Communication in The Lesser Bushbaby
(*Galago senegalensis moholi*)

by

A.B. Andersson, B.Sc.Hons. (Rand)

A thesis presented to the
University of the Witwatersrand,
Johannesburg, in fulfilment of the
requirements for the degree of
Master of Science.

Johannesburg.
October 1969.

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

A.B. Andersson

A.B. ANDERSSON

A C K N O W L E D G M E N T S

I wish to express my sincere thanks to the many and various persons who have assisted me in the preparation of this thesis. In particular thanks are expressed to the following:-

Dr. G.A. Doyle, my supervisor, for all his help and encouragement.

Mr. T. Bekker for his willingness to assist with laboratory changes, recording installations and particularly photography.

Mr. S.K. Bearder, a fellow student, for his interest and helpful arguments and discussions.

The Staff of the Department of Electrical Engineering of the University of the Witwatersrand for the use of their Kay Sonagraph.

Mrs. H. Mann and Mrs. D. Ball for typing assistance.

The University of the Witwatersrand for valued financial assistance.

Finally to my husband for his patience and encouragement over many trying months.

CONTENTS

Call 4 - Shivering-Stutter. Single animal followed by two animals duetting
Call 5 - Whistles and selection of Whistle variants
1st 4 units - Whistles given in succession by adult female
Next 3 units - Whistle variants
Following 3 units - Whistle - Moan and Whistle-Moan variants
Next 2 units - Hiccup Whistle variant
Call 6 - Yap
Call 7 - Plaintive Yap and Yap Alarm
Call 8 - Wuffs
Call 9 - Wails followed by characteristic 3 or 4 notes rising in pitch at start of Alarm
Call 10 - Caw with Whistle Variants.

Infant calls:-

Call 1 - Clicks and Crackles
Call 2 - Loud Squeaks

Mixed Call Sequence:-

(1) Sequence given by juvenile after escaping from home cage and being chased and caught by the observer
(2) Sequence given by female adult while being chased and attacked by aggressive adult female

LIST OF FIGURES

LIST OF PLATES

1. INTRODUCTION

During the last two decades interest in behavioural research in primates, especially in the field, has increased rapidly. The majority of primates are social animals establishing complex social organisations. An understanding of the communication systems used by the various primate species is basic to an understanding of the social structure of a primate group since the maintenance of the social structure is dependent on the communicatory system. A study of communication is therefore essential in detailed studies of behaviour.

An increasing number of workers have thus recently turned their attention to the analysis of primate displays, especially those concerned with facial expression, body postures and calls. Hinde and Rowell have described the calls, postures and facial expressions which play a communicatory role in the rhesus monkey (*Macaca mulatta*.) (Rowell and Hinde 1962, Hinde and Rowell 1962, Rowell 1962.) Van Hooff (1962, 1967) and Bolwig (1959, 1964) have given extensive accounts of the major categories of displays in which the facial structures take part, and Andrew (1962a, 1963a, 1963b, 1963c, 1964) deals with calls and associated facial expressions and displays of representatives of most groups of the primates with emphasis on their derivation and evolution taking the concept of 'stimulus contrast' and protective responses as the basis of his argument. Struhsaker (1967) has given a detailed account of thirty-six physically and/or audibly distinct sounds which were recognisable among vervet monkeys (*Cercopithecus aethiops*.)

A prominent worker in the New World Primate group, Moynihan (1964, 1966, 1967), has made a "preliminary attempt to survey and summarize features of the social signal systems of platyrrhine monkeys", while Epple (1968) has done work on comparative studies on vocalizations in marmoset monkeys. Ploog et al. have published a series of papers (1963a, 1963b, 1963c, 1967) on the social behaviour of the squirrel monkey (Saimiri sciureus.)

Many field studies such as Schaller (1965) on the gorilla (Gorilla gorilla beringei), Reynolds and Reynolds (1965) and Goodall (1965, 1968) on the chimpanzee (Pan troglodytes), Hall and De Vore (1965) on the baboon (Papio ursinus and Papio anubis) and Jay (1965, 1967) on the langur (Presbytis entellus) to mention a few from a rapidly increasing list, contain data on the social signals used by these primates as communicatory systems, indicating the importance of knowledge of such systems in field studies.

Hockett (1960), Marler (1965) and Altmann (1967) have published papers dealing with primate communicatory systems from a general theoretical as well as from a practical view point, discussing the nature and structure of social communication in primates and indicating ideal methods of approaching the subject so that valid comparisons between the repertoires of species may eventually be made. These authors have pointed out that although descriptive material of signalling behaviour is increasing, meaningful comparisons between species cannot as yet be made, as little work has been done concerning the message content involved, which requires detailed knowledge of the responses evoked by the signals.

Other workers such as Zinkin (1963), Bastian (1965), Seboek (1965, 1967), Lancaster (1968) and Hockett (1960), are interested in non-human primate auditory communication systems primarily because of the light they may shed on the emergence of human language.

There are at present comparatively few detailed published accounts of prosimian behaviour. This is undoubtedly due to the difficulties encountered in observing small groups of arboreal animals of which all the Asian and African, and many of the Madagascan species, are completely nocturnal. Due to the paucity of primate fossils, (Brace and Montague 1965), knowledge of prosimian behaviour is important as the living prosimians can be expected to provide the main source of clues to the behaviour of the prosimian ancestral group from which the Old and New World monkeys and the apes have evolved. A knowledge of the living prosimians thus contributes towards an understanding of the phylogenetic development of behaviour in the Primate Group as a whole.

The unique opportunities afforded to the prosimian worker by the Malagasy lemurs have attracted several researchers to this field and the number of published accounts of lemuroid behaviour is increasing. Petter (1959, 1962a, 1962b, 1965), Bishop (1962, 1964) and Jolly (1966a, 1966b, 1967) are prominent workers in this field. Knowledge of lorisoid behaviour, however, is still comparatively scarce and the present study of communication in the lorisoid prosimian, _Galago senegalensis moholi_, is intended to contribute towards filling this gap.

Previous work on _Galago senegalensis_ includes that of Lowther (1939, 1940), Andrew (1963a, 1963c, 1964), Doyle _et_ al. (1967), Hall-Craggs (1965), Sauer and Sauer (1963), the latter being the only account of field work on this species, and Sauer (1967). None of these authors deal with communication, (particularly auditory) in detail, although Lowther and Andrew both discuss a repertoire of 8 - 10 calls and Andrew (1964) gives an extensive account of many of the displays of this species.

The term "communication" as Altmann (1967) has noted has been defined in several different ways. Crawford (1939) states, "the term communication lacks precise definition in its application to animal behaviour, for it may be stretched to include almost any sort of anticipatory movement which may signalise an activity to another individual, or it may be limited strictly to vocalizations or gestures which clearly direct or predicate." Moynihan (1967) for example, states that, "any behaviour pattern which often conveys information from one individual to another may be considered a social signal, even if it has many other functions as well." Most workers on primates have taken social communication as the process by which the behaviour of one individual affects the behaviour of others. It is in this sense that the term has been used in the present study.

Primates, in general, use a wide variety of olfactory, tactile, auditory and visual cues in their social communication and as Marler (1965) has pointed out "perhaps the most striking generalisation that can be advanced from a survey of the communication signals of monkeys and apes is the overwhelming importance of composite signals." That vocal signals, especially among ground dwelling primates, may play only a secondary role to visual signals in communication has been suggested by the work of Jay (1962), Cole (1963), Itani (1963), Hall and De Vore (1965) and Altmann (1967). In fact in the patas monkey (Erythrocebus patas) the "general vocal pattern is one of adaptive silence in which muted calls have an occasional function" (Hall 1965). In Galago senegalensis, however, auditory signals may be expected to be of primary importance due to the restriction of visual signals imposed by their arboreal and nocturnal habit. This has been found to be the case in Aotus trivirgatus, the only nocturnal species of monkey (Moynihan 1964). The main emphasis of this study has therefore been centred on auditory communication although observations on the olfactory, tactile and visual communicatory signals have also been included in order to be able to attempt to place the relative importance of auditory as against those other communication channels in the correct perspective. The behaviour patterns found will therefore be described and discussed under the major headings of olfactory, tactile, visual and auditory signals.

2.. METHODS AND MATERIALS

2.1 FACILITIES

The study was carried out on a colony of bush-babies which has been established under semi-natural conditions by the Department of Psychology at the University of the Witwatersrand.

Basically the laboratory consists of three rooms. The animals are housed in four cages situated in rooms flanking the central observation room which has one-way screen panels set in its walls affording the observer a clear view of the animals in the cages. (See Fig. 1)

Although the laboratory was moved during the period of study to temporary quarters, and finally to a new permanent situation, the essential plan of observation room with one-way screens overlooking the cages remained unchanged. The following details of the cages are those obtaining in the present laboratory but as measurements and details of the cages in the three laboratories did not differ greatly, it is felt that a full description of all three laboratory conditions is superfluous and only major differences will be noted.

2.1.1 Housing Facilities (See Plate I)

The four cages are numbered one to four in clockwise rotation starting from the first cage situated on the left as the observation room is entered. All the cages are the same size viz. 72" wide x 72" long x 96" high at the far side sloping to a height of 66" on the side in common with the observation room.

PLATE I. OBSERVATION CAGE.

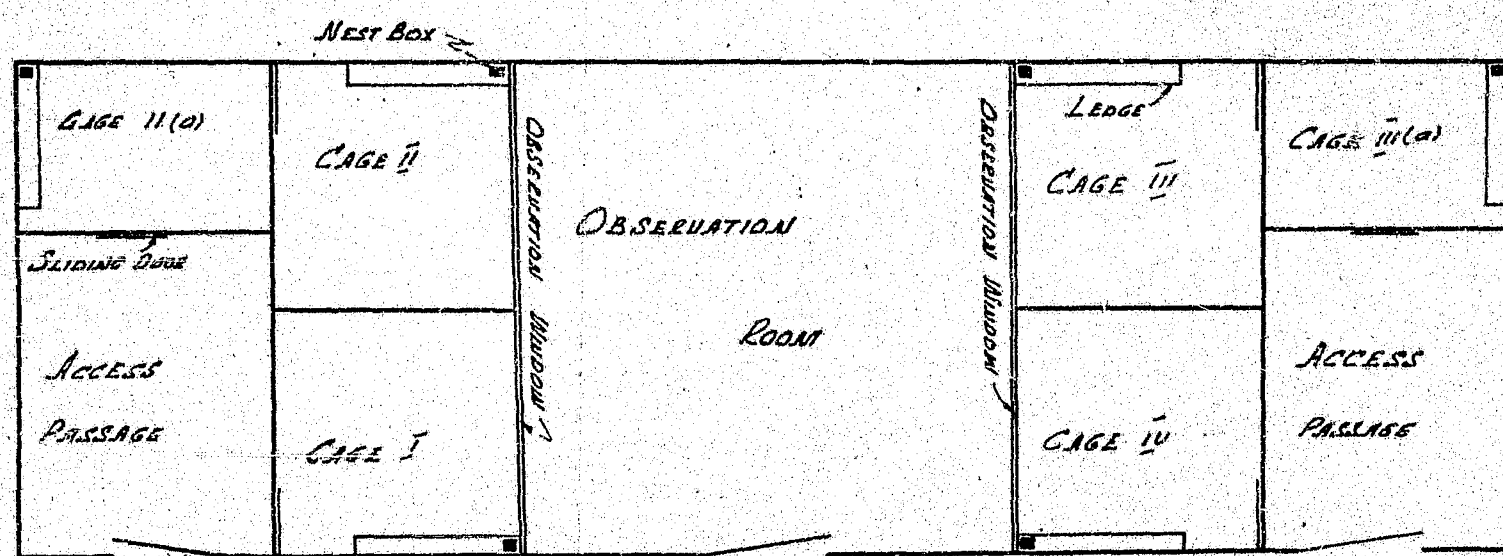

DIAGRAM OF LABORATORY SEEN FROM ABOVE

FIG. I

The walls of Nova-board surfaced with light grey Panelyte are supported in a frame of aluminium and the sloping roof is of ½", 14 gauge galvanised screening. Observation windows of one-way glass 66" long x 28" high are set into the walls separating the cages from the observation room at a height of 32" from the ground.

Each cage contains a nest box set against the observation windows on a food shelf of pressed board surfaced with Panelyte and measuring 48" in length and 12" in width. Each nest box consists of two portions:-

(a) A removable perspex box 10" long x 9" wide x 9" high which slides on aluminium runners on the ledge into position under;

(b) A fixed light housing made of painted pressed board, with a Panelyte top and containing one 15W bulb which is manually operated from the observation room. The bottom of the light housing which is situated immediately on top of the perspex box (a) is made of perspex covered with a red 'cinebex' filter. The light which illuminates the interior of the nest boxes is therefore red.

Branches and a rope have been placed at random round the interior of the cages and a layer of wood shavings covers the floor.

The cages are illuminated from above by 1 x 30W white fluorescent tubes yielding an average brightness of 7 foot candles to simulate day-time conditions. Night-time illumination is provided by 1 x 30W red fluorescent tubes giving an average foot candle reading of 2. The artificial daylight conditions prevail from 2300 h until 1200 h during which period the animals sleep. (This period will be referred to as the light-inactive period throughout the paper.) The red light simulating night-light conditions prevails during the remaining 11 h (1200 to 2300 h.) The bushbaby, lacking cones in its retina (Dodt 1967), is relatively insensitive to this light and is active during these hours. (This period will be referred to as the dark-active period throughout the paper.) These lights are automatically controlled by pre-set timer switches.

Suspended above the galvanised roof screening of each cage is a loudspeaker which acts as a microphone. These are connected to a control board in the observation room. Any one of the four cage microphones may be connected to an amplifier and calls may be monitored either by earphones or a loudspeaker.

Extract fans keep the cage-rooms well ventilated and both floor and air ventilation heating are available in winter.

In addition to these four cages, cages 2 and 3 have small cages adjoining them. (See Fig. 1) These are used to isolate injured animals or to house animals which may be temporarily excluded from an observation programme. The cage doors are all on slides and those between cages 2 and 2a, and 3 and 3a may be left open if a larger living area is required, although there are no viewing facilities from the observation room, for cages 2a and 3a.

During the time period that this study was undertaken, the disposition of animals in the cages has varied but has consisted in general of one adult male with one or two females and a varying number of infants and juveniles. The total number of animals per cage at any time has not exceeded six.

Although the laboratory described has proved to be an excellent solution to the observational difficulties imposed by the nocturnal habit of the bush-baby, several problems were encountered in studying the auditory signals. One of the main difficulties was to pinpoint the caller. Many of the calls are given with the mouth closed or only slightly open and are infrequently accompanied by characteristic body postures or facial expressions which might assist in indicating which animal is calling. When two animals are close together, for example, during fighting, mating, grooming or eating it is very difficult to ascertain which animal is calling. The positioning of microphones above each cage was of great assistance in establishing which cage housed the caller but the problem of pinpointing the caller in that particular cage remained.

In an effort to overcome these difficulties a box 30" wide x 48" long x 20" high, having the back and sides of masonite and the roof and front of plexi-glass, was constructed. The box stood in a tray of sawdust on an angle iron stand. It contained an horizontal branch, small food ledge and a nest box 10" long x 6" high x 7" wide. Two microphones were installed in the nest box roof, one leading to a tape recorder and the other connected to an amplifier and earphones. Lights suspended over the box produced night conditions similar to those obtaining in the main cages. Animals were kept singly or in pairs in this box for periods of time varying from one to seven days. (See Fig. 2)

The main differences in the three laboratories are:-

(1) The walls of the cages in the first two laboratories were made of Nova-board painted with a high gloss enamel paint. In the third laboratory Panelyte has been used to facilitate easy cleaning.

(2) The one-way glass observation windows in the first two laboratories were smaller than in the current laboratory, measuring 18" x 45".

(3) None of the laboratories has been sound-proofed and background noise interference in the first two ground level laboratories was very much higher than in the current laboratory which is situated on the third floor of the building in which it is housed.

2.1.2 <u>Recording Equipment</u>

Two <u>tape recorders</u> were used:-

(1) A Kudelski Nagra III tape recorder with a Neumann M.M. 5c microphone having a frequency range of 20 - 40,000 cps.

(2) An Uher 4000 Report - L tape recorder with a M514 microphone having a frequency range of 70 - 14,000 cps.

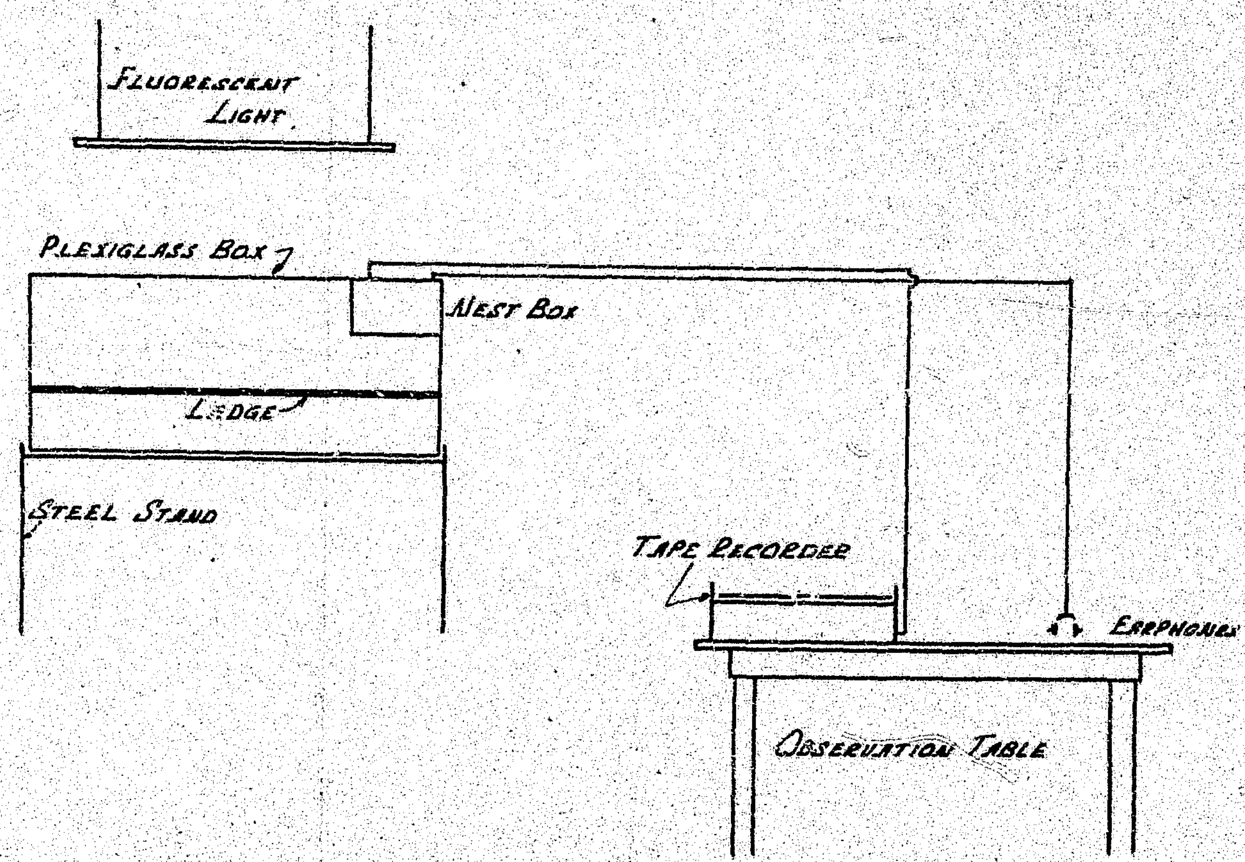

DIAGRAM OF PLEXIGLASS BOX.

FIG. II

A speed of 7.5"/sec was used in recording material for sound spectrographic purposes and that of 3.75"/sec during lengthy observation periods.

The sound spectrograph used to graph the vocalisations was a Kay Electric Company Sona-graph Model Recorder 662A used in conjunction with the Nagra tape recorder. Kay Electric Company Sonagram Paper Type B and Type B/65 was used and the 0.085 - 6 KHz and 6 - 12 KHz frequency bands were scanned on the vertical axis and time to a total duration of 2.4 secs on the horizontal axis. In general the H.S. shaping switch was used and narrow band filtered (450) sound spectrographs were obtained. A few wide band filtered (3000) sound spectrographs have also been included.

2.2 SUBJECTS

A total of twenty-seven animals were observed during the period of study, thirteen being male and fourteen female. Of these nine were born in the wild and their early history is unknown. Eighteen were born in the laboratory.

As many of the young animals matured and grew to adulthood during the period of study, the actual number of animals studied in the four main groups are as follows:-

Adult	= 17	(9 of these were adult at the commencement of the study.)
Sub-adult	= 11	
Juvenile	= 16	
Infants	= 9	

2.3 PROCEDURE

Samples of calls were recorded during periods of observations totalling approximately 800 hours. Observation periods varied between 25 mins to 100 mins per session during which both written and tape-recorded data of patterns were obtained.

During formal observation sessions the observer sat in the darkened observation room at a writing ledge lit by a well shielded red neon tube of 6W and situated directly in front of one of the observation windows.

A tape recorder and microphone were placed to record all calls heard during the session. Samples of calls were also obtained while sitting with the tape recorder in the access passage inside the rooms containing the cages. (See Fig. 1) In this way higher quality recordings were obtained but the behaviour accompanying these calls could not be observed. More than 50 hours were spent sitting on the floor inside the cages in order to obtain samples of the soft calls as these were very difficult to record.

Recordings of calls were made during sessions in which two previously unacquainted animals were introduced to each other and on one occasion during the introduction of a cat and a snake into the cage.

During observation sessions of animals in the plexiglass box (See Fig. 2) the observer sat at a table situated at a distance of three feet from the cage behind a black cloth screen that had a small viewing window in the centre. The observer wore the earphones that were connected to a microphone in the nest box roof and recorded samples of the calls heard via the second microphone which was also positioned in the top of the nest box. Unfortunately, due to acoustic distortion, these recordings were subsequently found to be unsuitable for sonagraphic analysis.

Samples of recordings were played back to the animals and their reaction noted.

A photographic record was built up to aid in the descriptions of communicative signals.

Sound spectrographs of calls that contained frequencies between 0.085 to 12 KHz were built up by excising the excess paper at the top of the 0.085 - 6 KHz spectrograph so that it could be placed directly in line with the 6 - 12 KHz spectrograph and a composite spectrograph depicting the entire range of 0.085 to 12 KHz obtained.

The spectrographs that were chosen for the illustration of the study were photographed and, although a small amount of extra detail was lost by this method, it is felt that the photographs show all the essential details of the original spectrographs. Many of the spectrographs show a heavy band of background noise between 85 and 200 cycles due to the interference encountered with the air conditioning unit. This interference is particularly noticeable with the softer calls and recordings suitable for sonagraphic analysis of some of the quieter calls were therefore not obtained.

3. OLFACTORY COMMUNICATION

Olfactory cues may be expected to play a more important role in communication in the prosimii than in the higher primates as is evidenced by their moist rhinarium, relatively large olfactory lobes and the widespread occurrence of special scent glands found prominantly in the Lemuroidea. (Montagna and Ellis 1959, 1960, Montagna and Yun 1962, Montagna 1962). Indeed, as Jolly (1966a) has pointed out, prosimians stand out among primates for the wealth and variety of their olfactory communication.

Olfactory signals may be divided broadly into the deposition of odoriferous substances and social sniffing.

3.1 DEPOSITION OF ODORIFEROUS SUBSTANCES

3.1.1 Urine-Marking

In common with other members of the Lorisoidea, Lemuroidea and some Ceboidea (See Table 1), Galago senegalensis has evolved an olfactory display involving the application of urine to the palms of the hands and thereafter to the soles of the feet. Two types of 'urine-marking' have been observed. The first and most frequent type has been described by several authors, (Lowther 1940, Sauer and Sauer 1963, Andrew 1964, Doyle et al. 1967) each with slight differences in detail. Basically in the animals observed in this study the movements consist of:-

(1) The foot and hand of one side are raised simultaneously from the substratum.

(2) The hand is cupped under the uro-genital region, a little urine being discharged into it.

(3) The hand then wipes the sole of the foot or grasps it firmly, one to several times.

(4) The hand and foot are replaced on the substratum. The pattern is usually, but not always repeated on the opposite side. (See Plate II fig a)

This type of urine-marking is performed far more frequently by the male than by the female e.g.

Female I urine-marked 20 times in 30, 25 minute observation sessions.

Male F urine-marked 110 times in the same observation sessions.

Urine-marking has been observed to occur in the following situations:-

(1) On emerging from the nest boxes for the first time at the beginning of the dark-active period, preceding or following various comfort movements such as stretching and self-grooming. The number of urine-marks during the first hour of the dark period is generally much higher than during the remainder of the active period unless a female in oëstrus is present when the urine-marking remains at a high level throughout the active period.

(2) Animals, especially the male, will urine-mark on entering the nest box at any time during the dark-active period even when no other animal is present in the box.

(3) Animals frequently urine-mark after eating.

(4) Animals urine-mark on a strange object placed in the living cage, or when they are placed in a strange environment, or on encountering the smell of a strange fellow.

(5) The males urine-mark during or immediately after genital smelling and/or grooming the female and, to a lesser extent, after genital smelling and/or grooming juveniles and infants.

(6) The males may urine-mark after chasing a female or subordinate male. They may also scent mark while staring at a submissive male generally prior to chasing.

(7) The male may urine-mark after smelling a spot where a female has just urine-marked.

(8) Both males and females (to a lesser extent) urine-mark during or immediately after naso-nasal greeting. One female An, previously a house-hold pet, urine-marks during nose-to-nose greeting with the human caretaker.

(9) The female may urine-mark after the male has genital smelled and/or groomed her, but she does this infrequently.

(10) The female may urine-mark during or after genital smelling and/or grooming or chasing another adult female or (rare) an adult male.

(11) Infants over 21 days old and juveniles may urine-mark after genital smelling and/or grooming any other animal.

(12) Under laboratory conditions the animals, particularly the males will extensively re-mark the living area after it has been cleaned.

It is interesting to note that on the occasions when a female becomes very aggressive and takes over the dominant role in her cage from the normally dominant male, her urine-marking increases and, although seldom reaching the high level of the males, assumes a distinctly masculine pattern.

A second form of urine-marking is found in Galago senegalensis moholi which is seen more rarely than the form described above. This type consists of the lowering of the hind part of the body to the substratum and deposition of a few drops of urine while at the same time moving forward with a wriggling movement of the body thus leaving a trail of urine drops. This form of urine-marking appears to be similar to that described for Loris tardigradus by Ilse (1955 cited in Andrew 1964) who has termed the movements "rhythmic micturation." The females perform this type of urine-marking more frequently than the males. Female Pr. habitually deposited a wide semi-circle of urine in this manner round the food dishes placed on the feeding ledge in her cage. The other animals in the cage, however, displayed little interest in the urine although they had to pass through the urine 'barrier' to approach the food.

A variation of rhythmic micturation in which the animal urinates copiously on a branch and, on