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Territorial and intergroup behaviour of the Lesser Bushbaby, Galago senegalensis moholi (A. Smith), in semi-natural conditions in the field

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Fig.8(a). Mean maximum and minimum temperatures throughout the year.

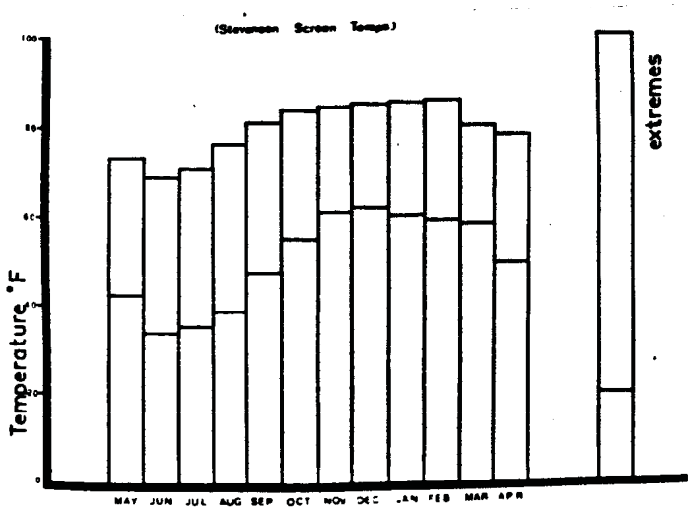


Fig.8(b). Occurrence of births, mating and new nests May 1968-Apr.1969.

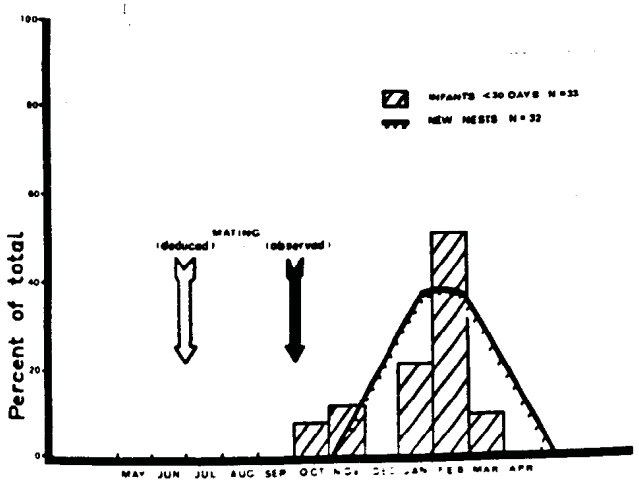
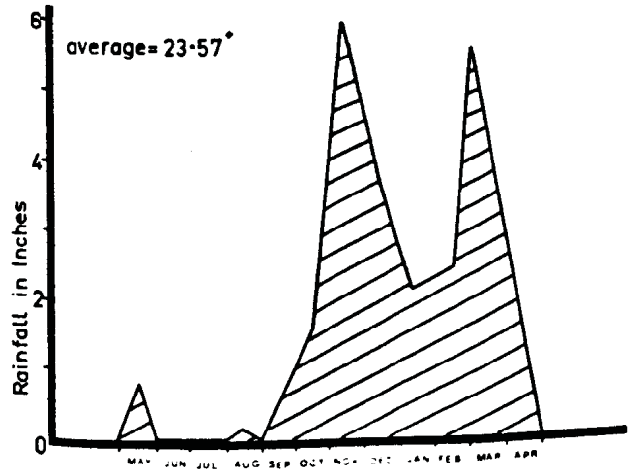


Fig.8(c). Monthly rainfall. May 1968-Apr.1969.



and the beginning of February. Allowing for the gestation period, it can be assumed that the first matings occurred during June and July. Mating was actually witnessed on September 29th and October 5th which is in accordance with the timing of the second birth peak.

In two cases it appears that females gave birth twice during the year. The second sets of infants were found approximately 4 months after the first, within the same home range. Two sets of twins were produced in the same nest site.

The majority of females did not give birth for the first time until late January and February when there was a large increase in the overall population. The timing and number of births presumably depends on local ecological conditions. In the study area the previous year had been dry (5.2 inches below average rainfall). Nesting material was not available until November, which may be an important factor affecting the survival of infants.

Laboratory data shows that the females do not become sexually mature until approximately 200 days old. Females born in February 1967 would therefore, not be receptive until September 1968, which precludes an early birth period. Those born in November 1967, however, could come into oestrus for the first time in May 1968 and so would be capable of giving birth twice during the

following summer.

Observations over a single year are insufficient to give a full account of the birth periodicity of this species.

3. BEHAVIOUR IN THE FIELD

3.1 THE MOTHER-INFANT RELATIONSHIP

A detailed description and analysis of the maternal behaviour of the Lesser Bushbaby in the laboratory is given by Doyle *et al*. (1969). The significance of many of these observations is qualified by field data collected during 95 hours. During the year 20 mothers were found with 33 infants. Detailed behavioural records were made for 19 infants from an age of about 2 weeks. They were observed regularly during 4 months as they matured.

An analysis of 26 periods of observation of mothers with small infants of less than 30 days of age, lasting 59 hours, shows an overall pattern of mother-infant behaviour. The various mothers spent only 0.33 of this time with their offspring. A total of 3 hours were spent grooming the infants and 45 minutes apparently suckling. The soft maternal call was given by the mothers on approaching the infants during 9 of the observation periods. They carried the infants during 12 periods. The infants gave 'clicks' in 7 periods and alarm 'yaps' in 2 periods.

No infants were found of less than about 10 days of age, judging by physical characteristics, dark ears, small eyes, lack of colouration and relative size.

The presence of infants in a particular home range was always accompanied by one or more substantial nests or, in one case, a number of nesting holes. Infants above two weeks of age were often seen without a nest, sleeping with the mother on shaded forks or branches.

3.1.1 Nursing

Nursing of infants, during which the mother sits in the fork of a branch with the infants completely hidden beneath her, is rarely seen. Occasionally the infants may make an obvious attempt to suckle, but are rejected by the mother. It seems probable that most suckling occurs during the daytime.

3.1.2 Grooming

Short periods of grooming, of not more than 15 minutes duration occur whenever mothers and young infants are together. Grooming may take place between transporting the infant from one place to another, or when the mother returns to it after a period of absence.

3.1.3 Changing of Nest Site

Mothers with small infants are not restricted to one particular nest or sleeping site. Movement from one sleeping place to another within the home range is common and may occur at any time of the night. Older infants are not usually retrieved until shortly before dawn.

3.1.4 Infant Transport

While the infants are unable to move around of their own accord the mother carries them to various places within the home range where they may be left for long periods. They are carried in the mouth by a dorso-lateral fold of skin with the legs held close against the body and the tail often curling passively around the mother's neck. The head can be turned and the eyes remain horizontal (Doyle et al. 1969). The mother carries each infant through several trees and then releases it, the distance travelled seems to depend on the size of the offspring. It may then be carried further or is left alone as the mother returns for the second infant. At the beginning of the night's activity the female leaves the sleeping place alone in order to forage. Some time later she returns to the infants and carries them one at a time, to particular trees in the vicinity. They may either be placed together or left separately. Certain trees may be used repeatedly by the same female for the deposit of her infants.

3.1.5 Infant Development

For convenience the development of the young bushbaby can be divided into 5 stages according to its physical capabilities. The behaviour observed can be compared with that in the laboratory, where the exact age of the developing infant is known.

1). During the first stage, between birth and about 10 days of age, little is known of the behaviour of infants in the wild. The indications are that they spend almost the whole time on a nest or in a hollow.

2). During the second stage, from about 10 days to 21 days (plate 12a), the infant remains entirely dependant on the mother for sustenance and transport. It is carried from one tree to another during the night and the sleeping place may be changed repeatedly. The distance travelled and the pattern of movement is extremely variable. Usually the infants are carried away from the nest and left together for long periods, sometimes longer than 3 hours. They remain still when left by the mother, often sleeping huddled together in the fork of a tree.

Infants at this age may be handled by the observer and make no noise when stroked. The mother may approach anxiously and quickly carries her offspring away, once the disturbance has ceased. On one occasion an infant had been placed on a broad fencing post and left by its mother. It was handled, in order to note its size and sex, before being replaced for the mother to retrieve. No alarm or threat calls were made by the mother. Females with small infants have been seen to chase away adult conspecifics which approach the youngsters. This behaviour ceases as they grow older and more active.

3). Between 21 days and 28 days the infants are still dependant on the mother for transport from tree to tree, but are able to jump around, explore and lick gum within a tree. Twins may be placed in different trees, up to 40 yards apart where they remain for most, or all, of the night. The mother visits each one sporadically and spends short periods with them.

It occasionally appears that the mother has completely forgotten one of the infants, but she never fails to go directly to it, in order to retrieve it, before dawn. One infant may attempt to follow the mother as she carries the other. Infants of this age have been seen to fall to the ground twice. One of them was dropped while being carried, but it was quickly retrieved.

4). From 4 weeks to approximately 6 weeks (plate 9) the infants are at a stage where they are able to follow the mother. They do not attempt jumps of much more than 3 feet but they go onto the ground for the first time, taking short hops of about 1 foot, and are thus able to cover longer distances between trees. They follow the mother away from the sleeping place in the evening to certain trees in the vicinity where they spend the rest of the night alone. They feed, play, sleep and move from one tree to another over short distances.

When the mother returns shortly before daybreak she gives a soft 'coo' and the infants approach her giving high pitched 'clicks'. She moves slowly towards the sleeping place, occasionally returning to the infants, which follow her making frequent 'clicks'. 'Clicks' are seldom heard in the absence of the mother.

5). After about 6 weeks (plate 12b), the infants leave the sleeping place of their own accord and begin independant movements with an ever increasing range. The use of new sleeping trees by the group in different parts of the home range, ensures that the movements of youngsters become more widespread. The mother continues to go off alone but the family still comes together in the morning before moving to the sleeping tree.

3.1.6 Discussion

Infant bushbabies spend the majority of time alone at night. They are at first more active in the presence of the mother, but they gradually begin to explore more and more of their own accord. It appears that the youngsters gain a thorough knowledge of the particular trees in which they are left and as their jumping abilities increase so does their range of exploration. They find and lick gum independantly, long before they are able to catch insects, which is possibly learnt from the mothers. There is slight

evidence to suggest that juveniles of a few months old may follow the mothers and thereby increase the size of their normal range.

The movement of very young infants from one tree to another during the night and the changing of sleeping places, is possibly equivalent to the behaviour of females in the laboratory, which repeatedly move their infants from one nestbox to another, sometimes leaving them separately in different boxes (Doyle et al. 1969). Small infants are highly vulnerable to predation and this behaviour may reduce the probability of the infants encountering predators.

In the laboratory the infants first leave the nest box of their own accord at about 2 weeks of age, at which time there is a marked decrease in the amount of time spent nursing by the mother during the first and last waking periods (Doyle et al. 1969). This coincides with the first appearance of infants in the wild and accompanying transport and foraging activity by the mothers.

As soon as the infants are able to follow the mother there is an increase in the amount of 'clicking'. 'Clicks' may cause the mother to go to the infants, but are also given as the infants approach or follow

the mother. In this sense they may act as 'contact' sounds, in a similar way to the maternal 'coo' which is given by the mother in the same situation.

3.2 RELEASE OF TAME ANIMALS

The release of captive bushbabies was done in order to see if it was possible for laboratory reared animals to adapt to the conditions of the wild. A male/female pair named Z. & E. were released during February 1969 and observed for 1 week. A second pair M & W, were released in the following April and observed for 4 days.

Each pair was released in the known home range of a wild adult male so as to observe any possible interactions. A suitable sleeping tree was chosen and a provisioned nest box placed in it, into which the animals were released.

In both cases the initial behaviour was similar. At dusk they left the box and moved around in the nest tree and a few adjacent trees, for at least the first 6 hours after release. They all found and ate insects and gum but occasionally returned to the nest box in order to feed. The second pair, M & W, returned to the nest box to sleep for the first two days after release, having spent the nights in a group of 4 trees.

The male Z, of the first pair, moved far away from the nest box late on the first night and did not return. During his absence the female E was approached by 2 wild bushbabies, one of which showed friendly but persistant interest in her for the following 2 nights. This bushbaby repeatedly gave the 'male' call and stayed with E until well after the normal sleeping time at dawn. E remained completely submissive, giving the alarm 'yap' and retreating each time the male approached. He spent the following day in his usual sleeping place but returned again soon after dusk, together with another wild bushbaby. Each of them chased E, who eventually left them to rejoin the tame male Z.

Z & E thereafter remained in one group of 5 trees for a week, after which they could not be located. Movement from the tree of release was over 100 yards and involved covering several stretches of up to 30 yards along the ground. The two slept separately, each returning to a particular fork at the end of each night. The male Z slept only 3 feet above the ground. Feeding seemed quite normal, except that long periods were spent on the ground, searching for insects.

The second pair, M & W, were approached by a wild

male soon after being released and he returned to them repeatedly during the following 2 nights. The 'male' call was given frequently by both males and fighting occurred several times. Each time, both males fell to the ground locked together and then separated. The wild male chased the female W, who remained submissive.

It was not possible to determine the ultimate fate of the released bushbabies. The effects of being reared in the laboratory where food is provided and there are no predators, is reflected in a marked difference in their range of movement and awareness compared with the wild animals. This would make it harder for them to find sufficient food and render them more liable to predation.

Three interesting facts emerge from the interactions which took place. The wild males showed persistant and friendly interest in the females which were not in oestrus. Rivalry between adult males was clearly shown by the fighting which occurred between the wild male and M. The 'male' call was given repeatedly by both wild and laboratory males whenever they were in the same vicinity. The possible significance of these observations is discussed in section 5.

Several other experiments could be performed involving the release of tame bushbabies in different parts of a home range, or the movement of wild ones from one home range to another, in order to establish the exact mechanisms which control movement in a particular area and the formation and dispersion of family groups.

3.3 AUDITORY COMMUNICATION

The means of communication in the Lesser Bushbaby are described in detail by Andersson (1969). She has identified and recorded a repertoire of 25 calls in the laboratory, made in a variety of situations. Each of these calls has been found to occur in a similar context under natural conditions. A list of their relative frequences and possible meaning is given in table 5.

Three loud calls are made which can be heard from approximately 0.25 mile away. The most common of these is the 'bark' which is normally made only by adult males in the laboratory, but also by adult females when they are dominant within a cage. The two other loud calls are the 'yap' and the 'whistle'. In general the 'yaps' occur under alarm conditions, while 'whistles' are of lower intensity, seeming

Table 5 Auditory Communication

(A) LOUD CALLS. (In order of relative frequency).

NAME	SITUATION AND RESPONSE OF CONSPECIFICS
1. Bark (Male call).	Particularly common in areas of high population density. Repeated often once started, answered by some animals, ignored by others. Common soon after sunset and during mating. Made in the proximity of conspecifics by known males and females with offspring. Sometimes used by male as if 'calling' the female, or made continously while on the move
2. Whistles and variations.	Made in 'anxiety' situations e.g., in the presence of domestic cats, jackals or when disturbed by the observer. Frequently associated with Yaps suggesting a low intensity alarm. No apparent reaction from conspecifics.
3. Yaps. 4. Plaintive Yaps and Yap alarm.	Made during 'alarm' situations, when actively disturbed by the observer or towards domestic cats, genets or jackals. Also given during and after being chased by a conspecific. Often no apparent cause. Attracts mother when given by youngster. May be given in chorus but rarely causes any obvious response by conspecifics.
5. Explosive coughs.	Nearly always given by the subordinate animal before and during pair interactions. Given by mother when infant falls from tree. Coughs given when on the move, sometimes preceding whistles. Response not known.

6. Clucks. 7. Ge-Whits.	Made during agonistic encounters often preceding or following Yaps but also heard separately. Response not known.
8, Wuffs. 9. Wails. 10. Caws.	Loud, high intensity calls following 'Yaps' and associated with Whistles in 'alarm' situations. Response not known.
11. Moans/Sobs. 12. Chatter (fighting) 13. Screams. 14. Rasps.	Calls made during aggressive encounters by the subordinate animal. Often associated with Spits and Coughs .

(B) SOFT CALLS. (In order of relative frequency).

15. Sneezes.	Extremely common. Made at any time. Significance unknown.
16. Shivering stutter.	Common before, during and after mating. Often given at the approach of the observer, accompanied by signs of nervousness. Sometimes followed by alarm Wails . Causes a startle reaction in conspecifics.
17. Soft Hoot. 18. Contact Grunt. 19. Coo.(Maternal call)	Made in contact situations where the encounter is friendly. Hoots made only by males. Coos given by females with infants when approaching them and in close contact.
20. Spits. 21. Spit-Grunts. 22. Grunts.	Made by the subordinate animal at the close approach of an assertive conspecific (or the observer). Made by infants when harassed.
23. Clicks. 24. Crackles. 25. Squeeks.	Made by infants or juveniles in 'distress' situations or when approaching and following the mother.

to reflect anxiety. The two calls are often associated with one another and may be given in a mixed series by a single animal.

The 'bark' or 'male' call is commonly heard in the wild during the summer months but it is infrequent in the winter. It is particularly common in areas having a high population density where once started it is frequently answered by several other bushbabies in the vicinity.

'Yaps' and 'whistles' may sometimes be made when jackals, genets or cats are seen nearby. They are not necessarily given at the mere presence of a potential predator but only when it interferes with the "planned" activity of the bushbaby concerned for example, when it is thwarted from moving from one tree to another. If the observer shakes the branches of a tree in which a bushbaby is moving, it often gives a short bout of 'yaps'. The calls may be made for up to 1 hour at a time, while on the move or when remaining still.

Subjectively a disturbed bushbaby seems to work up to a peak of agitation or fright which is expressed through vocalisations. This state may last for a long time and is easily reinforced once the animal

is aroused. In the majority of cases the cause and significance of the state of arousal cannot be ascertained.

On one occasion the approach of the observer caused a pair of bushbabies to begin an alarm duet of 'yaps' but it is more common for a 'shivering stutter' to be given when an animal first sees the observer or is otherwise startled.

One other call of particular interest in the field is the 'explosive cough'. Whenever two bushbabies approach one another this call is usually given by one of them while they are between 5 - 20 yards apart. In all cases the individual which gives the 'cough' proves to be submissive in the encounter which follows. It is approached and frequently chased by the other. Often the two are friendly and mutual grooming follows. In this context the 'explosive cough' is evidently a sign of submissiveness, which immediately establishes the relationship. It is not known whether there is any initial recognition of status prior to the 'cough'.

The calls of a bushbaby in the field are not unlike those of a bird. For every loud call made there is a bird call which sounds almost identical, but to the trained ear the difference is generally unmistakeable. No calls are heard during the daytime except

for 'sneezes', which may be given by an individual when it is disturbed.

3.4 GENERAL BEHAVIOUR

Very little of the behaviour shown in the wild has not been seen previously in the laboratory but the way of life is extremely different due to the greater range of movement involved. Considering the home range to be approximately 7 acres, the laboratory environment represents only 0.000125 of this area, even discounting the third dimension.

Activity counts and time scores for different types of behaviour during each hour of the night throughout the year, indicate that there is a broad pattern of activity. The frequency of feeding and scent-marking per hour normally reaches a peak within the first hour after leaving the sleeping place each night (figure 9). The number of trees through which the animal moves also reaches a peak at this time, with an additional peak before returning to the sleeping place in the morning. At other times of the night each bushbaby shows periods of rapid movement, rest, sleep, interest in feeding, exploration and social activity, independant of any pattern or rhythm.

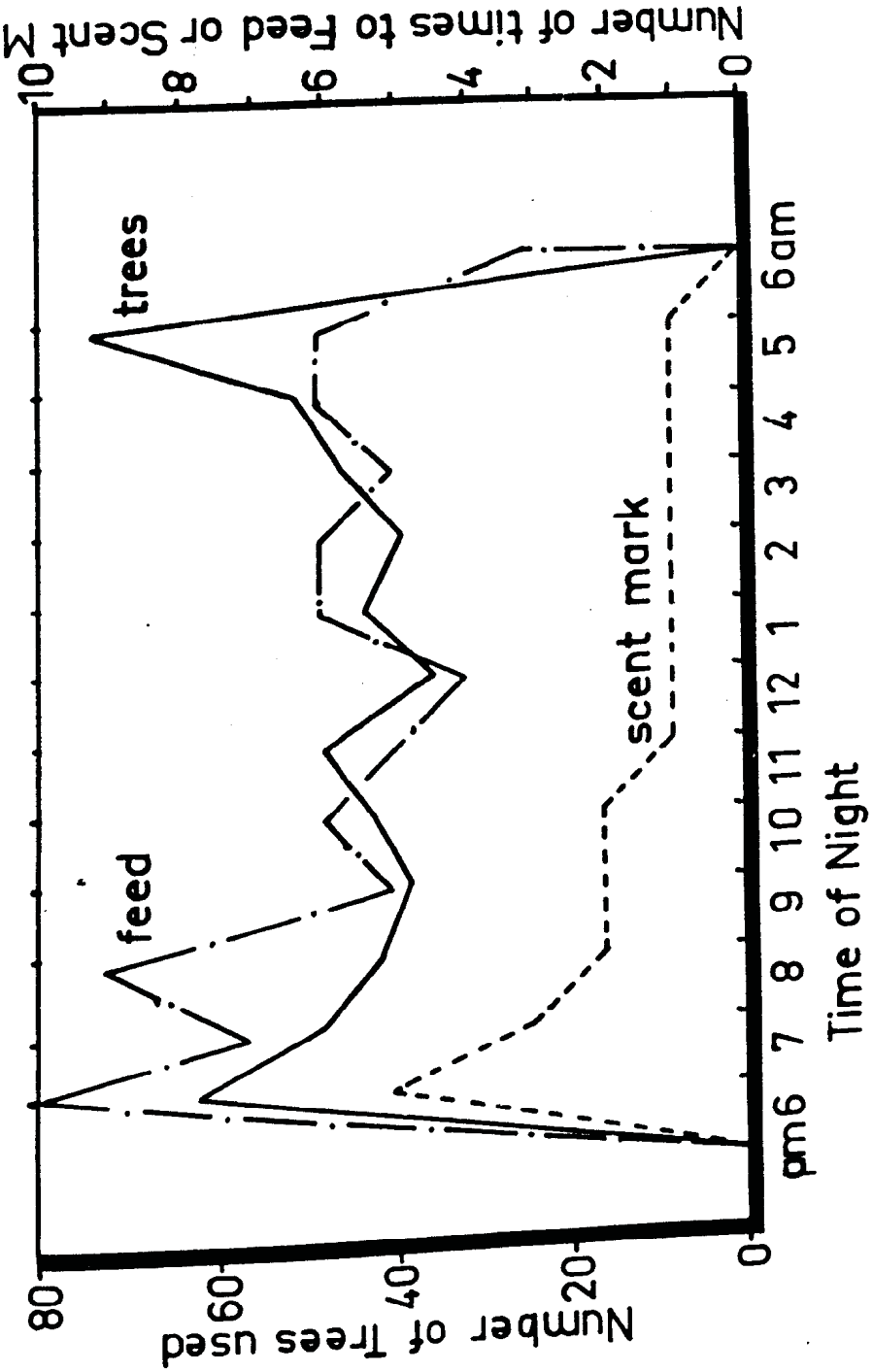


Fig.9. Variations in the mean frequencies of activities throughout the night.

There is evidence that certain types of behaviour show quantitative variations between winter and summer. During the long winter nights the overall activity is greater than in the summer, when bushbabies may occasionally sleep for long periods on a convenient fork or branch.

Heavy rain and strong wind apparently make little difference to the normal activity of bushbabies but few calls are heard on windy nights. A pair were observed near the base of a tree during a downpour in the daytime, but it is not known if they had moved down in order to shelter. It may be that these small animals need to find shelter during serious hailstorms, although there is no proof of this.

In the laboratory, bushbabies are extremely inquisitive. This is less obvious in the wild but interest is frequently shown towards the observer and inanimate objects. At the start of each observation period it was not uncommon for the subject to come within a foot of the observer, while making a soft 'sneezing' sound, apparently indicative of curiosity. Some individuals, particularly juveniles and those which had not been observed previously remained orientated towards the observer for as long as 20 minutes. If disturbed during this time they made a hasty retreat. Marker cards placed on certain trees

were often investigated and manipulated by bushbabies.

One form of behaviour not seen in the laboratory was a type of "dance". This consisted of rapid, jerky movements on a horizontal branch, in which the hands and feet were rubbed against the bark. The performer frequently turned in circles and sometimes gave a peculiar 'coughing' sound. Considering the thorny habitat, it may be that this behaviour dislodges splinters from the palms or soles.

3.4.1 Social Interactions

A laboratory analysis of the interactional behaviour of paired classes of bushbabies is given in section 4, where the behaviour shown by each animal is described in detail. Social interactions observed in the wild follow the same pattern and may be assumed to be equivalent, obeying the same rules. An interpretation was made of more than 120 interactions in the field, based on laboratory data, so that it was frequently possible to determine the age, sex and status of an individual from its behaviour, which would otherwise have been impossible.

Various types of social behaviour were observed which are listed below in order of relative frequency.

1. Friendly approach between individuals of one family group.
2. Friendly chasing of an unidentified submissive animal by an adult or sub-adult male.
3. Mother/infant contact.
4. Complete avoidance between rival males or females.
5. Overt fighting after much chasing between rival males or females.
6. Overt fighting between adults in which each approaches the other.
7. Aggressive chasing between adults, particularly by females with young infants.
8. Chasing of a female by a male prior to mating.

Social contact is typically brief but occasionally one animal will follow another for a period of some hours. Friendly contact includes play, grappling, chasing and periods of vigorous alternate grooming, in which one animal will groom the other briefly and then allow itself to be groomed.

An example, taken from field notes, of the activities of an easily identifiable individual with a tumour on it's neck, illustrates some of the possible interactions which occur on a single night.

Extract from field notes: 3rd October 1968. Four hours of observation in which the subject moved 1,568 yards in a complete circle:

20.05 No.1.(Subject) approaches a second bushbaby (No.2.) which moves away quickly giving an'explosive cough' and 'yaps'. No.1 follows it into a small tree. No. 1 genital smells No. 2 which makes soft 'sneezes'.

20.15 A third animal (No. 3) approaches the other two. No. 1 moves away immediately. No.2 follows it but is chased by No. 3 which gives a soft 'hoot' ('chasing' call) followed by a 'bark' ('male' call) while sitting on the ground. This call is answered by a fourth bushbaby from a distance. No. 2 is again chased by No. 3 and descends to the ground. No. 3 moves away and No. 2 jumps back into a tree.

Meanwhile No. 1 is some distance away, in close proximity to No. 4, which approaches it.

20.40 No. 1 is quicly approached by another bushbaby. It immediately descends to the ground. It allows itself to be groomed by the stranger before leaving.

21.40 No. 1 is yet again approached and immediately descends to the ground. The other also descends and the two sit staring at one another. The newcomer then begins to chase No. 1 which makes submissive vocalisations and 'yaps', while fleeing along the ground.

21.45 The two move away in opposite directions.

22.05 No. 1 is nearby to a second bushbaby but it moves away quickly.

During each interaction, submission is indicated by the animal descending to the ground and making a variety of calls. The soft 'hoot' is known to be given only by males, thus indicating that No. 3 was a male. Mutual grooming indicates that a pair are familiar with one another, whereas vigorous chasing and rapid retreat usually occurs between strangers.

A general discussion on social behaviour in the field and in the laboratory is given in section 5.

3.4.2 Sexual Behaviour

Mating was observed on only two occasions, so that it is not possible to generalise when discussing sexual behaviour. A brief summary of field notes is recorded here for the sake of completeness.

One pair were observed for two hours. At the approach of the observer they became extremely agitated, giving an alarm duet of 'yaps' for 10 minutes. During this time they jumped about in a single tree, continually looking in the direction of the observer. The 'yapping' slowly subsided as they moved away. One of the two, (which turned out to be a female), repeatedly gave a long drawn out 'whistle'. It was chased by the male for some minutes.

During chasing the male gave a soft 'hoot' while the female gave a 'chatter' and 'spitting' sounds in between 'whistles'. After a while the 'whistling' subsided and the male mounted the female and began a high pitched 'shivering stutter'. At the end of 6 minutes the mounting ceased. The male continued to follow the female with intermittant chasing.

Soon after mating the pair were approached by a third

bushbaby which gave the 'male' call. This was answered by the first male and the calls continued in answer to one another for the next 1.5 hours. In addition the first male frequently gave the 'shivering stutter'.

A second mating was witnessed in which two bushbabies repeatedly chased a third, often on the ground, while each of them gave a constant 'shivering stutter'. The one being chased made 'spits' and 'grunts' at the approach of the others and was finally mounted by one of them for 3 minutes. Mating was followed by the male genital grooming itself and giving a high pitched 'stutter'. All three moved away together with occasional chasing.

(a)





PLATE 1.

(b)

(c)





(a)



(b)



PLATE 2.

(c)

(a)





PLATE 3.

(b)

(c)

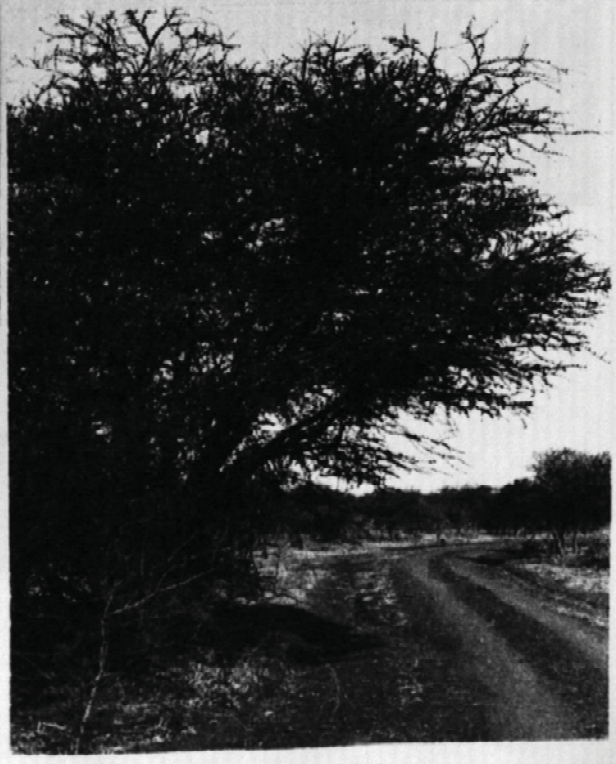
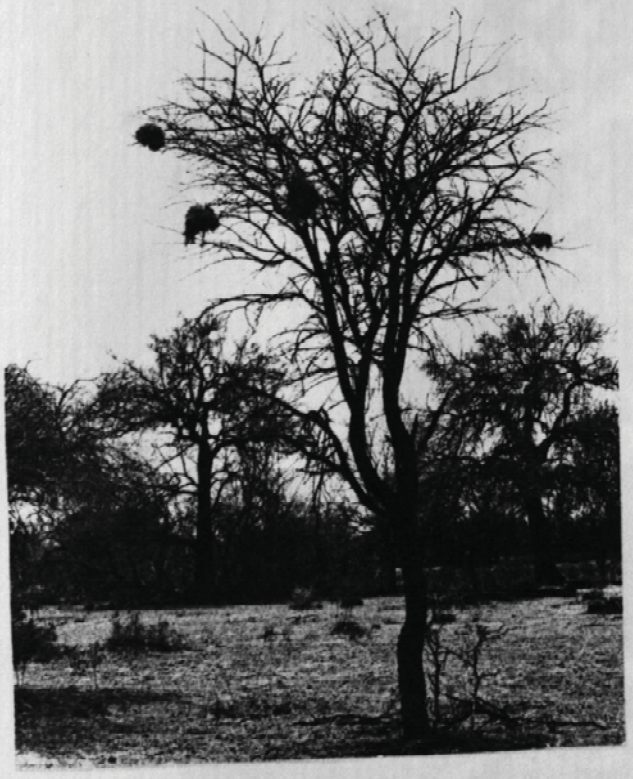


PLATE 4.

(a)





(b)



(c)