

The "soft notes" uttered by the male when approaching the female are Soft Hoots (Whoo-Whoo) while the "harsh note" uttered by the female while hitting at his face corresponds to Spit-Chatter or Spit-Grunt. The "zee zee zee ..." notes uttered by the infant are Clicks and Crackles, while soft "pips" notes uttered while being groomed may be soft Squeaks, but this is not certain. The "Grega" (a as in lad) heard by these authors when one young male play-fought over-vigorously with a younger male may be the Explosive Cough (Chow-hah) of this study. This is, however, uncertain as a loud bisyllabic call given during play-fighting has not been recorded for the animals in this study. Likewise the "chirping song" ... long-lasting without distinct breaks, soft, and always of about the same volume, offering all the attributes of pure play", has not been recorded for any juvenile in this study.

Andrew (1963a) refers to soft clicks given when a wild trapped animal is chased by the hand. He found that these calls occurred singly or in bouts which may blur together and pass into typical sharp calls with soft grunts occurring during the same period. These calls appear to correspond in this study with Spits, Spit-Chatter and Chatter passing into Yaps with Soft Grunts occurring in the same period.

The sneezes observed by Andrew appear to correspond with the Sneezes referred to in this study.

Difficulty has been experienced in placing the wuff-moan detected by Andrew (op. cit. Fig. B, Page 41) and no sound spectrographs were obtained which matched this call.

In the present study the 'Wuff' was mainly noted to be given in conjunction with Wails and an intermediate form of Wuff that has an ascending limb only. Soft Wuffs were not given by the animals during exploration of a new cage nor were Loud Wuffs given in lengthy bouts at the sight of a strange animal. Rapid Yaps and Clucks with occasional units of Whistles were given in response to the presence on different occasions of a cat and a snake. The small differences found in this study to the calls reported by Andrew might be explained by differences in rearing and housing of the animals concerned.

Although it is difficult to compare the calls reported for other closely related species with those found in the present study, Cansdale (1944 cited by Hill 1953) reports two calls for Galagoides (Galago) demidovii which appear to have a similar function to two calls found in G. senegalensis muholi. A call which appears to be similar to the Bark is described by Cansdale as a "chatter with a definite tonal pattern, starting very low and slowly and gradually rising in pitch and tempo and dropping off again as it ends." This is repeated after an interval of 5-10 secs and males answer each other alternately. He also reports a single note low "hoo" which may correspond to the Soft Hoot.

Grimm (1967) reports that one call of the pigtail macaque (Macaca nemistrina) is only given by pregnant females. Itani (1963) reports this for Macaca fuscata. Winter et al. (1966) have noted a distinctive call made by the squirrel monkey during labour. With the exception of the female, C, who experienced a protracted and difficult labour, all other females were silent during labour. The female C emitted a very soft 'wimpering jumble' of sounds during labour which was taken to be indicative of pain but it was not feasible to record these sounds. They appeared to be little more than a by-product of breathing. However, another animal, male L, emitted similar sounds when he had a facial abscess lanced, so these sounds are not restricted to females. Adults generally remain silent when open wounds are dressed. (A plastic antiseptic aerosol dressing is used which stings sharply for a few seconds when used on humans.) Infants utter Crackles and Loud Squeaks.

Grimm (1967) and Rowell and Hinde (1962) discuss the possibility of a dialect developing in animal groups kept in the laboratory. Moynihan (1964) points out that "captive animals may perform displays in situations that are different from those in which wild animals perform the same displays, but they do not perform displays that are not also performed by wild animals in some situations." Obviously field observations are essential in forming a biologically correct picture of the significance of the behaviour

patterns found in the laboratory and it is hoped that the patterns discussed in the present study will be found to be basically correct when supplemented by field observations. Bearder (1969) confirms that all the loud calls and many of the soft ones heard in the laboratory occur in the field and, to the unaided ear, do not appear to differ noticeably from those heard in the laboratory.

S U M M A R Y

A description of the signals used by the Lesser Bushbaby in communication under semi-natural living conditions is given under the major headings of Olfactory, Tactile, Visual and Auditory Communication.

Olfactory signals fall under the broad divisions of
(A) Deposition of odoriferous substances, and
(B) Social sniffing.

Methods of urine deposition are described and the situations in which it occurs noted. A behaviour pattern that is generally performed mainly by the male, that of Chest-Rubbing, is described. It is suggested that an odoriferous substance is deposited from a gland centrally situated in the chest of the male, and that this marking is concerned with territorial demarcation. Naso-nasal sniffing is a common greeting pattern and ano-genital sniffing occurs between all members of a group, especially in males. The general behaviour of the bushbaby indicates that olfactory signals and cues are an important communicatory channel.

Tactile signals include contact in both friendly and hostile situations, and are described under these headings. Allogrooming occurs frequently, in a wide variety of circumstances and is not restricted to sexual situation. All possible combinations of groomer and groomee occur but male-female and female-infant combinations are the most common. The method used in allogrooming is common to many of the prosimians where the hand is only used to hold the groomee.

Playwrestling is common in infants and juveniles but is rare between adults unless juveniles are present.

Two types of mounting involving females are described as well as the tactile signals occurring in infant transport and suckling.

Two types of fighting occur. In the first type one animal is the aggressor and the other submissive and open wounds seldom occur. The second type involves two equally dominant animals, is completely silent and open wounds may occur especially on the hands and face. Instances are given in support of the suggestion that tactile signals such as allogrooming reduce intraspecific damage.

The large repertoire of facial expressions and body postures that constitute an extensive visual communication system in the higher primates does not occur in the Lesser Bushbaby. The facial expressions and body postures are described. The facial expressions seen give support to the theory given by Andrew (1963a, 1963b, 1964) that they have been derived from "protective responses" and it is suggested that this remains their main function in Galago senegalensis moholi.

It is suggested that visual signals are not an important means of communication in the Lesser Bushbaby (at least under laboratory conditions). This paucity of facial expressions results from a simple facial musculature which in turn may be indicative of a simple social structure of small family groups taken in conjunction with a nocturnal and arboreal habit.

The 25 vocal signals used in auditory communication are described under the general headings: (1) calls associated with Agonistic situations; (2) calls associated

with Friendly and Contact situations, and (3) calls associated with Alarm situations. Sound spectrographs of most of these calls are presented.

Vocalizations which are obviously intermediate between distinct calls are not common and the overall impression of the repertoire is one of relatively stereotyped calls. The method of utilization of the various calls compares closely with that found by Moynihan (1964) in the Aotus trivirgatus (Night Monkey). The bushbaby does not utter intermediate notes when motivated by a complex combination of tendencies but rather a series of different types of notes each one of which expresses only one or two tendencies.

Calls used mainly by infants are described as well as two non-vocal sounds which may act as auditory signals.

An attempt is made to identify the calls found by other workers with those found in this study.

It is concluded that while many of the messages sent by the bushbaby in communication are complex messages utilizing more than one channel at a time, the auditory channel carries the heaviest load with the visual channel being possibly the least important.

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ERRATA OMISSIONS (from Table I.)

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TABLE I
METHODS OF OLFACTORY MARKING IN PRIMATES

Name	Type	Author
<u>Loris tardigradus</u>	Urine deposited on plantar surface of hand and wiped onto plantar surface of foot. Rhythmic micturation. Gland on inner side of arm at elbow.	Ilse 1955 Ilse 1955 Montagna and Ellis 1960
<u>Myotis coucang</u>	Rhythmic micturation. Gland on inner side of arm producing fetid smell.	Hill 1953 Montagna et al. 1961
<u>Perodicticus potto</u>	Rhythmic micturation. Concentration of apocrine glands around the genitals used in marking.	Bishop 1964 Montagna and Ellis 1959
<u>Galago crassicaudatus</u>	Urine deposited on plantar surface of hand and wiped onto plantar surface of foot. Rhythmic micturation.	Eibl-Eibesfeldt 1953 Andrew 1964
<u>Galago senegalensis</u>	Urine deposited on plantar surface of hand and wiped onto plantar surface of foot. Rhythmic micturation. Gland on centre of chest used in Chest-Rubbing.	Lowther 1940 Andersson (this paper) Andersson (this paper)
<u>Galagoideus (Galago) demidovi</u>	Urine deposited on plantar surface of hand and wiped onto plantar surface of foot.	Cansdale 1944 (cited in Hill 1953)
<u>Cheirogaleus major</u> <u>Cheirogaleus minor</u>	Anal rubbing and marking with faeces.	Petter 1962
<u>Microcebus murinus</u>	Urine deposited on plantar surface of hand and wiped onto plantar surface of foot.	Petter 1962

Table I continued on next page

TABLE I continued

<u>Lemur catta</u>	Palmar and armpit scent glands. Shoulder gland.	Fiedler 1955 Evers and Goy 1968
<u>Lemur mongoz</u>	Mark with palmar and armpit glands.	Bolwig 1960
<u>Lemur macaca macaca</u> <u>Lemur macaca fulvus</u>	Mark with urine and faeces and with palmar glands.	Petter 1962
<u>Hapalemur griseus</u>	Mark with palmar and armpit glands.	Petter 1965
<u>Propithecus verreauxi</u>	Mark with throat gland. Rhythmic micturition especially in the female. Urine on plantar surfaces of hands and feet.	Jolly 1966a Jolly 1966a Petter 1965
<u>Avahi laniger</u>	Mark with glands on the head at the level of the angle of the mandible.	Petter 1962
<u>Daubantonia</u> <u>macgasecarieus</u>	Anal marking with faeces	Petter 1965
<u>Tupaia glis</u>	Mark with chin and throat glands	Sprinkel 1961
<u>Aotus trivirgatus</u>	Urine on plantar surface of hands and transferred to soles of feet. Marks by Anal Rubbing with glands in genito-anal region.	Hill 1960 (but not Moynihan 1964) Moynihan 1964
<u>Alouatta palliata</u>	Anal Rubbing, marking with glands in genito-anal region.	Moynihan 1967
<u>Saimirus hoffmanni</u>	Anal Rubbing	Hill 1957
<u>Callicebus moloch</u>	Anal Rubbing (rare). Chest Rubbing, marking with a central chest gland.	Moynihan 1966 Moynihan 1966

Table I continued on next page

TABLE I continued

<u>Amimiri sciureus</u>	Anal R. boing (rare). Urine 'washing'.	Moynihan 1967 Andrew 1964
<u>Cebus apella</u>	Urine washing.	Nolte 1958
<u>Cebus runcinus</u>	Urine washing.	Hill 1957
<u>Ateles sp.</u>	Marks with throat glands.	Marler 1965 cites Eisenberg and Kuehn unpublished
<u>Hapale iaculus</u>	Mark territory 'in a manner similar to lemurs.'	Bolwig 1964
<u>Cercopithecus aethiops</u>	Mark with gland in corner of the mouth. (Unconfirmed.)	Gartlan and Brain 1968

TABLE 2

SIGNALS ACCOMPANYING DIRECTIONAL OR UNIDIRECTIONAL CALLS		
Call	Directional or Unidirectional	Other signals involved
Grunt (Defensive)	Directional	Defensive threat facial expression, Swaying and Gringing body posture.
Spit, Spit-Chatter, Spit-Grunt	Directional	Defensive attack facial expression and upright defensive attack body posture. Boxing at face of male by female.
Chatter (Fighting)	Directional	Tactile signals involved in fighting. Protective responses involving eyes and ears.
Moans - Sobs	Directional	Tactile signals involved in fighting. Protective responses involving eyes and ears.
Screams	Directional	Tactile signals involved in fighting. Protective responses involving eyes and ears.
Roar	Directional	Offensive attack facial expression. Tactile signals involved in fighting.
Explosive-Cough	Directional	Agitated subdominant animal, otherwise no conspicuous signals.
Bark	Unidirectional	No definite allied visual, tactile or olfactory signals, although alert upright posture frequently occurs.
Soft Hoot	Directional	Chasing and tactile signals involved in friendly contact.
Coo	Directional	Tactile signals involved in transport of infant. Olfactory signals particularly probable.
Soft Grunt	Directional	Tactile signals involved in friendly contact. Olfactory signals probable.
Squeaks	Directional	Tactile signals involved in grooming and friendly contact. Olfactory signals probable.
Sneezes	Unidirectional	Peering in infants and juveniles. Nose licking in adults.

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TABLE 2 continued

Call	Directional or Undirectional	Other signals involved
Growl Cluck Shivering-Stutter Whistles Yap Plaintive Yap Yap Alarm Wuffs Wails Caws	Undirectional*	No distinctive visual or tactile signals apart from a generally 'agitated' animal.
Clicks and Crackles	Directional	Grin facial expression.

* When occurring in agonistic situations may possibly be directed at aggressor.

TABLE 3

SIZE OF AUDITORY REPERTOIRE OF VARIOUS PRIMATE SPECIES
(Based partly on Struhsaker 1967.)

Species	Number of Sounds	Authority
<i>Macaca mulatta</i>	17 - 20	Rowell and Hinde 1962
<i>Macaca fuscata</i>	37	Itani 1963
<i>Cercopithecus aethiops</i>	36	Struhsaker 1967
<i>Erythrocebus patas</i>	15 - 20	Hall 1965
<i>Presbytis entellus</i>	10	Jay 1962
<i>Papio sp.</i>	15	Hall and DeVore 1965
<i>Hylobates lar</i>	9	Carpenter 1940
<i>Pan troglodytes</i>	22	Goodall 1965
<i>Gorilla gorilla</i>	21	Schaller 1963
<i>Aotus trivirgatus</i>	9 - 10	Moynihan 1964
<i>Callicebus moloch</i>	10	Moynihan 1966
<i>Alouatta palliata</i>	20	(Carpenter 1934 (Collins and Southwick 1952 (Altmann 1959

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