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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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by the male or female when dominant, but it is not made by a subordinate adult. It is possible that vocalisations from the submissive animal may appease the aggressor and thus reduce the amount of fighting. No sound is made when both animals are aggressive. Certain of the calls made in agonistic situations may be merely outward expressions of fear, induced by the presence and behaviour of a dominant conspecific. In each introduction, these calls including the explosive cough, are made only after the position of dominance has been established and they do not appear to be an important means of recognition in the initial encounter.

There are several indications that the sense of smell plays the most important role in intra-specific recognition.

Adult males show considerable interest in adjacent cages which contain other adult males. Fighting often occurs through small cracks in the partition, causing bloodshed and damage to the fingers. Females are never damaged in this way. Recognition can, therefore, be achieved in the absence of visual stimuli.

At the beginning of an introduction the bushbabies may avoid each other but they frequently smell the places

where the stranger has been sitting. This behaviour often precedes the coming together of strangers. Contact is always accompanied by naso-nasal and/or naso-genital sniffing and often by mutual licking or grooming of the fur. The motivation to smell a superior animal is high, even when it repeatedly results in being chased away.

Adult males urinate on the females by contact scent-marking. This occurs especially when a female is returned to her companion after a short absence, or when a strange female is introduced to a male. There is some evidence that males show greater antagonism towards females which have been with other males, indicating that the smell of the male on the female may be important. However, youngsters are never attacked under the same conditions. Objective experiments are required to clarify the significance of these observations.

The experiment indicates that certain strangers are compatible while others are not. Apart from youngsters, strangers of an equal age and sex status are generally incompatible. In addition an adult female will not tolerate the presence of a young sub-adult male. It appears that mutual recognition is achieved primarily by smell which may carry information of the age and sex of each animal. The status of a stranger may be recognised

through visual clues, which modify the subsequent behaviour. The results illustrate the probable mechanism which maintains the separation of family groups in the wild, while allowing the formation of new groups.

Wynne-Edwards (1964), notes that a group of males will parcel out the available ground as individual territories and thus put a limit on overcrowding. In many animals the males have vocal abilities which the females lack. These males use their voices not to woo females, but in contest with their fellow males for real estate and status.

The bushbaby lives in small groups, occupying a particular area while making loud calls and often showing aggressive behaviour towards strangers. It clearly has a similar behavioural mechanism geared to adjusting the density of the population to the food supply.

The groups do not seem to occupy a territory in the sense of an area defended against encroachment by conspecifics (Burt, 1943). Separation within a uniform habitat appears to be the result of a certain amount of antagonism and avoidance between strange individuals. This also results in the maintenance of discrete groups having a particular age/sex composition.

Since the adult male is the dominant figure within each group, it seems likely that rivalry between adult males is the most important factor resulting in the spacing out and spread of the species. Overt aggression has been witnessed in the wild, but it is not common. Few of the wild bushbabies show the typical loss of fur which occurs during fighting in the laboratory. Aggression may be prevented by the use of the 'male' call or 'bark', which advertises the presence of an assertive adult and probably results in rivals avoiding one another in most cages. All the loud calls made, may give an important indication of the position and number of animals within a certain area.

The size, shape and position of the home range is known to change during the year. As the young males mature and reach the sub-adult stage of development, their range of movement may become separated from that of the parents due to rising mutual antagonism. Overlapping home ranges allow animals from different groups to meet.

Adult and sub-adult males have been shown to be persistant in their attentions towards adult females which are not in oestrus. This behaviour is significant in the formation of new groups. The success of

the male in forming a pair presumably depends on the absence of other males and acceptance by the female, who may then share the same sleeping place. The movements of the pair form a new home range.

There is some speculation on the relative roles of the senses in moving within the home range. Since bushbabies are nocturnal, yet are able to orient precisely, it has been suggested by Sauer & Sauer (1963) that they follow scent "trails" through the trees. The scent "helps the animal to become and remain familiar with its territory. It facilitates exploring a new place and tracing the trail home". Sauer & Sauer consider that bushbabies establish predistinct main trails which are well marked, frequently used and retraced. A network of subtrails is suggested, which are not so often marked with urine as the main trails, nesting sites and particular food sources.

Contrary to this idea there are various indications from the present study that olfaction plays little role in establishing "trails" in the wild. In the absence of controlled experimental evidence it is only possible to speculate as to the significance of the senses. The bushbaby obviously has a thorough knowledge of the area in which it lives but it is

suggested that it has primarily a visual memory and not an olfactory one.

Scent-marking, which involves the wiping of the palms of the hands and soles of the feet with urine, occurs several times in quick succession within the nest tree, or one or two adjacent trees, before leaving for the night's activity. Thereafter it occurs on an average of only twice per hour. Considering that during this time the animal generally moves through 45 to 50 trees spaced over a distance of 200 yards, the importance of scent-marking as a means of demarcating a trail becomes debatable.

Field observations suggest that certain movements which are repeated frequently become memorised so that jumps between particular trees and branches may be performed habitually. However, bushbabies are capable of a tremendous flexibility of movement, both in direction and method of progression, according to circumstance. They do not always use the same route in coming and going. No regular scent-marking at particular places has been observed, except at the sleeping trees. Also, wild bushbabies show a distinct lack of obvious sniffing, it occurs only during social interactions and when investigating certain restricted areas within the home range.

It is known that bushbabies are unable to make jumps if they are unable to see. An experiment is described by Petter (1959), in which it was found that jumps of at least 2 metres could be performed in a very dark room, but not when it was made completely light-proof. Using an infra-red scope the animals were seen to remain completely immobile and would only move slowly and clumsily when very frightened.

A repeat of this experiment in the laboratory, using 20 bushbabies in 6 light-proof cages, confirms that no jumps are made, even after 2 hours in total darkness. There is, however, considerable movement from one branch to another around the walls of a familiar environment. It is not possible to force a bushbaby to jump from the hand under these conditions unless it is extremely timid, in which case it jumps undirectionally and lands on the floor.

Providing there is star light, the visibility at night in the bush is such as to enable even the human being to negotiate an area by recognising certain trees or open spaces. The possibility that visual recognition is also used by the bushbaby in moving from one place to another is supported by the special structure of it's eyes. Luc (1963) notes that for G.crassicaudatus agisymbanus (coquerel) : "The eyes have all the hall-

marks of a thorough going nocturnalist: a pure rod retina, a well-developed tapetum cellulosum (although of an exceptional composition), a large anterior segment of the eye, a large lens and a slit pupil."

Since sight is necessary in jumping, it can be assumed that a bushbaby can see clearly for at least 15 feet at night, which is the distance of the longest jump. There is some evidence that greater distances are travelled on bright moonlit nights and just after sun-set or before sunrise. It is possible that a bushbaby can see clearly for 30 to 40 yards. Such vision would explain many aspects of behaviour seen in the wild.

Apparent visual checking is made before attempting a long jump. Long distances may be travelled rapidly across the ground after a period of staring in the direction of travel. The method of progression between particular trees, whether by a long jump or across the ground, may vary from one night to the next, particularly if the animal is harassed. Infants, which are not able to make the same jumps as the mother, follow in her general direction by independant routes. These facts indicate that sight and a visual memory coupled with a Kinaesthetic sense, enables these nocturnal animals to move around with little reliance on olfactory markers or trails. Scent-marking may give an important indication of the presence of particular animals within a certain area

6. SUMMARY

A preliminary survey of the ecology of the Lesser Bushbaby, Galago senegalensis moholi, is given for a 12 month period in South Africa. Bushbabies are found alone or in small groups of up to 6 animals. They sleep during the day, on nests, or in forks and tree holes. Members of a group generally separate at night in order to forage. Their movements are purposeful and directional within a home range of approximately 7 acres. It is suggested that orientation is achieved primarily by a visual memory and not an olfactory one.

The feeding habits of bushbabies in the study area and their relationships with predators and other species are discussed. Of the 8 potential predators, it seems that only man has a serious effect on population numbers.

The occurrence of nest building, births and mating is shown in relation to environmental factors. Infants were found during the summer months from October to March with an apparent double birth peak. Population numbers reached a maximum towards the end of the rainy season.

A record is made of seasonal and diurnal variations in behaviour during the year. Activity conforms to a broad pattern during each night but it varies quantitatively between winter and summer. The position of home range

boundaries show a continual change.

Certain aspects of behaviour in the field, including those which are not seen in the laboratory, are recorded in detail. The mother-infant relationship and auditory communication are described and discussed in relation to existing laboratory data. Bushbabies commonly make three loud calls, two of which are associated with alarm and one which appears to act as a spacing mechanism. An account is given of social interactions witnessed in the field and the behaviour of tame animals when released into the home range of wild ones.

Aspects of the social organisation of the species in the laboratory are reported. By a dyadic analysis between different age/sex classes, an objective dominance/submission rating is calculated for each class in a variety of situations. Evidence is given that there is an underlying pattern of social organisation governed by certain rules. The age and sex of each individual and differences in "character" and environmental factors, combine to affect the results. It is evident that olfactory cues have an overriding influence in controlling intraspecific encounters.

It is suggested that the formation and separation of family groups in the wild is achieved through antagonism

and avoidance between strange individuals, particularly adult males.

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