

https://dspace.org/

Aspects of the ecology and behaviour of the thick-tailed bushbaby Galago crassicaudatus

Bearder, Simon Kenneth

2014-12-09
http://hdl.handle.net/10539/15915

Downloaded from a DSpace repository. https://dspace.org/

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

Simon Kenneth Bearder

A Thesis Submitted to the Faculty of Science
University of the Witwatersrand, Johannesburg
for the Degree of Doctor of Philosophy

Johannesburg 1974

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

S. K. Bearder

S.K. BEARDER

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.

ACKNOWLEDGEMENTS

I am sincerely grateful to the many people who have made this study possible and helped in the preparation of the thesis.

My special thanks go to Professor G.A. Doyle, my supervisor, for his constant support and encouragement and for his critical reading of the draft manuscript.

The field work was made possible through the generosity and hospitality of Mr and Mrs P.G. McNeil and Mr and Mrs R. Speedy of Ofcolaco in the North-Eastern Transvaal; Mr and Mrs J. Wylie of the Wildwoods Sanctuary in Umtali, Rhodesia and Mr R.E. Webster, ranger of the Umlalazi Nature Reserve in Zululand.

A number of people have shown enthusiastic interest in my work. I am indebted to my colleague, Mrs D. Swierstra, for her fruitful discussions; to Mr A. Renny for his excellent identification of plant material; to Mr R. Bérard who helped with field work during his vacations and to Mr B. Cnoops who freely gave his advice concerning photography.

I wish to thank several people who helped to prepare and edit the manuscript. Miss J.G. Rouse and Mr M.B. Ormerod drew the maps and many of the diagrams; Mr R. Lowe helped to develop and print the photographs; Mr N. Passmore kindly produced the sound spectrograms and Mrs M. Olivier and my wife, Catherine, patiently typed the draft thesis.

Financial support was granted by the University Council of the University of the Witwatersrand, Johannesburg and by the National Geographic Society of America, which I acknowledge with gratitude.

CONTENTS

		PAGE
ABSTRACT		iii
ACKNOWLEDGEMENTS		iv
LIST OF TABLES		ix
LIST OF ILLUSTRATIONS		xi
1.	INTRODUCTION	1
2.	METHODS	7
	2.1 The Choice of Study Areas	7
	2.2 Day and Night Patrols	7
	2.3 Direct Observation	8
	2.4 Trapping and Marking	9
	2.5 Photography	12
	2.6 The Interpretation of Vocalizations	12
3.	SPECIES DISTRIBUTION	13
4.	HABITAT	16
	4.1 Vegetation and Topography	16
	4.2 Climate	16
5.	ANIMALS STUDIED	18
6.	BIOMETRIC DATA	19
7.	STUDY AREAS	21
	7.1 North Eastern Transvaal	21
	7.2 Zululand	21
	7.3 Eastern Rhodesia	24
8.	POPULATION DENSITY	25
9.	ACTIVITY PATTERNS	28
	9.1 The Control of Activity	28
	9.2 Nightly Activity	30
10.	FEEDING BEHAVIOUR	34
	10.1 The Use of Gum	38
	10.2 The Use of Fleshy Fruits	40
	10.3 The Use of Seeds and Dry Fruits	44
	10.4 The Use of Nectar and Other Secretions	46
	10.5 The Use of Insects	47
	10.6 The Licking of Moisture	47
	10.7 Predatory Habits	47

PAGE

10.8 Discussion of Feeding Habits 48

11. LOCOMOTION 51
11.1 Walking and Running 51
11.2 Jumping 53
11.2.1 Quadrupedal Hops 53
11.2.2 Short Leaps 53
11.2.3 Long Leaps 57
11.2.4 Saltation 59
11.3 Climbing 59
11.4 Locomotion on the Ground 61
11.5 The Locomotion of Lame Animals 62
11.6 Discussion of Locomotion 62

12. SLEEPING PLACES 67

13. BIRTH PERIODICITY 72

14. PATTERN OF SOCIAL GROUPINGS 75
14.1 Group Structure 75
14.2 Social Dynamics 76
14.3 The Mother/Offspring Relationship 80

15. HOME RANGE MOVEMENTS 84
15.1 Night Range 85
15.2 Use of Space 87
15.3 Characteristics of Movement in Different Habitats 94

16. SOCIAL BEHAVIOUR 99
16.1 Grooming 100
16.2 Play 103
16.3 Marking and Rubbing Behaviour 105
16.3.1 Urine Washing 108
16.3.2 Foot Rubbing 111
16.3.3 Chest and Body Rubbing 112
16.3.4 Ano-Genital Rubbing 113
16.4 Vocalizations 113
16.4.1 Calls associated with Social Cohesion 114
16.4.2 Calls associated with 'Anxiety' or 'Alarm' Situations 122
16.4.3 Calls associated with Agonistic Contact 127
16.4.4 Discussion of Vocalizations 129
16.5 Agonisitc Behaviour 136
16.6 Discussion of Social Behaviour 140

17. OTHER ASSOCIATED SPECIES 143
17.1 Predators 143
17.2 Primates 145

PAGE

17.3 Viverridae 146
17.4 Birds, Bats and Rodents 147

18. DISCUSSION 148

19. SUMMARY 155

LIST OF REFERENCES 162

APPENDICES
1. Climatic data for each study area 176
2. Exotic trees and fruits of the study areas 178
3. Predominant indigenous trees and climbers of the study area in the North Eastern Transvaal 179
4. Predominant indigenous trees and climbers of the study area in Zululand 181
5. Predominant indigenous trees and shrubs of the study area in Rhodesia 183
6. A comparison of the vocalizations of G. crassicaudatus and G. senegalensis 184
7. The organization of field observation 194
8. Some examples of data analysis for aspects of the study 196

LIST OF TABLES PAGE

Table 1. Size and weight measurements for G.c. umbrosus captured in the North Eastern Transvaal (* = recaptured; † = captured together; DT = dark tip to the tail; LT = uniform, light coloured tail) 20

Table 2. The population densities of G. crassicaudatus and G. senegalensis (Bearder and Doyle, 1974a) in different localities, including areas where they are sympatric 25

Table 3. Food items known to be consumed by G. crassicaudatus (from personal observation or a reliable source = *). 35

Table 4. A comparison of the locomotion and feeding habits of Perodicticus potto (Walker, 1969; Anderson. 1971; Charles-Dominique, 1971), G. crassicaudatus and G. senegalensis (Bearder, 1969, personal observations) 65

Table 5. Examples of sleeping sites used by G. crassicaudatus 67

Table 6. The relative frequency of occurrence of different types of sleeping sites used by G. crassicaudatus (N = 35) in comparison with data for G. senegalensis (Bearder, 1969) (N = 168) 69

Table 7. Sightings of different individuals and groups in G. crassicaudatus compared with sleeping groups in G. senegalensis (Bearder, 1969) 75

Table 8. Aspects of the mother/offspring relationship in G. crassicaudatus, including some indices of development 81

Table 9. A comparison of the activity and sleeping habits of G. crassicaudatus in different sectors of the home range in relation to their size and the availablity of sleeping places 93

Table 10. The frequency of use of different s
places by G. crassicaudatus within a single hom
158 days during the study period 93

PAGE

Table 11. Marking and rubbing behaviour of G. crassicaudatus in comparison with that of G. senegalensis (Andersson, 1969) 106

Table 12. The mean number of cries per hour which were heard in the three study areas 117

Table 13. A comparison of related calls in the continuous 'mobbing' sequence of G. crassicaudatus showing increasing intensity from left to right 123

Table 14. A classification of the calls of G. crassicaudatus to show their functional significance (following Marler, 1968; see appendix 6) 134

Table 15. A comparison of the vocal repertoire of G. crassicaudatus with that of G. senegalensis (Andersson, 1969: Bearder, 1969) showing possible homologues and analogues 135

LIST OF ILLUSTRATIONS * PAGE

Figure 1. Galago crassicaudatus E. Geoffroy

Figure 2. Spring-operated trap 10

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 11

Figure 4. Map showing the approximate distribution of G. crassicaudatus (hatched) compared with G. senegalensis (squares) in relation to broad zones of vegetation. The study areas are marked by circles. (Modified after Hill, 1953) 15

Figure 5. Examples of habitats in the study areas. (a) Tropical fruit trees and indigenous bush in the N.E. Transvaal. (b) Flat-crowned Acacia abyssinica and exotic vegetation in E. Rhodesia 22

Figure 6. Examples of habitats in the study areas. (a) The Hlinza forest, Eshowe, Zululand. (b) A view of the coastal dune forest, Mtunzini, Zululand 23

Figure 7. Map showing the distribution of G. crassicaudatus groups in a valley system of the N.E. Transvaal. The circles represent the approximate limits of home ranges 27

Figure 8. Diagram showing examples of nightly movement and rest by G. crassicaudatus in the main study area. (a) to (e) Female group. (f) Adult male (above), juvenile (below). (g) Adult male with female group. (h) Adult male moving to a new sleeping place (above), female group (below). Broken lines represent periods without observation 31

Figure 9. Histogram of the observed monthly intake of different foodstuffs by G. crassicaudatus. The continuous lines represent months in which the average temperatures were above $18^{o}C$. No observations were made during February 37

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

PAGE

Figure 10. Photographs of a G. crassicaudatus at night as it descended an Acacia Karoo in order to lick gum. Note the extreme divergence of the hallux from the remaining digits of the foot in the lower photograph 39

Figure 11. Drawings taken from photographs to show a variety of postures adopted by G. crassicaudatus at a single gum lick. The photographs were obtained over a period of several months and depict four individuals of a group 40

Figure 12. Photographs showing postures used by G. crassicaudatus to obtain gum from beneath a broad, overhanging, trunk. Note the uniform colour of the tails, one of which has been cut for identification 41

Figure 13. Drawings taken from photographs to show a sequence in the positions adopted by G. crassicaudatus while licking gum beneath an overhanging trunk. Note that the limbs are held wide apart with the body close to the tree. The tail appears to be important for maintaining balance 42

Figure 14. Drawings taken from photographs to show the similarities between the gum-licking postures of G. crassicaudatus (above) and G. senegalensis (below) 43

Figure 15. Photographs of G. crassicaudatus taken at night. (a) An adult male feeding on wild figs (Ficus sycamorus). (b) An adult female moving within a flowering Albizia. Note the reflection of flash from the tapetum of the eyes, which in the lower photograph are half-closed. This animal has a dark tip to its tail 45

Figure 16. Drawings taken from photographs to show the use of the hands in G. crassicaudatus while feeding on wild figs (1-5) and in G. senegalensis while feeding on a locust (6-10) 46

Figure 17. Night photographs of locomotion in G. crassicaudatus. (a) The usual method of progression over open ground. (b) 'Potto-like' walking along a branch 52

Figure 18. Photographs illustrating locomotory postures in G. crassicaudatus. (a) Descent through a thorn tree. Note the positions of the fingers. (b) Walking along a branch. Note the position of the hands and feet 54

PAGE

Figure 19. Drawings taken from photographs of G.crassicaudatus to illustrate a typical sequence of movements through the trees and on the ground 55

Figure 20. Drawings taken from photographs and field sketches to illustrate some jumping abilities of G. crassicaudatus. (1) The arms are raised sharply on take-off. (2) The arms and legs take almost equal impact on landing. (3) Saltation. (4) Quadrupedal hopping 56

Figure 21. Drawings taken from photographs to show common types of locomotion in G. senegalensis (1-8) and G. crassicaudatus (9-14). Note the difference between the typical short jumps of the two species (2-7 & 10-11) 57

Figure 22. Drawings taken from photographs to illustrate some jumping abilities of G. senegalensis. The arrows indicate possible sequences. (2) The arms are raised sharply only during extremely long jumps (above four metres) (5-10-6) Jumps may be made onto the ground and immediately back into a tree using only the hind limbs. (8-10) Saltation 58

Figure 23. Night photograph of a G. crassicaudatus to show the start of movement between trees without jumping. The animal maintains perfect balance while grabbing for another branch which it pulls nearer and then steps carefully across 60

Figure 24. Examples of sleeping places used by G. crassicaudatus. (a) Isolated cypress trees. (b) A high fork in a pine. (c) The space beneath a roof. (d) A dense tangle of bourganvillia 68

Figure 25. Diagram to show the breeding activity of G. crassicaudatus (N.E. Transvaal) in relation to that of G. senegalensis (N. Transvaal; Bearder, 1969) and the period of summer rains. Stippled areas = gestation periods; cross-hatching = mating periods; hatching = birth periods; shading = periods of lactation. The crosses indicate months in which nest-building was recorded 73

Figure 26. Diagram to illustrate the structure and dynamics of a single group of G. crassicaudatus in the main study area during one year. The continuous and dotted lines represent the observed limits of range movements for the adult male, maternal group, and maturing offspring 78

PAGE

Figure 27. Graph to illustrate some aspects of the observed social contact within the main study group during one year. (a) Sleeping associations between mother and offspring. (b) Offspring sleeping alone. (c) Nocturnal associations between adult male and maternal group. (d) Sleeping associations between adult male and maternal group 79

Figure 28. Map showing the major pathways used by the main study group within its annual home range (continuous heavy lines) 85

Figure 29. Map showing some examples of nightly routes taken by G. crassicaudatus: the maternal group = dotted lines; adult male = broken lines, and isolated juveniles = continuous lines 86

Figure 30. Map showing the annual home range of the adult male G. crassicaudatus (hatched) superimposed upon that of the maternal group in the main study area 88

Figure 31. Map showing the range of the maternal group during April 1970 89

Figure 32. Map showing the range of the maternal group during June 1970 90

Figure 33. Map showing the range of the maternal group during September 1970 90

Figure 34. Map showing the range of the maternal group during March 1971 91

Figure 35. Map showing the range of the maternal group during April 1971 91

Figure 36. Map showing the division of the annual home range into five sections based on their relative frequency of use (see text). Section A has been termed the core area 92

Figure 37. Diagram to illustrate the characteristic movements of G. crassicaudatus in different habitats. (a) Temperate forest. (b) Dune forest. (c) Open woodland and garden vegetation 95

PAGE

Figure 38. Diagram to illustrate the characteristic movements of G. crassicaudatus (broken line) and G. senegalensis (continuous line) in different habitats. (a) Acacia savannah. (b) Riparian bush 96

Figure 39. Map showing sightings of G. crassicaudatus, with the number of individuals (in circles) and their movements (dotted lines) in relation to sleeping sites (triangles) in an open habitat (E. Rhodesia) 98

Figure 40. Drawings taken from photographs to show the similarities between the 'comfort' activities of G. crassicaudatus (1-3) and G. senegalensis (4-8) 101

Figure 41. Drawings taken from photographs to illustrate mild agonistic contact between juvenile G. crassicaudatus at a gum lick (1-2) and social play (3) 104

Figure 42. Drawings taken from photographs and field sketches to show the common marking and rubbing actions of G. crassicaudatus (1-6) and G. senegalensis (7-11). (1-2) Urine washing. (3) Chest/body rubbing. (4) Anogenital rubbing. (5) Chest/body rubbing. (6) Foot rubbing, (7-8) Urine washing, (9) Biting, (10) Chest rubbing. (11) Chin rubbing 107

Figure 43. Spectrogram of a six unit cry (G. crassicaudatus) with each unit in sequence from top to bottom. The call builds up to a crescendo and subsides on the last unit. The black squares represent time signals 115

Figure 44. Histogram to show the frequency distribution of cries (G. crassicaudatus) with different numbers of units. (a) N.E. Transvaal (N = 300). (b) Zululand (N = 374). (c) E. Rhodesia (N = 120) 116

Figure 45. Histograms to show the frequency of cries (G. crassicaudatus) during the night in different localities. (a) N.E. Transvaal (isolated group). (b) N.E. Transvaal (several groups). (c) Zululand, dune forest (mating season). (d) Zululand, temperate forest. (e) Zululand, dune forest (outside mating season). (f) E. Rhodesia. The continuous lines represent periods of moonlight. Arrows indicate the times of sunset and sunrise 118

Figure 46. Histograms to show the frequency of cries. (G. crassicaudatus) during fifteen minute intervals. (a) After the animals had left their sleeping places on forty nights (N = 176); (b) Before they returned to their sleeping places on seventy nights (N = 629) 119

PAGE

Figure 47. Spectrograms showing a sequence of calls in the 'anxiety/alarm' series of G. crassicaudatus. (a) Knock, (b) Low squawk, (c) Harsh squawk, (d) Whistled-yap, (e) Whistled-yap variation, (f) Whistle 125

Figure 48. Spectrogram of various calls in G. crassicaudatus. (a) Chatter, (b) Moan, (c) & (d) Screams, (e) Yell 128

Figure 49. Diagram to show the most common relationship between calls of the continous 'anxiety/alarm' series in G. crassicaudatus and associated discrete calls 131

Figure 50. Diagram to show the most common relationships between calls of two continuous 'anxiety/alarm' series in G. senegalensis and associated discrete calls (Personal observations) 131

Figure 51. Photographs depicting aspects of social contact in G. crassicaudatus. (a) Agonistic behaviour between juveniles at a gum lick. (b) Association between juveniles while grooming 138



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.

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 7.

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.

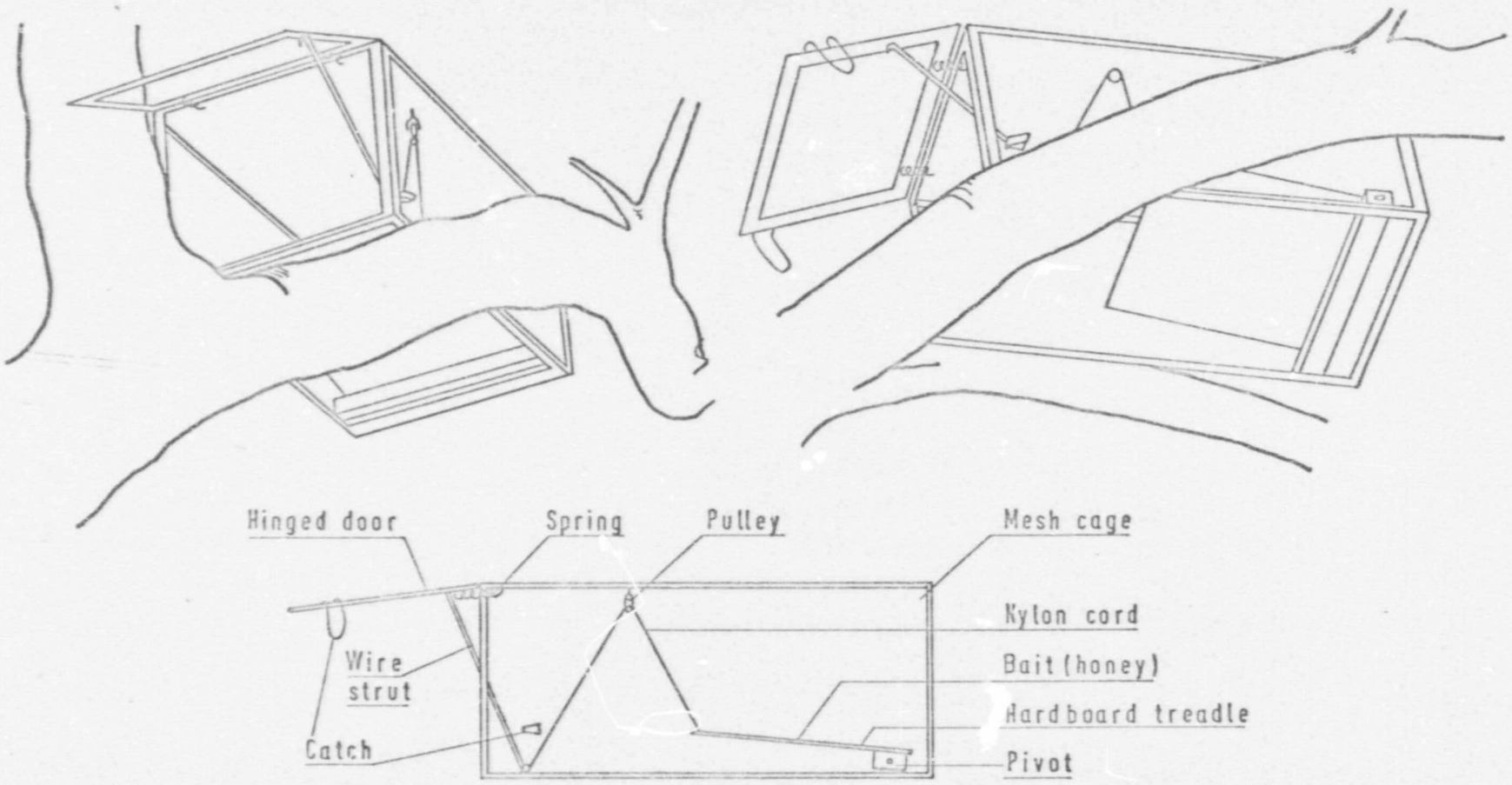

Figure 2. Spring-operated trap



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.

Author Bearder Simon Kenneth
Name of thesis Aspects Of The Ecology And Behaviour Of The Thick-tailed Bushbaby, Galago Crassicaudatus. 1974

PUBLISHER:
University of the Witwatersrand, Johannesburg
©2013

LEGAL NOTICES:

Copyright Notice: All materials on the University of the Witwatersrand, Johannesburg Library website are protected by South African copyright law and may not be distributed, transmitted, displayed, or otherwise published in any format, without the prior written permission of the copyright owner.

Disclaimer and Terms of Use: Provided that you maintain all copyright and other notices contained therein, you may download material (one machine readable copy and one print copy per page) for your personal and/or educational non-commercial use only.

The University of the Witwatersrand, Johannesburg, is not responsible for any errors or omissions and excludes any and all liability for any errors in or omissions from the information on the Library website.