ASPECTS OF THE ECOLOGY AND BEHAVIOUR OF THE THICK-TAILED BUSHBABY *GALAGO CRASSICAUDATUS*

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I hereby declare that this thesis is my own work and has not been submitted to any other university.

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ABSTRACT

The extant prosimian primates, with the exception of some lemurs of the Republic of Malagasy, are nocturnal and secretive in their habits. Several lines of evidence suggest that they have remained similar to the basal primate stock, but their study under natural conditions has, until recently, been largely overlooked. Only eight prosimian species remain on the Continent of Africa. Two relatively slow-moving lorises (Perodicticus potto and Arctocebus calabarensis) and three active galagos, or bushbabies (Euoticus elegantulus; Galago alleni and G. demidovii) are confined to the equatorial forest belt, while three other galagos (Euoticus inustis; G. crassicaudatus and G. senegalensis) show adaptations for more open environments. A field study of G. crassicaudatus has been carried out in three distinct habitat types in southern Africa by means of direct observation with red light. Aspects of the ecology and behaviour of this species are presented and compared with those of other lorisoids and lemurs, particularly G. senegalensis, which is sympatric in some areas. In the absence of an adequate fossil record a consideration of species typical behaviour patterns and functional morphology leads to inferences concerning the probable behavioural and ecological condition of ancestral species, and conclusions regarding the separation and divergencies of recent forms. The morphological characteristics of G. crassicaudatus conform to the typical Galagine pattern of adaptation for active leaping progression but some features of their behaviour are reminiscent of members of the Lorisinae, with which they show a superficial similarity in their karyotype. It is concluded that the species directly ancestral to G. crassicaudatus were smaller and more active leaping animals which underwent a secondary, behavioural, adaptation towards slower quadrupedal locomotion. It is assumed that this was accompanied by an increase in body weight which facilitated infant transport on the fur leading to closer contact between mother and offspring and a better developed social group structure. On the basis of this interpretation the behavioural similarities with the Lorisinae are seen as the result of convergence and not due to a close phylogenetic relationship.

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CONTENTS

LIST OF TABLES PAGE

PAGE

LIST OF ILLUSTRATIONS * PAGE

*Photographs, and drawings taken from photographs, by the author.

PAGE

PAGE

PAGE

PAGE

PAGE

Figure 1. Galago crassicaudatus E. Geoffroy

1. INTRODUCTION

There are many different approaches to the study of animal behaviour. Each worker is presented with several possibilities in terms of the duration of his study, his access to facilities and equipment, the animals at his disposal and his particular interests and abilities. These factors are in turn affected by the part of the world in which he is working and even the local political situation. The number and type of species which have been studied has been restricted by these considerations. While a large amount of information has been collected on relatively few species, the vast majority remain more or less unstudied. In some cases there is a pressing need for information on the behaviour and ecology of species which are in danger of extinction. Even if it is too late to ensure their survival in the wild, their study may at least contribute towards a better understanding of animal behaviour. An appraisal of the particular contributing factors which lead to their decline may be used to avert or prevent similar declines in other species.

In 1964 a colony of Lesser Bushbabies (Galago senegalensis moholi) was established by Professor G.A. Doyle in the Department of Psychology at the University of the Witwatersrand (Doyle and Bekker, 1967). These small nocturnal primates bred successfully in captivity, their requirements for space were not excessively large and they could be handled with ease. They could be observed through one-way glass using a reversed day/night cycle with red light to simulate nocturnal conditions. This facility enabled many types of information to be collected which would not have been possible in the wild (Doyle et al., 1967; 1969; 1971) but it was unknown whether it was sufficiently natural to allow meaningful conclusions, while the functional significance of some behaviours remained obscure. In 1968 a field study was undertaken to provide a natural background for studies in the laboratory (Bearder, 1969). The logical continuation of this work was to compare the ecology and behaviour of G. senegalensis with closely related forms and particularly with the Thick-tailed Bushbaby (G. crass-

icaudatus) which was found locally. The laboratory colony has now been extended to include the latter species and also the Dwarf Bushbaby (Galago demidovii) and the Lesser Mouse Lemur (Microcebus murinus). The object of the present study is to provide field data on G. crassicaudatus (figure 1) which can be compared with the ever-increasing body of information on related prosimians.

Man's affinity with the remaining Primates, prosimians, monkeys and apes, has attracted considerable interest in the Order from scientists of many disciplines. Yet the study of behaviour and ecology in non-human primates is still in its early stages. Despite a number of preliminary field studies there are few detailed, long-term, investigations such as the study of howler monkeys (Alouatta palliata) on Barro Colorado Island (Carpenter, 1965) or the semi-free Japanese macaques (Macaca fuscata, see Frisch, 1959). When considering the ethological approach to the study of animal behaviour the preliminary studies are most important but they merely set the scene for investigations in depth. Extensive observation and description of behaviour provides the basis for questions concerning its causation, ontogeny and survival value while comparisons between related species or groups can lead to a better understanding of the possible origins and evolution of their behaviour.

The evolutionary approach was firmly established through the writings of Lorenz (1937, 1950) and Tinbergen (1951) following workers such as Whitman (1919), Heinroth (1911) and Huxley (1914). It is based on the fact that much of behaviour is species-specific, yet it is often similar in related species. This suggests that it can be studied comparatively in the same way as structures or physiological characteristics, leading to conclusions concerning its probable evolution. Obviously it is not possible to study the way that animals have behaved in the past but, as Tinbergen (1963) points out, it is possible to answer questions concerning the survival value of behaviour and thereby to consider the effects of natural selection. Inevitably any conclusions which are reached concerning the evolution of behaviour remain tentative, since they deal with possible events in the past, but an emphasis on survival value, which can often be demonstrated by experimentation, can at least show the potentialities of selection. The results may be strengthened by other indirect evidence but: 'they really deal merely with "possible future evolution", and only indirectly with past evolution.' (Tinbergen, 1963).

The earliest fossil representatives of the Order Primates have been discovered from the middle of the Palaeocene period and are approximately seventy million years old (Schultz, 1969). A large variety of still very archaic prosimians have been discovered from the Palaeocene and Eocene stratas in Europe, North America and Southern Asia. It appears that the lemurs of Malagasy became isolated on the island in early Eocene times. It is thought that here they diversified from a small number of ancestral species which succeeded in colonizing the island from the mainland of Africa (McKenna, 1966; Martin, 1972b). Martin suggests that this probably occurred at a time when the two land masses were closer than they are today. Subsequent widening of the Moçambique Canal due to continental drift would have considerably reduced the likelihood of further migration of animals to Malagasy, which thus became effectively isolated (Martin, 1972b). In East Africa, Walker (1969) indicates that both the Lorisinae (lorises) and the Galaginae (galagos) were developed by the lower Miocene times. They evidently underwent a considerable amount of adaptive radiation within the extensive equatorial forest belt which existed at that time.

An interpretation of the history of primates as revealed by their fossil evidence alone is extremely difficult. Despite the work of several experts there remain many unanswered questions. The chances for fossilization of arboreal, tropical forest living animals are far less favourable than for terrestrial or aquatic species in temperate zones (Schultz, 1969). Recent finds from new sites and strata are continually adding to the overall picture which is clarified by cytological and serum protein studies and the evolutionary interpretations of the behaviour of extant species.

Simpson (1945) divides the Order Primates into two Sub-Orders: the Prosimii (tree shrews, lemurs, lorises, galagos and tarsiers) and the Anthropoidea (old-world monkeys, new-world monkeys, pongids and hominids). Recent evidence suggests that the tree shrews should best be excluded from the Order (Martin, 1967; 1968) and that the lemurs and lorisoids are far more closely related than Simpson's classification implies. Charles-Dominique and Martin (1970) have compared the morphological characteristics of a nocturnal lemur (Microcebus murinus) with a galago (Galago demidovii) and found that the classical distinctions between lemurs and lorisoids did not apply. In addition the two species showed such extensive similarities in their ecology and behaviour as to

suggest the retention of homologous ancestral primate characteristics, or at least ancestral lemur/loris characteristics, by the Cheirogaleinae and the Galaginae. These authors considered that convergent or parallel specialization most probably emphasized the similarities based on a common ancestry.

Martin's subsequent examination of the adaptive radiation and behaviour of the Malagasy lemurs led to the conclusion that the ecology and behaviour of the ancestral lemurs was probably quite similar to the existing Cheirogaleinae and particularly to the genus Microcebus (Martin, 1972b). By further comparing the Cheirogaleinae with the Lorisoidae he built up a picture of their probable common ancestor, which seems to have had an earlier common origin with the Adapinae and Notharctinae of Northern Europe and North America. None of these forms were far removed from the ancestral primate stock. It can be seen that comparisons between other closely related extant species can provide a basis for distinguishing those characteristics of primates which are primitive from those which are specialized.

Despite the obvious importance of the prosimians within the Order they have received much less attention than the more conspicuous diurnal monkeys and apes. Recent development of techniques for observing the often small, nocturnal and forest-adapted forms has led to a number of field studies which supplement the previous work of Bluntschli (1933), Petter (1962c) and Petter and Petter-Rousseaux (1964) on nocturnal lemurs and Sauer and Sauer (1963) on Galago senegalensis.

Prominent studies under natural conditions include observations of several of the small nocturnal Malagasy lemurs: the Aye-Aye, Daubentonia madagascariensis (Petter and Petter-Rousseaux, 1967; Petter and Peyrieras, 1970); the Forked-crowned lemur, Phaner furcifer and Coquerel's Mouse lemur, Microcebus coquereli (Petter, Schilling and Pariente, 1971); the Sportive lemur, Lepilemur mustelinus (Charles-Dominique and Hladik, 1971) and the Lesser Mouse lemur, Microcebus murinus (Martin, 1972a). Among the African Lorisoidea field work has been carried out on Bushbabies, Galago demidovii, Galago alleni and Euoticus elegantulus; the Potto, Perodicticus potto and the Angwantibo, Arctocebus calabarensis (Charles-Dominique, 1971; Jewell and Oates, 1969). Detailed studies of individual species have been made by Charles-Dominique (1972) and Vincent (1969) on the Dwarf Bushbaby, Galago demidovii and by Bearder (1969) on the Lesser Bushbaby, Galago

senegalensis. Thus in Africa, considering the present study, only Euoticus inustus remains relatively unknown in the wild. There are few field studies of the prosimians of Asia but some observations are available on the Slender Loris, Loris tardigradus (Petter and Hladik, 1970) and the Western Tarsier, Tarsius bancanus (Fogden, 1974).

In the pages which follow ecological data are presented for G. crassicaudatus as a background for a consideration of its behaviour. An attempt has been made to deduce the functional significance of behaviour patterns in this species. Descriptions and illustrations of behavioural acts and postures are presented, often in relation to the morphological structures which they involve, with a particular consideration of feeding habits, locomotion, social organization, use of space, marking behaviour and vocalizations. These and other behaviours are compared with those of closely related species in order to indicate possible evolutionary trends. A special emphasis is placed on a comparison with G. senegalensis, for which some additional information has been collected during this study. The most important factors which bring about ecological separation between these two species are outlined. The need for further information regarding the taxonomy of the Galaginae is exemplified by the cytotaxonomic studies of Ying and Butler (1971) and De Boer (1973a and b). Karyological variations found within G. senegalensis and G. crassicaudatus suggest that their sub-species diverged much more than is generally supposed, for example by Hill (1953). Chromosome number polymorphism is even reported within a single sub-species (G. senegalensis braccatus). In addition there are certain anomalies when considering the separation of the Galaginae and the Lorisinae. Galagos are characterized by their large ears, long bushy tails and long hind limbs, in which the navicular and calcaneal bones of the feet are strongly elongated. In contrast the lorises have much smaller ears and the tail is reduced or absent. The tarsus is much less elongated and the extremities show special adaptations for maintaining a powerful grip. Accordingly, galagos are characterized behaviourally as active leapers while lorises are well known as slow-moving climbers. On closer examination, however, it is found that G. crassicaudatus occupies an intermediate position in terms of its normal locomotory behaviour. This is of special interest as a marked difference exists between the diploid chromosome numbers of G. senegalensis (2n = 38) and G. crassicaudatus (2n = 62), while the

karyotype of G. crassicaudatus corresponds numerically with that of Perodicticus potto in Africa or Loris tardigradus in Asia. De Boer (1973a) notes that a clear structural relationship seems to exist between the karyotypes of G. crassicaudatus and G. senegalensis and that the difference in chromosome numbers may have been mainly a result of centric fusions. He concludes that the differences in their karyological characteristics arose after their phylogenetic separation from the Lorisinae (De Boer, 1973b). Whether or not the behavioural similarities between G. crassicaudatus and members of the Lorisinae can be related to genetic similarities remains to be seen.

2. METHODS

The approach to this study of G. crassicaudatus was based on a previous investigation of the ecology and behaviour of G. senegalensis (Bearder, 1969). The techniques were somewhat modified to suit the relatively inaccessible habitats preferred by the former species. First, the most suitable study areas were chosen and mapped out by means of regular day and night patrols. Then knowledge of the vegetation was obtained through collection of plant specimens and consultation with local botanists. The emphasis was placed on direct observation of bushbabies at night in conjunction with trapping and marking individuals. Detailed field notes were supplemented by photography and by tape recordings which provided an important source of information even when the animals could not be seen.

2.1 The Choice of Study Areas

Study sites were chosen for the ease with which the animals could be found and followed. Coastal and mountain forest areas were least accessible due to the density and height of the vegetation and the nature of the topography. Care was taken to avoid the danger of large nocturnal carnivores. The most productive regions proved to be the riverine forests and open woodlands of farming areas.

2.2 Day and Night Patrols

Regular reconnaisance of each study area was maintained in order to assess the nature of the vegetation and to find sleeping sites during the day, or to estimate population densities and the distribution of bushbabies at night. After a bushbaby had been followed at night its food plants and sleeping trees could be identified during the day. Travel routes and distances were recorded and paths cut through dense vegetation to allow access to regions which were used habitually.

2.3 Direct Observation

G. crassicaudatus were observed at night using red light from a head-band torch covered by a red celluloid filter and powered by a six-volt accumulator battery. A six-volt hand lantern provided a strong beam of white light when necessary. Under ideal conditions the animal's eyes could be seen at a distance of 100 metres due to the extremely reflective tapetum. G. crassicaudatus could be distinguished from other nocturnal prowlers at a distance by the size and spacing of its eyes and its characteristic fixed stare. The use of red light for watching nocturnal animals has been described by Southern (1955). Unlike white light it did not cause bushbabies to contract their pupils, blink or retreat rapidly. In addition it did not reflect strongly from nearby vegetation and thus ruin the night vision of the observer. The animals could be seen in relation to the surrounding vegetation and their movements followed with ease. A Starlight Scope (6,75-volt image intensifier) on loan from the National Geographic Society of America proved to be of little use in the dense vegetation. It is considered that this instrument would be most practical for observing larger animals in open areas.

Particular bushbabies were observed for long periods in order to make a gradual assessment of their behaviour. These well-known individuals could then be compared with other bushbabies in different areas. The usual procedure was to follow one or more bushbabies for a few hours at a time and occasionally throughout the night. Observations were made in a variety of weather conditions and regardless of the state of the moon over the entire study period. The most productive hours of the night were found to be in the evening after the animals left their sleeping places and in the morning before they returned to them at dawn.

Individual and group recognition could be achieved in the absence of marking by a combination of clues. Certain bushbabies had characteristic facial features, tail shapes and colouring or they were distinguished through the loss of a portion of a limb or the tail. Each group had a particular size and composition and its members used regular ranges in one area and often slept in the same tree day after day.

When first observed the animals usually became habituated to the observer after one hour and subsequently they continued their activities undisturbed. The observer could then approach them to within five metres,

but never closer than two metres, without difficulty. Certain individuals were more timid than others and these would remain still and stare at the observer for long periods. Shorthand records of behaviour were kept during each hour of observation and transcribed at the end of the night. A more detailed breakdown of methods employed in the collection and treatment of behavioural and ecological information in included in appendix 1.

G. crassicaudatus were observed for a total of 663 hours over a period of eighteen months between February 1970 and August 1971. The study can be conveniently divided into three sections:

(i) An investigation of a single isolated population of bushbabies over a period of fifteen months in the North Eastern Transvaal (411 hours).

(ii) Scattered observations on a population of bushbabies twelve kilometres from the main study site over the same period (145 hours).

(iii) Comparative observations in widely separated areas over a period of three months, Mtunzini, Zululand (30 hours); Eshowe, Zululand (10 hours); St. Lucia, Zululand (5 hours) and Umtali, Rhodesia (62 hours).

2.4 Trapping and Marking

In order to facilitate the interpretation of data a number of bushbabies were trapped and marked in a characteristic fashion. Wire mesh automatic traps were employed with honey as bait (figure 2). The animals were handled during the daytime without anaesthetization and released on the following night where they had been captured. When handled they struggled vigorously, and occasionally they screamed or ground their teeth, while attempting to bite the gloved hands of the observer.

Individuals were marked by cutting hair from a segment of their bushy tails and these marks remained visible for several months before growing out (figure 3). The animals were sexed, measured and weighed on a small spring scale. They showed no apparent aversion to being trapped. They did not become timid of the observer at night and would enter the trap on subsequent occasions. Four bushbabies were taken to the laboratory and housed under semi-natural conditions for closer observation.

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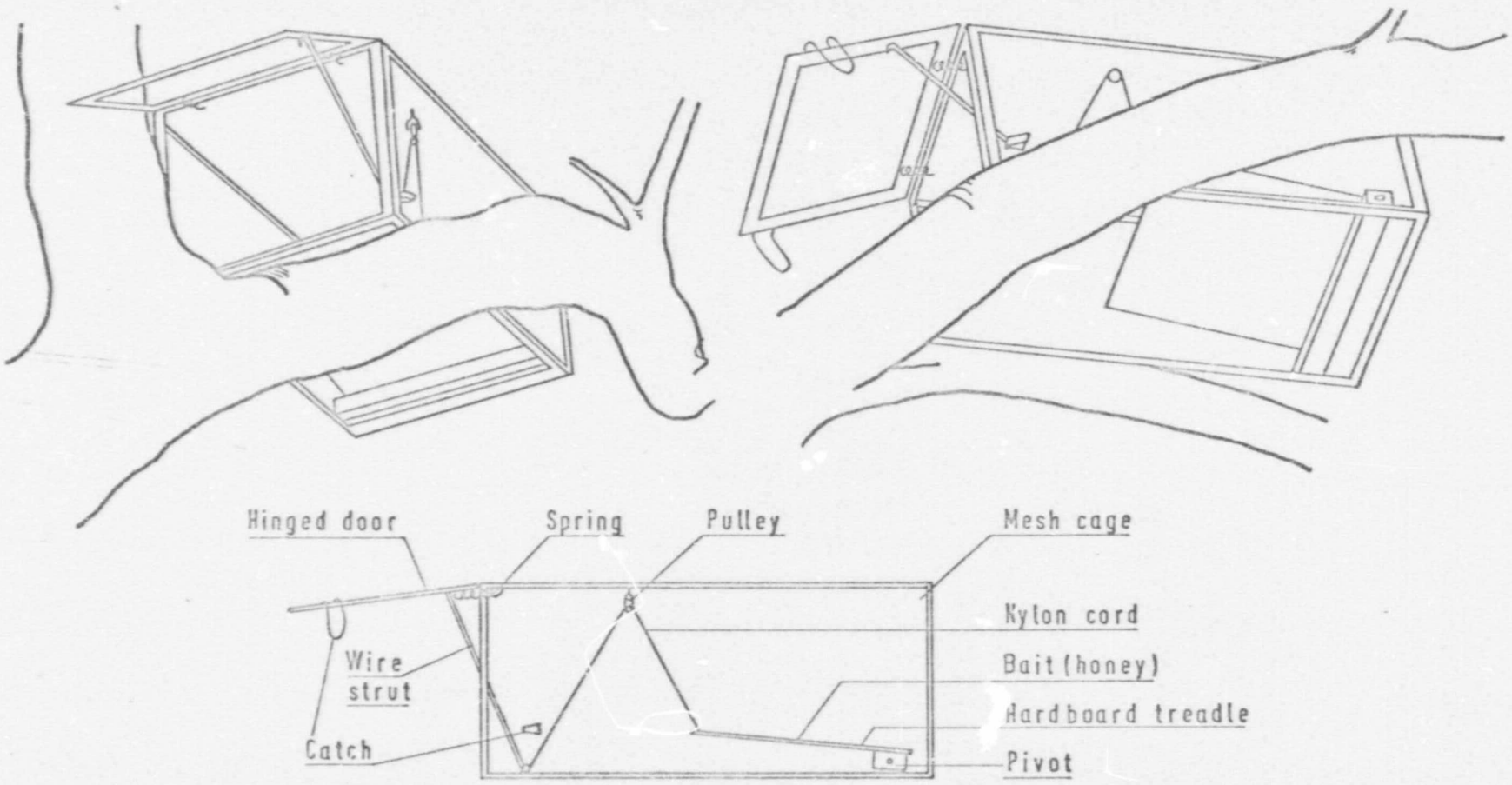

Figure 2. Spring-operated trap

Figure 3. (a) Photograph of an adult male G.c. umbrosus (weight 1,82 kg) taken after capture. Note the saggital line on the head, the bald patch on the chest and the hairless part of the scrotum. (b) Photograph taken at night of an adult female G.c. umbrosus (weight 0,91 kg) to show the bushy tail which has been cut for easy identification.

2.5 Photography

More than 300 photographs were taken in colour and black and white to provide a tangible record of behaviour and ecology. For night work the photographic apparatus comprised a Nikon F. camera with a Nikon 200 millimetre f.4 automatic lens. A Mecablitz 181 electronic flashgun was mounted behind a large condenser lens to produce a telescopic effect. This flash unit and a small red lamp for focusing were offset from the camera and the entire assembly supported on a gunstock for easy handling. Kodak High Speed Ektachrome film (A.S.A. 160 - 23 D.I.N.) or Kodak Plus-X Panatomic film (A.S.A. 125 - 22 D.I.N.) was used, with an exposure of f.5,6 at five metres.

Fifty eight line drawings have been taken from the photographs and arranged in logical sequences to illustrate particular movements and postures. These are compared with similar movements and postures in G. senegalensis.

2.6 The Interpretation of Vocalizations

Detailed records were made of all bushbaby vocalizations. Each sound was named by comparison to a common sound (bark, sniff, moan etc.) which facilitated the recognition and description of what would otherwise have been a confusing series of noises (see Rowell and Hinde, 1962; Moynihan, 1964). Information was collected for each call using the following parameters:

(i) The relative loudness, pitch, quality, speed of repetition, duration and frequency of occurrence of each call.
(ii) The stimulus situation in which the call was heard.
(iii) The behavioural context in which it was heard.
(iv) The response which it elicited from other animals.
(v) The time of night at which the call was given.
(vi) The season of the year when it was most frequently heard.
(vii) The age and sex of the caller.
(viii) Whether or not the call was directed towards a conspecific or another species.
(ix) The frequency with which each call was heard in association with other calls and the nature of any relationships.

Sound recordings were made on a Hitachi portable cassette tape recorder and illustrated by means of a Kay Electric Sono-Graph, model 7029A, with a 5 - 16,000 Hertz Spectrum Analyser. The H.S. shaping switch was used together with the wide bandpass filter.

3. SPECIES DISTRIBUTION

The African Lorisidae are distributed over almost the whole of Africa south of the Sahara with the exception of the southern-most tip. They show preferences for particular habitat types although they may be found living sympatrically. In Gabon, for example, Galago demidovii, Galago alleni, Euoticus elegantulus, Perodicticus potto and Arctocebus calabarensis occupy different ecological niches within the same tropical forest habitat (Charles-Dominique, 1971). Likewise in East and South Africa G. senegalensis and G. crassicaudatus may be found together (Buettner-Janusch, 1964; Bearder and Doyle, 1974a).

The species G. crassicaudatus has been divided into ten sub-species by Hill (1953) on the basis of anatomical and morphological variations in relation to geographical range. Considerable confusion has arisen in the attempt to classify the races of this and other species of Galago and the apparent differences between some of Hill's type specimens may be misleading. Buettner-Janusch (1963, 1964) examined a number of G. crassicaudatus from a single forest in Kenya which had the pelage colouration of at least five sub-species described by Hill and he considers that most of the differences should be treated as minor variations of a single major population. On the other hand he describes G. crassicaudatus argentatus as being distinctly different from G. crassicaudatus crassicaudatus, the 'typical' thick-tailed bushbaby. This difference leads him to suggest that if they are found in the same area they may actually be separate species.

Other authors distinguish between two main groups of races. Matschie (1905) included crassicaudatus and argentatus in a southern group of races together with lönnbergi, umbrosus, garnetti and monteiri, while lasiotes, agisymbanus, kikuyuensis and panganiensis were separated as a northern group and even given subgeneric status. Hill (1953), Schwartz (1931) and Kingdon (1971) follow the division of a northern and southern group of races, but crassicaudatus (Hill) or panganiensis (Kingdon) are reported to be intermediate forms between the two groups.

The chromosome studies of De Boer (1973a) showed two different karyotypes within G. crassicaudatus which were clearly related to racial dif-

ferences, but not in accordance with the division into northern and southern groups. De Boer considers it unlikely that fertile hybrids could be obtained from kikuyuensis and crassicaudatus on the one hand and monteiri on the other, due to the large difference in the structure of their chromosomes.

Even in the absence of cytological distinctions, the division of a species into sub-species is meaningful if it defines breeding populations whose members have characteristics in common and which are effectively separated from one another by physical barriers such as rivers or mountain ranges. The tendency for isolation of breeding populations in bushbabies is very great owing to the nature of the habitat to which they are adapted. Patches of forest may be cut off from one another by tracts of unsuitable bush or open grassland which the animals are unlikely to cross. While the individuals of one population may show a considerable range of characteristics which they share with those of another population they will nevertheless tend to conform to one particular type and this may partially explain the large variety of subspecific characters which have been described.

G. crassicaudatus is one of the most widely distributed of the African prosimians, being second only to G. senegalensis. In East Africa it is found just north of the equator in Southern Somalia, in Kenya and Uganda in the region of Lake Victoria. It extends southwards in the east through Tanzania, Moçambique, the Eastern Transvaal, Swaziland and as far south as Zululand in Natal. Further west it is reported to be widespread in Malawi, Central and Eastern parts of Rhodesia and Western parts of Zambia but it is sparse in Western Rhodesia (Smithers, 1968). Hill (1953) indicates that it may also be found in the Eastern and Southern parts of the Congo, extending westwards to the coast of Angola south of Luanda. It is absent from Botswana and most, or all, of South West Africa while in tropical Central and West Africa it is replaced by a number of other species (Hill, 1953). The approximate known distribution of G. crassicaudatus is indicated in figure 4 in comparison with that of G. senegalensis. The overall limits of distribution are shown, within which the species may be found in suitable habitats, although there are many discontinuities.