The mode of action of the pheromone was investigated in the laboratory and the field. The information collected was analysed on the basis of social interactions between galagos in the field. It is suggested that the chest gland secretion supplies a relatively short lived (1 hr) signal that gives an indication of the age of the scent mark and a relatively persistent message (3-4 days) for territorial markings. Differences in the message conveyed by chest rubbing and urine washing are discussed.

Dedicated to my parents.

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CHAPTER 1. INTRODUCTION

1.1 Chemical communication

1.1.1 General

Chemical communication is undoubtedly the most widespread means of communication among animals and has a variety of functions at least as broad as those of the visual and auditory systems. Thus chemical signals may be used as sex attractants e.g. in the algae (Muller et al., 1971), Lepidoptera (Roelofs and Carde, 1974), Diptera and other insect orders (Shorey, 1973), as well as in crabs (Kittredge et al., 1971), amphibia, reptiles, fish (Pfeiffer, 1974; Madison, 1977) and mammals (Stoddart, 1976). They may further be used for alarm signals as in the earthworm (Ressler et al., 1968). In the social insects they serve a diversity of functions (Wilson, 1971), while mammals generally use chemical signals in territorial and dominance behaviour (Eisenberg and Kleiman, 1972; Stoddart, 1976).

Chemical communication has been defined by Eisenberg and Kleiman (1972) as 'the process whereby a chemical signal is generated by a presumptive sender and transmitted to a presumptive receiver who, by means of adequate receptors can identify, integrate and respond to the signal'. This definition, however, does not exclude chemical signals in communication between individuals of different species, a topic which will not be considered in this dissertion at all.

Karlson and Lüscher (1959) originally defined the term 'pheromone' as chemical signals used in intraspecific communication. They defined the chemical signals as 'substances which are secreted to the outside by an individual of the same species in which they release a specific reaction'.

In addition, pheromones are usually divided into two categories, depending on their mode of action; releasers, that is odours which elicit a specific behavioural response, and primers which result in a delayed physiological response (Wilson and Bossert, 1963).

The use of the term pheromone as defined above in mammalian olfactory communication is somewhat controversial. The controversy has arisen from the use of terms like 'primate sexual pheromone' and 'copulins' when applied to primate vaginal secretions (Michael et al., 1975). Freeman (1978) has objected that in situations such as these where associative learning is involved, the use of the 'pheromone concept' is inappropriate, since this concept implies that learning and prior experience with the olfactory stimuli are not necessary for its effect. Thus he would argue that the fact that learning may be involved in mammalian olfactory communication, implies that the chemical signals used should not be called pheromones.

Recently Müller-Schwarze (1977) has suggested restoring the use of the term pheromone in mammalian olfactory communication by using th term 'informer pheromone' for a stimulus which can be stored in the memory and recalled later in a variety of contexts i.e. an olfactory stimuli which involves learning. Thus he divides pheromones into three categories; releasers, primers and informers, depending on thei mode of action. This terminology is adopted in this dissertion.

Chemical signals have the advantage that they can be transmitted in darkness, around obstacles and over distances varying from a few millimeters to several kilometers. In addition the half life of a signal may vary, enabling an animal to transmit a signal into the future, or even to encounter at a later time, the signal it deposited. Moreover, olfactory communication is energetically more efficient than visual and auditory communication (Wilson, 1975) and does not require a sophisticated releasing

apparatus. The main disadvantage of chemical communication however, is in the s eed of transmission. Molecules move by diffusion or by mass flow in the surrounding medium at speeds which cannot be compared with the speed of light or sound and, as a result, the possibility for quick responses is limited.

There are also some important differences between the transmission of odours in insects and mammals which should be noted. Most insect pheromones are released into the air and can be perceived at some distance from the source (50 - 500m). The concept of an 'active space' has been discussed mainly with examples from insects (Bossert and Wilson, 1963; Lewis and Macaulay, 1976). Social insects also transfer chemical signals directly by grooming, licking and sometimes via food (Gary, 1974). Mammals transfer chemical information by sniffing each other at the source of the scent itself, (e.g. dog's meeting ceremony), or possibly by marking a conspecific with secretion (Epple, 1974). The most characteristic behaviour however, is indirect communication by scent-marking whereby urine or a secretion is deposited on objects by a distinctive and stereotyped display. The receiver picks up the signal by sniffing and/or licking the marked place and hence the distance over which communication occurs is small (0 - 1m). In addition the recipient of the signal seldom communicates directly with the transmitter.

Many insect pheromones have been chemically identified and extensively studied (Shorey, 1976), in contrast to the relatively few mammalian pheromones studied (Preti et al., 1977). Consequently insect chemical communication research has a more extensive theoretical background. Young and Silverstein (1975) have summerised the methodology used for the isolation and identification of insect pheromones and have suggested the following approach.

1. Development of a sensitive bioassay.
2. Isolation of the active compounds through progressive steps each monitored by bioassay.

3. Identification of the active compounds.
4. Confirmation of biological activity of synthesized compounds in both the laboratory and the field.

In a later review, Claesson and Silverstein (1977) discussed the difficulties which arise when applying this approach to mammalian systems. The responses of insects are relatively stereotyped in contrast to the variability of response found in experiments with mammals, owing to the complexity of their social interactions and their highly developed learning abilities. Furthermore, the number of insects available for experimentation is usually much greater than in mammals and when experiments are based on greater numbers the variability of the results is reduced.

Mammal secretions have often been found to consist of a greater number of compounds than is commonly found in insect pheromones (Birch, 1974). This makes it more difficult to synthesize an artificial pheromone for mammals. Sometimes the only recourse is to identify every compound present, synthesize them and then systematically bioassay the synthetic compounds in all possible combinations (Claesson and Silverstein, 1977). Further difficulties have been indicated by Birch (1974): A specific behaviour pattern in mammals may be evoked more readily by a combination of inputs from the visual, auditory and olfactory senses, while insects tend to specialize in a particular communication channel. One must always consider the other senses before coming to a conclusion as to the contribution of olfactory communication to a behavioural pattern. Moreover, the behaviour of mammals in captivity varies greatly from that in their natural environment and hence a laboratory bioassay may not be adequate. Bioassays in the field for mammals are highly desirable from a biological point of view, but are practical only in rare cases, due to the distances, terrain or vegetation involved (Muller-Schwarze, 1977).

Bioassays for mammals should be carefully designed to control the 'excitement state', i.e. the degree of anxiety, fear or threat of the animal (Eisenberg and Kleiman, 1972). An excited animal may increase its frequency of marking and displays. [e.g. chewing the ends of branches displayed by G. crassicaudatus (Schilling, 1979)]. An animal may use scent-marking merely as a means of 'self advertisement' (Jolly, 1966) and hence care should be taken a priori not to relate a message to a signal.

The investigation of chemical signals, particularly those involved in scent-marking, cannot be carried out using the traditional ethological approach (Tinbergen, 1951), since the signal is spatio-temporal, i.e. the signal is not necessarily followed by a response. Thus it is difficult to relate the responses given at a different time to the olfactory signal produced by the scent mark. However, Smith (1977) has suggested an approach to analysing communication that solves some of these problems. It involves the use of a set of analytical procedures, each emphasising a different aspect of the process. The unifying theoretical framework comes from the field of semiotics, a theory which uses three levels of abstraction, each analysing particular components and kinds of relationships within the process of communication.

The first level, the syntactic level, is concerned only with the signals. These are analysed independently of the events in which they occur and are treated only as physical entities. The second level, the semantic level, is concerned with the kinds of information made available by the signal. It is concerned only with what the messages are - i.e. the information content of the signal. As with the syntactic level it deals only with a component of the process. The third or pragmatic level uses the signals, their messages and meanings, and investigates their use by participants who are actually communicating.

Scent-marking is particularly suitable for this type of

analysis, since the secretion which is used for scent-marking can be removed from the animals and analysed according to the first and second analytic levels. By learning about the properties and the information content of the secretion we are better equipped to understand the meaning of the signal.

This step-by-step approach seems to be the most appropriate for dealing with complicated mammalian chemical communication systems and was adopted in this study. Finally to place this study in context, some earlier studies of mammalian chemical communication systems are described below.

1.1.2 Mammals

Mammals perceive odours through the olfactory epithelium of the nose as described in detail by Eisenberg and Kleiman (1972), Stoddart (1976), Graziadei (1977) and Freeman (1978). Liquids and odours of low volatility can be perceived by the vomeronasal organ, found in all terrestrial mammals other than bats, Old-World monkeys and apes (Estes, 1972). Mammals also ingest urine and faeces, but there is no evidence that scents are perceived in this way.

Most of the 4,000 or so species of mammals have a keenly developed sense of smell and the olfactory channel of communication appears to be of major importance (Stoddart, 1976). Romer (1970) in his comparative description of the vertebrate brain has emphasised the importance of the sense of smell in the evolution of the cerebral hemispheres as follows:

> 'Following down the ancestral line to early mammals and on down to their early vertebrate ancestors it appears that this sense has been throughout a main channel through which information concerning the outside world has been received. It is thus but natural that its brain centres should form a base

> upon which higher correlative and associative mechanisms have been built.'

In lower vertebrates, the cerebral hemispheres are merely for olfaction, while later in evolution they become more important as memory and learning ability develops.

This close association between the olfactory and memory centres in the mammal's brain may be responsible for the inconsistent responses in experiments with mammalian pheromones. Sometimes the effect of the pheromone is that information is received and stored in the memory without an immediate response. This is the mode of action of informer pheromones, and the vast majority of mammalian odours may fall into this category (Muller-Schwarze, 1977).

Scent sources in mammals are found over the entir surface of the body, usually in scattered apocrine or sebaceous glands, although sometimes a prominent gland is found (Stoddart, 1976; Quay, 1977). Urine and faeces are also used as chemical signals (Eisenberg and Kleiman, 1972). The body posture, when scent marking, can further serve as a visual signal as is often found in the Lemurs (Schilling, 1979).

Scent glands are most highly developed in the male and their odour production usually increases during the breeding season. However, observations suggest that the odour is primarily for communication with other males and not for female attraction. In nature, males usually seek out females and hence male-produced scents could hardly serve for the attraction of females which do not seek out males (Stoddart, 1976).

The recognition of a female in oestrus by her mate often occurs through a chemical signal, at least in rodents (Bronson, 1971; Stoddart, 1976; Johnston, 1977). The male of feral mice (Mus musculus) can be captured readily in a trap containing the odour of an oestrous female (Rowe,

1970), which suggests that the urine or vaginal secretion of an oestrous female carries information as to her condition.

Perception of the oestrous signal is usually through the olfactory epithelium; in many rodents anosmia whether permanent or temporary can clearly stop them from copulating (Stoddart, 1976). However, recent studies of the sexual behaviour of the hamster (Cricetus auratus) have shown the involvement of the vomeronasal organ in the perception of this stimulus (Powers and Winans, 1975). Male ungulates often lick the genital area of an oestrous female, raise their heads and curl the upper lip in a stereotyped manner which is termed 'Flemen'. It is suggested that Flemen is associated with stimulation of the vomeronasal organ (Eisenberg and Kleiman, 1972). Estes (1972) summarised evidence for the involvement of this organ in mammalian reproduction.

When considering the reproduction of mammals, the contribution of the other senses must not be overlooked, since reproduction is under multisensory control (Mykytowycz, 1977). Yet it is advisable to study first the contribution of chemical signals, which are often of crucial importance.

Olfactory communication in rodents has been studied in greater detail than in other mammals (Stoddart, 1974; Ropartz, 1977), due to the fact that the social interactions of rodents are extremely dependent on olfaction, and they are convenient animals for experimental work. Most of their chemical signals act either as releaser or primer pheromones. At least five primer effects have been found in rodents. 1. The Bruce effect, which is a pregnancy block that occurs when a recently impregnated mouse is exposed to the odour of a male from a strain different to that of the stud male (Bruce, 1959). 2. The Lee-Boot effect, which results in suppression of oestrus and production of a false pregnancy when four or more females are housed together without a male (Van Der Lee

and Boot, 1955). 3. The Ropartz effect, which is a reduction in reproductive capacity when the odour of other mice increases corticosteroid production of the animal (Ropartz, 1966). 4. The Whitten effect, which is the introduction and acceleration of oestrus in a group of females that has been exposed to an odour present in the urine of male mice (Whitten, 1956). 5. The Vandenbergh effect, which is the acceleration of sexual maturation in young female mice by the scent of males (Vandenbergh, 1969). The control of social behaviour by releaser pheromones in rodents has been reviewed by Bass and Stevens (1977), and Ropartz (1977).

Although many attempts have been made to identify rodent pheromones, these have had only limited success, probably because scent sources other than urine are in numerous small glands scattered over the body surface, which prevents the efficient collection of the secretion. Only recently, with the combined efforts of chemists and biologists from different laboratories, has the sex pheromone (dimethyl disulphide) of the hamster (C. auratus) been isolated from the vaginal secretion (Singer et al., 1976). The major compound (phenylacetic acid) of the ventral scent mark of the mongolian gerbil (Meriones unguiculatus) has also been identified (Thiessen et al., 1974). In this study the behavioural response to a conditioning task was used for the bioassay.

In larger mammals e.g. carnivores or ungulates, chemical identification of scents has been more successful (e.g. Ruzicka, 1926; Lederer, 1949; Albone and Fox, 1971; Wheeler et al.,1975; Burger et al., 1977), undoubtedly because of the conspicuous scent glands in these species. The functions of the scents, on the other hand, are not properly understood. Laboratory bioassays are usually unsuitable for larger mammals, as was discussed earlier, and until recently, very little information from field studies on these animals was available.

Observation in the field can often help to classify the mode of action of the pheromone i.e. primer, releaser or informer (Müller-Schwarze, 1977). Krouk (1972) in his exhaustive field study of the spotted hyena (Crocuta crocuta), observed that animals often marked the border of their territories with a secretion from the anal gland (and faeces). On one occasion when hyenas were hunting in their neighbours' territory, they were encountered by the aggressive owners of the territory, lost their prey and were chased back to their own range. On a second occasion, a few days later, the same hyenas were chasing game again, but this time stopped at the border of their territory and allowed their quarry to escape. This observation indicated that the pheromone involved in making of territorial borders is of the informer category.

In the primates the first attempts to study chemical communication were directed at the conspicuous diurnal monkeys. Curtis et al. (1971) and Michael et al. (1971) have reported that short chain fatty acids are the sex attractants for the rhesus monkey and have suggested the existence of a 'primate sexual pheromone'. Recently, however, Goldfoot et al. (1976) testing the effect of aliphatic acids on the sexual behaviour of the male rhesus monkey found a lack of response. Recent work on chacma baboons (Papio ursinus) (Bielert and Crewe in prep.) supports the results of Goldfoot and his coworkers.

Volatile fatty acids were also found in human vaginal secretion (Michael et al., 1975) and the 'likelihood of human pheromones' has been suggested (Comfort, 1971). In a recent review of chemical communication in humans, Doty (1977) has stated that although people do not have an innate ability to distinguish between males and females by scent, adults can easily learn to do so.

The only other attempt at chemical identification of secretions in primates has been on the marmoset (Saguinus

fuscicollis), which utilises scent marks for communicating information such as sex, social status and individual identity (Epple, 1974). The major volatile components of the scent mark were identified as long chain butyric acid esters (Smith et al., 1976). The function of the esters in olfactory communication is not known. The active pheromone may be a much more volatile compound that remains unidentified (Preti et al., 1977). The secretion was collected from perches marked by the animals. These perches were washed with dichloromethan and methanol (Harger et al., 1977). Some volatile compounds were probably lost as a result of this collection method.

The difficulties that have emerged in studies of chemical communication in higher primates are mostly due to the well developed learning abilities of these animals. More complex bioassays based on social interactions under natural conditions are needed to alleviate the problem. As chemical communication in higher primates is not a major means of communication, the other senses should not be overlooked.

Since chemical communication in the prosimians is a major communication channel, and since they are related to the anthropoid primates, the study of chemical communication in these animals can contribute to the understanding of the evolution of communication in the primates. Some of the work on prosimian chemical communication is summarised below.

1.1.3 Prosimians

Schilling (1979) has recently reviewed olfactory communication in the prosimians and emphasised the major role that 'olfactory behaviour' plays in their way of life. The nocturnal prosimians are a favourable group of animals for studying chemical communication, not only among primates but among mammals in general. Their sense of smell is

well developed and the nasal structure resembles that found in non-primate mammals, rather than that of the simian primates (Cave, 1967). Prosimians and New-World monkeys have a functional vomeronasal organ which is absent in Old-World monkeys. (The possible role of this organ in mammalian reproduction has been discussed earlier). In addition they have conspicuous scent glands which make it relatively easy to collect their secretions efficiently. Olfactory communication in this group is undoubtedly an integral part of the animals adaptation to a nocturnal life style (Charles-Dominique, 1975; Clark, 1978a).

The study of prosimian communication is important for comparisons with higher primates. It can be used to indicate the modifications in communication that are necessary for the transitions from nocturnality to diurnality and from solitary to more social behaviour. It will also indicate the role of learning in communication in the two groups. Recent studies (Ehrlich et al., 1976) have suggested a greater learning ability in nocturnal prosimians than was previously supposed.

In this context the lemurs are especially important since they display convergent evolution with the simian primates towards diurnality and complex social behaviour, but use olfactory communication to a great extent (Bourlière, 1974; Charles-Dominique, 1975).

Nevertheless very few studies of chemical communication in prosimians have been carried out (Schilling, 1979). No prosimian pheromones have been identified to date - with the exception of a single component from the chest gland of Galago crassicaudatus (Wheeler et al., 1977) - and almost no field studies have concentrated on this subject. This is probably due to their inaccessibility - lemurs are restricted to Madagascar - and the difficulties involved in performing observations and experiments at night. The problem of nocturnal field studies has recently been overcome by the use of red light head

torches (Bearder, 1969; 1974) and radio-telemetry (Charles-Dominique, 1977).

The study of olfactory behaviour in prosimians has revealed that complex communication patterns exist especially in scent-marking behaviour. Manley (1974) noticed allomarking behaviour in Perodicticus potto and Arctocebus calabarensis. These species of the subfamily Lorisinae are slow-moving animals which live in the tropical forests of Africa and almost never descend to the ground (Charles-Dominique, 1974). Hill (1957) has suggested that allomarking in these animals enables the sexes to locate each other at night. Manley, however, has suggested that this behaviour may serve as a means of recognition in long-lasting pair bonds, but more field observations are needed to confirm this.

In the social ring-tail lemur (Lemur catta) Schilling (1974) described three types of scent marking; Genital-marking performed by both sexes, brachial marking, performed by males, (brachial glands are possessed only by males), and self marking of the tail by the brachial glands, again only by males. Brachial markings on trees can be seen from several meters away and are usually concentrated on border zones between territories, which suggests that this behaviour is important in territoriality, although Schilling has suggested that it is merely a means of impressing the opposite troop. The tail marking is used in the 'stink fight' between rivals from two troops (Jolly, 1966). This display uses a combination of visual and olfactory signals for the same function. In a recent study Mertl (1977) has shown that the response to brachial markings on a branch diminishes over a few days, but can be elicited again by changing the position of the marked branch, which suggests that memory is involved in the recognition of these signals.

Harrington (1974) studied scent marking in Lemur fulvus.

Initially he investigated the social interactions between animals in the field. His observations suggested that scents might function for orientation. alarm signals, territorial markers, or for identification of individuals and sexes. He then performed laboratory experiments to examine the kind of information available in these sign ls. He presented a scent receiver with a series of pads marked by another individual until it habituated to that animal's scent, then presented the receiver with the scent of a second individual. He was thus able to demonstrate that L. fulvus is able to distinguish between individuals on the basis of scent.

This method of following up field observations with laboratory experiments is preferable for studying prosimian chemical communicat on, since it prevents misidentification of a behavioural pattern in the field on the one hand, and enables one, on the other hand, to interpret laboratory results on a natural basis.

The behaviour of 'urine washing' among prosimians ha been reviewed by Andrew and Klopman (1974). This b iour is found in all the Galaginae, except for Gala (Euoticus) elegantulus, hardly at all in Lor.sinae (except for Loris), in few nocturnal lemurs and also in some South-American monkeys (Cebus, Samiri and Aotus). There are at least five different hypotheses as to the meaning of this behaviour:

1. Moistening the soles for a better grip (Boulenger, (1936).
2. Cleaning of the plantar surfaces (Hill, 1938).
3. Odour trail for orientation (Eibl-Eibesfeldt, 1953).
4. Marking of a territory (Ilse, 1955)
5. Thermoregulation (Schmidt and Seistz, 1967).

Recently Charles-Dominique (1977) was able to show that Galago alleni displayed this behaviour on the border of its territory more than elsewhere, by using sophisticated radio-telemetry.

This short survey of studies concerned with prosimian olfactory communication, demonstrates the variety of signals involved in these behaviours, as well as the confusion which exists in their interpretation. The main reasons for the latter are:

1. Most of the studies were purely observational. Field observation usually only gives a suggestion of what is being communicated and in most cases an experimental approach is needed to determine the actual meaning of the signal.
2. Little attention has been paid to the chemical identification of scents. In a complicated communication pattern such as scent marking, experiments with artificial scents would be of great value. They would help to decrease the degree of false interpretation by isolating the response to a chemical signal from the numerous undefined factors that are involved in a communication pattern. Hopefully, comparing the responses of animals to natural and artificial scents will lead to an understanding of the contribution made by the different senses to a behavioural pattern.

1.2 Galago crassicaudatus

Galago crassicaudatus is the largest member of the subfamily Galaginae. This subfamily is distinguished from the subfamily Lorisinae by its mode of locomotion. Whereas the lorises are slow climbers with degenerate tails, the galagos are active, leaping animals. All the members of the family Lorisidae are strictly nocturnal and are found in Africa and Asia, while the members of the other prosimian family, the Lemuridae, are restricted to Madagascar. Three galago species G. demidovi, G. alleni and G. elegantulus are found in the central African equitorial forests, sympatric with the two African lorises, Perodicticus potto and Arctocebus calabarensis (Charles-Dominique, 1974). The remaining two galago species, G. senegalensis and G. crassicaudatus are found, often

sympatrically, in savannah and less dense forests in Africa. They have been studied together (Bearder and Doyle, 1974; Doyle and Bearder, 1977) and, in fact, the two species have very similar social structures and communication systems (Bearder, pers. comm.). However, G. crassicaudatus bears a greater resemblance to P. potto than to G. senegalensis in certain features such as karyotype, serological reactions and skin structure (Groves 1974). G. crassicaudatus and P. potto are similar in size and due to the fact that they occupy comparable ecological niches, do not overlap in distribution (Kingdon, 1971). In comparing the three species, Bearder and Doyle (1974) found the locomotion and feeding behaviour of G. crassicaudatus to be somewhere between the other two species, having characteristics of both.

G. crassicaudatus is a widely distributed species, being found on the East-coast of Africa from Somalia to Zululand, and spreading to Angola in the West (Kingdon, 1971). It shows considerable adaptation to different habitats, food sources, temperature ranges and humidity conditions. It is also able to adapt to changes made by man. It is found in a variety of plantations (Kingdon, 1971) and has also been found sleeping on roofs (Bearder, 1974). In parts of the range with a single rainy season, Kingdon (1971) found seasonal variations in the social structure. The animals were more gregarious during the breeding season and immediately after giving birth. He suggested that animals in tropical habitats which bred biannually would be more gregarious than those in savannah areas. [Correlations between social structure, density, habitats and seasons in mammals have been shown by Crook (1970), and in primates, especially in the more adaptive species such as Cercopithecus aethiops, by Eisenberg et al., (1972)].

Hill (1953) described eleven subspecies of G.crassicaudatus on the basis of their geographical distribution. Recently Dixson and van-Horn (1977) have suggested that

G. crassicaudatus crassicaudatus and G. crassicaudatus argentatus are actually different species.

This study was done on G. c. umbrosus, one of the three South African subspecies (Bearder and Doyle, 1974), which has characteristics which seem to resemble G. c. argentatus (Masters, pers. comm.). An important character used in this study is the existence of a prominent functional chest gland in G. c. umbrosus similar to that described by Clark (1975) for G. c. argentatus, which has not been found in G. c. crassicaudatus (Montagna and Yun, 1962).

G. c. umbrosus is the size of a small cat (± 1340 g.) males being slightly heavier than females. It is well suited to an arboreal, nocturnal existence, having a cryptic woolly coat, large eyes with a reflective tapetum lucidum, large foldable ear pinnae and a moist nose. The hands and feet have opposable thumbs for gripping. The long hind legs and a long bushy tail are adaptations for jumping (which can be up to five metres, pers. observ.). However it is more often quadrupedal, slow moving and prefers walking or running along branches to jumping. Concentrated glandular areas are found on the chest, chin, scrotum and labia. The genitalia and chest gland are covered with hair in young animals but are naked in adults and yellow droplets of secretion are often seen. In males the naked area on the chest is usually larger than in females (Clark, 1975). Recently Wheeler et al., (1977) identified 2-(p-hydroxyphenyl) ethanol in the chest gland secretion and Crewe et al.,(1979) have found two additional compounds (Table 10).

Until recently there had been no field studies on G. crassicaudatus, although some behavioural studies on captive animals had been undertaken. Buettner-Janusch (1964) described mating and maternal behaviour. Social interactions were studied by Roberts (1971), who found

old males to be dominant over younger males but no clear dominance relationships were found in females. Tandy (1974) found personal preferences in their social interactions and in a recent paper (Tandy, 1976) has described some of their vocal and olfactory signals. Research on the mating behaviour of G. crassicaudatus was undertaken by Eaton et al. (1973). They found differences between 'vaginal oestrus' and 'behavioural oestrus' in terms of days of receptivity. They also noticed an unusually long copulation for the species (several hours), a behaviour which was not explained. Recently Dixson (1978) has studied the behaviour of ovariectomized females treated with oestradiol and found it to be different from that reported for Old-World monkeys (Michael, 1975).

The most detailed study of olfactory communication in this species has been done by Clark (1975). Using the habituation technique (Harrington, 1974) she was able to demonstrate that, using scents, galagos are able to distinguish between individuals, sexes and subspecies. After observing the behaviour of a group of bushbabies in a zoo ('semi-natural conditions') she suggested that olfactory communication would be more important in indirect communication than in direct interactions.

Scent marking patterns have been described by Bearder (1974), Clark (1975) and Tandy (1976), although there are differences between the three authors in the naming and description of the behaviour. To prevent ambiguity, the terms I have used in this text are described in detail in Chapter 2 and illustrated in Figure 3.

The ecology and behaviour of G. crassicaudatus in the field was studied by Bearder (1974). He found that G. crassicaudatus 'were commonly encountered in dense evergreen bush, indigenous forests, tracts of evergreen bush and occasionally in open woodland or parkland'. In South

Africa and Rhodesia their population density varied between 72-125 animals/km^2. Their diet consisted of gum, fruits, flower secretions and insects. Mating took place in mid-winter (June/July), and the birth period was at the beginning of summer (November).

The basic social structure is the family group, consisting of a mother and her offspring. Adult males were generally seen alone but occasionally joined the family group. In the group studied by Bearder the young male left his mother's home range when approximately ten months old while the young female stayed with her mother until she was approximately sixteen months old and her mother had new infants. Eventually she left the original range too. The adult male and female home ranges were more or less unchanged during the two years of the study, but the male's home range was bigger and overlapped most of the female's home range. A single adult male associated with the adult female during this period of time. The maternal group's home range was found to be approximately seven hectares and different parts were used for sleeping and feeding in the different seasons. A small portion, about 4% of the area, was used constantly and almost exclusively in mid-winter, and was considered to be the 'core area'.

Communication between members of the group was mostly by direct contact where the animals groomed, played and slept together. Vocalisation was also found to be important for communication. Twelve different calls were distinguishable and were interpreted as alarm, social, cohesion, agnostic contact, etc. signals.

One call, the 'Cry' or 'loud call' has been described by Tandy (1974) as 'a series of notes first rising rapidly and then falling gradually in frequency and amplitude'. It has been suggested by Bearder (1974) that it is used to attract members of the social group to the adult male and to maintain distance between rivals. The cry is

usually made by males but also by females. (In captivity it has been given only by males - Tandy, 1976). I will discuss the meaning of this call in connection with scent-marking, particularly chest rubbing later.

Bearder (1974) observed all the different types of scent-marking in the social group he studied, but could find no clear association with communication.

It is suggested in this study that chemical communication based on chest gland secretions is more important in communication between individuals from different groups rather than in intragroup communication.

1.3 The aim and the plan of the study

The aim of the study was to analyse chemical communication in Galago crassicaudatus. Chest rubbing behaviour was selected for detailed study owing to the presence of chest gland secretion in sufficient quantities for chemical analysis.

The theoretical approach advocated by Smith (1977) as outlined previously, was adopted. Thus the chemical composition and physical properties of the chest gland secretion were studied first, followed by experiments in the laboratory and the field aimed at understanding the possible messages conveyed by the signal. Attention was directed to differential responses elicited by what was apparently the same signal and the influence of factors such as position of the mark, seasonal variation in responsiveness, and the previous experience of the receiver. This information was analysed together with observations of interactions between animals under natural conditions, in order to discover the meaning of the signal to a presumptive receiver galago.

My approach to the investigation of this problem was as

follows:

1. To study the social organisation and population dynamics of G. crassicaudatus in the field in order to produce a meaningful interpretation of chemical signals on a natural basis. As Bearder (1974), in his study of the social structure of this species, concentrated mostly on a single isolated group, I observed the interactions within a larger number of animals.
2. To study the responses of laboratory animals in an observation room under different conditions. This method was chosen in order to avoid the influence of previous scent marks on the responses of the test animals and to maintain a definitive set of conditions for all animals. Furthermore, the clean observation room imitates the natural 'olfactory environment' of the animal more so than a cage, where the saturated olfactory environment may screen the test odour.

It may be argued that moving the animal out of its cage to the observation room may change its 'excitement state' and as such, influence the results. However, as there is no definition of the 'basic excitement state' of an animal, it can reasonably be assumed that the same changes in the excitement state will be caused by the researcher on each occasion and thus this factor should not adversely influence the results.

3. To experiment with artificial scents in the laboratory and the field, in order to check the responses of recipients and compare these with their responses to natural scents. In order to investigate the meaning of the signal, an experiment was carried out in the field to determine the influence of the position of the scent mark on the responses of recipient animals.

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CHAPTER 2. MATERIAL AND METHODS

2.1 Field Observation

This study was conducted at a field site established by Dr. A.B.Clark in March 1976 (Clark, 1978b), in the Soutpansberg Mountains, Northern Transvaal, South Africa (Fig. 1).

The area is 960 m above sea level with summer night temperatures of 20-25°C (days 25-35°C) and winter night temperatures of 0-8°C (days 8-20°C). The average annual rainfall is 450 mm, falling mainly between October and April. In summer the relative humidity ranges from 50% to 80% whereas in winter it often falls below 40%. The indigenous flora is mostly bushveld which thickens to forest along the rivers. The study area consisted of a strip of riverine forest between cultivated and open fields. The trees are mostly Acacia sp. and Combretum sp., the average height being ten metres. The animals were captured using the method described by Bearder (1974) and marked on the tail for easy identification, as well as on the ears for more permanent identification.

During January, June and November 1977, short periods of time were spent in the area to test field observation methods. The method of observation used to obtain ecological and behavioural information from a small group of animals by following one or two members of a group (Bearder, 1974), proved to be unsuitable for the observation of a larger number of animals. As a result the alternative method of remaining at strategic sites which a number of animals usually passed, was adopted. During 1978, three periods of three weeks each, were spent at the field site, (during March-April, June-July, and



Figure 1. The field site in the Soutpansberg mountains, view from south.



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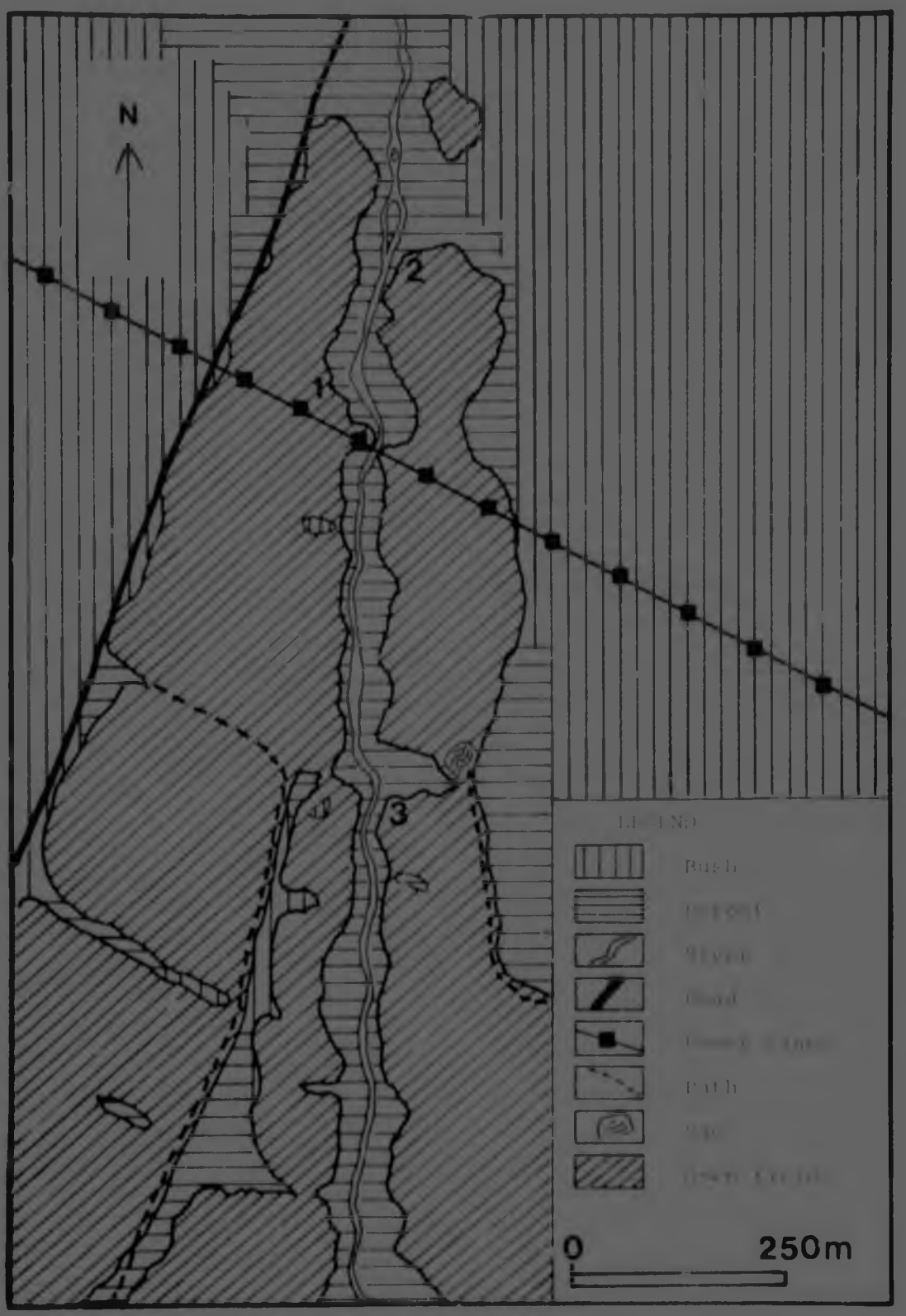
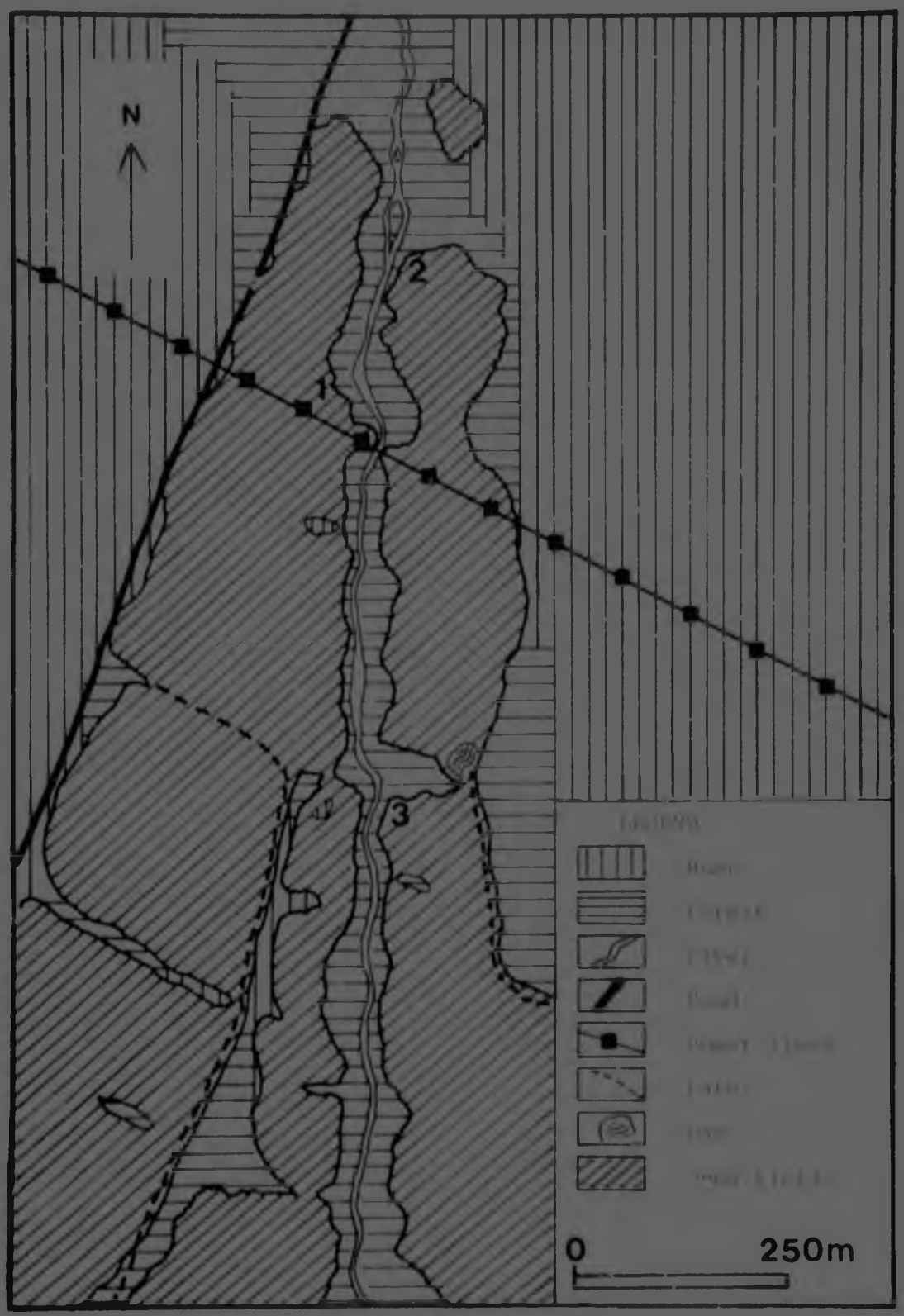


Figure 2. A map of the study area: 1, 2 and 3 were observation sites.



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September), for observation and experimentation. In March-April and June-July observation site 1 (Fig. 2) was chosen for most of the observations. This is an area rich in gum-producing Acacia trees. Many animals, usually alone or in small groups, passed through the area during the night. During September, observation site 3 was used for experimentation. The animals were observed in the red light of a head torch, and field notes were immediately recorded in a note-book. Food bait was used to entice the animals closer for identification, and control observations were made without bait.

2.2 Scent-marking patterns

Scent-marking behaviour in G. crassicaudatus is usually divided into five categories:

1. Chest rubbing: The animal rubs its chest against an object, usually vertically in a forward/upward direction (Fig. 3a). Bearder and Doyle (1974) have suggested that this may be important in territoriality.
2. Anogential rubbing: The animal drags its anogenital area on an object or merely touches the object a few times with its genitalia (genital rubbing). This behaviour often follows chest rubbing in males (Fig. 3b).
3. Hind-foot rubbing: Named leg rubbing by Bearder and Doyle (1974). The hind-foot is rubbed back and forth on the object with the animal often biting the edge of the object at the same time (Fig. 3c).
4. Face rubbing: This behaviour is probably composed of a number of different displays which are dealt with together in this study. The animal may rub the edge of its mouth (mouth rubbing) on the object, followed by rubbing with the head and ears (head rubbing), or alternatively, the cheeks and the chin (cheek rubbing, chin rubbing) (Fig. 3d, e).



Figure 5. Scent marking in G. crassicaudatus: a. Chest rubbing. b. Genital rubbing. c. Hand-foot rubbing. d. Mouth rubbing (face rubbing). e. Head rubbing (face rubbing). f. Urine washing.

5. Urine washing: This is a behaviour common to many prosimians (Andrew and Klopman, 1974). The animal raises its hind foot, sole upwards, holds it in the hand of the same side, and then urinates on the hand and the sole while rubbing them one against the other (Fig. 31). This behaviour is then usually repeated on the other side. Other ways of urination were also observed, namely; rhythmic micturation and spontaneous urination.

Combined rubbing displays were often observed and are referred to as complex marking in the text. The most complex pattern observed started with mouth rubbing then chin rubbing, chest rubbing, genital rubbing, hind-foot rubbing and biting. Urine washing was not observed in combination with other scent markings.

2.3 Collection of c[illegible] gland secretion

The chest gland secretion was collected in capillary tubes (Fig. 4), while the animal was held in a restrainer (Fig. 5). Collection of the secretion in capillary tubes has the advantage of keeping the secretion unchanged as it comes out of the animal. Holding an animal in the restrainer while collecting the secretion has been found to be less disturbing to it than handling with gloved hands.

To get the animal into the restrainer, it is caught by the tail. The animal then pulls forward and the restrainer without the lock is put over it. The animal responds by pushing its head and arms out of the front opening thus enabling the lock to be put into place and the nuts tightened (Fig. 6a). The feet may be held in the special holes as seen in Fig. 6b.

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Figure 4. Collection of chest gland secretion in a capillary tube.

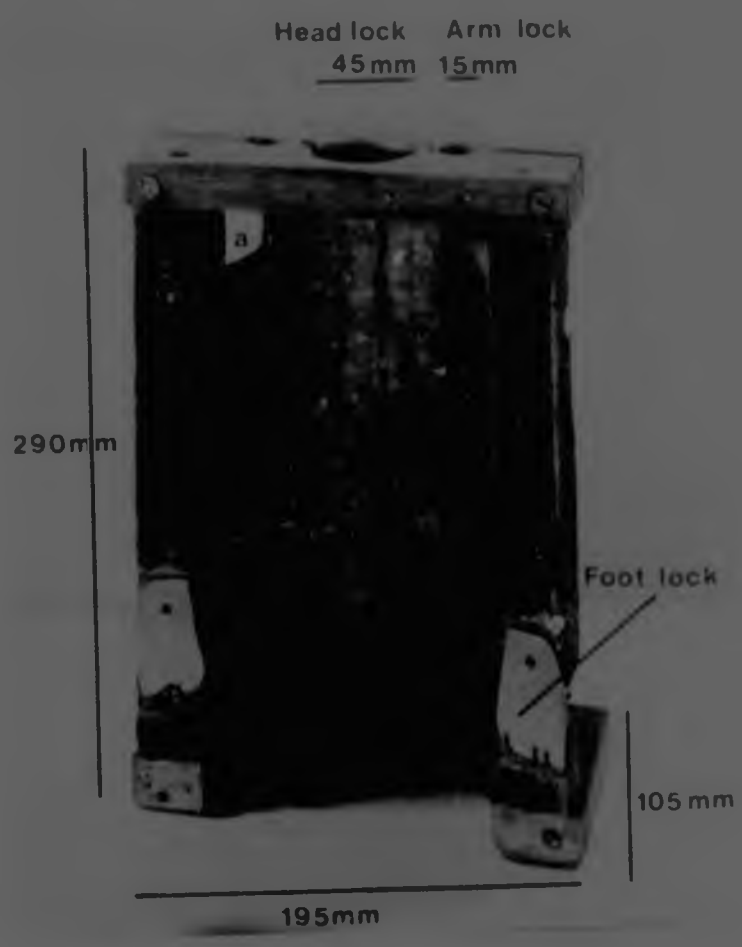

Figure 5. The restrainer used for immobilising the galagos with the ventral surface uppermost to facilitate collection of chest gland secretion.



a. b.

Figure 6. Animals immobilised in the restrainer.

2.4 Oestrous cycle

The oestrous cycles of three G. crassicaudatus females were followed from June 1977 to June 1978. Vaginal smears were taken regularly once a week, and on every second day when the animal was in oestrus The smears were stained according to Greenstein (1964) and classified into one of five categories, according to Eaton et al. (1973). The results are summarised in the appendix.

2.5 Experiments in the laboratory

The experiments were performed using G.c.umbrosus maintained by the Primate Behaviour Research Group, University of the Witwatersrand. Two to six animals were kept in room cages under a reverse day/night light cycle (Doyle, 1974). The red light illumination was turned on at 12.00 hours. Observations were all started at 16.00 hours and ran for a forty-minute period. The test animal was put into a clean observation room 175 x 175 x 200 cm (Fig. 7), and was observed from behind a one way glass window. Every time the animal scent marked, the time and the place of marking were immediately recorded in a note book. Sniffing and licking behaviour were not recorded unless they were exceptionally frequent. Polyethylene pipes were used in the observation room and were cleaned with soap and hot water (Clark, 1975) after each observation.

Five animals were used.

♂O 8 years old (caught as an infant).
♂H 3 years old (caught as an infant)
♀V 10 years old (approximately).
♀J 8 years old (caught as an infant).
♂G 8 years old (caught as an infant).

All these animals had been caught in the wild and were maintained in the laboratory. Each animal (with the exception of V and G who shared a cage) lived in a different cage with different cage mates. ♂G was missing



Figur 7. Interior of the observation room showing arrangement of pipes (A) and shelves (B).

both hands and was used as a scent donor.

The experiments were done on an individual basis, the results of each being compared with its own control.

In the first experiment the responses of the galagos to a clean observation room were recorded. Thirty observations were made between August 1977 and August 1978 on ♂O, twenty-seven on ♂H, nineteen on ♀V and sixteen on ♀J.

Complex marking behaviour was dealt with separately.

2.6 Experiments with artificial scents

2-(p-hydroxyphenyl) ethanol and p-hydroxybenzyl cyanide were purchased from Aldrich Chemical Co. Milwaukee, U.S.A. and benzyl cyanide was obtained from the university chemical store. For analysing their volatile properties 10 mg of each compound was dissolved in 1 ml of diethyl ether (Proter A.R.). 5 µl of this solution was applied to a filter paper disc (Whatman No. 1 qualitative) 5.5 mm in diameter, and weighed at successive time intervals, on a Mettler ME 22 microbalance. A disc to which 5 µl of ether had been applied was used as a control. Each experiment was repeated three times. The temperature during the experiments varied between 24° - 26°C and the relative humidity between 50 - 70%.

For field experiments, standard solutions of these compounds were prepared in dichloromethane (Merck) with a concentration of 1 mg/ml, and the mixtures (Table 11) were made using these standard solutions. Ten µl of artificial scent were applied during each test. During the March-April observation period, the chemicals were applied to polyethylene pipes, similar to those used in the observation room. These pipes were attached to trees (No. 10, 12, 29 and 30, Fig. 8) at observation site 1. Pipes which had been left in the cages of laboratory animals for

a week were also tested. (These were packed in polythene bags for transport.) The experiment was repeated for nine nights and each night the control pipe was cleaned, the artificial scents renewed and a new laboratory conditioned pipe put in place. In September the scents were applied directly to trees at various positions at observation site 3 (Fig. 9). (Tree 1 - on the regular route used by the animals, tree 2 - on the regular route and on a branch close to the ground, tree 3 - on a branch close to the ground). The experiment was repeated three times, every third night, and dichloromethane was used as a control scent.

The scents were applied to the trees or the pipes at sunset (18.15). Sniffing and marking behaviour was recorded on each occasion.

CHAPTER 3. RESULTS

3.1 Field study

The social structure and population dynamics as deduced from observations of the animals in the field site (Fig. 1) are given below:

Table 1 indicates the animals that were seen at the field site during the entire study, their ages, relationships and the last date on which they were seen. The animals which were adults at the beginning of the study were permanently present in the area. However young animals eventually left the area or died. Young males tended to leave their mothers' home ranges at an average age of 14 ± 8 months, while young females remained for a period of, on average, 18 - 28 months. (♀Ma probably gave birth in the area before disappearing). Between siblings, it seems that one brother (or sister) leaves the area a considerable time before the other, e.g. Al and N, Ke and Ti.

Table 2 summarises the movements of animals through observation site 1 during the March-April observation period. Two relatively stable groups were often seen at the site; ♀D and her two, four-month-old offspring, A and T, comprised one group and the other group consisted of ♀M and her infants, Je and To. The ♀D group was most frequently observed in the site, almost always seen together and were usually the first animals to arrive at the site, which suggests that their sleeping sites were not far away. The second family group - the ♀M group - visited the site on different nights or at least at different times of the night from the ♀D group. On the one occasion that D and M were observed to meet (e.g. on 76.3) they were antagonistic to each other. Towards the end of the observation period, the ♀M group started to

Table 1. Marked animals observed in the study area. Data before August 1977 was obtained from A.B. Clark (Pers. comm.). Animals still in the area at the end of September 1978, the end of the study, do not have a date in the last column.

No.	Name	Born	Mother	Date last seen
1	♂ B	Adult		
2	♀ D	Adult		July 1978 *
3	♀ M	Adult		
4	♀ G	Adult		
5	♀ K	Adult		
6	♂ J	Nov. 1974 ?		
7	♂ C	Nov. 1974 ?		July 197[illegible]
8	♂ P	Nov. 1975 ?		June 19[illegible]
9	♀ Jc	Nov. 1975	K	
10	♂ Po	Nov. 1975	D	Nov. 1977
11	♀ V	Nov. 1975	D	Aug. 1977
12	♀ Ma	Nov. 1975	D	March 1978
13	♂ Ax	Nov. 1975	M	Feb. 1977
14	♂ Pb	Nov. 1975	M	March 1977
15	♂ Al	Nov. 1976	D	Nov. 1977
16	♂ N	Nov. 1976	D	June 1978
17	♂ Ke	Nov. 1976	M	Nov. 1977
18	♂ Ti	Nov. 1976	M	May 1978
19	♂ Gr	Nov. 1976 ?		May 1978
20	♂ Br	Nov. 1976		Aug. 1977
21	? U	Nov. 1976		
22	♂ A	Nov. 1977	D	
23	♀ I	Nov. 1977	D	
24	♂ Io	Nov. 1977	M	July 1978
25	♂ Je	Nov. 1977	M	
26	♂ Mo	Nov. 1977		
27	♂ L	Nov. 1977		
28	♂ R	Nov. 1977	Ma ?	
29	♀ Q	Nov. 1977	Ma ?	March 1978

* D was ill in July 1978, and presumably died from a disease caused by a Rickettsia-like organism found in a blood smear.

Table 2. Movement of bushbabies at observation site 1 during March-April 1978. + = identified in the observation site, - = identified in observation site 2 (Fig. 2), +) = identified near the observation site, (+) = doubtful identification. _____ = animals foraging together, ↑+ = come from south, ↓+ = come from north, +← = come from east, +↑ = go to north, +↓ = go to south.

Animal	M	Je	To	I	A	D	N	Ti	Gr	C	J	B
Date	?	♂	♂	♀	♂	♀	♂	♂	♂	♂	♂	♂
21.3				(+)	(+)	(+)	↑+↓	+←	+)	↓+↓		
22.3				(+)	(+)	(+)	+↓				+)	
23.3	↓+	+	+									
24.3				-	-	-	↓+	-				
25.3				↑+	+	+	+					
26.3	↓+	+	+	↑+	+	+↑	↓+	+	+	+)		
27.3				-	-	-	↓+		↓+	(+)		
28.3	↑+	+	+↑				-					
29.3	(+)	+←	↑+↑				↓+			-	(+)	
30.3				↑+	+	+		-	↓+	+		
31.3	+	+←	+←	+			↓+	+)			(+)	
1.4				↑+	+	+	+					
2.4				↑+	+	+		-				
3.4	-	-	+	+	+	+↑		+				(+)
4.4							↓+	↓+↓		↓+↑		↓+↑
5.4	+←	+←	↑+	+	+	+↑	↓+↑				↓+↑	(+)

break up and began foraging independently. ♂Io was seen foraging with the ♀♀ group.

The other animals that passed the site were all males. They can be classified according to age, as juveniles (N, Ti and Gr), subadults (C and J), and an adult (B). The young males were usually seen alone but occasionally formed a group, or joined a family group. The subadults C and J appeared at the site on every fifth or sixth day, which suggests that their usual foraging route is much longer than that of the other animals. Male B tended to remain in the area after first appearing on the 29.3.78. He was not marked during this observation period and as a result his identification is in some doubt. However, it was assumed to be ♂B because of his characteristic behaviour and appearance. He had an enormous chest gland and most of the cr es heard originated from him.

The animals used to pass the observation site along a regular route (fig. 8) and to stop, sniff and scent mark at particular places (marking stations). The three most interesting observations from this period, which may be important in the interpretation of chemical signals are given in detail:

26.3.78

18.40 Three bushbabies, O, A and I appeared from the south and began feeding. The young sniffed and chest rubbed on the marked plastic pipe between tree 29 and tree 30, (pipes were connected to trees 10, 12, 29 and 30 for the experiment which is described later). Then all started grooming each other on tree 29.

19.45 Continued to north, following the regular or main route.

19.50 N, Gr and Ti appeared from the north. N urine washed on tree 13 (marking station). Then Gr and Ti stopped and urine washed at the same spot. Ti sniffed and bit the marked pipe on tree 12.

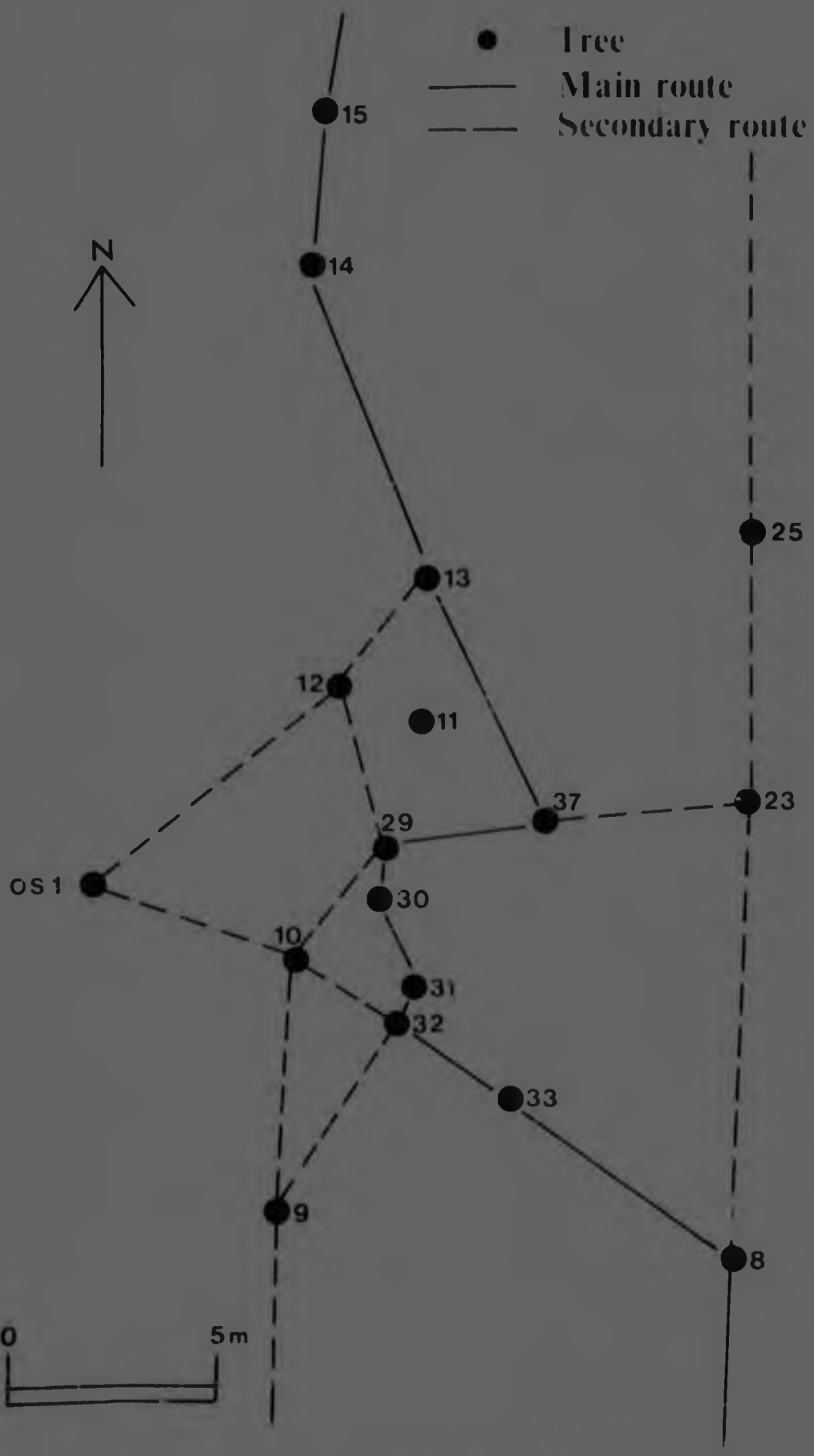

Figure 8. Plan of observation site 1 (OS1). Trees that are numbered are referred to in the text.

20.30 The three groomed and played together.

20.40 Bushbabies heard screaming in the north. (Group ♀D meeting group ♀M).

21.00 M, Je and To appeared from north.

4.4.78

19.10 Ti appeared from the north. Feeding followed by grooming on tree 12.

19.40 Continued to the south following the main route.

19.45 B(?) came from north. A large animal with a very large chest gland and wounded right hind foot, (he moved on only three feet). He sniffed the marked pipe on tree 10 and chest rubbed high on the tree (marking station).

20.00 N appeared from north, grooming with B. B continued to south.

20.15 C appeared from north. Fed until he reached tree 10 then turned back to the north.

21.00 B reappeared from the south.

5.4.78

18.20 D, A, I and To appeared from the south. D urine washed on tree 32 (marking station). They all fed then groomed in tree 13.

18.40 Cry of bushbaby from north.

19.00 The four left, heading north.

19.15 Je appeared from the east (tree 23). Continued to the north following the main route.

19.30 M appeared from the east. Fed until she reached tree 32 then turned south.

20.00 B appeared from the north.

20.15 N and J appeared from the north, groomed on tree 37. N approached B and they groomed on tree 23. J approached B and started the 'meeting ceremony' with him by sniffing muzzle to muzzle, but then moaned (Bearder, 1974) and returned to tree 37.

21.00 N and J continued to move towards the south.

Nine other animals were seen in other parts of the study area but never at observation site 1. ♀G was seen at observation site 2, ♀Ma (?) and her infants R and Q across

the field on the east side, and five animals to the south of the power lines (Fig. 2). The latter five animals appeared in the area very close to observation s te l on the night of 25.3.78 and were chased back to the south by the ♀D group and ♂N, after a fight lasting half an hour. The fight involved much screaming, ending with one cry. The five animals were not identified at the time but from later experience they were probably ♀K or ♀Jc and juveniles.

During this observation period there was no detectable difference between observat ons using food bait and observations without bait, either in the number of animals that visited the observation site or the time that they appeared and spent at the site.

The observations during June-July 1978, focused on the changes in social structure and behaviour during the mating season. The mating season of G. crassicaudatus in South Africa is the middle of winter. The weather is very cold and dry, with temperatures often falling below 0°C at night. The gum on most trees was dry and the bushbabies were often seen foraging on the ground. The Combretum trees, the favoured sleeping trees, were dropping their leaves and the bushbabies changed to sleeping in Acacia trees. As a result the sleeping places could often be located during the day. Female D moved to sleep at observation site 1 which was presumably part of her core area.

Five main changes in social organisation and behaviour were noted.

1. The young males N, Ti and Gr had disappeared (Table 1).
2. There was an increase in crying and marking behaviour.
3. Males behaved aggressively towards each other. Male B showed dominance and chased other adult males from observation site 1.
4. Females in oestrus were tolerant of males and

females. ♀D and ♀M were seen grooming and sleeping together.

5. Young animals born in November 1977 began foraging independently, although they sometimes slept with their mothers.

Vaginal smears (see appendix) were taken from females Jc, M, G, D and T and all were in oestrus except T. The other four came into oestrous within a few days of each other, starting with M then Jc, G and lastly D.

Female D was the bushbaby that had been studied most at the site (Clark, pers. comm.), and it thus seemed obvious to investigate her oestrus and mating behaviour in detail. Unfortunately she became ill on June 28th, her third day of 'oestrous behaviour' (Eaton et al., 1973). She stopped eating and spent long periods of time on low branches, behaviour never observed in healthy animals. She failed to display the mating posture (Eaton et al., 1973) when investigated by males and on 30.6. was found shivering in a feverish state on a low branch. She was taken to a veterinarian who found a Rickettsia-like organism in the blood smear using a Stevenel stain. She remained in my care for a week and was fed Oxytetracycline mixed with bananas and milk, but unfortunately the observation period came to an end, and on 7.7. she was returned to the field. Observation for three days showed no improvement in her condition and she is presumed to have died as she has not been seen since.

The behaviour of males towards her did not however, seem to be influenced by her illness. She was still attractive to them and they tried, albeit unsuccessfully, to mate with her. There were many interactions between the males that followed her which are important for an analysis of the communication in this season. Below are the details of the first two days observations on ♀ D's oestrous behaviour when she was still behaving naturally.

26.6.78

During the day ♀D was sleeping in the extreme north of her home range and returned that evening to the observation site followed by males.

18.00 Early observation at observation site 2: Bush-babies arrived from north-east. A, then D followed by B, who sniffed her genitalia when they stopped moving. Fourth animal Je. All moved to the south.

18.15 J from north, continued to the south. I then moved to observation site 1.

18.55 A arrived from the north, followed by J. J chest rubbed on tree 32.

19.10 M appeared and foraged on the ground.

19.15 Je arrived from the north. J went to the south.

20.15 D and B approached the observation site. Cry from south (J). B looked to the south and gave answering cry. B started calling before the end of the cry from the south. The cry has 'preparative' notes, weaker in intensity than the cry itself. B's body rocked throughout the call.

20.20 B groomed his genitalia and urine washed.

9.30 Cry from south, B answered immediately.

21.00 All the animals left in a southerly direction.

27.6.78

B and D slept on tree 13.

17.50 Je arrived from the north, proceeded south.

18.15 J arrived from the south. Chased Je who screamed. B approached J. J screamed and retreated.

19.10 A and I passed by, moving from south to north. B and D remained in tree 13. J on tree 32 (Fig. 8) gave a preparative call which did not develop into a cry. J chased \ who screamed. J repeated the call and proceeded to the north.

19.45 M appeared and fed. B and D moved north. I followed them.

21.00 B licked D's genitalia and attempted to mate. J approached and B stopped mating to chase away. J moved round D in a circle, but B always remained

between them. Hind-foot rubbing by B caused J to retreat. J always retreated when B approached, but as soon as B returned to D, J returned.

22.00 J moved southwards giving the preparative call and chased Je who was approaching from the south.

On 29.6. B was seen mating with D for a considerable length of time (½h), which was the fourth day of her behavioural oestrus. On 30.6. B had gone to the far south of the study area and J mated briefly with D who was removed later in the night. J was at the observation site when B cried from the south. He then turned northwards and was not seen again at the observation site during this particular observation period.

The movements of animals in the observation site during this period, June-July, are summarised in Table 3.

An interesting occurrence was noted on the 4.7. - four days after D was removed from the field. G who had never been seen before at observation site 1 appeared. No females were in oestrus at that date. Details of the observation are as follows.

4.7.78

M, A and I were sleeping near the northern side of observation site 1.

17.45 A and I moved to the south. M approached, fed then returned to the north.

18.00 Je approached, fed, moved northwards. B approached, to tree 10.

18.15 C appeared from the south following the main route and stopped in tree 29, started knocking (Bearder, 1974). B climbed tree 10, chest rubbed and approached C who fled screaming. B chased C to the south and cried.

18.25 B foraged on the ground.

18.35 M and Je approached. B began genital rubbing, approached M who screamed and fled. M approached

Table 3. Movement of bushbabies at observation site 1 during June-July 1978. + = identified in the observation site, - = identified in observation site 2 (Fig. 2), +) = identified near the observation site, (+) = doubtful identification, _____ = animals foraging together, _ _ _ = sleeping (together) in observation site 1, _._._ = sleeping together in observation site 2, ↓+ = come from north, +↓ = go to south, ↑+ = go to north. D was taken out of the field on 30.6.

Animal	To	Je	M	I	A	D	B	J	C	G
Date	♂	♂	♀	♀	♂	♀	♂	♂	♂	♀
20.6					+↑	+		(+)		
21.6				_+↓	_+↓	_+↑	↓+↓			
22.6		(+)	_-_·_-_·↓+_·↓+_				↑+			
23.6		↑+	+)	_+↓	_+↓	_+↑				
24.6	+)		+)	_+↓	_+↓	_+↑			↓+↓	
25.6	+)		+)	_+↓	_+↑	_+_				
26.6	+)	↓+↓	+	+)	↓+↓	↓+ +↓		↓+↓		
27.6	+)	↓+	↓+	↑+↑	↑+↑	+ +↑		↑+		
28.6			+	↓+	↓+	+) +		+		
29.6	+			↓+	+	+) +		+		
30.6	↓+	+)	↓+	↓+	↓+	+)	↑+	↓+↑		
1.7	_+_	_+_	_+_	+	_+_		_+_			
2.7			+		+		+			
3.7			_+_	_+_	_+		_+_			
4.7		↓+	_+_	_+↓	_+↓		↓+		↑+↓	↓+↑

again to feed. B followed h , she stopped feeding and approached him. M and B fought (a fight with only the hands, no biting). Some screaming from M, whereafter she gave up, and B descended to feed. Je on tree 10 chest rubbed at the same place B had marked.

19.20 Bushbaby G appeared from the north. B approached her and sniffed her. G jumped and threatened him. B genital rubbed on tree 10 and then urine washed and groomed his genitalia. G chest, genital and hind-foot rubbed at the same place.

19.30 B and Je groomed together, M approached G moaning, sniffed G nose to nose, attacked G and chased her to tree 32. G screamed. Je approached, groomed G and then groomed M. B also approached.

19.40 M and G started to fight again, G seemed to be wounded on the hind foot and moved slowly to the north. A cry from tree 32 (either M or B). Je groomed G.

20.30 All four moved to the north. Screaming from the north.

21.00 M, B and Je returned to the observation site.

During the observations with and without food bait, no difference was observed in the number of animals and the time at which they appeared at the observation site. The time spent at the site was, however, longer when food bait was used. The tendency of M and B to sleep near the site towards the end of this observation period was apparently due to the presence of bait.

September in South Africa is the beginning of spring. Although in 1978 no rain had been recorded by that time, the trees on the fringe of the forest started to come into leaf and bloom, (small low bush and Combretum). The Acacia trees started producing gum in quantities again, (this is dry during the day but is wet and starts to flow at night), and insects were attracted to the blooming

trees. The bush away from the river, however, was still dry.

The bushbabies appeared at observation site 1 late in the evening or not at all. M retained her old core area (near observation site 2), and if she appeared at observation site 1 it was at about 21.00, which indicated that her sleeping place was far from the site. A and I were sleeping in the field to the east and usually crossed the open field in the vicinity of the power lines (Fig. 2). B was not seen at all near observation site 1, and J was seen only once. These movements are summarised in Table 4.

The main purpose of the September field study was to perform some experiments with artificial scents. As very few bushbabies appeared at observation site 1 and then only late in the evening, this site was no longer suitable for experimentation. Instead, observation site 3 (Fig. 2) was used, where seven or eight animals were seen in the early evenings. These included ♀Jc, ♀K, ♂M, ♂I, and U (marked animal which was not identified), one or two unmarked animals and ♂P. These animals usually moved in groups of three to six, the members of a group changing nightly. Their sleeping sites must have been in the immediate vicinity as they appeared directly after sunset. Later in the evening at about 21.00-22.00 they were sometimes seen near the power lines, south of observation site 1.

Most of the observations at observation site 3 were made during experimentation with artificial scents, and will be discussed later. Some of the observations made in the absence of artificial scents are interesting as far as chemical communication is concerned. These are given in detail below.

16.9.78

18.25 U came from south.

18.55 Mo and B arrived together. B marked on tree 1

Table 4. Movement of bushbabies at observation site 1 during September 1978. + = identified in the observation site, +) = identified near the observation site, _____ = animals foraging together, ↑+ = come from south, ↓+ = come from north.

Animal	A	1	M	Je	J
Date	♂	♀	♀	♂	♂
7	↑+	+)	↓+		
8	↑+				
9			+		
10	+)	+)			
11					
12	+	+	+	+	
13					
14		+	+)	+	
15	+	+	+		
16	+				
17			+	+	+

(marking station, Fig. 9, also Figs. 18 and 19). Almost every bushbaby that passed this place (which is on the main route) sniffed or marked it. B also chest rubbed a point on tree 2, another common marking place.

19.00 U and Mo played on tree 5. Jc approached, K following. Jc approached U and chased it. U screamed and fled to tree 1 and stopped after passing the marking station. Jc stopped at the marking station and urine washed. Moved back to tree 5. During the fight K squawked (Bearder, 1974) and kept her distance.

19.30 Mo groomed Jc. K approached together with L.

17.9.78

Late observation. Unmarked animal appeared from the south. Chest rubbed on several branches which were not usually marked. It also genital and hind-foot rubbed, and bit the end of a branch.

20.30 Cry from the south (B). The unmarked animal looked southwards and again marked and bit branches.

20.40 Moved to the east, not on the usual route, across to the east of the dam.

On 19.9 B, Jc and U were foraging together. B was fighting continually with Jc. This usually occurred on a gum lick and B seemed to dominate Jc with regard to the food. Between fights all three groomed together.

On 23.9 U arrived at the site first. It left the area using a route other than the main one. The only marking behaviour noticed was urine washing. The other animals which appeared five or ten minutes after it, all chose the same route. The movements of this group in observation site 3 are summarised in Table 5. Note that all the animals arrived from the south.

The home ranges of the adult galagos constantly present in

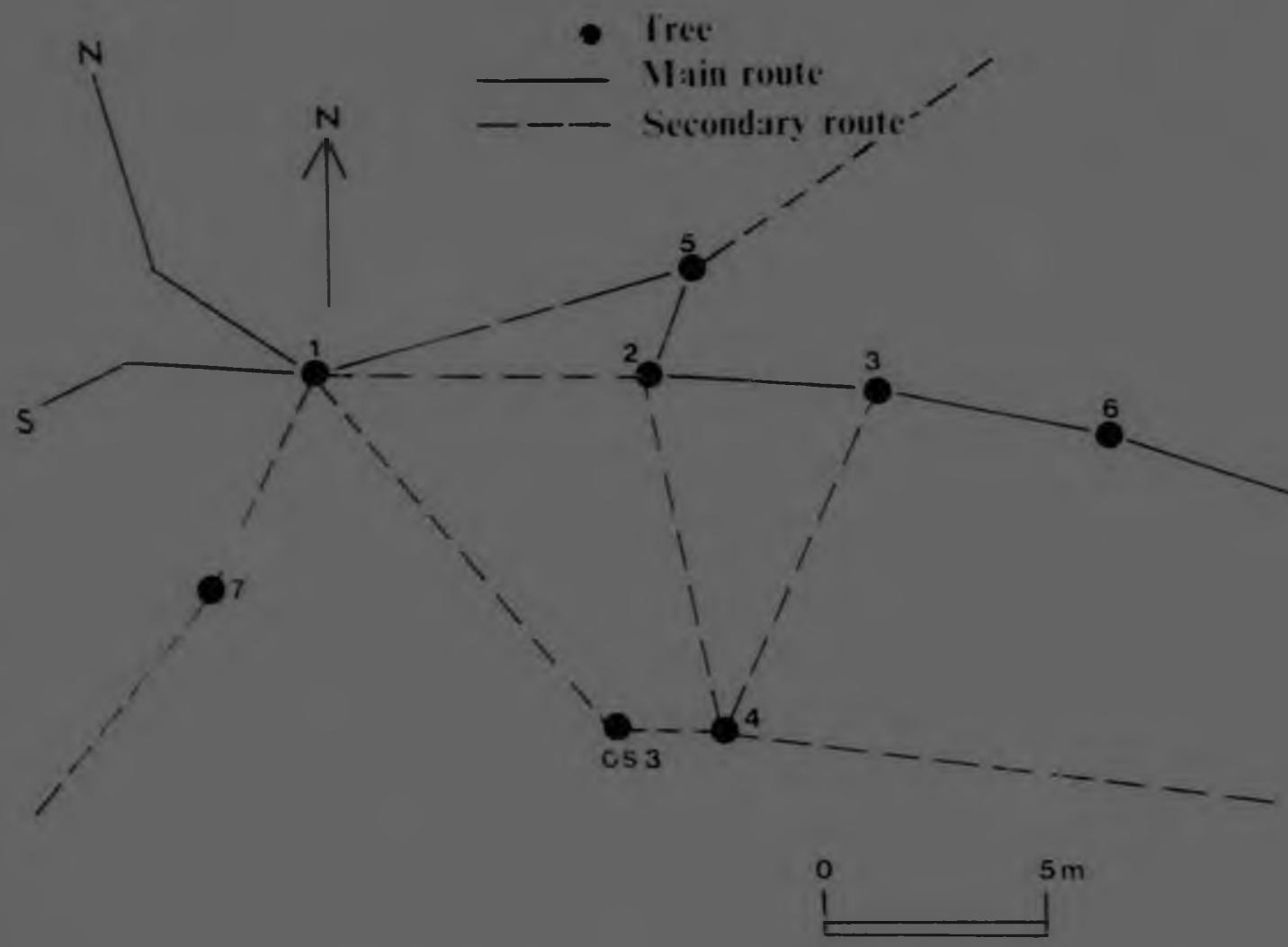

Figure 9. Plan of observation site 3. (OS3). Trees that are numbered are referred to in the text.

N : north
S : south

Table 5. Movement of bushbabies at observation site 3 during September 1978. + = identified in the observation site, (+) = doubtful identification, _____ = animals foraging together, ↑+ = come from the south, +↑ = go to north, ∓ = go to east.

Animal	K	L	unmarked	Jc	B	U	Mo	unmarked
Date	♀	♂	1	♀	♂	?	♂	2
15				↑+	↑+	+	+↑	
16	↑+	+		+	↑+	↑+	↑+	
17				↑+	+)	↑+	↑+↑	↑(∓)
18	↑+↑	↑+		↑+↑	↑+	↑+	↑+↑	
19	↑+↑	↑+		↑+	+	+↑		
20	∓	+		+	+	+	+	
21	↑+↑	↑+	(+)	+	↑+↑	↑+	+↑	
22	↑+			↑+	+)	↑+	↑+	
23	↑+			↑+	↑+	+↑	↑+↑	
24	↑+			+	+	+↑	↑+↑	

the area were assessed by marking all the places a particular animal was seen during the study, on a map. The four adult females and ♀Jc lived in three distinct home ranges which overlapped slightly (Fig. 10a). ♀K and ♀Jc were probably mother and daughter (Table I), but the relationship between ♀M and ♀D was unknown. Females from different home ranges fought when they met in a territorially defined area, but were often tolerant in the overlapping areas of their ranges (e.g. when ♀D, M and G met at observation site 2).

The home range of ♂B was large and overlapped those of the five females (Fig. 10b). As he was present in only part of his range at any one season it would be better to call this area '♂B controlled area', and to call ♂B the resident male.

The other males in the area could be divided into two groups: a) Juveniles: These were approximately 6-22 months old, foraged mainly in their mothers' home ranges and were tolerated by the resident male in any season. b) 'Vagrant males': These were approximately 1½ - [illegible] years old and as they appeared in the area only occasionally were assumed to have a very large home range. They were tolerated by the resident male only in summer (November-May). ♂J and ♂P used parts of ♂B's control area when he was not in the vicinity; however, when ♂B returned, they moved away. In September 1978, ♂J seemed gradually to establish his own control area in the north (Fig. 10).

Females did not have a vagrant stage and migrated after the juvenile stage in one direction only.

The social interactions between the animals showed seasonal variation. Females were more aggressive to other females in the summer (November-May), while the resident male was tolerant of other males. In winter, particularly

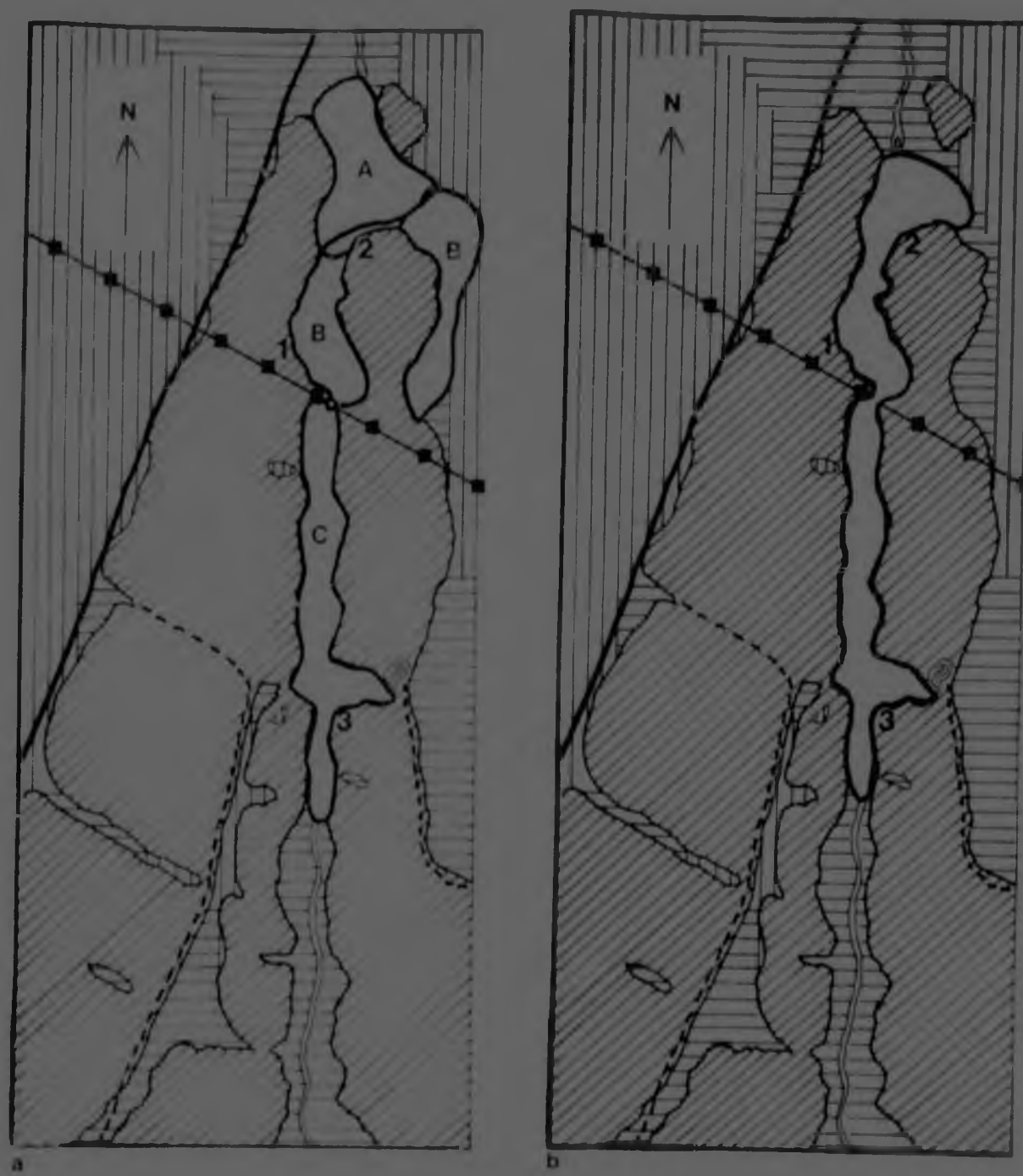

Figure 10. Home ranges of adult C. crassicaudatus in the study area. a. Home ranges of females: A = ♀G; B = ♀D and ♀M; C = ♀K and ♀Jc. b. Control area of ♂B. (Legend the same as Fig. 2).

in the breeding season, females were less aggressive when in oestrus while males were more aggressive to each other. At this stage the resident male was clearly dominant.

3.2 Laboratory Experiments

Experiment 1. Observations of scent marking in clean observation room. The scent marking behaviour of ♂0 over thirty observation periods is summarised in Table 6. It is clear from Table 6 that chest rubbing is the most common marking behaviour of ♂0. The number of occurrences of chest rubbing in each of the thirty observations throughout the year is shown in Fig. 11. There were no seasonal changes in his marking behaviour, (although seasonal changes were noticed in the amount of chest gland secretion produced). The distribution of chest rubbing was closer to normal than for all other types of marking behaviour, and is shown in Fig. 12.

The animal was always very active at the beginning of the observation period, and investigated the room by sniffing and licking objects. Most of the marking behaviour was done in the first twenty minutes of the observation period. Towards the end of the observation period the animal was more relaxed and spent more time on grooming and toilet behaviour. Fig. 13 gives the kinetics of chest rubbing during the observations and shows that almost 70% of the markings were done in the first twenty minutes. Fig. 14 gives the kinetics of urine washing and shows that almost 80% of this was done in the last 20 minutes of observation. Urine washing in this experimental situation, does not seem to have a communicatory function.

The marking behaviour of ♂H is summarised in Table 7. Chest rubbing as in ♂0, was the most commonly observed marking behaviour. This animal was generally more active than ♂0 and marked more often, but hind-foot rubbing was

Table 6. Number of scent marks by ♂♂ in a clean observation room over thirty observation periods of 40 minutes each.

Marking behaviour	Total No. of occurrences of the behaviour	Mean No. of / occurrences/observation / period
Chest rubbing	453	15.1 ± 8.2 *
Hind-foot rubbing	202	6.7 ± 12.4
Face rubbing	116	3.9 ± 4.2
Anogenital rubbing	67	2.2 ± 6.2
Urine washing	54	1.8 ± 2.8

* mean ± the 95% confidence limits.

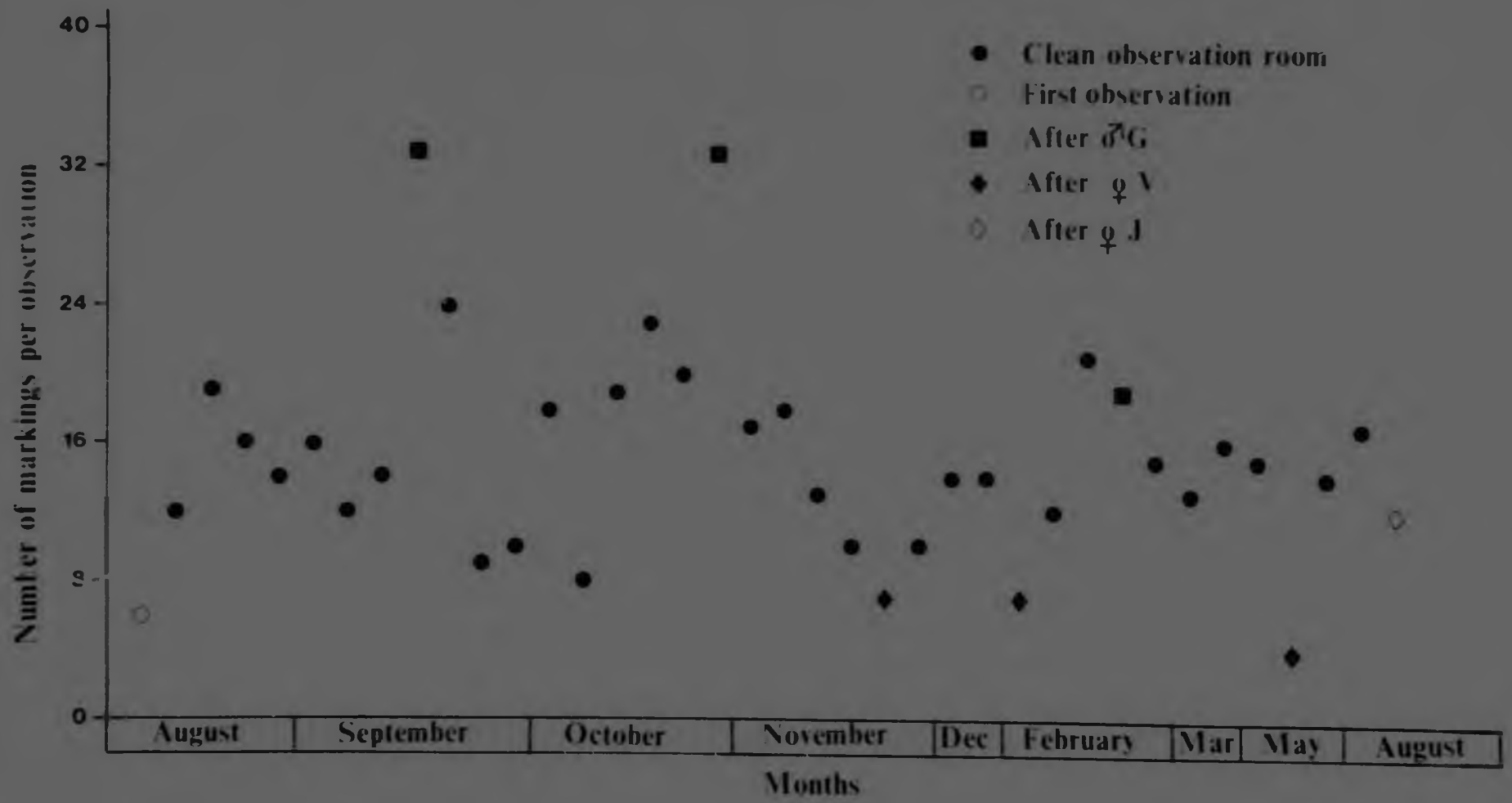

Figure 11. Chest rubbing of ♂0 in the observation room during 40 minute observation periods, conducted between August 1977 and August 1978.

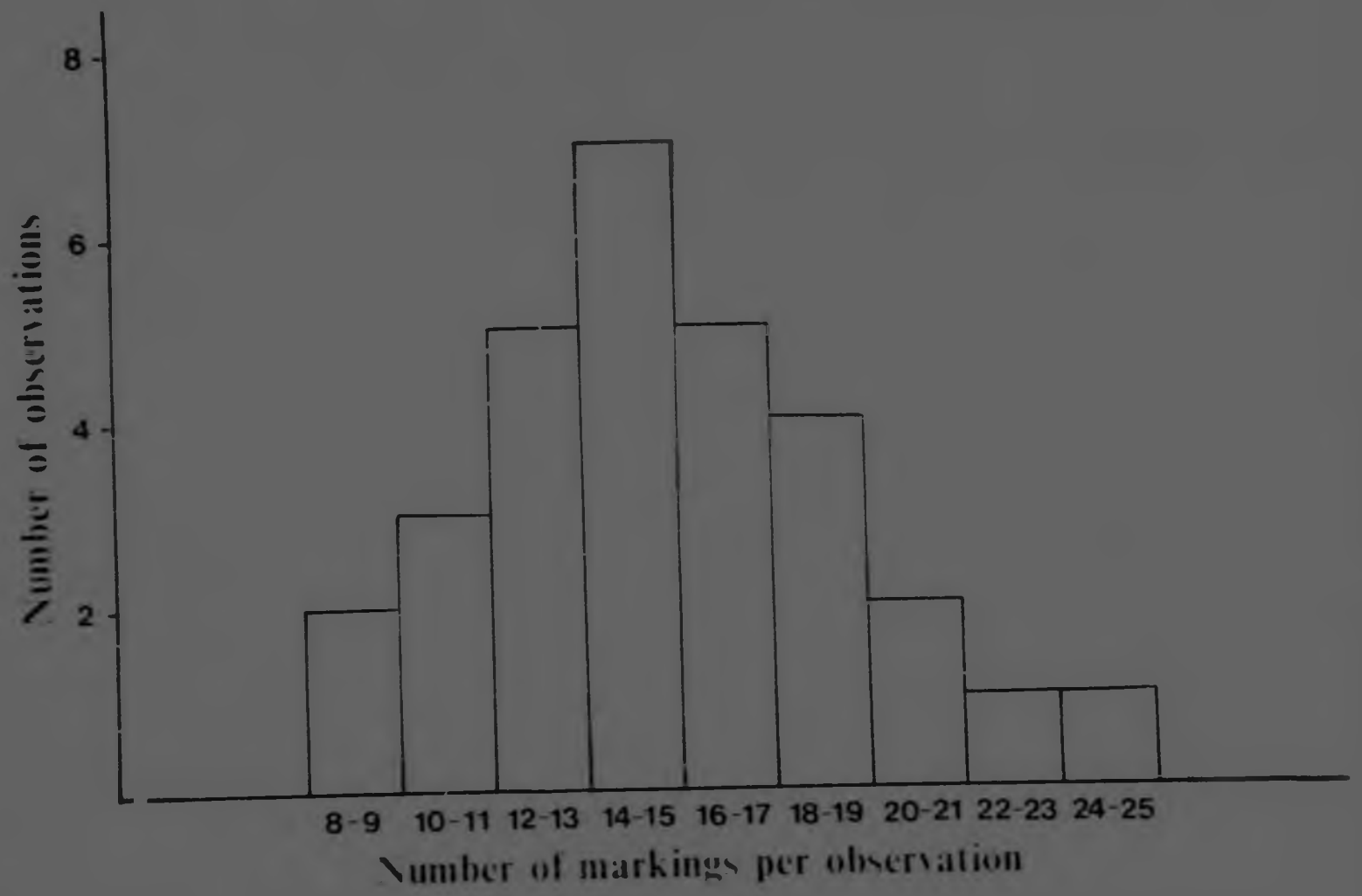

Figure 12. Distribution of chest rubbing by ♂0 during thirty observation periods in a clean observation room.

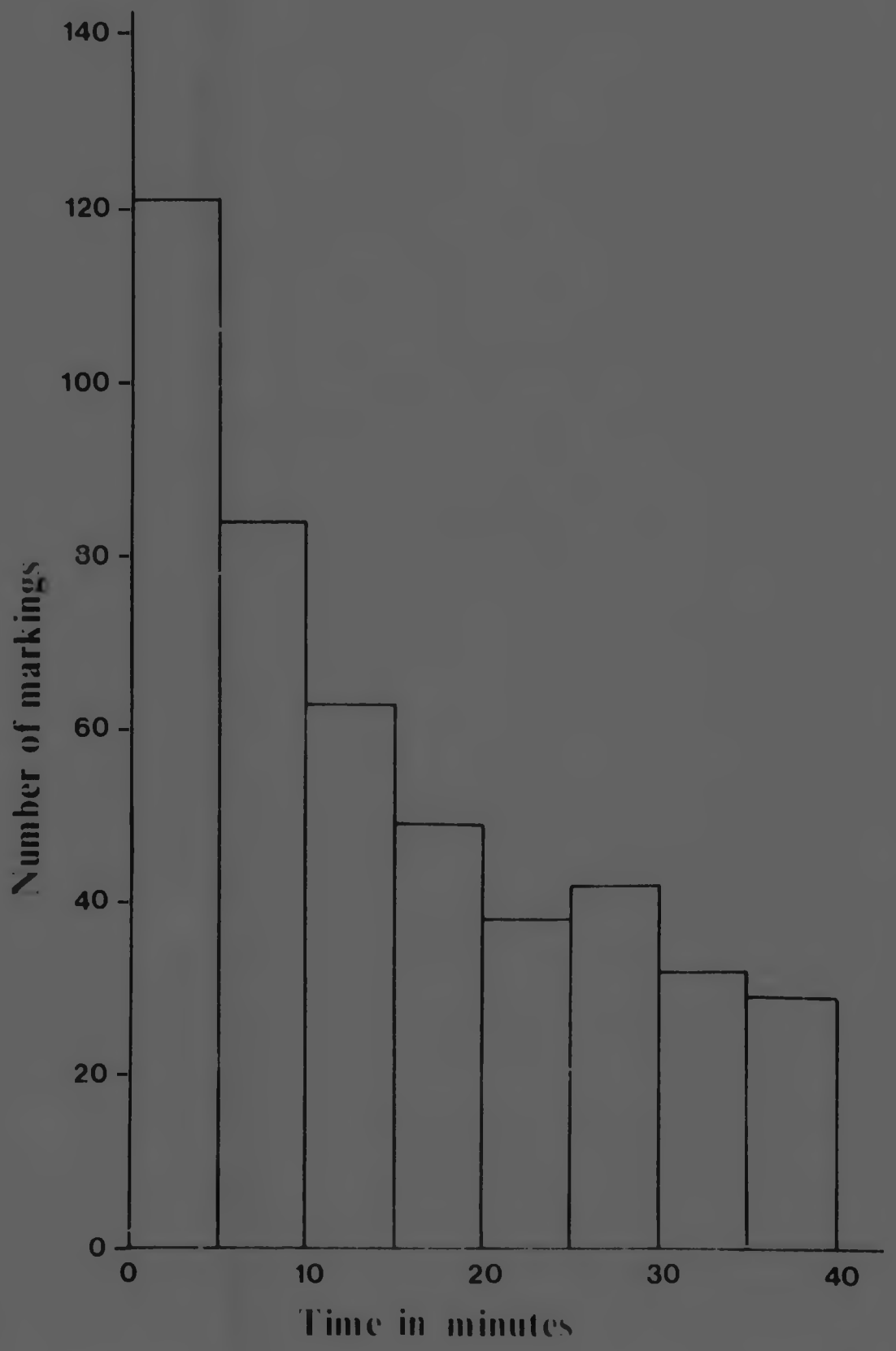

Figure 13. Kinetics of chest rubbing by ♂♂ during 30 observation periods in a clean observation room.

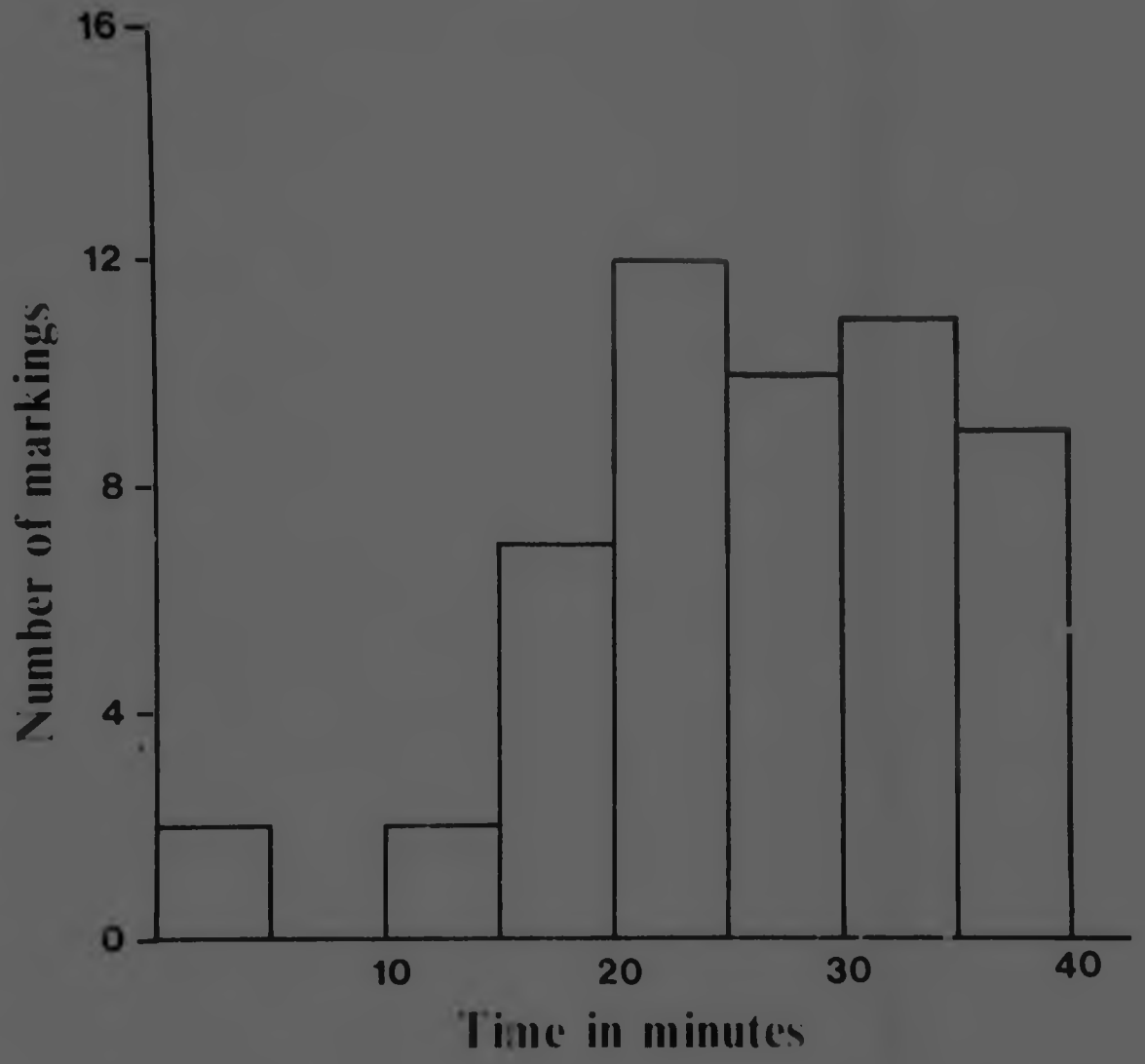

Figure 14. Kinetics of urine washing by d0 during 30 observation periods in a clean observation room.

Table 7. Number of scent marks by ♂♂ in a clean observation room over twenty-seven observation periods of 40 minutes each.

Marking behaviour	Total No. of occurrences of the behaviour	Mean No. of occurrences/observation /period
Chest rubbing	451	16.7 ± 10.0*
Hind-foot rubbing	26	1.0 ± 3.8
Face rubbing	42	1.5 ± 3.0
Anogenital rubbing	180	6.7 ± 11.3
Urine washing	62	2.3 ± 4.1

* mean ± the 95% confidence limits.

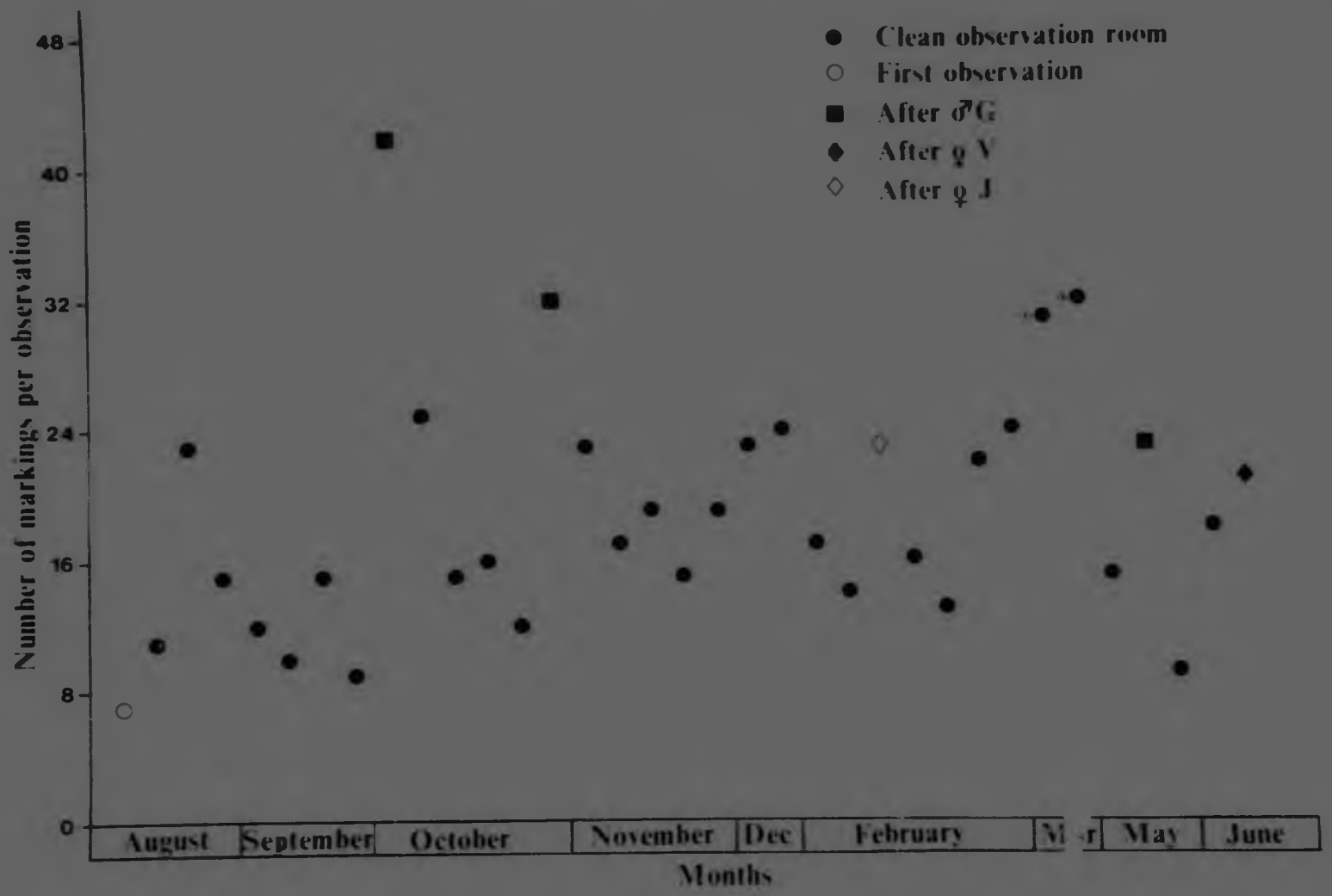

Figure 15. Chest rubbing by ♂H in the observation room during 40 minute observation periods, conducted between August 1977 and June 1978.
(1) ♂H was housed with ♀G1 in oestrus.

displayed more seldom. Most of the anogenital rubbing was displayed in a combination with chest rubbing, the former following the latter.

The kinetics of chest rubbing and urine washing for ♂H were similar to those of ♂O. The distribution for chest rubbing during the year is given in figure 15.

An interesting increase in chest and anogenital rubbing was observed in March 1978. On February 21st ♂H was placed in the same cage as ♀GI (see appendix) who began to come into oestrus on the 26th, and displayed oestrous behaviour from the 9th March. The chest rubbing of ♂H was significantly higher than usual during this period (t - test $p < 0.01$).

Male G was used as a scent donor during experiment 2. Chest rubbing was also observed as his most common marking behaviour, with an average of eighteen rubbings per observation.

The results for ♀V are summarised in Table 8.

Chest rubbing was clearly the most common marking behaviour, followed by face rubbing, whereas anogenital rubbing was not observed at all. In fact females who were not in oestrus very seldom displayed anogenital rubbing at all. ♀V showed a seasonal variation in the amount of chest rubbing behaviour. (Marking more in September, less from October to December, more often from February to March and less again in June). The correlation of chest rubbing with urine washing (in connection with seasonal variation) was negative ($r = -0.54$, $p < 0.02$).

The marking behaviour of ♀J was different from that of the other animals, with a relatively low amount of chest rubbing (Table 9) and face rubbing her most common marking behaviour. She was a fat animal and was not normally active during the observations.

Table 8. Number of scent marks by ♀♀ in a clean observation room over nineteen observation periods of 40 minutes each.

Marking behaviour	Total No. of occurrences of the behaviour	Mean No. of occurrences/observation /period
Chest rubbing	325	17.1 ± 12.0 *
Hind-foot rubbing	35	1.8 ± 6.4
Face rubbing	177	9.3 ± 12.9
Anogenital rubbing	-	
Urine washing	82	4.3 ± 9.6

* mean ± the 95% confidence limits.

Table 9. Number of scent marks by ♂♂ in a clean observation room over sixteen observation periods of 40 minutes each.

Marking behaviour	Total No. of occurrences of the behaviour	Mean No. of occurrences/observation /period
Chest rubbing	139	8.7 ± 4.8
Hind-foot rubbing	11	0.7 ± 2.1
Face rubbing	181	11.3 ± 11.1
Anogenital rubbing	-	
Urine washing	10	0.6 ± 1.5

* mean ± the 95% confidence limits.

Experiment 2. Scent-marking behaviour of an animal in an observation room previously occupied by another animal. A record of ♂0's chest rubbing behaviour in this context is shown in Figure 11. When ♂0 was placed in the observation room previously occupied by ♂G, he showed an increase in chest rubbing behaviour (33 rubbings, compared with the average of 15.1, t-test $p < 0.001$). The same result was observed when the experiment was repeated (33 rubbings, $p < 0.001$), but not when it was performed a third time (19 rubbings, $p = 0.16$).

When ♂0 was placed in the observation room previously occupied by ♀V, there was a decrease in chest rubbing behaviour (t-test, $p < 0.001$ for the three results; 7,7 and 4 rubbings, Fig. 11). ♂0 failed to show a decrease in chest rubbing, after ♀J had been in the observation room (12 rubbings, $p = 0.25$).

The results for ♂H when placed in the observation room previously occupied by ♂G were similar to those of ♂0 (Fig. 15), but he showed neither an increase nor a decrease in chest rubbing after either ♀V or ♀J. A significant increase in anogenital rubbing, was noted (t-test, $p < 0.01$).

There were no significant changes in the responses of either ♀V or ♀J when placed in the observation room previously occupied by ♂G. Similarly a negative result was obtained when the animals were tested with respect to each other and ♀L.

Figs. 11 and 15 seem to indicate that, during the observation period in a clean room which followed the experiment in which the room had been marked previously by ♂G, the number of markings was higher than usual. This result will be discussed later.

Experiment 3. Pair interactions. Four test animals were

placed, two at a time, in the observation room for thirty minutes.

♂O and ♂H. ♂H marked far more than ♂O, especially with regard to hind-foot rubbing. He also chewed the edges of pipes (Fig. 16a), which indicated his high 'excitement state'. H began grooming O (Fig. 16b), which indicated that he was subordinate.

♀V and ♀J. The two animals groomed each other, the behaviour having been initiated by J. However, ten minutes later V attacked J and they had to be separated.

♂H and ♀J. Both animals attempted to sniff each others genitalia which resulted in their moving in a circle. Later H began grooming J.

♂O and ♀J. The animals tended to stay away from each other and not to interact.

♂O and ♀V. O moaned continuously. He threatened V when she approached, although later he groomed her briefly.

3.3 Field experiments

The chest gland secretion obtained from animals in captivity was analysed (Crewe et al., 1979) and three major volatile compounds were detected (Table 10).

To test the biological activity of these compounds, standards and mixtures were prepared according to Table 11.

Experiments in the observation room using these mixtures yielded no special behaviour, nor did the animals respond as they do to being placed in the room after another animal.

Experiments in the field however, yielded interesting results. The results of the first experiment are given in Table 12. Higher responses to laboratory conditioned pipes than to the control pipes were noticed each night. For eight out of nine nights the responses of the animals

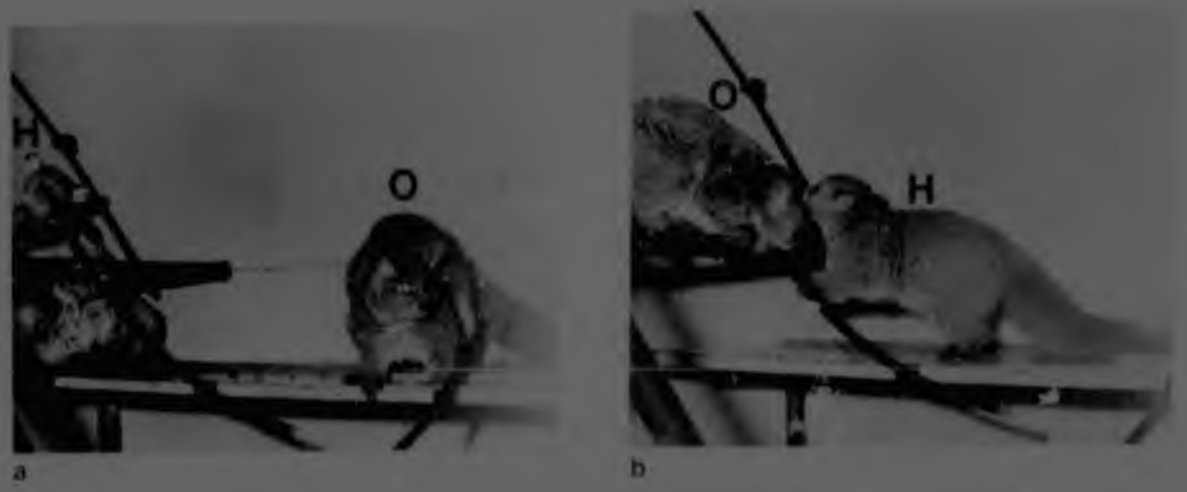

Figure 16. Results of interaction between oO and H
a. H chews edge of a pipe. b. H grooms O.

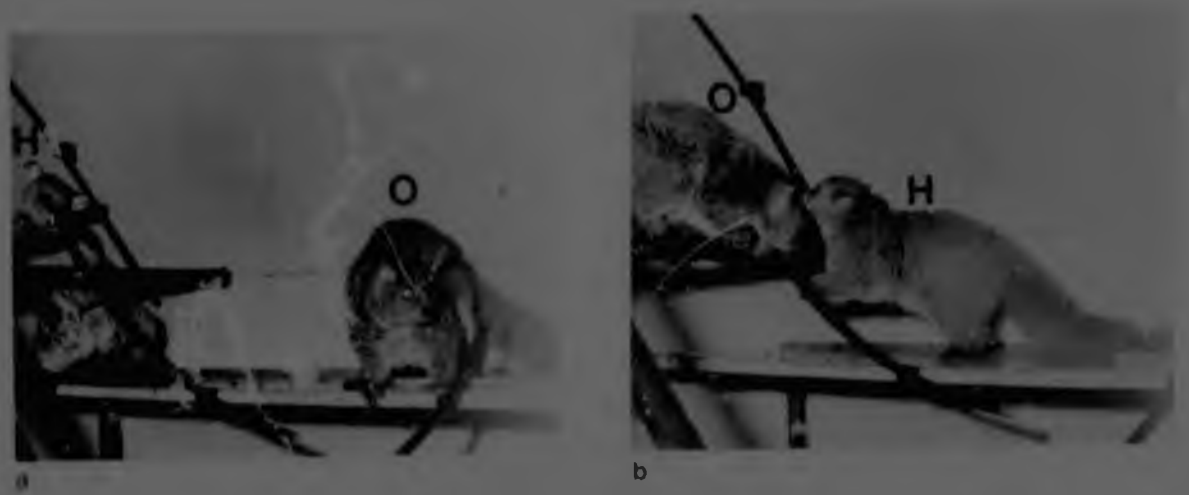

Figure 18. Results of interaction between δO and δH a. H crowds edge of a pipe. b. H grooms O.

Table 10. Volatile compounds found in the chest gland secretion of Galago crassicaudatus and their relative concentrations in male and female galagos (Crewe et al., 1979).

Name	Formula	Relative concentration	
		male	female
Benzyl cyanide (bc)		69%	47%
p-hydroxybenzyl cyanide (phbc)		10%	16%
2(p-hydroxyphenyl) ethanol (phpe)		21%	37%

Table 11. Composition of the artificial scents used in the field experiments. bc = benzyl cyanide, phpe = 2-(p-hydroxyphenyl) ethanol, phbc = p-hydroxybenzyl cyanide.

Mixtures	Standards*		
	bc	phpe	phbc
M-1	0.5 ml.	0.5 ml.	-
M-2	0.7 ml.	0.2 ml.	0.1 ml.
M-3	0.5 ml.	0.35 ml.	0.15 ml.

* 1 mg/ml in dichloromethane.



Figure 17. Sniffing at an artificially marked pipe in the field by °1 (April 1978).

Table 12. Number of occurrences of sniffing and marking behaviour in response to pipes treated with artificial scents over a period of nine nights. Control = a clean pipe, l.c = laboratory conditioned pipe, bc = 10µl of standard solution of benzyl cyanide, pipe = 10µl of standard solution of 2-(p-hydroxyphenyl) ethanol, for the composition of H-1 see Table 11.

Control	bc	pipe	H-1	l.c
6	8	5	20	23

to M-1 were higher than to the controls. ($p < 0.026$, Sign test).

Bushbabies were often seen biting the edge of a pipe; a marked pipe usually elicited more biting than a control. Fig. 17 shows a bushbaby sniffing a marked pipe in the field.

The second experiment was carried out at observation site 3, as explained in Chapter 2. The animals used a regular route (Fig. 9) and marked particular places on tree 1 (Fig. 18) and tree 2. The usual marking places on these trees were higher than six metres (the maximum height that could be climbed) and the artificial scent had to be left lower down on the trees, yet still on the main route. The experiment was repeated every third night as animals still seemed to respond to the same mark on the second day. The results are summarised in Table 13.

It is not possible to test whether the responses given to scents left on the main route are significantly higher than those given to scents left on low branches, as experiments were only performed on three nights. However, the following are the details of the observations from the field note book, which illustrates the significance of the above results.

17.9.78

18.35 U arrived at tree 1. Sniffed for several seconds at M-2 on the main route. Sniffed again, moved to the usual marking place and marked it by chest rubbing. Moved to tree 5, then to tree 2. Sniffed briefly at the low M-3 mark then fed.

19.00 Mo approached and sniffed the M-2 on the route (Tree 1). Moved to another branch, then directly to tree 2 (Fig. 9).

19.20 Jc appeared on tree 1 and moved towards tree 5. Stopped suddenly at the M-2 mark, and sniffed carefully. Continued to tree 5. Passed the dichloromethane control without stopping. Stopped



Figure 18. The main roots on tree 1. A. The artificial scent. B. The control. C. The marking 'station'.

Table 13. Number of occurrences of sniffing and marking behaviour observed over three nights, in response to scents left along a regularly used route. o.r. = on route, l.b. = low branch, for the composition of M-2 and M-3 see Table 11.

Control	M-2		M-3	
CH_2Cl_2	o.r.	l.b.	o.r.	l.b.
2	16	5	11	4



Figure 19. 'Olfactory behaviour' at observation site 3.
a. ♂B chest rubbing at the 'marking station'.
b. ♀Jc sniffs the artificially marked place.
c. ♀K sniffs the artificially marked place.
d. ♂Mo start chest rubbing on low branch (artificially marked).

and marked the 'marking station'. Moved from 5 to 2 to 3. Went down tree 3 without sniffing the lower M-2 mark. Fed on gum.

19.30 Jc moved back along the same route, sniffed at the M-2 again and continued to the north.

22.9.78

18.30 Jc arrived from the south and proceeded along the route from tree 7 to 1 to 4 (Fig. 9). K appeared on tree 1 and sniffed M-2 on the route. Continued to tree 5 and urine washed on the way. Chest rubbed the usual marking place. Moved to tree 5.

18.50 U arrived on tree 1 and stopped at the marked place. Sniffed, looked around, then licked the place. Went back and crossed the branch to tree 4.

19.00 Jc, K and U met on tree 2 and groomed together. Jc moved along the route and stopped at the spot marked with M-3, sniffed and went back to groom with K.

19.15 Mr on tree 1. Sniffed carefully at the M-2 on the route. Moved to tree 2. Stopped suddenly on the M-3 marked spot on the main route, sniffed and looked around, sniffed again. Went down and sniffed the M-2 mark lower on the tree. Started chest rubbing. Went up and played with U.

These observations are illustrated in more detail in Figure 19.

3.4 Volatile properties of the artificial compounds used to mimic galago chest gland secretion.

The volatilisation of the three compounds from cellulose discs is shown in Figure 20. The benzyl cyanide evapourated completely within an hour ($\pm$ 5 minutes), while the two hydroxy compounds evaporated more slowly (the 95% confidence limits for the curves = $\pm$ 3%) Significant quantities of these two compounds were still present after two days. Preliminary experiments with

glass discs produced similar results. Experiments with dichloromethane as a solvent instead of ether, gave similar results.

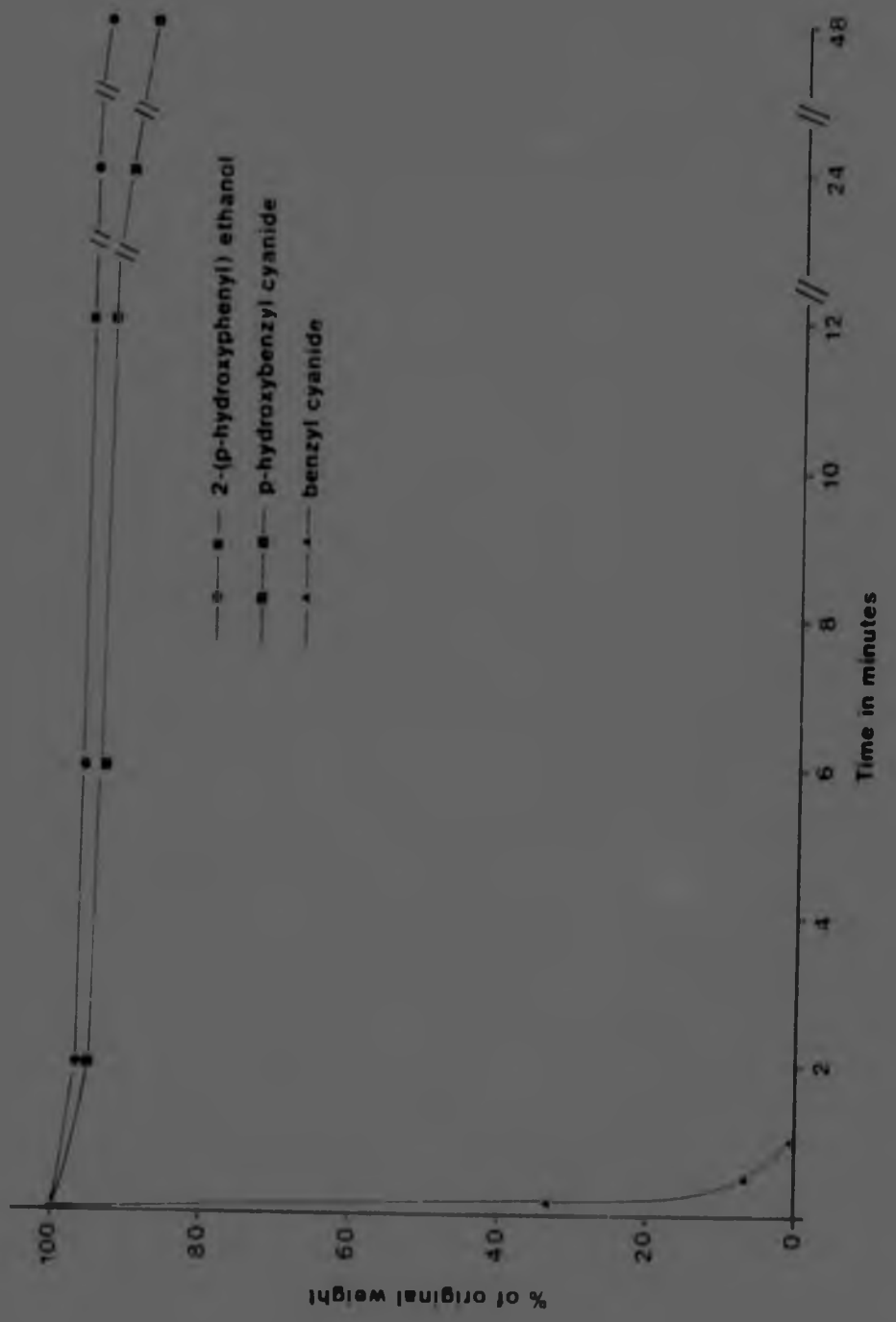

Figure 20. The relative mass of each standard compound which had evaporated from cellulose discs after successive time intervals.

CHAPTER 4. DISCUSSION

4.1 *Galago crassicaudatus* social structure and communication.

The social structure of *G. crassicaudatus* as described in the results, is basically in agreement with Bearder's (1974) description. Adult animals live in restricted areas with females having relatively small home ranges and males larger ones which overlap those of the females.

Further information which was collected in the field study suggests that a home range may be shared by more than one female. Bearder (pers. comm.) has found that a number of females of *G. senega'ensis* may share a home range and *G. alleni* females have also been known to share a territory (Charles-Dominique, 1977). Female *G. crassicaudatus* which share a home range may have different core areas and may share the area on a differential time basis in some seasons. A territory shared on a time basis has also been described for felids by Leyhausen (1964).

The results indicate that young males and females eventually leave the home range of their mother (Table 1). A similar situation was described by Bearder (1974). However, Clark (1978b) has suggested that 'female kin will be closely associated for much of their lives'. The discrepancy between these results and those of Clark may be due to the fact that she left the field before the young females (V and Ma) had departed from their mother's home range.

An adult male *G. crassicaudatus* dominates all other males in an area which is termed the 'control area'. Young males have a 'vagrant' stage in their lives. A similar social organisation was reported for other nocturnal

prosimians: Charles-Dominique (1972) described 'Central A' and 'Central B' males for G. demidovi as well as 'peripheral and vagabond males'. Bearder (pers. comm.) could not distinguish peripheral males in G. senegalensis but found that a resident in an area dominates all other males.

It has been suggested (Charles-Dominique and Hladik, 1971) that the situation in which the home ranges of several females are encompassed by the home range of a central reproductive male, is the common and ancestral form for prosimian social organisation. G. crassicaudatus has probably the most developed social structure of all galagos, as territorial behaviour between males is very limited and social grouping seems to last longer (Clark, 1978a). The results of the observations which are summarised in Tables 2 - 5 suggest that bushbabies can switch from being solitary to foraging in social groups. Animals which can change their social structure usually have a more developed communication system than those which have a fixed structure (Kruuk, 1972). In G. crassicaudatus this is demonstrated by the many auditory and chemical signals used in communication.

The best approach to understanding why a specific communication channel is chosen in the evolution of a species is to define it in terms of energy and efficiency (Otte, 1974). Since chemical communication is energetically cheaper than other communication channels one would expect to find that it is inefficient in any situation where it has been replaced by other communication systems.

In Galago crassicaudatus visual communication is used only in direct interactions. With the reduction in efficiency of vision at night it is clearly adaptive to use visual signals only when a quick response is needed. A quick response is not necessarily needed in communication over a distance, where olfactory or auditory signals are

used. The need for both channels can be explained on the basis of the social structure of the galagos.

The cry, which is the most important auditory signal used in communication over a distance, is normally used only by males. It has been suggested that it is for self advertisement and spacing (Bearder, 1974). The use of the cry by males may be connected with their larger home ranges which cannot be efficiently marked by scent only. However, there are nights when a resident male does not cry at all (Bearder, 1974; and pers. observ.) and the space between resident males is still maintained. This suggests that there is still a chemical signal - probably of a longer lasting nature - which controls spacing to a certain extent.

Interactions between a dominant male and vagrant males on the other hand, cannot be dependent on olfactory communication alone, since the latter forage over wide areas regardless of territorial borders and may not pass a common marking place at all. Hence it seems to be an advantage for the resident male to advertise its presence by a cry. The vagrant male may cry and wait for a reply which will indicate to him where the dominant male is. The resident male seems to be able to distinguish between the cry of another resident male which he usually ignores and that of a vagrant male which he will always answer. Scent markings are deposited by the resident male on the regular routes used by the galagos and a vagrant male seems to respond to a fresh scent mark, (e.g. observation on 4.4. p.40). During the interaction between males, chest rubbing is probably used as a threat display (e.g. observation of 4.7. p.44) which causes the subordinate to retreat. The cry given by the dominant animal at the end of a chase is undoubtedly a warning signal which will be remembered by the subordinate. The cry therefore, is important for maintaining social status as well as for social spacing.

In the breeding season when the dominant male is busy following the females, the efficiency of his scent marks is much reduced. There is also more interaction between the males in this season and thus a corresponding increase in the number of his cries. Scent marking of the 'rubbing' type in this season seems to be used as a ritualised threat display (e.g. observation on 27.6. p.43).

In G. senegalensis Bearder (pers. comm.) has found that the territorial barriers between resident males may break down in the breeding season. Although this has not been observed in this field study, this may be true for G. crassicaudatus in denser populations (e.g. in Zululand, Bearder, 1974).

Territorial behaviour in females is more obvious than in males. Clark (1978a) noticed that ♀D, (referred to as ♀5 in that study), marked areas in the extreme south of her range by chest and genital rubbing. The scent marks seem to be efficient for a few days as is suggested by the observations in June-July, when ♀G came to observation site 1 four days after ♀D has been removed from the field. The cry is not important in female interactions as there are no vagrant females.

This study was too limited to give an interpretation of each scent marking behaviour separately; however, some distinction between urine washing and marking of the 'rubbing' type can be made. Rubbing behaviour, particularly chest rubbing is used in interactions between a resident male and vagrant males, in threat displays and possibly in territorial markings. All of these are agonistic behaviours. Using Smith's (1977) interactional perspective, one can suggest that these signals transfer the message that the communicator is ready to interact agonistically. Urine washing on the other hand, is often used in non-agonistic situations, or transferring a message that the signaller is ready to interact non-

agonistically e.g. observation on 26.3. p.38. It may also enable animals foraging together (which in G. crassicaudatus often means they pass a point 5 - 10 minutes after one another, e.g. observation on 23.9. p.49), to follow one another. The existence of special 'marking stations' on a main route supports this hypothesis (suggested by Clark, 1978a). As galagos are able to distinguish between individuals on the basis of urine (Clark, 1975), it is also possible that females which share a home range can use it in order to avoid each other (e.g. observation on 5.4. p.40).

Charles-Dominique (1977) has suggested a function for urine washing in G. alleni He argues that this behaviour pattern is used here for territorial marking and that the function of urine washing is the same in all primates displaying this behaviour pattern. The field observations on G. crassicaudatus do not support this hypothesis. The function of urine washing in prosimians and New-World monkeys differs between species (e.g. the five hypotheses described on p.14, also, Doyle, 1974) and a comparative study of the behaviour in the different species may indicate how these various functions evolved.

Chemical communication is also used for direct interaction, as is shown by G. crassicaudatus in the stereotyped 'meeting ceremony'. When two bushbabies meet they sniff each other muzzle to muzzle, whereafter they either interact agonistically, or the dominant one will present his head and arm to the subordinate to be groomed (Fig. 16b). In the case of the latter this will be followed by the dominant animal grooming the subordinate after which the animals may separate or engage in mutual grooming. In addition they may try to sniff each others' genitalia. That G. crassicaudatus identify each other by scent is suggested from a common laboratory observation: When a strange galago is introduced into a cage occupied by an established group, the aggression evoked is not only

directed against the introduced animal but between members of the group as well. This may continue even after the stranger has been removed and stops only after either sniffing each other or performing the whole meeting ceremony. In this connection it has been suggested that the smell of the fur is critical for identification (Kingdon, 1971). G. crassicaudatus, as is the case with many other prosimians, has a special 'tooth comb' in the lower jaw together with a 'second tongue', (sublingua) bearing denticles that fit into the space between the teeth (Kingdon, 1971). Martin (1972) has suggested that this is an adaptation for collecting gum, a hypothesis which has been repeated by Petter and Petter-Rosseaux (1979). However it has been reported by Bearder (1974) that G. senegalensis and G. crassicaudatus do not use the 'comb' for this purpose. Kingdon (1971) and Buettner-Janusch and Andrew (1962) have observed Galago crassicaudatus using the 'comb' and 'second tongue' for grooming the fur and have suggested that combing the fur is important in order to keep a steady fresh scent on it. The development of such a complex apparatus for grooming indicates how important it is for galagos to keep a constant body odour.

The other direct chemical signal - used in mating behaviour - is the oestrous signal. Mating in G. crassicaudatus is preceded by the male licking the genital region of an oestrous female (Eaton and Slob, 1970; Eaton et al, 1975). Field observations during the mating season suggest that this chemical signal is effective only over a short distance. The communication involves two steps; a) attraction of the male by the female which results in the male following her, and b) the actual copulation, which occurs a few days later.

4.2 Laboratory experiments

The results of Experiment 1 indicate that scent marking and particularly chest rubbing is part of the normal

response of a bushbaby to its surroundings. This response decreases with the time, which is a typical feature of habituation (Fig. 13). The first observation may indicate the response to a completely new area, while the other observations indicate responses to an area which has been visited before. It is suggested that galagos respond differently in the two situations.

Eisenberg and Kleiman (1972) discussed the importance of 'self reassurance' that scent marking produces for an animal and suggested that there is an 'optimum odour field' for each animal depending on its age, sex and 'excitement state'. The results of experiment 1 support this hypothesis and suggest that the optimum odour field is different in different parts of the area, depending on whether it is inside or outside the home range. The results also suggest that scent marking of the rubbing type, and particularly chest rubbing, is used for this purpose, while urine washing is not. This is in agreement with the field observations which indicate that urine is probably more important for communication between members of a social group in this species.

The increase in marking behaviour of ♂H when his mate came into oestrus (Fig. 15) is also supported by field observations which indicate that an increase in this behaviour correlates with aggression by males in the mating season. However, Clark (1975, 1978a) did not notice an increase in scent marking by males in her experimental situation.

The results of Experiment 2 suggest that males will over-mark the scent marks of other males, and may hereby indicate an aggressive mood. This response will habituate if there is no reinforcement from aggressive interactions between males. The results also suggest that the pheromone involved in this behaviour is of the informer class (Müller-Schwarze, 1977), and depends on previous experience.

The frequency of marking behaviour in a clean observation room during the observation period which followed that in which the frequency of marking behaviour in an observation room previously occupied by ♂G was determined, was still somewhat higher than the mean marking frequency for the particular animal being tested (♂O Fig. 11 and ♂H, Fig. 15). This suggests that galagos can memorise and associate scents and places, an ability they share with Lemur catta (Mertl, 1977).

The results of this experiment also suggest that memory is an important factor in female-female and female-male interactions. Old laboratory data suggests that ♀V is the mother of ♂O. He was clearly subordinate and nervous in the pair interaction between them (Exp. 3), which may be the reason for the low frequency of marking behaviour when put into the observation room after her. The failure of the females to show any significant change in behaviour in this experiment can be explained in terms of their social structure. The lack of vagrant females and the tolerance shown by resident females to the vagrant males in their home ranges, suggests that in nature there is no change in their excitement state in response to such a stimulus, nor any detectable response.

The males in the experimental situation were adults, each dominant in its cage. It is suggested that their responses to the scent of ♂G were similar to those of a resident male to the scent of a vagrant intruder male.

Interaction between bushbabies is on an individual basis; each pair interaction (Exp. 3) is different from the others. Age seems to play a major role in dominance status. Roberts (1971) and Tandy (1974) came to similar conclusions for the social interaction in galagos in their experimental situations (p.18). Field observations of antagonistic behaviour between the dominant male and other males showed that these interactions were usually short

and ended with a short chase, followed by a cry from the dominant male. Fights between females on the other hand were longer, with bouts of aggression followed by breaks for grooming and other activities (e.g. observation on 4.7, p.44). Aggression between females and males, other than the resident male, out of the breeding season were never observed. The results of experiment 3 also indicate that fights between females may be more serious than those between males.

The responses of ♂H in the pair interaction with ♂U (Fig. 16) were in some ways similar to the behaviour of the strange galago at observation site 3 (Observation on 17.9, p.49). Just as ♂H was subordinate to ♂U in that experiment, the high 'excitement state' shown by the animal in the field (high rubbing and biting behaviour), indicates its subordinate status.

4 Experiments with artificial scents

Originally the artificial scents were to be tested in the laboratory. However, the animals failed to respond to them in any detectable way. General difficulties which are encountered in laboratory bioassays for mammals have already been discussed. In this particular case, the difficulties were probably that:

1. The laboratory 'odour field' even in a clean observation room was too high, and screened the test odours.
2. Laboratory galagos were not suitable for this bioassay, either because they lacked the social organisation of feral galagos, or since this pheromone is likely to be an 'informer pheromone' and the placing of the scent and previous experience were essential for releasing a response, or both.

The first field experiment was carried out in order to determine what message, if any, was available in the three major components that were identified. The results

given in Table 12 suggest that galagos do not find one artificial compound of the scent more informative than a clean pipe. However, the mixture of two components elicited almost the same amount of sniffing as pipes marked with the scent of a laboratory animal. This suggests that these compounds are indeed part of the active pheromone in the secretion, and that this pheromone is active as a mixture and no single compound has pheromonal properties.

The second experiment was concerned with the mode of action of this pheromone, i.e. does it release stereotyped responses regardless of the circumstances and contexts in which the signal is given, or do these factors alter the meaning of the signal? The results suggest that the meaning of the signal depends on the position of the mark. The value of the message is greater when it is placed in its natural context - on a regular route, rather than when it is placed in some other positions. Although the results of this experiment which is based on only three nights observation, cannot satisfactorily be tested statistically, the observations described on p.70 suggest that: 1. the animals, when descending to lower branches, often ignore the artificial scent there, 2. the response given to the mark on the regular route was conspicuous and involved prolonged sniffing, a peculiar display of looking around, followed by sniffing the marked place again. These observations suggest that the synthetic scent marks are behaviourally significant when placed on a route regularly used by the animals and indicate again the 'informer' mode of action of this pheromone.

Chest rubbing, as already suggested, may be used in either marking a territory, or as a time signal in communication between dominant and vagrant males. However, Clark (1978a) has stated that the chest gland secretion is unlikely to reflect the time of marking. In order to be able to test this hypothesis, the volatile properties of

the three identified compounds had to be analysed and the results, which have been summarised in Fig. 20 are very clear. Benzyl cyanide is a highly volatile compound while the other two compounds are much less so. It is likely that the relative concentration of benzyl cyanide is involved in time signalling, rather than in territorial marking, while the other two compounds are important in territorial marking. The field observations and experiments suggest that they are effective for three to four days, a fact which is consistent with their volatile properties. Although the two hydroxy compounds lose only about 10% of their weight by evaporation over 48 hours the threshold for response is dependent on the concentration of the pheromone, which is a function of the absolute amount of the scent (Bossert and Wilson, 1963). The mass of the compounds in one bout of chest rubbing is small (0.5µg, Crewe et al., 1979), and it may be that in four days a 20% loss is sufficient to bring the concentration below that of the olfactory threshold.

The method used in this experiment was chosen mainly for its simplicity. However, the volatile properties of these compounds may vary if they are mixed together or if they are placed in natural chest gland secretion. Analysis of the volatile properties of the compounds in this more complex situation would require the use of radioactive chemicals (Regnier and Goodwin, 1977) that were not available for this study.

The identified compounds can carry information such as time of marking, sex and age of the communicator. However, the gas chromatogram (Fig. 21) suggests that there are other compounds in the secretion in smaller quantities which may carry more individual information and/or modulate the release of the major compounds from the scent mark. Thus, additional chemical analysis will be necessary for a more complete understanding of how galagos communicate via chemical signals.



Figure 21: Gas chromatogram of G. crassicaudatus chest gland secretion.
1149 = Benzyl cyanide.
1914 = 2-(p-hydroxyphenyl) ethanol.
2074 = p-hydroxybenzyl cyanide.
from : Crewe et al., 1979.

The approach underlined in this study consisted of a combination of chemical analysis, field studies and laboratory experiments, each of which attacked the problem of chemical communication from a different aspect. Field observations gave an idea of what was being communicated by the chemical signal in natural conditions. However, to determine how the signal contributes to the process of communication, a laboratory analysis of the communication pattern was needed. A syntactic analysis of the signal through chemical identification, followed by experiments with artificial scents in the field and laboratory experiments concerned with the contribution of memory and other aspects which could be regarded as psychological in character to the process of communicating, led us to an understanding of what message is carried by the signal and what the mode of action of the pheromone is. Analysing interactions between the animals using all this information gives us a clearer picture of what is actually being communicated.

APPENDIX I.

The oestrous cycle of *G. crassicaudatus umbrosus*

The oestrous cycles of three female bushbabies from the Primate Behaviour Research Group were followed as described in Chapter 2.

The five categories used to describe the smears were:

1. Pre-oestrus. Large epithelial cells (stained a faint green) and almost no leucocytes.
2. Oestrus. Fully cornified epithelial cells stained orange brown, scattered throughout smears.
3. Metoestrus. Each epithelial cell was surrounded by a halo of granulated mucus.
4. Pre-dioestrus. The cells were clumped together with patches of mucus. Some leucocytes would be seen.
5. Dioestrus. Large numbers of leucocytes. Most of the other cells were stained green.

The three animals studied were:

♀J	8 years old	caught in the wild as an infant.
♀G1	3 years old	caught in the wild as an infant.
♀A	3 years old	laboratory reared.

♀J. She came into oestrus on the 28th May 1977 and after six day showed 'oestrous behaviour' (Eaton *et al.*, 1973). Leucocytes were seen in the smear again on 20th June 1977 (24th day of oestrus). After a gestation period of 139 days she gave birth to an infant on 25rd October, which died later the same day. She did not come into oestrus again until 7th April 1978, and this lasted for 27 days.

♀G1. She came into oestrus on June 11th 1977, and leucocytes were seen again on July 4th, 23 days later.

She gave birth to twins on 2nd November 1977, after a gestation period of 135 days. She and her infants were placed in a cage on their own. On 21st February 1978, ♂H was introduced to the cage, and ♀Gl came into oestrus on February 26th. She started to show oestrous behaviour on March 9th, but did not give birth to any young and has not been in oestrus since.

♀A. She was in a cage on her own when her oestrous cycle was first monitored. Slides taken from August 2nd until August 11th, looked like pre-oestrus metoestrus and pre-dioestrus but there were no typical, scattered, cornified cells indicating oestrus. A similar situation occurred again between 29th September 1977 and 5th October 1977, but cornified cells were seen for a four day period. On 14th November she was placed with a male, and she came into oestrus again from 17th May until 30th May, and gave birth to twins on 28th September after a gestation period of about 128 days.

The oestrous cycles of the two animals caught in the wild could not be calculated because the cycles were interrupted by the gestation period (p. 90). They were however definately irregular, with their oestrous smears lasting longer than those reported by Eaton et al. (1973) working on G. crassicaudatus crassicaudatus (12.4 days on average).

The first oestrous cycle of ♀A lasted about 56 days. The second cycle was 53 days, but may have been shorter than normal because of the introduction of a male. The third cycle lasted for about 177 days, which suggests that a female housed with a male may have a longer cycle. Eaton et al. (1973) give the oestrous cycle as 44 days, which is closer to the first two cycles of ♀A. ♀J and ♀Gl were usually housed with males and their cycles were similar in lengths to the third cycle of ♀A.

Eaton et al. (1973) reported that most of his animals had closed vaginas between oestrus. However, in the

laboratory colony, no adult G. c. umbrosus showed a similar situation. Young females born in November 1976 had closed vaginas until December 1977, when they opened and remained so.

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Author Katsir Z
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