BEHAVIOURAL ADAPTATIONS IN SOUTH AFRICAN GALAGOS

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I hereby declare that this dissertation is my own work, unless otherwise acknowledged, and has not been submitted to any other university.

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ABSTRACT

The behavioural and dietary adaptations of the two species of galago in South Africa were examined. Allopatric populations of *Galago senegalensis* and *Galago crassicaudatus* were studied. Both populations used the same type of food, gum and arthropods, but differences in the importance of the resource types were found. These could be related to the marked differences in body size of the two species and to seasonal changes in arthropod availability. Body size and resource abundance also affected the way the bushbabies used both time and space. The social structure of the galagos was very similar but the degree of their sociality differed between species and seasons. Body size, affecting the length of time offspring remained with their mother as well as the animals' foraging strategy, was the major cause of the difference.

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1. INTRODUCTION

The order Primates is divided into two suborders, the Anthropoidea and the Prosimii. The former group contains the Platyrrhini (new-world monkeys) and the Catarrhini (old-world monkeys, apes and man). In early classifications the Tupaiidae (tree shrews) were included in the Prosimii (Le Gros Clark, 1934; Simpson, 1945) but they have now been excluded from the suborder (Hill, 1953; Martin, 1967, 1968). This group contains three suborders: the Lemuriformes, Tarsiiformes and Lorisiformes. Of these the first is found only in Madagascar. They vary from large-bodied, group-living, diurnal species (e.g. Lemur catta) to small, essentially solitary, nocturnal species (e.g. Microcebus murinus). The other two groups contain only small-bodies, nocturnal species. The only surviving genus of the Tarsiiformes, the Tarsius, are found distributed throught the islands of the Far East (see Petter and Petter-Rousseaux, 1979, for details of distribution). In the third infraorder, the Lorisiformes, are found the genera Periodicticus (potto), Arctocebus (angwantibo) and Galago (bushbabies) in Africa and Nyticebus (slow loris) and Loris (slender loris) in India and the Far East.

Among the African Lorisoidea field work has been carried out on Arctocebus calabarensis, Periodicticus potto, Euoticus elegantulus and Galago alleni by Charles-Dominique (1977) and on Galago demidovii by Charles-Dominique (1977), Jewell and Oates (1969), Struhsaker (1970) and Vincent (1969). Galago senegalensis and Galago crassicaudatus are the two species found in South Africa and they were used in this study. Sauer and Sauer (1963) made brief observations on G. senegalensis in South West Africa. Haddow and Ellice (1964) looked at both species in East Africa in relation to the epidemiology of yellow fever. Bearder studied the territorial and intergroup behaviour of G. senegalensis (1969) and the ecology and behaviour of G. crassicaudatus (1975) in South Africa. A detailed study of the social organisation and population dynamics of G. senegalensis has recently been completed (Bearder and Martin, 1979, in press; Martin and Bearder, 1979). Clark (1978, pers. comm.) and Katsir (1979) have worked on the social behaviour and communication of G. crassicaudatus. R. H. Crompton (pers. comm.) has worked on the locomotion of the two South African species of bushbaby. The present study compared the diet and behaviour (in terms of space and time use and social behaviour) of G. senegalensis and G. crassicaudatus and relevant field studies are reviewed below.

Both of the South African bushbaby species are reported to eat gum, mostly from Acacia trees, and insects (Bearder, 1969, 1975) and both can live almost exclusively on these resources; (Clark, 1978; Sauer and Sauer, 1963). In addition, vegetable matter has been reported in the stomachs of G. senegalensis (Haddow and Ellice, 1964) and G. crassicaudatus eats fruit, nectar and seeds (Bearder, 1975). The latter species has also been reported to eat birds' eggs, small birds, reptiles and mammals (Kingdon, 1978). Seasonal differences in diet have been reported for both species but only differences in percentage time feeding on a particular resource have been presented (Bearder, 1969, 1975).

The use of time in the wild has not been studied in detail in either species. A general pattern of emergence from their sleeping site at sunset followed by a short period of 'comfort activities' (yawning, stretching, grooming), before moving off to search for food has been reported (Bearder, 1975; Sauer and Sauer, 1963). A bimodal pattern of activity through the night was recorded for G. crassicaudatus but no quantitative data on anything except distance travelled from the sleeping site was presented (Bearder, 1975). A seasonal difference in the time spent on different activities was found in the same study but this was not quantified.

Use of space, in terms of home range size, has been examined in both species although G. senegalensis has been studied in more detail (Bearder and Martin, 1979) than G. crassicaudatus (Bearder and Doyle, 1974). In terms of differential use of space, the time spent in different parts of the home range have been looked at in G. crassicaudatus (Bearder, 1975) but no details of which activities occurrred where in the range were reported. Both species were found to be active at all heights in the trees with the amount of activity at a particular level depending on the spacing of the trees and the availibility of food in the habitat (Bearder, 1975). No quantitative data on seasonal changes were reported.

The social organisation of G. senegalensis has been more intensively studied (Bearder and Martin, 1979) than that of G. crassicaudatus (Clark, 1978; Katsir, 1979) but the two species appear to be fairly similar in this respect (Bearder and Doyle, 1974). Adult females hold fairly small territories, which may or may not be shared with a female relative. In G. senegalensis large, dominant 'Central A' males have territories overlapping those of one or more females. The smaller, though adult, 'Central B' males are tolerated in the ranges of the 'A' males but they do not have ready access to the females. Both species tend to be gregarious during the day, sleeping in groups of up to nine conspecifics (Haddow and Ellice, 1964; Jolly, 1966a; Sauer and Sauer, 1963), and solitary during their active period at night (Bearder, 1969, 1975).

Comparative studies between related species can be used to isolate the factors which give rise to different adaptive strategies. The first attempt on primate species along these lines related differences in social or organisation to differences in ecology. (Crook and Gartlan, 1966). It was suggested that all primates could be classified into five adaptive grades on the basis of similarities in ecology, demography and social structure, and these cut across taxonomic groups. This suggestion has been further examined and amplified (Denham, 1971; Eisenburg, Muckenhirn and Rudran, 1972; Gartlan, 1968; Jolly, 1972) though little attempt has been made to examine differences within as well as between the ecological grades.

Recent reviews have attempted systematic investigations of the relationship between ecological and behavioural differences among the primates (Clutton-Brock and Harvey, 1977; Jorde and Spuhler, 1974; Milton and May, 1976; Spuhler and Jorde, 1976). Jorde and Spuhler (1974) found that the primates could be grouped into four clusters that agreed closely with Crook and Garlan's adaptive grades. Correlating these four groups with five different phylogenetic trees (Spuhler and Jorde, 1976) they came to the conclusion that phylogenetic and environmental factors were about equally important in determining social behaviour. Clutton-Brock and Harvey (1977) also showed that it was possible to define groups of species on behavioural and ecological characteristics. However, more important than this was their investigation of the relationships between different behavioural variables. Factors such as body size and density and distribution of food supplies were found to be important determinants of diet, group size, home range size, day range length etc. Milton and May (1976) also examined how body weight, diet and home range size were related.

These studies do not explain the variability found within species in different habitats. In one study (Tattersall, 1978) variations in the behaviour of Lemur mongoz were so great that the species fitted into more than one of the ecological categories suggested in the above papers. In one area the lemurs were active exclusively at night and in another, activity was observed throughout the hours of daylight. Group structure was also extremely variable with pair-bonded family groups and groups that were evidently not family units being found. The differences in activity patterns between areas were clearly related to climatic differences but the reason for the variation in social structure was not obvious. Another approach, that of optimality theory, can be used to try to explain differences in the behaviour of a species in different habitats and seasonal changes in the behaviour of a population of a particular species. One of the aims of the present study was to determine how the bushbabies adapted to seasonal changes in their environment.

The argument for using optimality theory in behavioural ecology is that natural selection should produce animals that are maximally efficient at propagating their genes. Selection will act on an animal's behaviour as much as on any other biological characteristic such as anatomy or morphology but, obviously, behaviour is more flexible than morphology. Most mammals, and particularly primates, are capable of changing their behaviour in response to their environment. The idea of optimal choice was first used in the context of foraging behaviour, with mathematical models being used to predict the animal's behaviour (Emlen, 1966; MacArthur and Pianka, 1966). Optimal foraging theory has been used to predict the choice of food type by an animal, where it should feed, how long it should feed in a particular place and its optimal pattern and speed of movement between food patches (see Pyke, Pulliam and Charnov, 1977, for a review). Optimality theory has now been extended to other fields such as the use of space and time (see Krebs and Davies, 1979).

The diet of an animal is largely dependent on its body size (Hladik, 1979). The two species in the present study use the same food resources and, therefore, belong to the same dietary grade. However, the difference in their body size was expected to lead to a difference in the proportion of each resource used, with the larger bushbaby eating fewer invertebrates than the smaller. It was predicted that their foraging strategy would change with changes in environmental energy levels (cf. Wilson, 1976). These two ideas were tested.

An animal has to optimise its time-energy budget (Wilson, 1975) and how it does this will depend on both internal and external factors. Seasonal changes in the habitat, for example the availability of food, will change the time allocated to feeding and foraging behaviour (energy intake) and, as a result, to all other activities (energy expenditure or conservation).

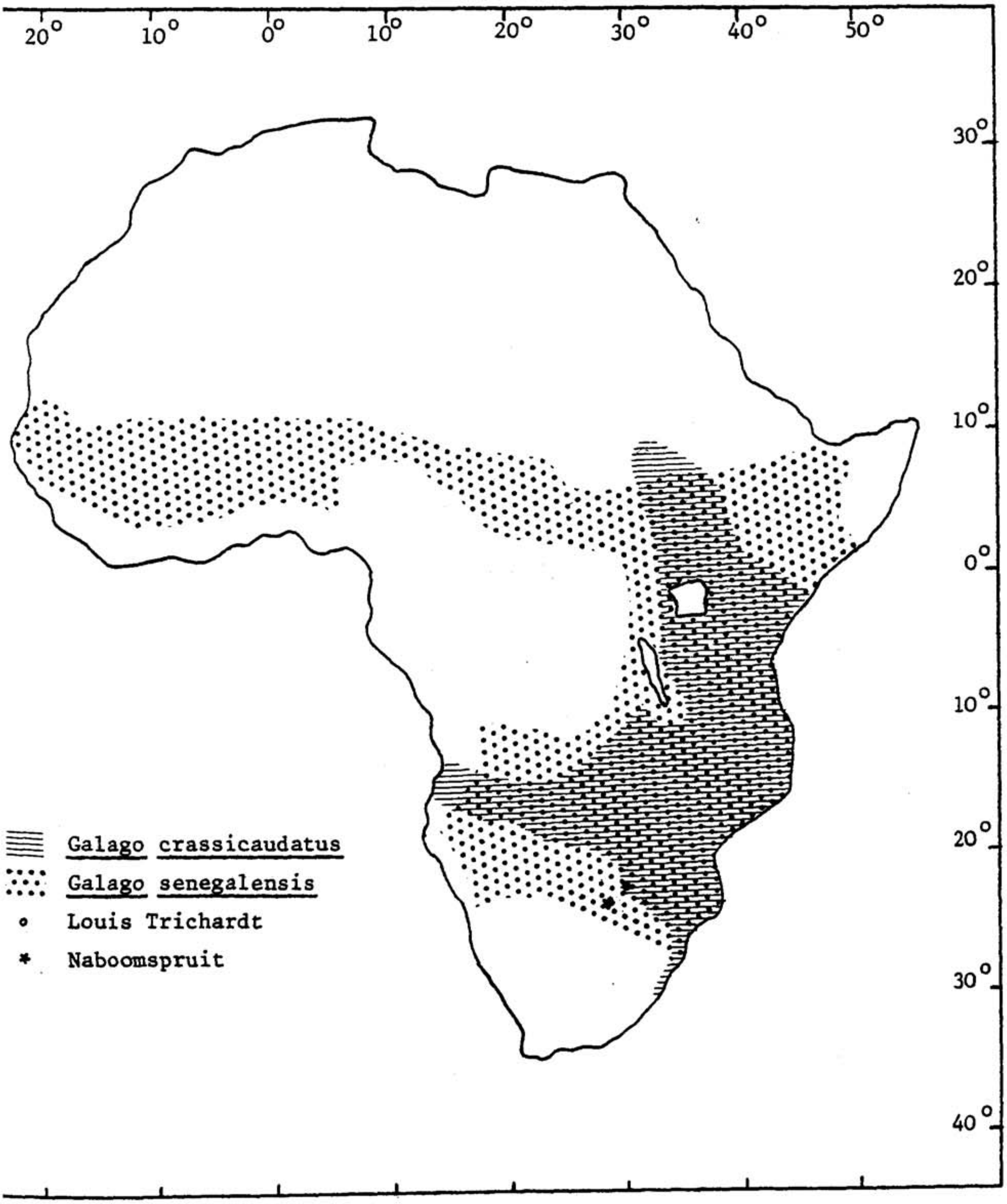
A detailed review of the literature relevant to each hypothesis is presented at the beginning of each chapter.

2. METHODS

2.1 Study Sites

This study was carried out at two sites in the Northern Transvaal. They were chosen because the galagos in both areas were reasonably easy to see and not too difficult to follow. Previous work at the same sites (A.B. Clark, pers. comm.; Bearder, 1969) had indicated that the two species were using similar food resources and this was also an important consideration for site choice. They were studied allopatrically as it was known that they were found at reduced densities when they were sympatric (Bearder and Doyle, 1974). This indicated that competition probably forced them into different niches which would increase dietary differences between them. The climate at both sites was characterised by hot, wet summers and cool, dry winters.

Galago senegalensis (Fig. 1) was observed on the farm Mosdene, near Naboomspruit (28° 47'E, 24° 35'S) (Fig. 2). The altitude of the farm is 1085m. Mean annual rainfall is 610mm., most of which falls between October and April. The mean annual maximum temperature is 32°C (range 25,2° - 36,6°C and the mean annual minimum is 4°C (range 0,2° - 12,8°C) (Weather Bureau, 1954, 1964). During this study the mean maximum temperature in summer (December 1977 and February 1978) was 33°C (range 22,5° - 38,5°C) and the mean minimum in the same months was 17,1°C (range 15,0° - 20,0°C). In winter



gure 2 Map showing the distribution of the study species and position of study sites (after Petter and Petter-Rousseaux 1979)

(July and August 1978) the mean maximum temperature was 24,6°C (range 17,2° - 31,0°C) and the mean minimum temperature was 9,2°C (range 3,0° - 17,5°C). This, however, was a comparitively mild winter, often the mean minimum temperature is below freezing point for at least one month in mid winter (E.A. Galpin, pers. comm.).

The main area used for this study was a small (3,5 hectares) T-shaped patch of <u>Acacia</u> thornveld surrounded by flood plain (Fig. 3). The bushbabies were known to cross patches of the open ground to reach nearby wooded areas. When this happened they were followed into those areas. The vegetation was varied with at least twenty five species of tree present (Appendix 1). It was dominated by <u>Acacia</u> species, especially <u>A. karroo</u>, <u>Dichrostachys cinerea</u> and <u>Terminalia sericea</u> (Fig. 4).

<u>Galago crassicaudatus</u> (Fig. 5) was observed in a strip of riverine forest on the farm Wallacedale, twenty kilometres north of Louis Trichardt (23°57'E, 29°56'S) (Fig. 2). The area is 985m above sea level. Mean annual rainfall is 450mm., most of which falls in summer. The mean annual maximum temperature for Louis Trichardt is 32°C (range 26,5° - 35,4°C) and the mean annual minimum is 8°C (range 1,6° - 13,3°C) (Weather Bureau, 1954, 1964). Temperatures taken at the study site gave a mean maximum of 29.8°C (range 21,0° - 38,5°C) and a mean minimum of 15,2°C (range 7,5° - 20,5°C) in summer (November 1977 and January 1978); a mean maximum of 22,7°C (range 15,0° - 28,0°C) and a mean minimum of 4,5°C (range -10° - 13,0°C) were recorded in the winter months of May and June 1978.

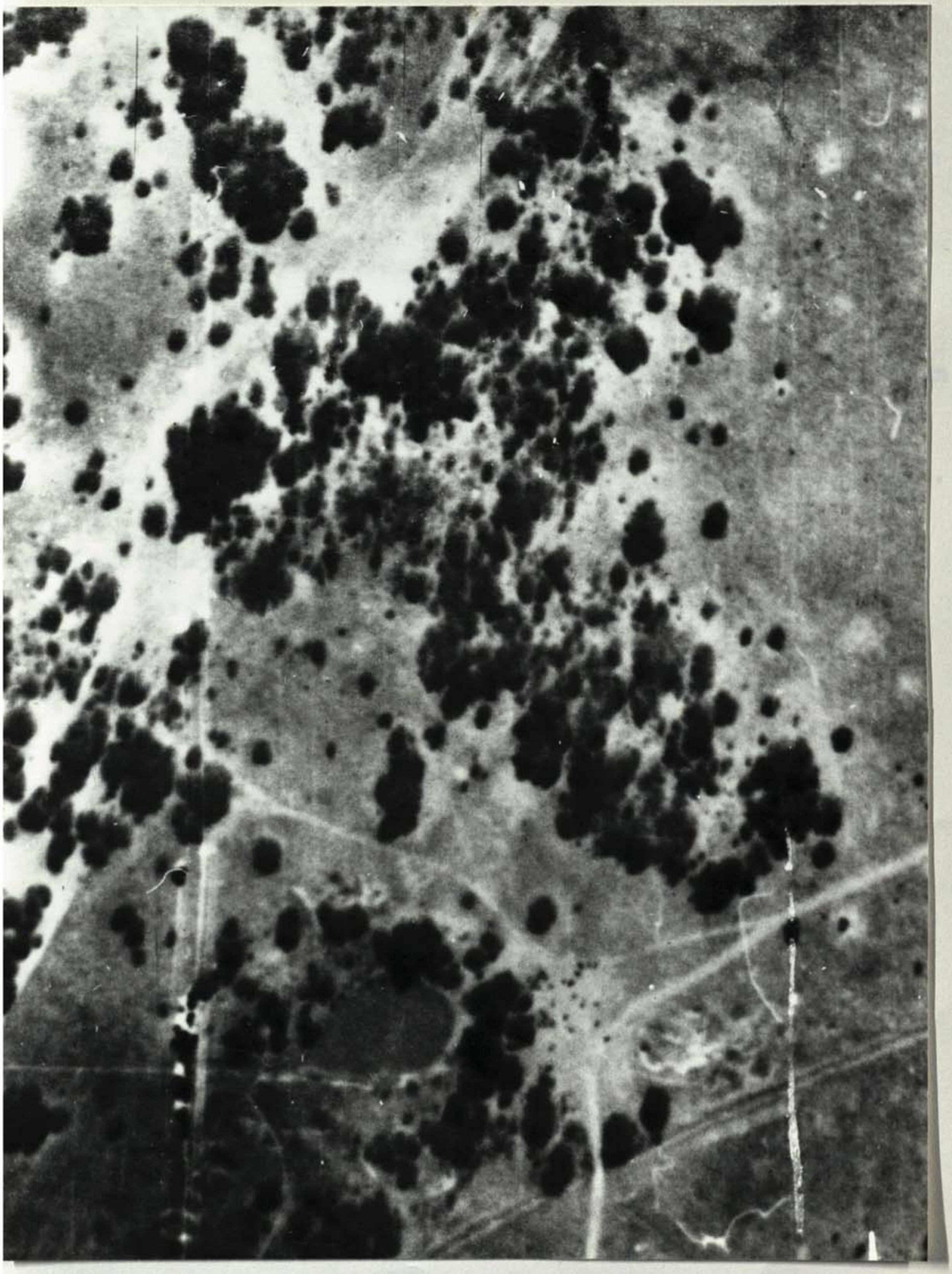


Figure 3. Aerial view of the study area on Mosdene.

The study area was approximately 600m. long by fifty metres wide (30 hectares)(Fig. 6). The predominant trees were Acacia karroo and Combretum erythrophyllum (Fig. 7), but there were also a variety of others (Appendix 2). A drier, more open area to the east of the riverine strip, where the vegetation was lower and more diverse, was used on occasions. Following the animals in this area proved extremely difficult.

All the trees in both areas were numbered and identified. Each site was divided into ten-metre quadrats and the position of every tree was plotted onto large scale maps. These were used to reconstruct and measure the animals' routes and ranges.

2.2 Study Animals

2.2.1 Galago senegalensis: G. senegalensis (the lesser bushbaby) is the most widely distributed of the African prosimians (Fig. 2). It is found in a variety of habitats but is usually associated with Acacia trees, especially A. karroo (Bearder and Doyle, 1974; Doyle and Bearder, 1977). The lesser bushbaby is a nocturnal, relatively solitary species, which feeds on insects and Acacia gum.

G. senegalensis attains a maximum weight of 300g., head and body length is approximately 170mm. and tail length is 230mm. (Charles-Dominique and Bearder, 1979). The sub-species studied was G. senegalensis moholi A. Smith, which is mainly grey with yellowish white underparts. The mean weight of the adult females in the study population was 171g. (range 154g. - 194g.) and that of the males was 193g. (range 178g. - 207g.) (Appendix 3).

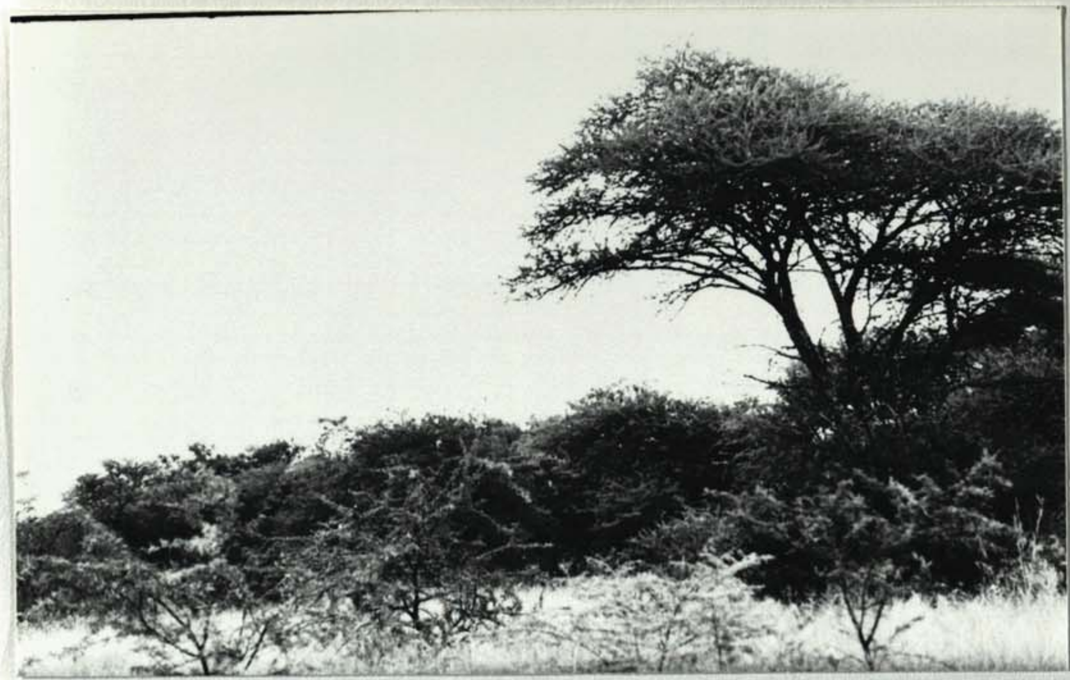


Figure 4. Views of the study site on Mosdene showing differences in vegetation cover between a)summer and b)winter.

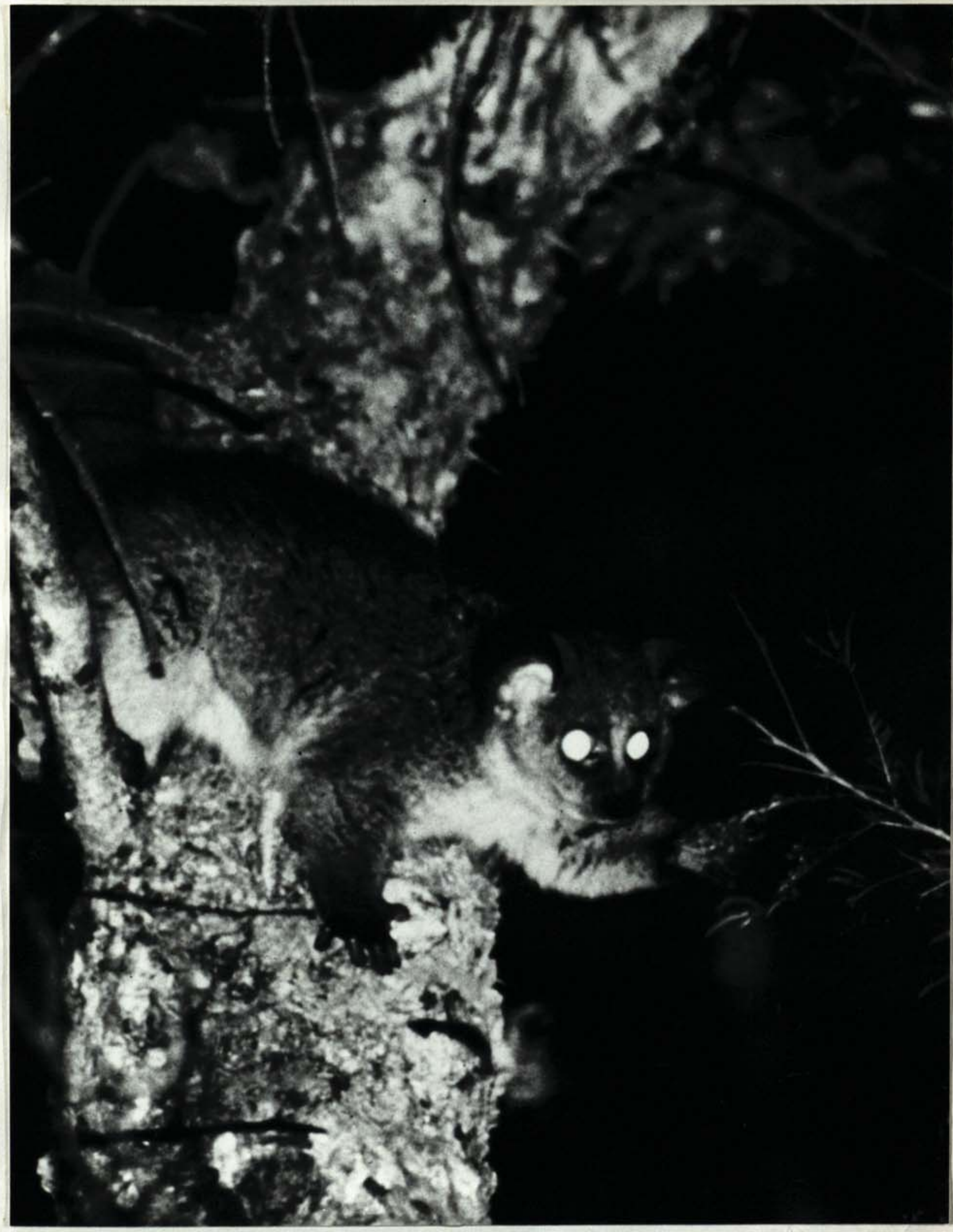


Figure 5. Galago crassicaudatus umbrosus.

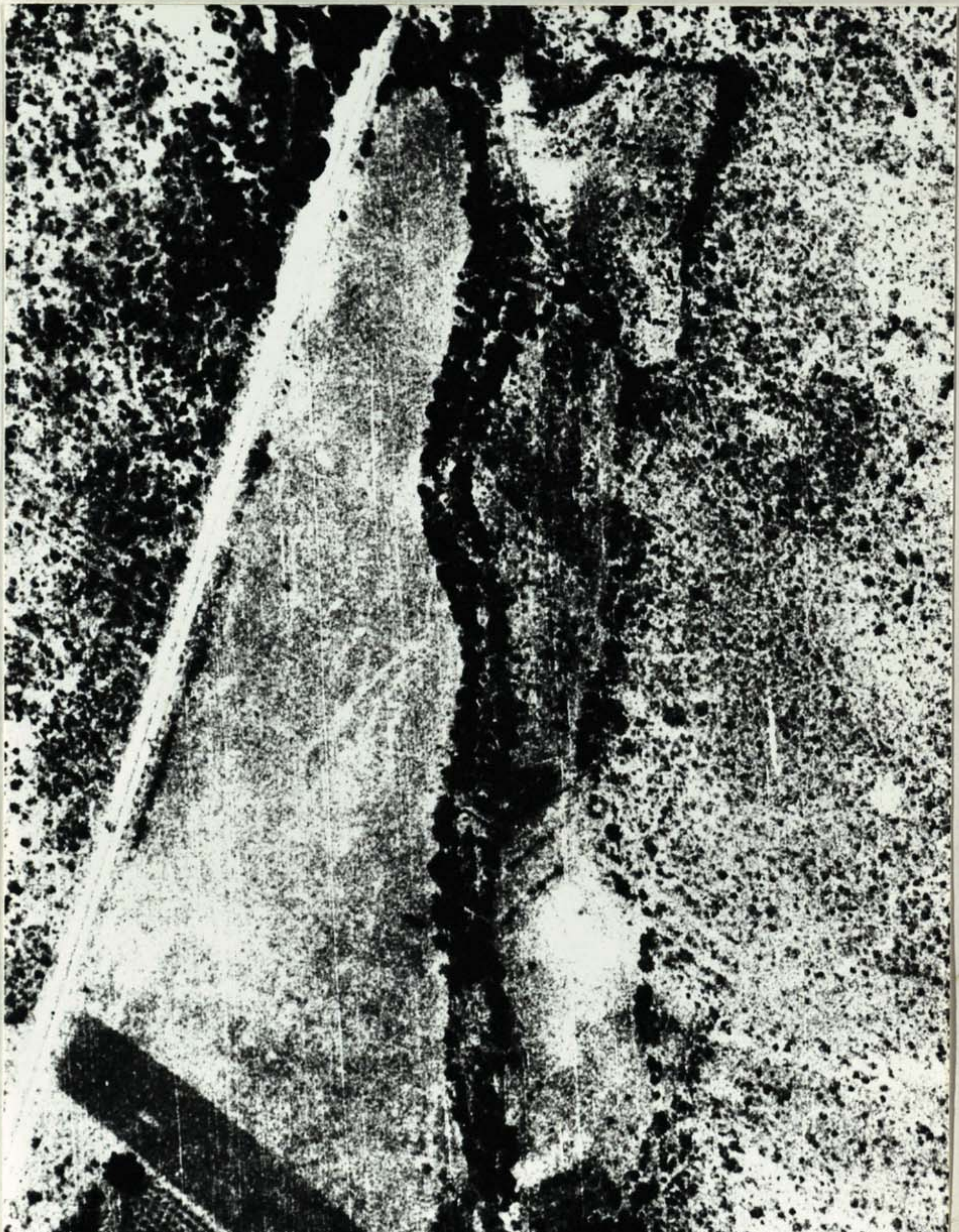
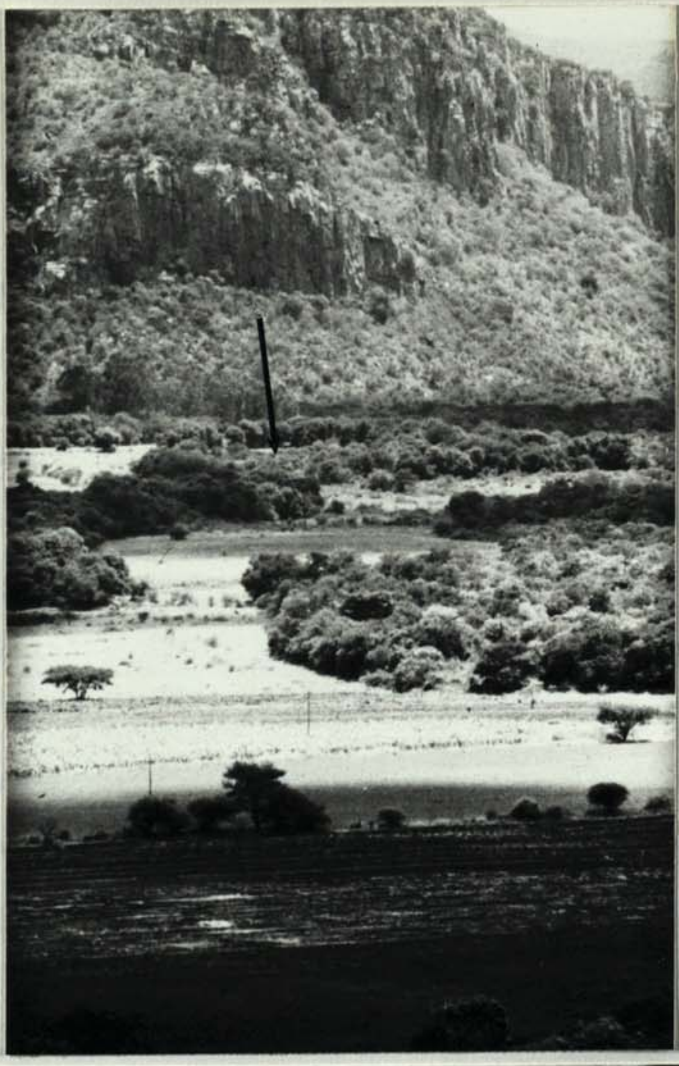


Figure 6. Aerial view of the study area on Wallacedale.



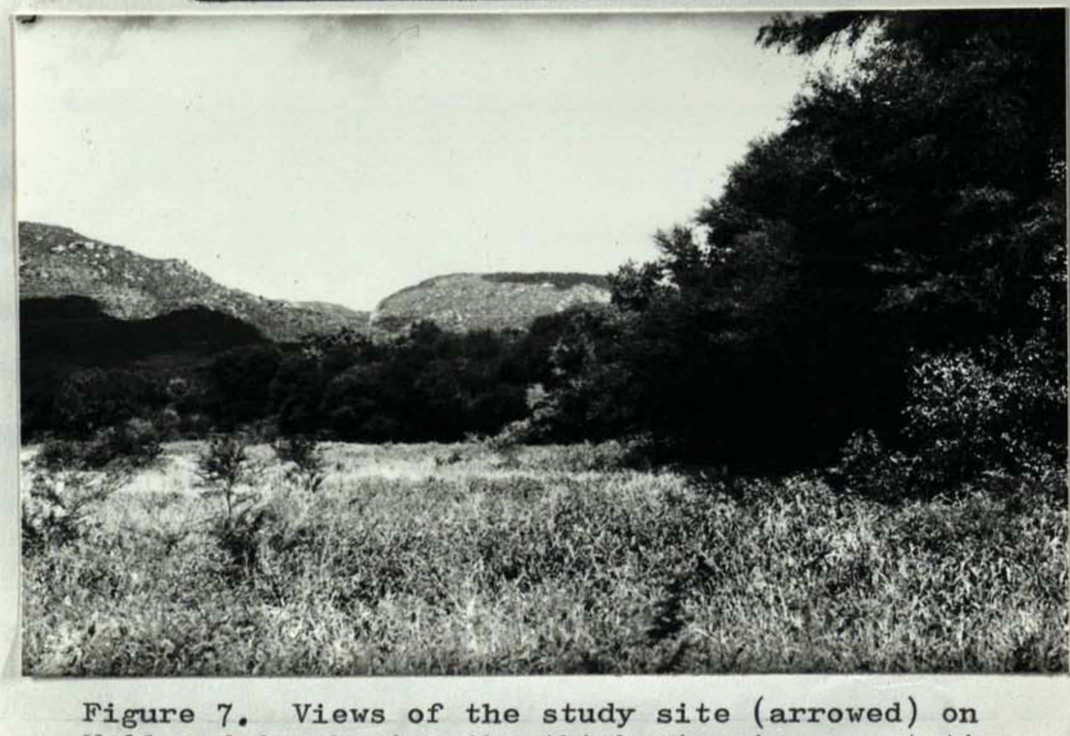


Figure 7. Views of the study site (arrowed) on Wallacedale showing the thick riverine vegetation.

The focal animal (Appendix 5) of this species was a multiparous female (Lydia in Appendix 3), which was at least four years old in April 1977 and had been resident in the field site for a minimum of two years at that time (ear-marked 1975, E. A. Armstrong, pers. comm.).

2.2.2 Galago crassicaudatus: G. crassicaudatus (the thick-tailed bushbaby) has a more limited distribution than the lesser bushbaby (Fig. 2). It is confined mainly to evergreen forest and riparian bush, normally in regions where trees bearing fleshy fruits are abundant (Bearder, 1975). There are, however, virtually no trees with fleshy fruit at the site used for this study. This species is also nocturnal but is more social than G. senegalensis (Bearder, 1975). It feeds on Acacia gum and insects and may or may not include fruit, nectar and seeds in its diet (Bearder, 1975; Clark, 1978).

The thick-tailed bushbaby is the largest of the galagines with a maximum weight of about 1800g., though there are considerable sub-specific differences. The sub-species studied was G. crassicaudatus umbrosus. This sub-species measures about 300mm. from nose to the base of the tail and the tail is about 400mm. in length (Charles-Dominique and Bearder, 1979). It is grey brown with paler underparts. The study population all had black tips to their tails but others of the same sub-species living nearby, did not. The mean weight of the adult females in the study population was 1261g. (range 1090g. - 1500g.) while the mean weight of the males was 1508g. (range 1350g. - 1800g.) (Appendix 4).

In this species the focal animal (Appendix 5) was also a multiparous female (Diana in Appendix 4). She was born in 1973 or earlier and had been resident in the site from at least 1975 (A. B. Clark, pers. comm.). She was known to have had one set of triplets in 1975 and one set of twins in each of the following two years.

2.3 Trapping and Marking

Trapping was carried out for two reasons: 1) to enable animals to be marked for permanent and field identification and 2) to enable data on the condition of the study population to be collected.

Animals were caught in automatic wire-mesh traps (Bearder, 1975; Charles-Dominique and Bearder, 1979) using banana as a bait. The sex, approximate age and the weight of the trapped animals were recorded as well as the position of the trap in which they were caught. All animals were then marked with ear notches (Fig. 32, the bushbaby allogrooming his partner has a notch in his left ear), which provided permanent identification and by a combination of protein dye and hair clipping on the tail (Fig. 8), which allowed for easy field identification. The focal animals were also fitted with a radio collar (see Section 2.4) which enabled them to be located at any time. All these procedures were carried out in the field on unanaesthetised animals which were released within half an hour of capture.

Retrapping allowed the weight and the condition of the bushbabies to be monitored throughout the year and the marking