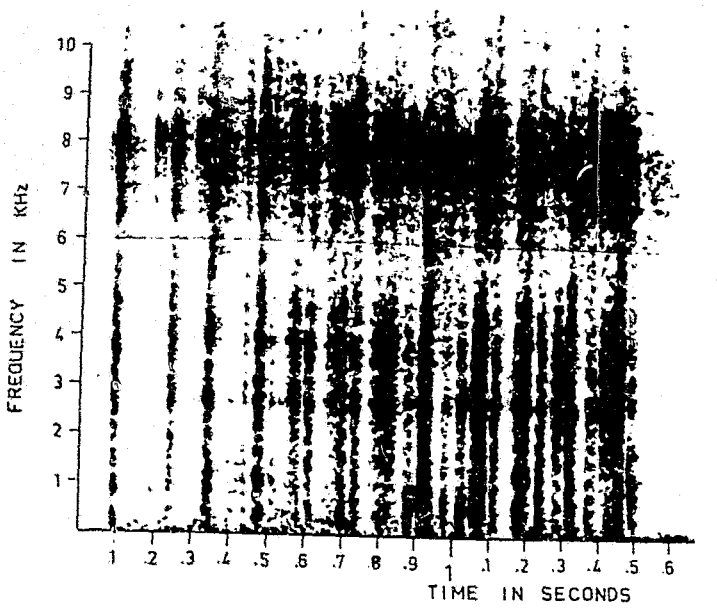
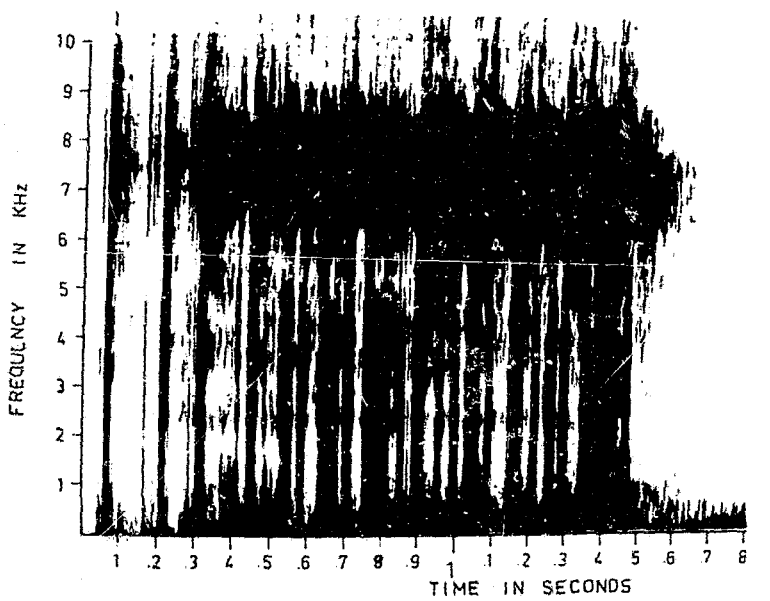


a. Narrow Band.



b. Wide Band.

PLATE IX. RASP.

6.3.10 Discussion

Calls given during contact in agonistic situations are, with the exception of the Rasp, all uttered by the inferior. Calls indicative of a frightened animal, such as the Yap and Whistle, that are heard in alarm situations are also heard during hostile encounters. Calls heard during imminent or actual contact are:-

Grunt (Defensive) (rare)

Spit-Grunt

Spit and Spit.Chatter

Chatter (fighting)

High Intensity Spit

Sobs

Screams

These are arranged in the order in which they are most usually given if the intensity of the situation increases. Units of the Explosive Cough, Whistle, Gerwhit and Yap may be given sporadically mixed with the units of the calls mentioned above, but are more frequently heard during or after chasing and not during contactual fighting. It is during hostile encounters that the majority of variants of calls occur. Sound spectrographically these are seen to be shortened versions of calls and it is thought that they occur when the animal under stress is uttering various units of calls in such a rapidly changing series that it does not have time to give the full unit. The animal is

frequently jumping very rapidly and the problems encountered in the breathing control necessary to cope with strenuous exercise and simultaneous vocalising may help to account for the variations heard.

As Hockett (1960) has pointed out a spectrograph does not show which features of the sound are communicatively significant and it is possible that the short versions of calls convey the same message content during high intensity situations, as the same call seen in the full form at less intense levels. Marler (1965) has pointed out that variations in the temporal pattern of delivery of the same signal under different conditions may be fundamentally related to the kinds of information they carry. The short versions of calls may therefore, indicate a situation of higher intensity than one in which the full length units are given. (This is the case as far as the human observer is concerned.)

Andrew (1964) notes that withdrawal of the mouth corners and vocalizations appear during intense attempts to gain contact in Galago spp. This mainly occurs when friendly contact between a hand-reared animal and the hand-rearer is prevented. This has not been observed in this study. The Rasp which may be given when endeavouring to get out of a cage to attack another animal may however be comparable to the shrieks of Lemur fulvus which are given under similar circumstances. In both cases the calls are accompanied by intense withdrawal of the corners of the mouth.

6.4 CALLS ASSOCIATED WITH FRIENDLY AND CONTACT SITUATIONS

6.4.1 Bark

This sharp tonal call consists of a series of single (± 0.25 sec) or apparently double (± 0.4 sec) monosyllabic notes with the main formants occurring at ± 0.5 and ± 1.2 KHz and the harmonics ranging up to 4 - 5 KHz. (See Plate XXI) The time interval between the units is very variable, becoming shorter with increasing excitement. The number of units in a phase or bout is entirely dependent on the total length of time spent calling.

This call is commonly heard in the laboratory shortly after the lights change to the dark phase at the beginning of the active cycle, as well as at odd intervals throughout the active cycle. An animal, generally an adult male, will start this call and will be answered by others in the adjacent cages. (See Plate XXI fig. a)

This call is generally given by the adult male in each cage and was for some time thought to be restricted to adult males only. However, the females may Bark when they are alone in a cage or accompanied by infants and/or juveniles only, or when they have assumed dominance over the normally dominant male in their cage during occasional very aggressive phases. The call is not uttered by infants, juveniles or subadults (males under 300 - 340 days old or females under 200 days.) When a male on maturing first starts to give the call he does not do so as

frequently or as loudly as the older (generally heavier) males.

Barks are given in response to other male calls and frequently also in response to Soft Hoots. (See Plate XXIII fig. a) Tape recordings of these calls played back will also elicit Barks from the males. If unanswered, Barks seldom last longer than 15 - 30 secs but those phrases or bouts that are answered by other animals last 30 - 60 secs/animal on the average. However, the frequency with which this call is heard under laboratory conditions increases very greatly when the females come into oestrus. The males may then call in bouts lasting four to five minutes in duration and are exceptionally quick to answer the call of another male. Barks are frequently given by the male immediately after mating particularly when other males could be seen in the mesh stock cages.

A typical phase consists of either a series of single notes and a few 'double notes', or a few single notes passing rapidly into 'double note' units that increase in intensity and loudness. An increasing amount of non-tonal components may occur until the call becomes very harsh and graty and resembles a non-tonal sound containing many frequencies at a similar intensity. (Plate XXI fig. d shows this beginning to occur.) During moments of high excitement triple note units may occur.

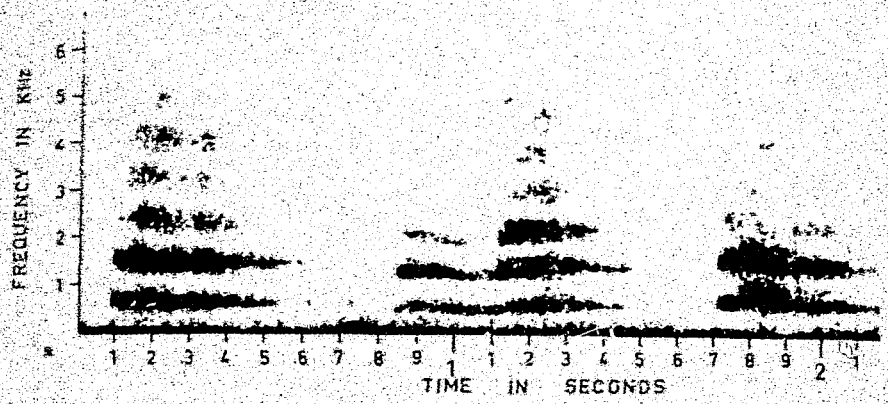
The mouth appears to be either closed or very nearly closed but on the second note of the 'double

note' unit the mouth may open sharply. The apparently 'double note' is represented on the sound spectrograph as a single tracing along the horizontal axis, and has therefore been taken to be a single unit. The harmonics however tend to separate into two groups. (See Plate XXI fig. a, 1st unit).

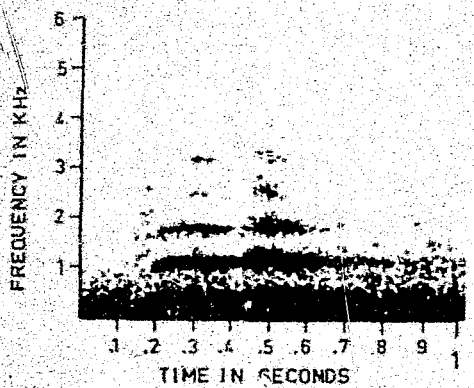
The adult males, on hearing a Soft Hoot or Bark given by another male, generally orientate their bodies in the direction of the call, moving the ears rapidly about and may jump to a high branch or ledge and face in the direction from which the original call is coming. They may then start answering the original caller. The original caller then also may turn to face the direction from which the answer is coming. The other animals in the cages, females, juveniles and infants appear to take very little notice. They may listen briefly but quickly resume whatever activity they were engaged in when the calling started. The caller himself may, towards the end of calling, jump round the cage or even eat during calling.

Although the function of these calls is not clear from a laboratory study, it is thought that they may function as a territorial call and aid in the spacing out of family groups. They are loud calls and exhibit both the low frequencies and sharp repetitive characteristics considered important for distance communication by Marler (1959). They appear to be more frequent during the breeding season

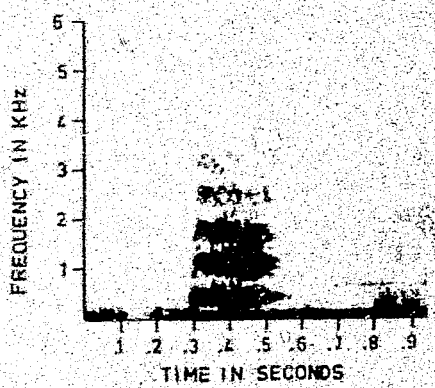
and many birds (Collias 1960), frogs and mammals (Bogert 1960) are known to acoustically define and defend territories during the breeding season. The response to the signal tends to be spacially orientated to the signal source and is given and answered by the most dominant animal in the cage. Throughout the active period soft single note (See Plate XXI fig. c) or 'double note' units may be sporadically uttered by the males during general activities and these may develop into the loud Bark call if it is answered immediately by a male in another cage. Several other primates are known to use calls as an aid to spacing and this type of call has been recorded for the gibbon (Ellefson 1968) and howler (Carpenter 1942, Southwich 1962, 1965), Callicibus (Mason 1964, 1968), marmosets (Epple 1968) and the langur (Ripley 1967 and Jay 1965b.) Among the Lemuroids calls apparently having a territorial spacing function have been noted for Lemur macaco macaco, Lemur macaco fulvus, Phaner furcifer, Propithecus verreaux, Daubentonia and Indri indri (Petter 1962.)



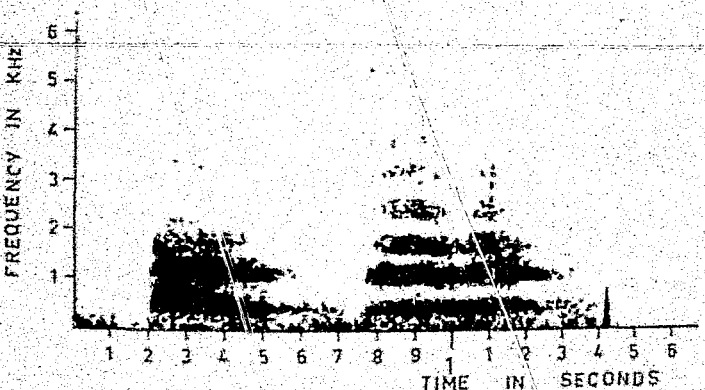
a. Male answered by another male. (center unit)



b. Female.



c. Single note bark.



d. Harsh Bark.

PLATE XXI. BARK.

6.4.2 Coo (Maternal Call)

The Coo is a very soft low call consisting of single note tonal units with a varying time interval between them. It is a maternal call given only by the female and occurs in situations where she gains, or attempts to regain, contact with her infants after a brief absence, e.g.

(1) After leaving her infants for a short period in order to eat and drink the female will utter the Coo on entering the nest box and approaching her infants. She has not been heard, however, to utter this call while grooming them.

(2) While retrieving the infant back to the nest box the female utters the Coo. If an infant which has been removed from the female for weighing purposes is offered to her outside the nest box, she will rapidly approach while uttering the Coo and pick the infant up. While still making the call she will return the infant to the nest box where she stops calling and starts to groom the infant.

The call has been heard while the female cleans the newborn infant and is most frequently heard during the first week after birth. It becomes less frequent during the second week and has not been heard after the 16 - 18th day by which time the infants are actively climbing on the branches. It is possible that it may continue to be given when the female retrieves

the infant as it is a very soft call given with the mouth closed, and is therefore difficult to detect.

The Coo does not appear to have the function of attraction that for example is found in the cluck of a chicken. The infants when left alone in the nest box frequently give defensive threat calls and postures if any other animal except the mother enters the box. The Coo therefore, appears to function as a recognition call. (Recordings suitable for sonagraphic purposes have not been obtained as the nursing female does not utter them if the observer approaches too closely with a microphone.)

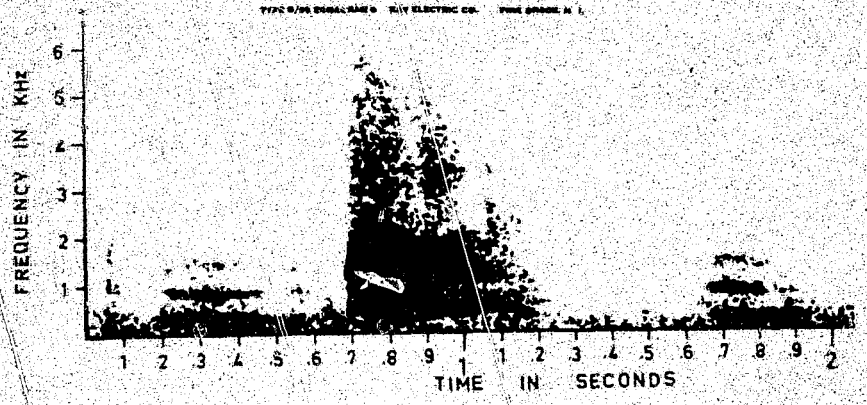
6.4.3 Soft Hoot (Chasing Call)

This tonal call consists of a low, soft, single note unit with a variable time interval between units which are frequently uttered in pairs. The Soft Hoot is given during chasing of the female by the male when he is endeavouring to come into contact with her to genital smell, groom or to mate with her and may continue during actual contact after chasing. An increase in the tempo of calling is correlated with an increase in excitement seen on the part of the male when he comes close enough to examine the female's ano-genital region. The female, while being chased, may suddenly stop, face the pursueing male and box at his face while uttering a chattering call. (See Spit-Grunt, Spit-Chatter sections 6.3.2 and 6.3.3.)

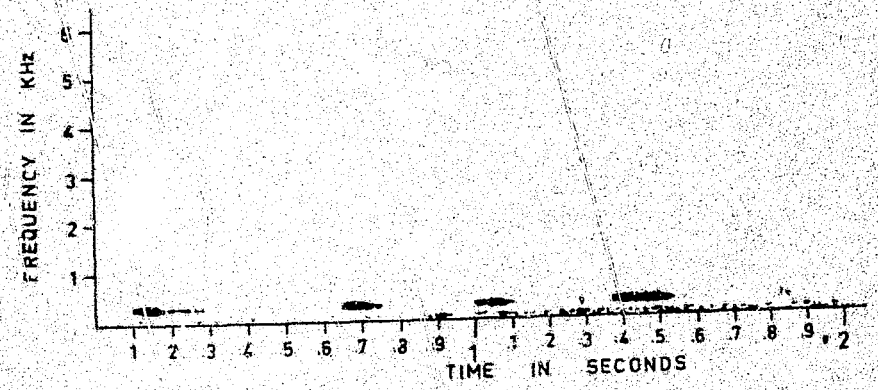
Soft Hoots may also be given by females and maturing juveniles during chasing but this is more rare. The adult males may also give this call on chasing a strange juvenile placed in the cage. It has not been heard when the chasing is hostile in nature and it appears to function as an indicator that the animal uttering this call is interested in a friendly manner in the animal that it is endeavouring to contact.

Good sound spectrographs of the Soft Hoot are difficult to obtain due to the large amount of background interference occurring in a chasing situation and also due to the fact that the call falls in the same frequency bands as the interference from the

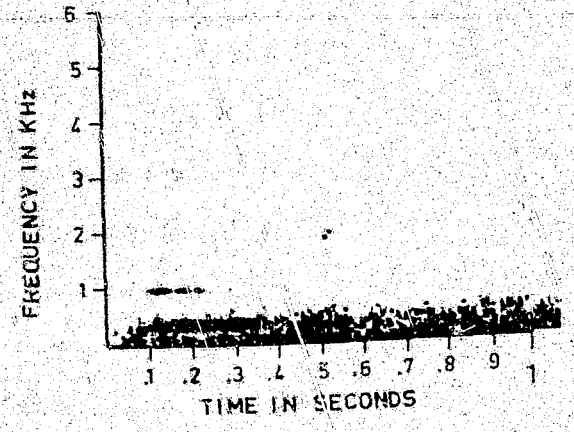
air conditioning unit. Plate XXII fig. c, shows a Soft Hoot unit lasting 0.27 sec. in total duration with the main fundamental at ± 300 Hz and a single harmonic at ± 800 Hz.. (The single harmonic is missing in Plate XXII fi . b as the photograph of the spectrograph has been printed to show the fundamental as clearly as possible.)



a. Soft Hoot with harsh Bark.



b. Soft Hoot.



c. Soft Hoot.

PLATE XXII. SOFT HOOT.

6.4.4 Soft Grunts (Contact Whispering Grunts)

Soft Grunts are similar, to the human ear, to Soft Hoots but are slightly lower in pitch and loudness. They are uttered with the mouth completely closed and occur during situations involving contact such as naso-nasal greeting behaviour, grooming and while settling down with another animal to rest in the nest box. Soft Grunts mixed with Squeaks are uttered by a female An, when attempting to burrow into the observer's clothing.

The units of this call occur singly with a variable time interval between them and seldom consist of more than 3 or 4 units/phrase.

Soft Grunts do not appear to occur very frequently but due to their very quiet nature, it is possible that they have not been heard on occasions when they have indeed occurred and it is difficult to give an accurate estimate of the relative frequency with which they appear in the overall repertoire.

Recorded examples of Soft Grunts were obtained from animals housed in the Plexiglass box and were found to be unsuitable for Sonagraphic analysis due to distortion. It is not certain, therefore, that they are spectrographically distinct from Soft Hoots. They are, however, distinctly quieter calls, (the observer can only hear them if he is inside the cage and within one to two feet from the caller), and are regarded as a distinct call as they are given in situations involving closer contact than those which elicit Soft Hoots.

6.4.5 Squeaks

Soft Squeaks given by adult animals while grooming moist areas of the human observer's face as reported by Andrew (1962) have been noted for one adult only, a female An, whose background before entering the laboratory was that of household pet. Squeaks given occasionally by juveniles, especially females C, Pa and O, have not occurred since the animals matured. Andrew (1963b) reports these sounds from hand-reared animals and Squeaks under these conditions may possibly be a case of persistance of infantile or juvenile behaviour. Animals have not been observed to utter Squeaks during allogrooming but as these calls are very soft, there is a possibility that if they occur only occasionally, they may have been overlooked. Soft Squeaks appear to be given with Contact Grunts in a soft mixed 'mumble' when the animal An, mentioned above, attempts to burrow into the observer's clothes and may pass into brief trills.

6.4.6 Discussion

The Bark, Soft Hoot, Coo and Soft Grunts appear to be similar calls in that they are all short linear sounds with a well-defined fundamental and harmonics, and appear to differ mainly only in loudness and pitch. The Coo and the Soft Hoot are similar calls. This similarity between calls used by the female with her young and the call given by the male in courting or attracting the female has been noted for several animals including goats, geese and the opossum. (Collias 1960)

The soft single note Bark that is given sporadically, mainly by the dominant animal in the cage but also occasionally by others, does not elicit any marked response from the other animals. It is possible that it may function in maintaining contact with the other members of the group. Calls which serve to maintain contact between members of a group and also to maintain a constant spacial distribution within a group have been described for several primates including the Japanese Macaque (Itani 1963), the vervet (Strushaker 1967), the rhesus monkey (Altmann 1962) and the baboon (Hall and DeVore 1965.) Marler (1968) has pointed out that these calls are all soft but readily locatable at close range.

The bushbaby may answer human imitations of the Bark particularly during the breeding season. The Bark is grunt-like in character and the Gelada Baboon (Theropithecus gelada) will give the charac-

teristic baboon segmented grunt in response to human imitations as will Hylobates concolor (Andrew 1962b.) Lemur fulvus and Lemur catta both give their contact calls in response to sounds of similar quality. It appears therefore that not only are grunt-like calls used to help maintain contact in several different primate species but also that these calls are not highly structurally distinctive.

On the few occasions when the power supply in the laboratory has failed leaving the bushbabies in exceptionally dark conditions, the number of Barks (both loud and soft) has increased so greatly in the first 5 - 10 mins that they have amounted to a distinct chorus. It is thought that the increase in vocalizations under these conditions may be correlated with the decrease in visual cues and that it lends some support to the suggestion that these calls have a contact function.

No specific mating calls have been heard. Mounting is generally silent. The calls that have been recorded during mounting are:-

(1) The Shivering-Stutter which may be made by the male and (more rarely) by the female if the pair are disturbed.

(2) The male may utter Clucks, Whistles and Yaps while chasing the female and may continue to utter these during mounting, especially when a very aggressive female is involved.

(3) The Hiccup Whistle has been given by males when

attempts at mounting have failed either due to aggressive non-acceptance on the part of the female or as occurred on two occasions when the female was removed by the observer. These calls in conjunction with highly active, alert, nervous behaviour on the part of the male are taken to indicate that mating is a very stressful time for the males.

6.5 CALLS ASSOCIATED WITH ALARM SITUATIONS

6.5.1 Sneezes (fft, fft-i-fft and Fu-ut)

This soft non-tonal and generally non-voiced call consists of units lasting ± 0.03 - 0.06 sec. in duration with energy distributed between 0 - 8 KHz and sometimes reaching to 11 KHz. A drop in energy between 2 and 2.5 KHz occurs with a subsequent increase to the level seen between 0 and 2 KHz. (See Plate XXIII) This common call is given in three distinct patterns:-

(i) The fft is given in single or double units.

(ii) The fft-i-fft is a series of ffts given in very rapid succession, while

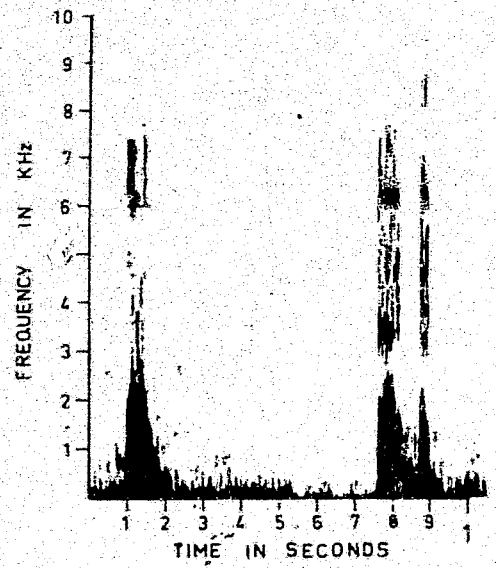
(iii) The Fu-ut is a more emphatic version of (i) and occasionally contains voiced components.

Sneezes of the first type occur in situations where 'curiosity' is combined with low intensity 'uncertainty", e.g. when a novel but not immediately frightening object is placed in the cage or when a human with whom the animals are familiar enters their cage. Sneezes (Type i) are given while looking at the object, while approaching and while first smelling, and then examining it. If, while one animal is examining the novel object, another gives a single definite Sneeze (Type iii), the first animal will immediately jump away and may utter Sneezes of the second type. If the object subsequently makes no threatening gestures, these calls soon revert to

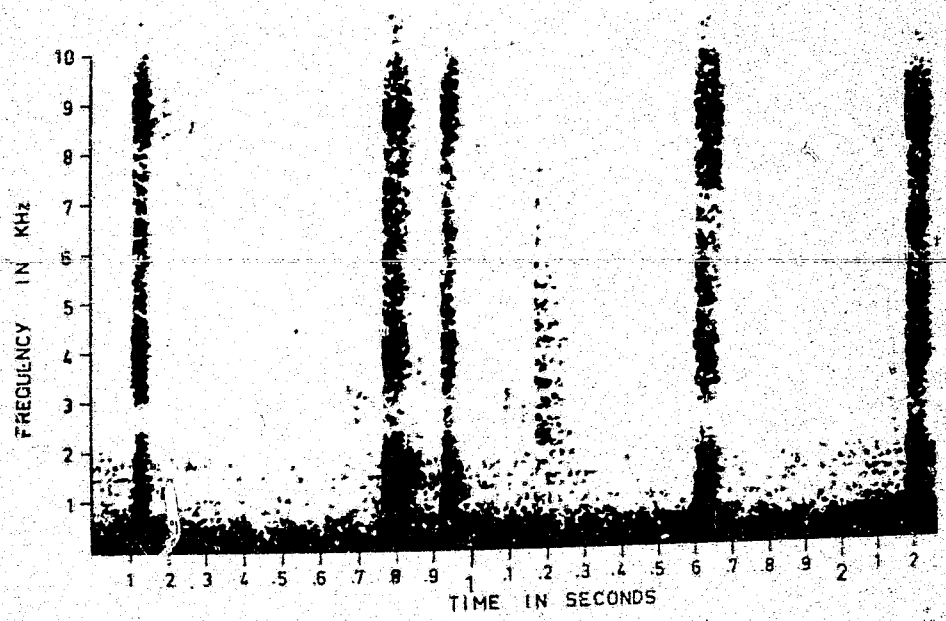
Sneezes Type i and the object is reapproached. As the animals become more familiar with the object they gradually stop Sneezing.

Sneezes may be given while exploring a new living area. Sneezes are also given when two strangers are introduced to each other when there is little likelihood of an attack on the part of either fellow, e.g. when a juvenile male is introduced to a placid adult female. The juvenile may give Sneezes (Type i or ii) while tentatively approaching the female. Sneezes are also given by the subordinate in response to a stare from a superior and may pass into Yaps if a chase follows. Mixed Sneezes of all types may be given with units of other calls when the intensity of a situation is decreasing. Sneezes similar to Type iii are also given during hostile encounters where they may actually serve to clear the nasal passages as the animals frequently become covered in wood shavings from the floor.

Sneezes appear to occur when both the tendency to approach and to flee are activated, with the former being the stronger. They may be accompanied by frequent nose licking. Sneezes given by one animal generally evoke Sneezes in its cage companions.



a. Wide band, Sneeze Type I followed by Sneeze Type III.



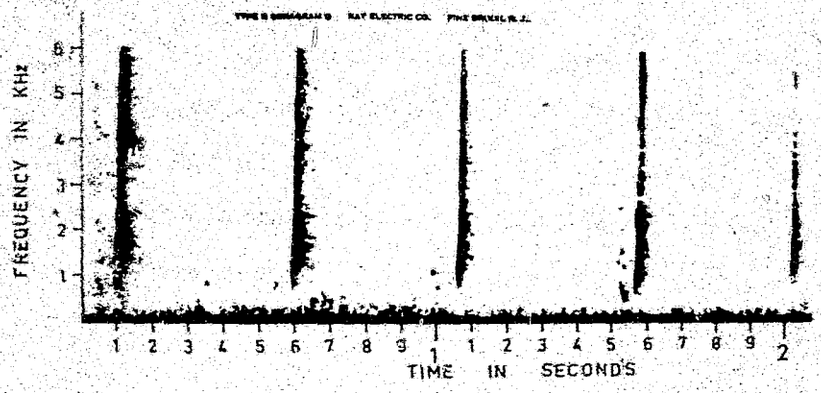
b. Sneeze.

PLATE XXIII. SNEEZE.

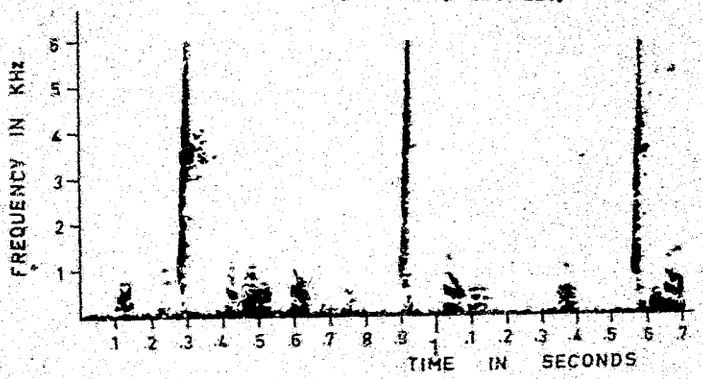
6.5.2 Gerwhit (Whits)

This call consists of mixed units of tonal and non-tonal sound having a very sharply rising almost vertical formant often with a vertical extension of non-tonal sound and also a lateral broadening between 200Hz and 2.5 KHz. This unit may be preceded by a spit-like unit when the call is relatively slow, having a 'deliberate' quality about it. When occurring more rapidly and swiftly this spit-like unit may become a very faint scatter of non-tonal sound or may be lacking altogether. (See Plate XXIV)

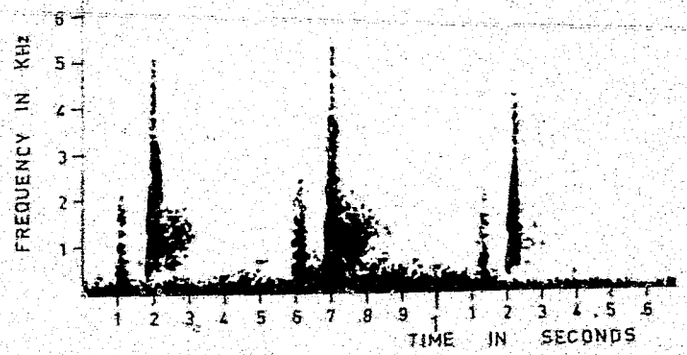
This call may be given in a series having a variable time interval between units, or, as is frequently found with the calls of Galago senegalensis moholi that are given in lengthy series, sections of the call may have a constant time interval that gradually increases as the intensity of the situation decreases. Units of this call are often heard in bursts of 3 or 4 units that are interspersed with units of other calls during agonistic or alarming situations. This call is given by the inferior during or after moderate intensity chasing by a superior. It was given by one animal during a mobbing call series when a cat was introduced into the living cage.



a. Gerwhit, Juvenile.



b. Gerwhit.



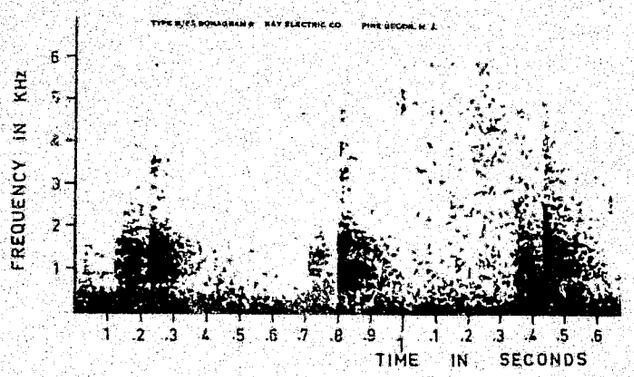
c. High intensity Gerwhit.

PLATE XXIV. GERWHIT.

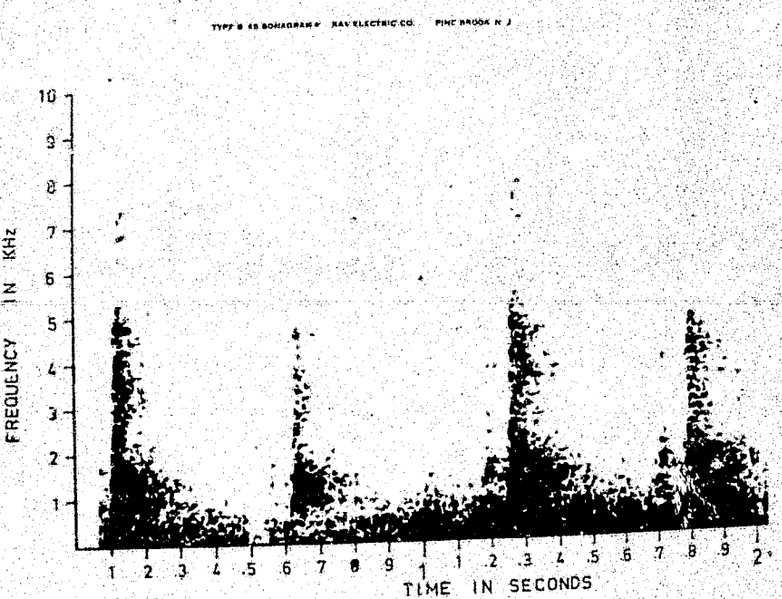
6.5.3 Cluck (Géwok)

This call consists of a low-pitched non-tonal sound that occurs singly or in a series. (See Plates XXV and XXVI)

The Cluck occurs during mobbing calls directed at a predator, and also in association with Gerwhit and Yap units during hostile encounters when the inferior animal is 'frightened.' It is also heard after a fright when one animal starts a loud bout of Yaps. Another animal may join in with Cluck units uttered immediately after the Yap units giving a Yap-Cluck duet.

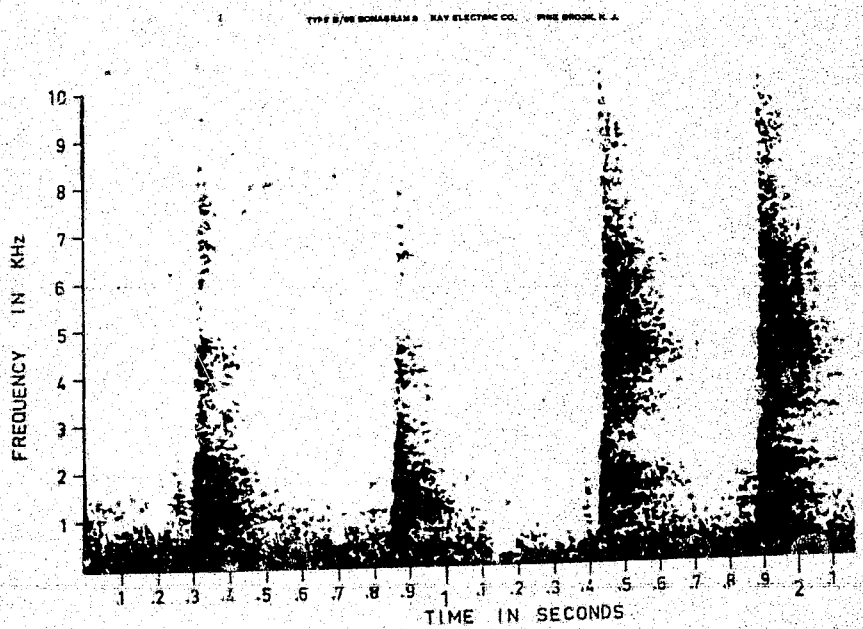


a. Cluck.



b. Cluck.

PLATE XXV. CLUCK.



Cluck. Followed by two Yap units.

PLATE XXVI. CLUCK.

6.5.4 Shivering-Stutter (B-B-B-B)

The Shivering-Stutter consists of a very rapid series of soft non-tonal units given with the mouth completely closed. (See Plate XXVII) It appears to function as a low intensity alarm call frequently occurring after the animals have had a 'fright' and 'startle-jumped' rapidly in all directions.

This call has been heard to alternate with Yap units in a very rapid bout and may be given by the inferior after being chased.

The frequency with which this call is given increases during the breeding season. One male, J, (wild born, and acquired as a mature animal) will alternate lengthy series of this call (5 - 6 mins) with a very intense version of the Bark when a female in oëstrus is in his cage. He has also been heard to pass straight from this call into full high intensity alarm Wails and Caws. Shivering-Stutter duets have been heard on several occasions where mating has been disturbed.

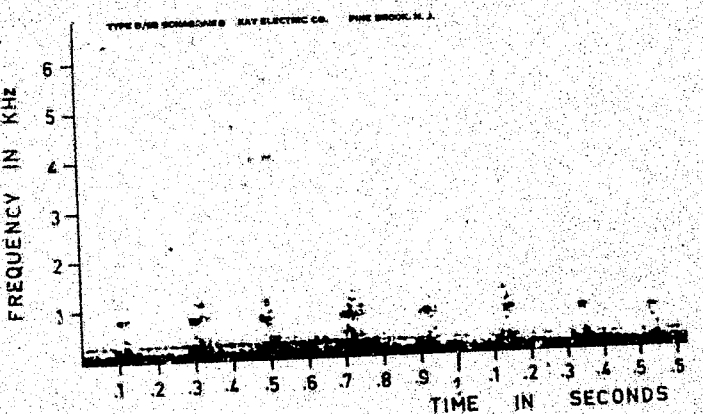


PLATE XXVII. SHIVERING STUTTER.

6.5.5 Whistles and Whistle-like Variants (Phew-hah)

Whistle-like calls constitute a group of calls in which many variants occur. These variants are commonly formed by lengthening or shortening phases of the basic whistle which in its full form sounds like a Pheew-hah. (See Plate XXVIII fig. a) In this form the call rapidly descends from 5.0 KHz to 1.3 KHz in ± 0.2 secs. (Phew), and then levels out at 1.0 KHz for a further 0.1 - 0.2 secs (hah). Instead of leveling out at 1.0 KHz, the call may rise again slightly, giving the sound spectrograph a hooked appearance.

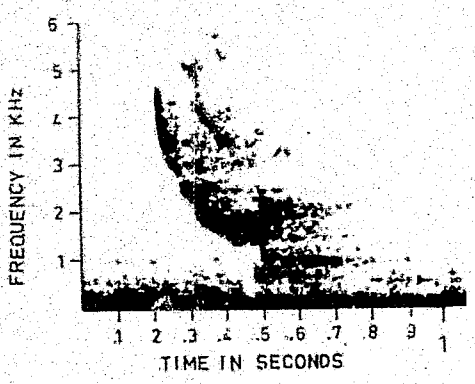
These Whistles are frequently given by a subordinate animal, during or after it has been aggressively chased and/or attacked by a superior. Whistle units are commonly associated with Yapping units in such situations, but the Yap units may gradually fall away leaving Whistle units only. These bouts of pure Whistle units may last up to 7 - 8 mins and there is a varying time interval between units. Sections may, however, maintain a constant time interval which then gradually increase to a varying interval as the intensity of the situation decreases.

A bisyllabic whistle-like variant consists of a short sound given with a sharp contraction of the abdominal muscles and sounding similar to a hiccup. On occasions, when an attempt to mount by the male has been firmly rejected by the female, the male may utter lengthy bouts of Yaps interspersed with the

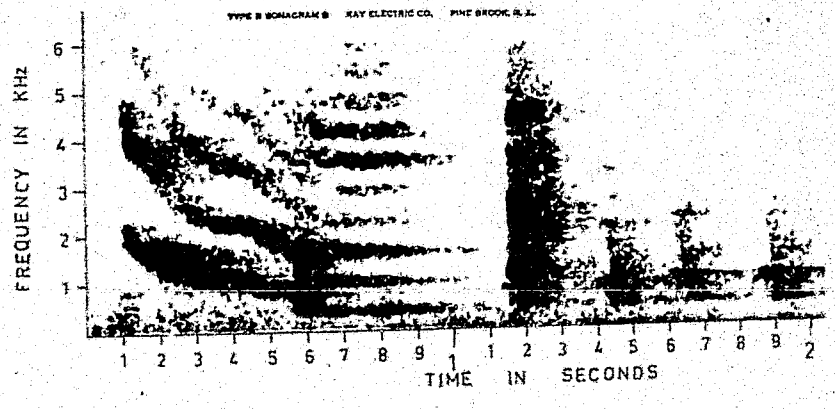
Hiccup Whistle. One male uttered a bout of pure Hiccup Whistle units for a period lasting over twenty minutes when a female was removed from his cage immediately after an unsuccessful mounting attempt. Only the males have been heard to give this whistle variant. (See Plate XXIX figs. a and b)

A chorus of Whistles and Whistle-like calls was given by a group of five young animals when they were introduced into a new cage, and female Pa frequently does so under these conditions. When the animals were moved from a previous laboratory to the building housing the new laboratory and placed in new cages, bouts of Whistles were given by most of the animals. When the animals are merely moved to a different cage in the laboratory Whistles are seldom heard.

Under laboratory conditions, it is not clear what message Whistles convey. An animal uttering Whistles generally appears to be 'anxious' and it is possible that the calls may have a warning function. (They were given by one animal when a cat was introduced into the cage.) They do not, however, belong clearly and without doubt to the group of alarm calls. They have been included in the alarm group because they tend to be closely associated with the Yap where the alarm function is more definate.

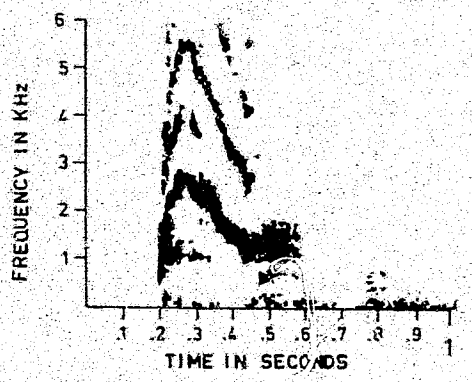


a. Whistle.

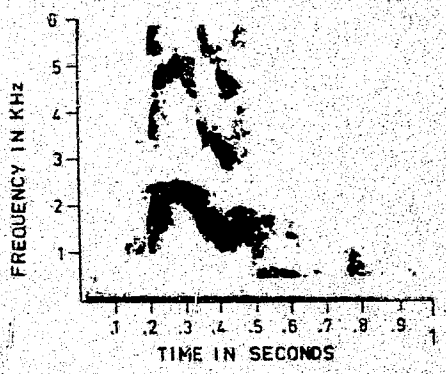


b. Whistle-moan and Yap

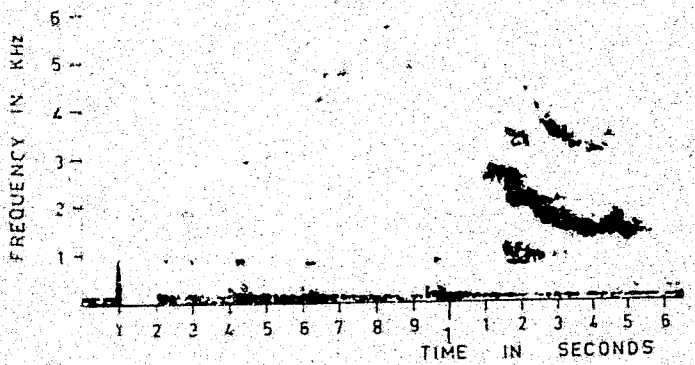
PLATE XXVIII. WHISTLE AND WHISTLE VARIANTS.



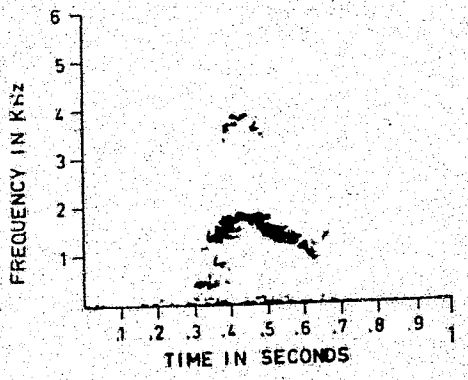
a. Hiccup Whistle.



b. Hiccup Whistle.



c. Shivering Stutter and Whistle Variant.



d. Whistle Variant.

PLATE XXIX. WHISTLE VARIANTS.

6.5.6 Yap

This call consists of a loud homotypical sound sequence of non-tonal units that extend over a frequency range of 0 - 6 KHz (occasionally extending to 8 KHz) and have the major energy distribution between the 3 and 5 KHz frequency band where the column of sound may broaden horizontally. (See Plate XXX fig. a) There is a varying time interval between individual units although they may be given in lengthy bouts during which the time interval between units may remain constant for lengthy stretches (4 - 15 mins) giving a very monotonous quality to the call. Yapping calls often start with a rapid monotonous section becoming slower with an increasing time interval between units until single units occur with intervals of 2 - 3 mins between them. The entire calling sequence may last up to an hour in total duration during which time the animal remains very tense and nervous. Units of this call may be mixed at odd intervals with Whistle call units. The mouth opens and closes sharply with each unit during Yapping and the whole body may jerk in rhythm with the individual units of the call. When Yapping occurs in very rapid bouts the call may acquire a metallic quality similar to the ring of a pick striking stone on concrete. (See Plate XXX fig. b)

This call is given in a wide range of circumstances in which the animal is 'frightened' and is thus heard both during agonistic and alarm situations.