

PLATE 5.

(a)



(b)



(c)



PLATE 6.

(a)

(b)



(c)



(a)

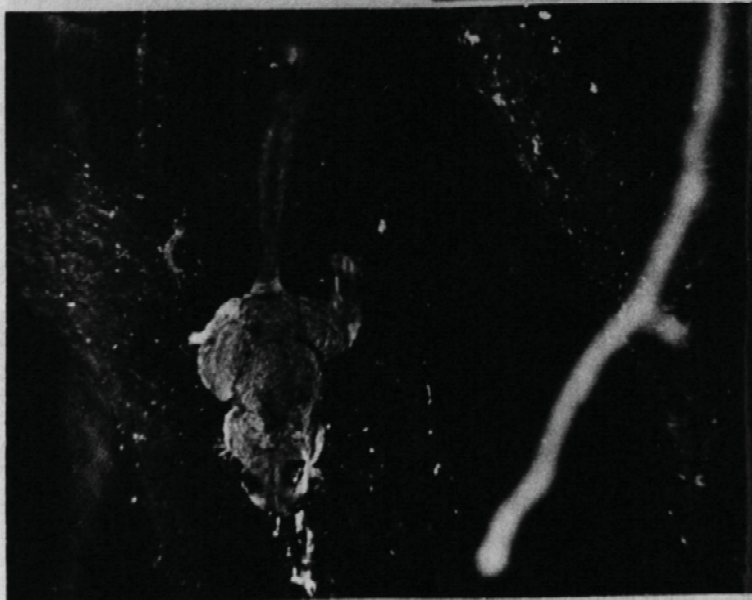


PLATE 7.

(b)

(c)



PLATE 8.

(a)



(b)



(c)



(a)

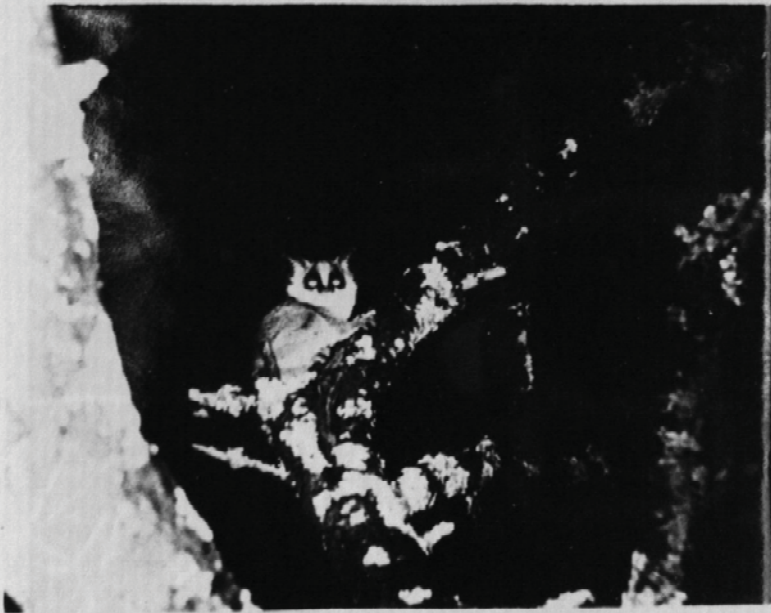
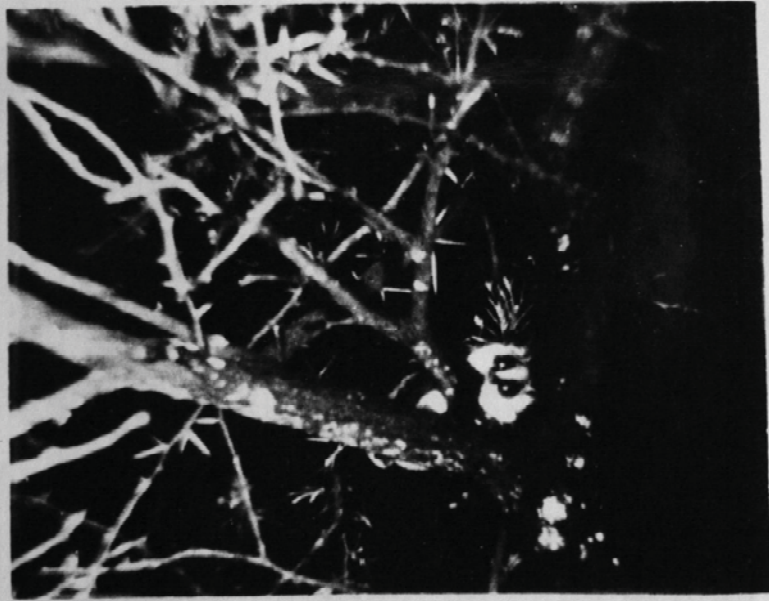
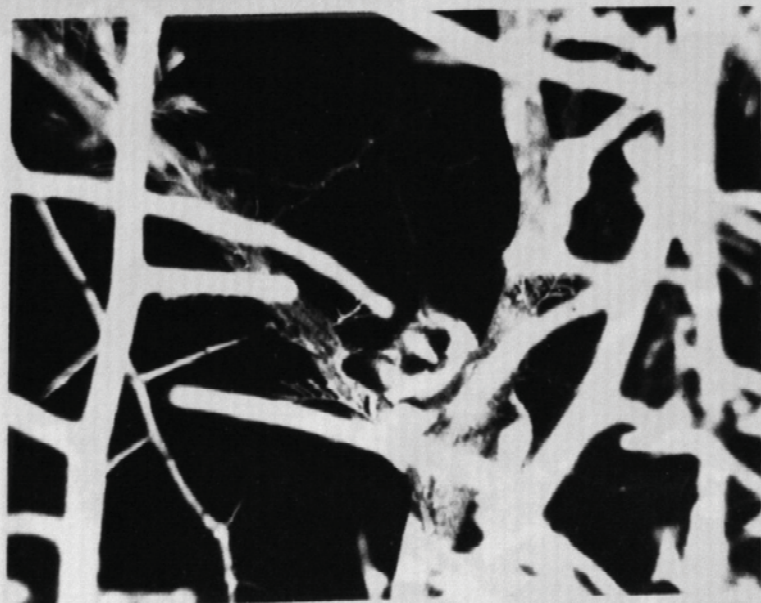


PLATE 9.

(b)

(c)



(a)



PLATE 10.

(b)

(c)



PLATE 11.



(a)



(b)

(a)



PLATE 12.

(b)

(c)



4. SOCIAL ORGANISATION IN THE LABORATORY

4.1 INTRODUCTION

In order to analyse the social hierarchy of a group of primates living together as a unit, it is usual to study the inter-actions between individuals of that group.

However, in the case of the bushbaby, it was found to be more realistic to study the social interactions which occurred between strangers, in a variety of laboratory situations.

In the undisturbed situation of the laboratory, members of each family group live in a confined space so that they are never, in effect, separated from one another. Under these stable conditions clear cut social interactions between companions are infrequent. The relative dominance of the male, female and offspring is fixed. Each animal appears to know its rank position and behaves appropriately, so that the group functions as an amiable unit.

Any change which occurs in the structure of such a group, by the introduction of a stranger, or by replacing a known individual after a short period of absence, or even movement into a new environment, causes a marked change of behaviour in order to re-establish the social structure of the group.

Observations in the field show that the group structure

is more pronounced during the day-time sleeping period than it is at night when each member spends most of its time alone. At night the group rarely functions as a unit and therefore, the laboratory situation is unrealistic. In the wild, each animal may come into contact with others, which may be either familiar or strange to it and of any age or sex. The resulting behaviour varies considerably and in order to interpret such social interactions it is necessary to enact possible meetings in the laboratory.

During four months before the commencement of the field study and at intervals thereafter, strange bushbabies were introduced to one another in the laboratory, under controlled conditions. The behaviour of individuals was categorised in relation to age and sex. It was hoped that an analysis of objective data collected during each introduction would help in understanding the social organisation of this species.

4.2 METHODS AND MATERIALS

4.2.1 Facilities

A detailed description of the maintenance and housing of the laboratory bushbabies is given by Doyle & Bekker (1967).

Essentially the laboratory consists of a central observation room on each side of which are two large cages

approximately 5 ft. by 6 ft. by 7 ft. each. These contain branches and nest boxes and form the home environment for groups of up to 6 animals.

A reversed day-night cycle enables observations to be made during the daytime under soft red light. White lights are turned on automatically at night. All observations are made through one way mirrors separating the ~~four~~ cages from the observation room, which remains in darkness.

Microphones are installed over each cage which are connected to a loud speaker in the observation room, so that all sounds made by the animals can be recorded on a tape recorder. Behavioural records are made on an Esterline-Angus 20-Channel events recorder (figure 10).

4.2.2 Subjects

For convenience the test animals may be divided into five age groups, based on behavioural differences, as summarised in table 6. Each age group represents a class for dyadic analysis. Twenty-five bushbabies were used in the experiment, but since in some cases these animals were tested at different stages of their development, (Juvenile, Sub-Adult, Adult), the effective sample is in fact forty three, in the following proportion:-

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Fig.10. Esterline-Angus record.

29

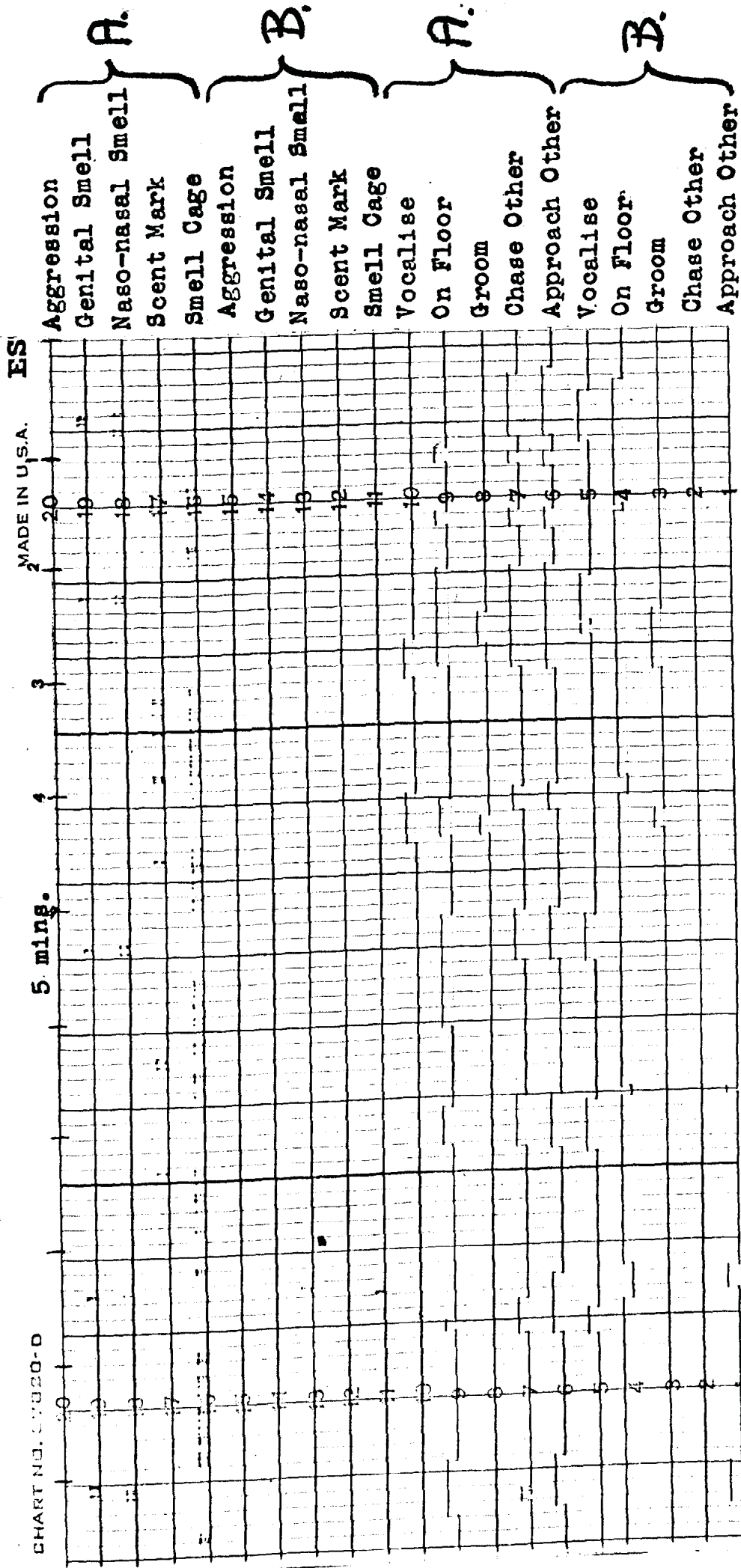


Table 6. Age Classification

DESIGNATION *	DESCRIPTION.	AGE IN DAYS.	WEIGHT IN GRAMMES / OUNCES
1. Infant	Wholly or partly dependant on mother.	0- 60	10-100 0-3.5
2. Juvenile.	Active and independant.	60-200	100-150 3.5-5.25
3. Sub-Adult Male.	Behaviourally between juvenile and adult.	200-300	150-180 5.25-6.25
4. Adult Female.	Reproductively mature.	200	150-260 5.25-9.00
5. Adult Male.	Dominant giving 'male' call.	300	160-300 5. 5-10.5

* The terms Infant, Juvenile, Sub-Adult and Adult have been chosen to represent stages in development which are roughly parallel with age. The Sub-Adult category is a distinct behavioural phase through which the male passes before becoming a 'confident' and 'assertive' adult, making the 'male' call. In the female, the transition between Juvenile and Adult is less marked and therefore, the Sub-Adult label is omitted. Females mature roughly 100 days before males of the same age.

10 Adult males
10 Adult females
9 Sub-adult males
6 Juvenile females
8 Juvenile males.

Each animal is named alphabetically and belongs to a stable family group in a particular home cage.

4.2.3 Procedure

A dyadic analysis was made from a series of 130 pair introductions, each one lasting for 40 minutes. Each pair of strangers were placed together in three separate environmental situations in order to assess the effect of the environment on subsequent behaviour. These were: (a) the home cage of one; (b) the home cage of the other, and (c) a neutral cage. The exact age, weight and previous associations of each test animal was recorded on a table, together with a breakdown of the Esterline-Angus record and a list of the calls made. Twenty four units of data were obtained for each bush-baby during every session.

Two series of introductions of a different nature were performed. In one case, two strangers were introduced to one another by removing the cover of a small opening between their home environments, having previously removed the other animals. Subsequently individuals

of each class were placed separately with an established family group, in order to test the disrupting effect of a stranger on a stable group.

4.3 RESULTS

The number of interactional possibilities for the effective sample of 43 individuals is given by the formula $\frac{N(N-1)}{1}$. (Carpenter 1965). This results in a possible 903 different introductions. If each one is to be observed in three different environments, the number becomes completely unmanagable. For this reason, although individual differences have been noted, the dyadic analysis is only made between the five age classes described. The results of the class interactions are used to characterise the normal interactional behaviour of strange individuals.

An underlying pattern emerges from the behaviour shown during each introduction. If a bushbaby is placed in a new cage it usually proceeds to explore by smelling all accessible parts of the cage. Adult males, in addition to smelling, also rub their chests or heads against projections and sharp edges, frequently biting the wood after each chest rub. Females occasionally rub the side of the mouth against objects within the cage. Exploration will not occur if the individual is frightened by the presence of a stranger.

The position of dominance usually becomes obvious within the first few minutes of each session. In an agonistic situation the dominant animal may be defined as that which chases or attacks the other. Aggression is invariably unidirectional during a 40 minute period. Where antagonism is lacking, the position of dominance is determined by which animal retreats most frequently. A subordinate animal in this situation may approach the other many times, but it generally leaves first. Submissiveness is clearly indicated by the bushbaby retreating to the floor, where it stays inactive for part or all of the observation period.

A variety of calls, which are described in detail by Andersson (1969), may be made during a pair introduction. Movement into a new environment may induce 'yaps' and 'whistles' from any bushbaby. Soft 'hoots' are given by dominant adult males when showing friendly interest towards conspecifics. Otherwise, calls are generally made only by the subordinate animal in response to a stranger.

The behaviour shown by each bushbaby when introduced to a stranger is a reflection of its dominance/submission status. When an animal is completely dominant over a stranger it spends the 40 minute period actively exploring the cage or chasing and sometimes attacking the stranger. It feeds and grooms relatively frequently.

A completely submissive animal, on the other hand, spends the entire session on the floor, inactive, unless it is chased, while it neither feeds nor grooms. There is a complete variation in behaviour between these two extremes.

A diagrammatic summary of six paired-class introduction is given in figure 11. Fourteen patterns of behaviour (approach, groom, play etc.) are grouped according to type under the headings: A. Agonistic behaviour, B. Contact behaviour, C. Exploratory behaviour and D. Comfort behaviour. The proportion of the different types of behaviour shown by the dominant animal is indicated in relation to that shown by the subordinate. The duration of certain events (sitting submissively on the floor, vocalising and grooming) is expressed as a percentage of the total time. Each section represents pooled data from the number of introductions performed in each of the six situations.

Since the amount of activity shown by the animals is dependant upon their relative status, it is possible to calculate an objective dominance/submission rating for each individual in a particular situation. The scores obtained for certain types of behaviour on the Esterline-Angus record are added together. Only those behaviour patterns which can be accurately recorded have been chosen:-

Fig. 11(a). Behaviour recorded during pair introductions.

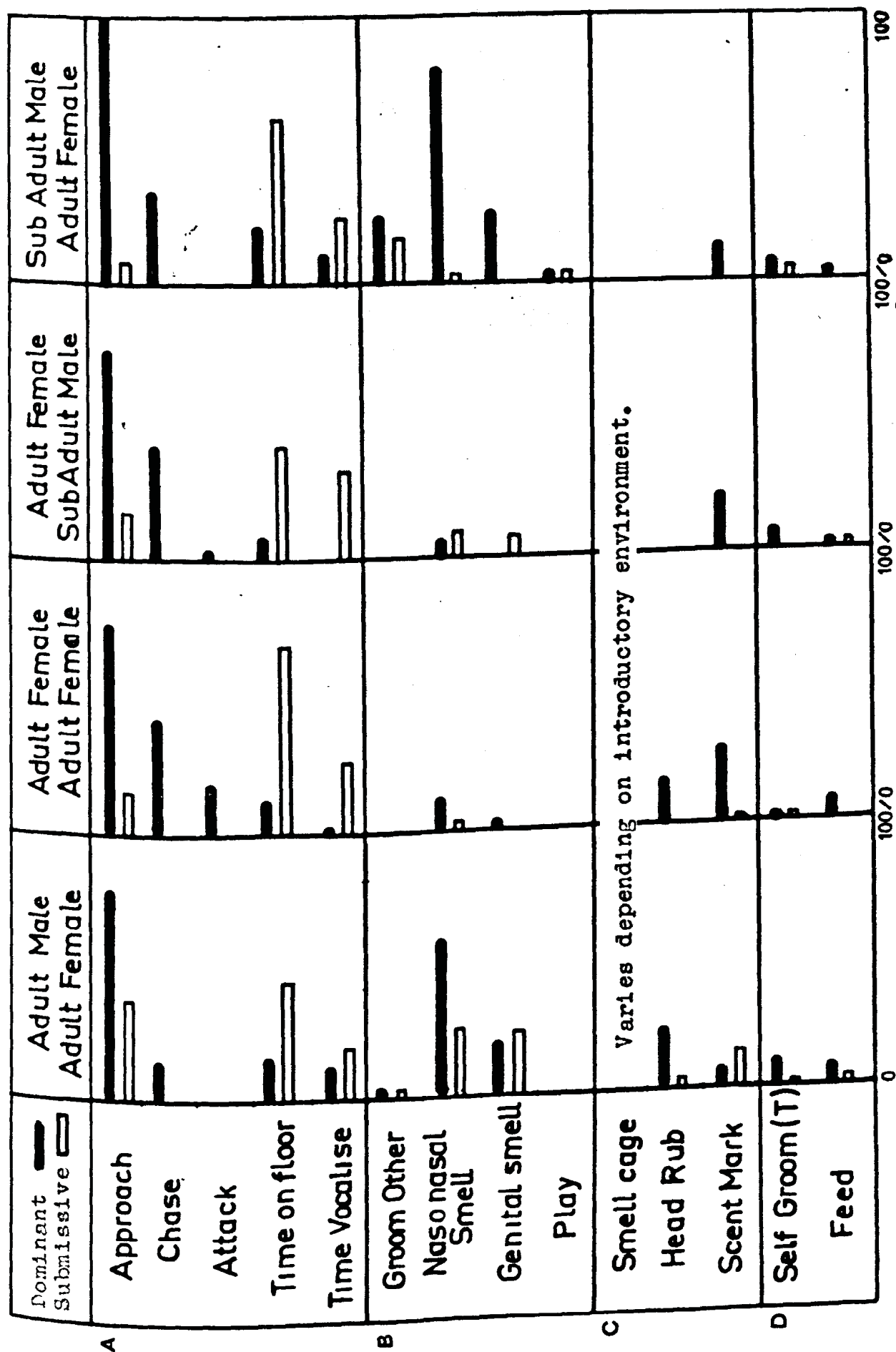
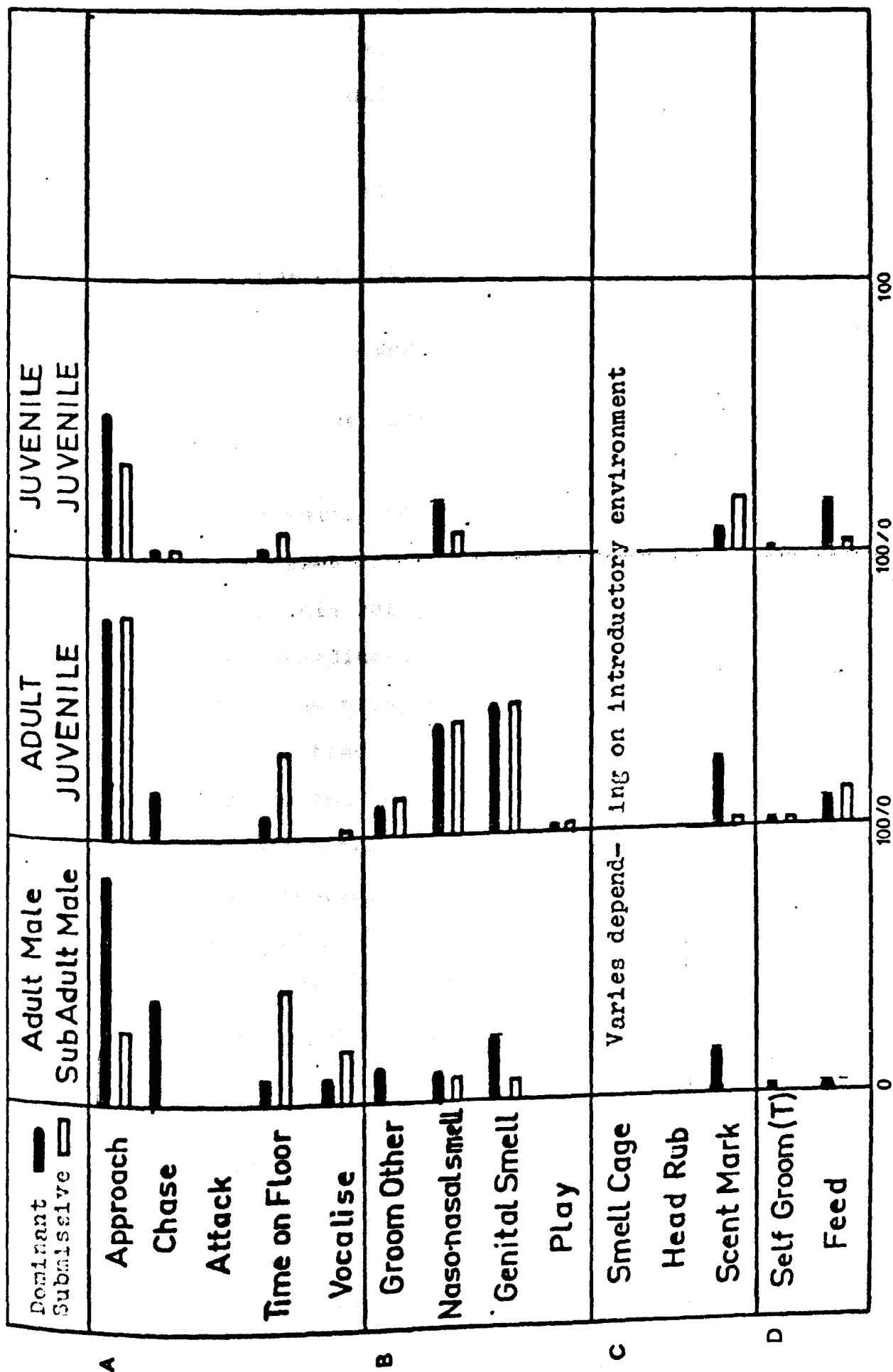


Fig. 11(b). Behaviour recorded during pair introductions. (Continued).



1. The number of times chasing a stranger and the total time spent chasing.
2. The number of times attacking the other.
3. The number of times that the animal feeds.
4. The total time spent self-grooming.
5. The total time active (off the floor).

An assertive animal has a rating of at least 40 which is the time spent active (5). Additional scores (1 to 4) may increase this rating to over 100. In contrast, a completely subordinate bushbaby may have a rating of 0. Small variations have been ignored since certain activities such as feeding or attack, inevitably vary from one session to the next. However, broad divisions in rating reflect a real difference in the animal's behaviour. The difference between the two ratings in each pair introduction indicates the amount of antagonism between the individuals. Where the difference is small the two are compatible and often friendly.

The dominance/submission status of each bushbaby may be dependant on and fluctuate in terms of a variety of factors. The relative size, age, sex and character of each individual and their degree of familiarity with the environment, may all be important determinants.

The ratings obtained in each of the 130 introductions (table 7) can be compared so as to determine how the behaviour varies with the particular conditions of each introduction and also to establish how the individual recognises and behaves towards the stranger.

4.4.1 Male - Male interactions

When two adult males are brought together by the removal of a partition between the adjacent home cages, they are both highly aggressive. Vicious fighting occurs, with the result that each animal inflicts severe damage upon the other. Fur is torn from the head and shoulders and cuts may be sustained around the eyes, sometimes causing damage to the corneal epithelium. Such combatants were rarely left together for more than a few minutes after which they had to be forcibly separated. The overt fighting between adult males, unlike all other agonistic encounters, is not accompanied by any vocalisations.

When rival males are left together for longer periods, the initial bout of intense silent fighting is followed by one of the bushbabies starting the full range of submissive vocalisations, while making every attempt to flee from attack. This only occurs after both animals have suffered extensive physical damage.

Table 7. Dyadic Analysis

Range of dominance/submission ratings for the subject in 130 introductions.

SUBJECT	STRANGER			
	Adult Male	Sub-Adult Male	Adult Female	Juvenile Male or Female
1. Adult Male	*	44-81 (D)	42-108 (D)	40-70 (D)
2. Sub-Adult Male	5-42 (S)	1-68 (S-D)	1-103 (S-D)	45-66 (D)
3. Adult Female	3-43 (S)	5-74 (S-D)	0-90 (S-D)	41-70 (D)
4. Juvenile Male or Female	7-50 (S)	11-43 (S)	2-49 (S)	10-67 (S-D)

* Result varies considerably depending on environment of introduction.
One or both animals highly aggressive.

(D) Dominant (S) Submissive

Rating Scale: 0-10 Completely submissive
 10-20 "Timid".
 20-40 "Wary".
 40 + Dominating or assertive.

When an adult male is taken from its own home cage and placed in a completely new environment, which is the home cage of another male, the resulting behaviour is quite different. The newcomer tries to maintain a distance from the resident male which soon attacks, causing the stranger to begin submissive calls and appropriate behaviour. Little serious fighting occurs during each 40 minute period and no appreciable damage is done.

Adult males are not aggressive towards sub-adult males. These interactions are always amicable. However, the older adult males are found to be more friendly towards sub-adults, than the younger ones. When sub-adult males are placed together they show considerable antagonism towards one another, with fighting. The age of the males concerned seems to be an important factor in determining behaviour. The greatest antagonism occurs where the age difference between individuals is the least. The older animal is usually dominant, irrespective of its relative size or environmental factors.

4.4.2 Male-Female Interactions

All adult males and many sub-adult males are dominant over adult females and show considerable interest in them. The remainder of the sub-adult males are submissive towards the females. The sub-adult category represents

a transition stage between juvenile and adult and this change is reflected by the difference in behaviour observed. In cases where the female dominates over the male, it is highly aggressive, whereas when the male is dominant, it is always friendly, although sometimes rough, with the female.

During each introduction where the male is dominant, he quickly approaches the female and smells her, after which he chases her while making a soft 'hoot'. The female usually flees onto the floor and begins a variety of low intensity submissive calls. Older males, which are less rough than the younger ones, induce less submissiveness in the female. In these cases the male jumps towards the female but pauses a short way from her. The female jumps away and the process is repeated until the male is able to groom and scent-mark over her without inducing fear. The younger males chase more rapidly and attempt to stand over and hold the females by force in order to groom and scent-mark over them.

Adult females are friendly towards juvenile males but aggressive to males as they begin to mature. These interactions are similar to those described for adult female pairs.

4.4.3 Female-Female Interactions

All pair introductions between adult females result in

one of the two being aggressive and the other completely submissive. The position of dominance is independent of environmental factors or the relative size of the animals concerned; it seems to be determined entirely by the 'character' of the individuals. Certain females are nearly always dominant while others are invariably submissive. Changes in 'character' are observed at different times of the year, which are possibly related to hormonal factors. Pregnant females, or those with small infants, are often unusually aggressive.

The position of dominance between strange adult females is soon recognised. One animal chases and attacks the other which retreats onto the floor while making a variety of calls, including high intensity 'chatters' and 'screams'. The submissive female remains on the floor for most of the observation period. The aggressor attacks by diving onto the other female from above and then returning to a vantage point in order to repeat the attack.

Aggression between females is not universal, although it always occurs in a 40 minute introductory session. Some adult females are known to live together peacefully and even to produce infants in the same nest.

4.4.4 Interactions involving Juveniles

Juveniles immediately recognise the presence of a stranger and behave appropriately. Their status varies depending

on their knowledge of the environment. Certain individuals are submissive in an unfamiliar cage but dominant over the same stranger when in the home cage.

Adult or sub-adult males or females are tolerant of Juveniles. They frequently show friendly interest accompanied by mutual smelling and grooming with occasional bouts of play. Juveniles may approach the adults many times out of curiosity but they are sometimes highly nervous, and spend the entire session on the floor making alarm calls. The nervous behaviour is completely unpredictable and seems to be related to the character of the developing juvenile.

When two juveniles are placed together they avoid contact, while showing obvious interest in one another. There is little mutual smelling and no mutual grooming.

4.4.5 Pair introductions in a Dual Environment

When two bushbabies from adjacent cages are each allowed access to the home cage of the other, the resulting behaviour conforms to the characteristic interaction of the particular age-classes to which they belong. Whereas the overall pattern is the same, each animal spends the majority of time in the opposite cage. The attraction to explore an unknown environment is extremely strong. Individuals have a higher dominance/submission rating

when in the home cage than when in the new cage.

4.4.6 Introduction of a Stranger into a Group

When a stranger is introduced into a stable family group, or when an individual is replaced with its own group after a short period of absence, there follows a period of olfactory "checking" of the stranger and also between members of the group. Interactions between individuals do not differ from normal, except that a dominant stranger causes considerable confusion within the group.

A certain generalisation of response is evident since members of the group may suddenly become wary or frightened of one another. Fighting may occur between previous companions, apparently by mistake.

5. DISCUSSION

Examination of the series of interactions yields a pattern, making it possible to generalise when discussing the behaviour shown between individuals of each class. There are, however, a number of variables which can alter the basic pattern, so that the resulting behaviour is not entirely predictable.

The pattern of each interaction is controlled by the behaviour of the dominant animal, depending on whether it is friendly, aggressive or ignores the stranger. The position of dominance is in turn, usually determined by the relative age and sex of the animals concerned, which therefore, exert the most influence on the interactional behaviour. It is also effected quantitatively and to a lesser extent qualitatively, by the previous associations of each animal, their knowledge of the environment and individual differences in character. The position of dominance between bushbabies of a roughly equal age/sex status, may be solely determined by these variables.

The relative importance of each variable is not easy to assess. They combine to modify the status of an animal, (as judged by its dominance/submission rating), in such a way that a normally nervous bushbaby, placed in a strange environment after having suffered a beating from a conspecific, will be completely submissive, even

to the friendly advances of members of its own family group. The initial position of dominance between strangers may become reversed after several hours, as the newcomer becomes more settled and familiar with the environment. A combination of visual, auditory and olfactory clues may be used by a bushbaby in order to recognise the status of a stranger.

There is no readily apparent, visible physical difference between males and females. Males are usually larger, but individual females may be larger than the majority of males.

When an adult male is introduced into an adjacent cage containing another adult male, the two will unerringly go straight to one another and begin fighting. This occurs irrespective of the size of other animals present. Small animals are frequently dominant over larger ones, so that relative size appears to be of little importance as a determinant of behaviour.

The activity of each bushbaby during an introduction may provide a variety of visual clues to the stranger whose behaviour may alter accordingly.

Different calls are made as a sign of dominance, submission or fear. The 'bark' or 'male' call may be given