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

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of the Galaginae on the other hand do build or occupy nests on which they may leave the young (but see Doyle, 1974) and the infants are not, at least initially, carried on the fur (fur-clinging has been recorded for G. crassicaudatus in this study but it does not begin until the infants are a few weeks old). Martin (1972b) points out that both the Lorisinae and the Galaginae exhibit 'baby-parking' during periods of nocturnal activity, but once again, at least in G. crassicaudatus and G. senegalensis, this behaviour does not begin until the infants are more than one week old. Before this time they still require a protective support and this serves to explain why nests are built in the first place. A number of different nests or equivalent sleeping places are used by a mother with small infants. She carries them from one place to another during the course of a night and over a period of several nights. It has been suggested that this behaviour in G. senegalensis reduces the likelihood of the infants being discovered by predators (Doyle et al., 1969). The continued use of nests after they are no longer essential for the infants may merely be due to the fact that they provide a suitable camouflaged support on which several animals may rest in a huddle. At this stage, however, bushbabies are equally likely to be found without a nest.

13. BIRTH PERIODICITY

There are many and varied reports concerning reproductive seasonality in prosimians. It appears that most, if not all species breed seasonally, at least in some parts of their range (but see Doyle, 1974). Some species show a capacity for recurrent oestrus cycles throughout the year. Butler (1960) found this to be true of G. senegalensis in the Sudan, where only a variation in breeding intensity gave the appearance of restricted seasonality. In South Africa the times of mating and births of this species are limited and synchronized in the wild (Bearder, 1969), whereas in captivity there is no marked breeding season (Doyle et al., 1971). Manley (1966) and Doyle (1974) have emphasized the importance of local environmental conditions. Undoubtedly some species are capable of giving birth twice during the year (e.g. G. senegalensis, Doyle et al., (1971); Microcebus murinus, Martin (1972a) and G. crassicaudatus, Beuttner-Janusch (1964)). This may allow them to take maximum advantage of suitable conditions for breeding, facilitated in some cases by a post-partum oestrus.

G. crassicaudatus has a distinct and restricted breeding season in South Africa, which is in accordance with the reports of Gerard (1932) and Cansdale (1960). Buettner-Janusch (1964) on the other hand finds little evidence of seasonal distribution of births in captivity. Smithers (1966) and Vincent (1969) indicate that there is a single birth season between November and March in South East Africa and October/November and March in the Congo. Doyle (1974) points out that these months could cover two consecutive birth periods if mating took place following parturition, as in G. senegalensis.

Jolly (1966a) records that four of her semi-captive female G. crassicaudatus were in oestrus during the same days, indicating a strict breeding synchrony such as that seen in Lemur catta (Jolly, 1966b). Her observation is fully confirmed by the present study. Within the main study area all infants were born within a period of three weeks at the beginning of November. There is circumstantial evidence which suggests that infants were born at approximately the same time in other areas as well. Juveniles

were seen in Zululand at the beginning of January 1970, while all the animals observed in Zululand and Rhodesia between June and August 1971 appeared to be fully grown.

Manley (1966), quoting several sources, reports a gestation period for G. crassicaudatus in the region of 130 to 135 days. This means that mating must have taken place in mid-winter (June/July) which coincides with observations of intense social activity in Zululand. Although mating was not witnessed there were many skirmishes and loud calls for a period which ended as abruptly as it began.

Figure 25 shows that the timing of births and the start of nest-building activity coincided with the onset of the rainy season when food

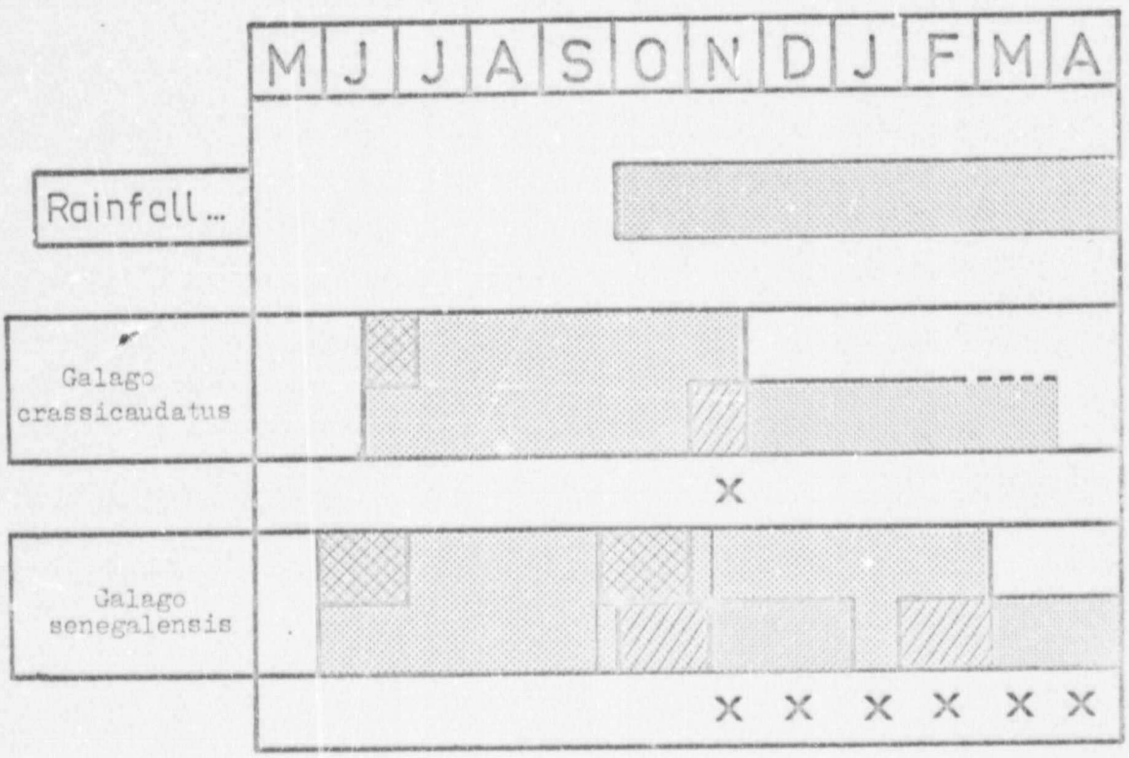

Figure 25. Diagram to show the breeding activity of G. crassicaudatus (N.E. Transvaal) in relation to that of G. senegalensis (N. Transvaal; Bearder, 1969) and the period of summer rains. Stippled areas = gestation periods; cross-hatching = mating periods; hatching = birth periods; shading = periods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

became abundant and cover was dense. In G. crassicaudatus the offspring were not weaned until they were approximately three months old and there was only one birth period. In G.s. moholi the offspring are weaned before two months old and there are two birth periods, the last-born infants are weaned only shortly after the rains have ceased (Bearder, 1969). A similar correlation between rainfall and birth periodicity has been shown for several species of lemurs by Martin (1972b), which he interprets as an adaptation to seasonal food availability. The infants are able to accumulate sufficient reserves to tide them over the period of food scarcity which follows. A second advantage of giving birth at this time is that the availability of suitable nesting material and dense cover may enhance the survival of small infants.

Sixteen infants were found during the study, including six sets of twins, one set of triplets and one singleton.

14. PATTERN OF SOCIAL GROUPINGS

The pattern of social groupings in G. crassicaudatus has been established through three approaches:

(i) By recording the frequency of occurrence of individuals or groups of varying size and composition in each of the study areas.

(ii) By examining in detail the social dynamics, sleeping habits and mother/offspring relationships of a well-known group of bushbabies over a period of fourteen months.

(iii) By checking the validity of these observations with data on known individuals from other groups in widely separated populations.

14.1 Group Structure

Approximately 157 different individuals of G. crassicaudatus were observed either alone or in small groups of up to six animals (table 7). The female and her offspring moved together as a group at night and slept

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

Number of animals at each sighting	1	2	3	4	5	6	
Percentage frequency of occurrence							
(a) G. crassicaudatus							
North Eastern Transvaal: Feb. 1970 to May 1971	29	27	29	8	4	3	(N = 48)
Zululand: June to July 1971	43	29	19	5	4	0	(N = 58)
Rhodesia: August 1971	73	21	3	2	0	0	(N = 42)
TOTAL	40	26	18	6	3	1	(N = 148)
(b) G. senegalensis	40	30	23	5	1	1	(N = 119)

together during the day. Adult males were generally seen alone but they occasionally joined family groups. Other groupings occurred as a result of attraction to a particular food tree. Haddow and Ellice (1964) have counted as many as nine G.c. panganiensis leaving a single sleeping place in East Africa, while Jolly (1966a) records a maximum of four in a nest near Lusaka.

Judging from table 7 there is a remarkable similarity between the frequency of sightings of different sized groups in G. crassicaudatus and G. senegalensis. While this undoubtedly reflects a basic similarity in their social structure the figures require further interpretation. It appears that in G. crassicaudatus a high percentage of single animals occurred in Zululand and Rhodesia, but it is not clear whether this represents a true difference in the occurrence of groupings or merely an error in sampling. Counts were made over a short period (June to August) at a time when the offspring of the previous year would be expected to begin some independent movements. The long-term records from the North Eastern Transvaal probably provide a more accurate picture of group structure in this species. These indicate that groups were encountered more than twice as frequently as single bushbabies (71% as opposed to 29%) which contrasts with observations of social grouping in G. senegalensis (60% groups as opposed to 40% singletons). In addition the figures for G. senegalensis in table 7 represent sightings of sleeping groups. These reflect the nature of social bonds between individuals but do not show the group structure at night, as in the case of G. crassicaudatus. In G. senegalensis the individuals which spend the day together generally split up at night and go their separate ways to forage. Social contact at night, with few exceptions, is typically brief and group members may not come together again until just before dawn (Bearder, 1969).

14.2 Social Dynamics

Within the main study area a tract of riverine vegetation was discovered in which one group of bushbabies was completely isolated. These animals were observed on 158 nights between April 1970 and May 1971, during which time no other bushbabies were found in the same area. It is quite likely that the group had been cut off by the destruction of riverine bush and represented the remnants of a more continuous population which

once occupied the river valley. This situation provided a unique opportunity to study the social dynamics of a single group but, unfortunately, it did not permit observations on inter-group contact. The relationships which are described, however, appear to be normal for all other groups which were observed.

The fluctuations in group size and structure during a period of twelve months are shown in figure 26. Initial observations showed that there was a total of four bushbabies in this patch of bush, three with dark tips to their tails and one with a light-coloured tail: adult female (D.T./1); juvenile male (D.T./2); juvenile female (D.T./3); and an adult male (L.T./1). The female and juveniles moved together as a group and they were occasionally joined by the male without any signs of serious hostility.

At the end of August 1970, when the dark-tailed male (D.T./2) was approximately ten months old (sub-adult) it moved downstream and did not return to its original range during the period of study. No hostility had been witnessed between this animal and the others but its departure coincided with a temporary increase in social contact between the adult male and the adult female and her remaining offspring (D.T./3). At the beginning of November the adult female gave birth to triplets, each with a light-coloured tail similar to that of the male. These were later identified as being two females (L.T./2 and L.T./3) and a male (L.T./4). By this time the dark-tailed female (D.T./3) was mature and its movements were largely independent of those of the mother and her new infants (figure 26b). During February 1971 when D.T./3 was fifteen to sixteen months old, she disappeared and was not seen again. By the end of April 1971 the adult male (L.T./1) was continuing to associate with the adult female and her offspring and their ranges remained almost identical to those which had been observed over one year earlier (figure 26c). The use of space is considered in more detail in section 15.2)

Certain aspects of social contact between members of this group are shown in figure 27 which is based on the observed frequency of events expressed as a percentage of the total number of observation nights during each month of the year. This indicates that the adult female slept with at least one of her offspring throughout the year. The youngsters slept away from the mother on 20% of the days overall, but this occurred pre-

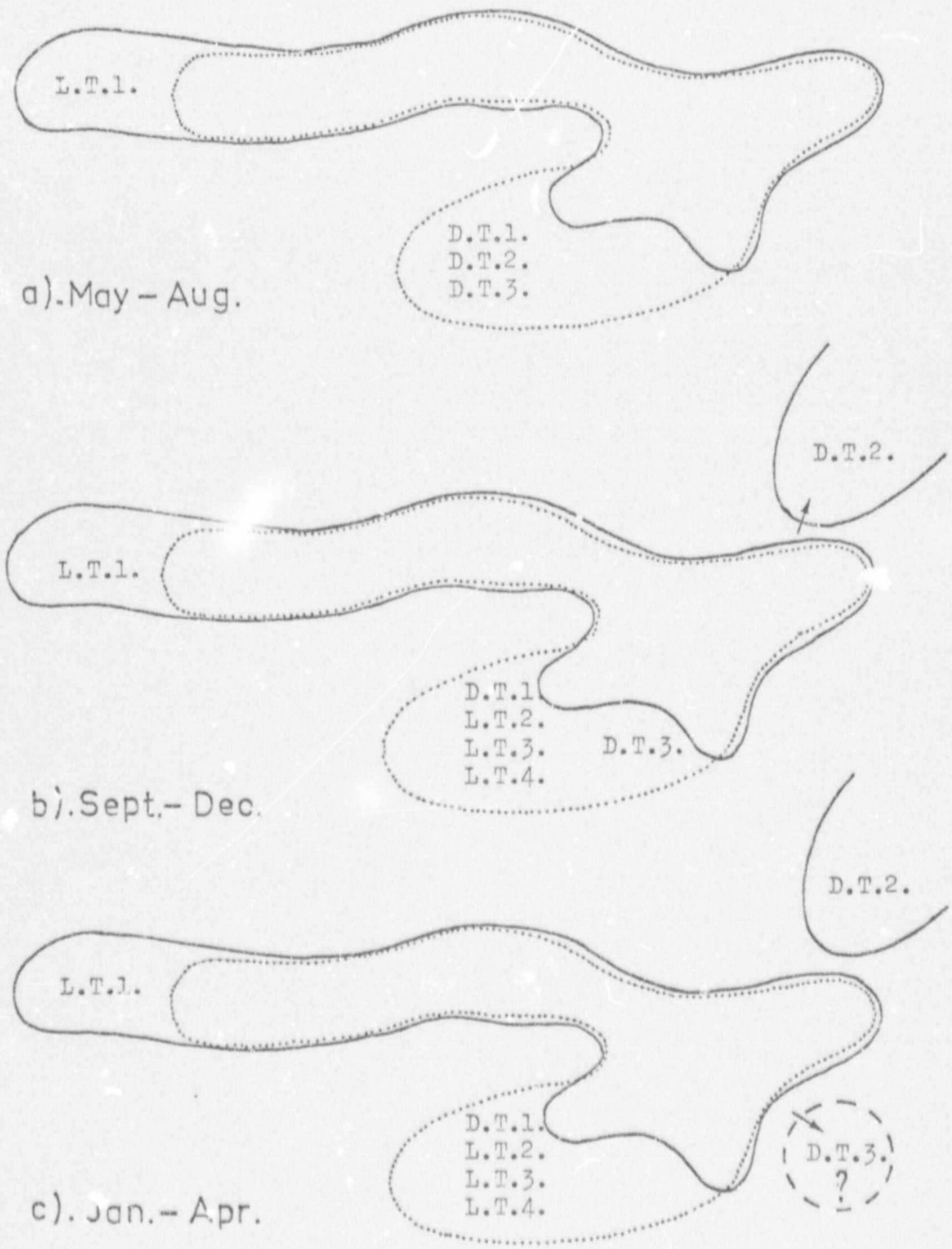

Figure 26. Diagram to illustrate the structure and dynamics of a single group of G. crassicaudatus in the main study area during one year. The continuous and dotted lines represent the observed limits of range movements for the adult male, maternal group, and maturing offspring.

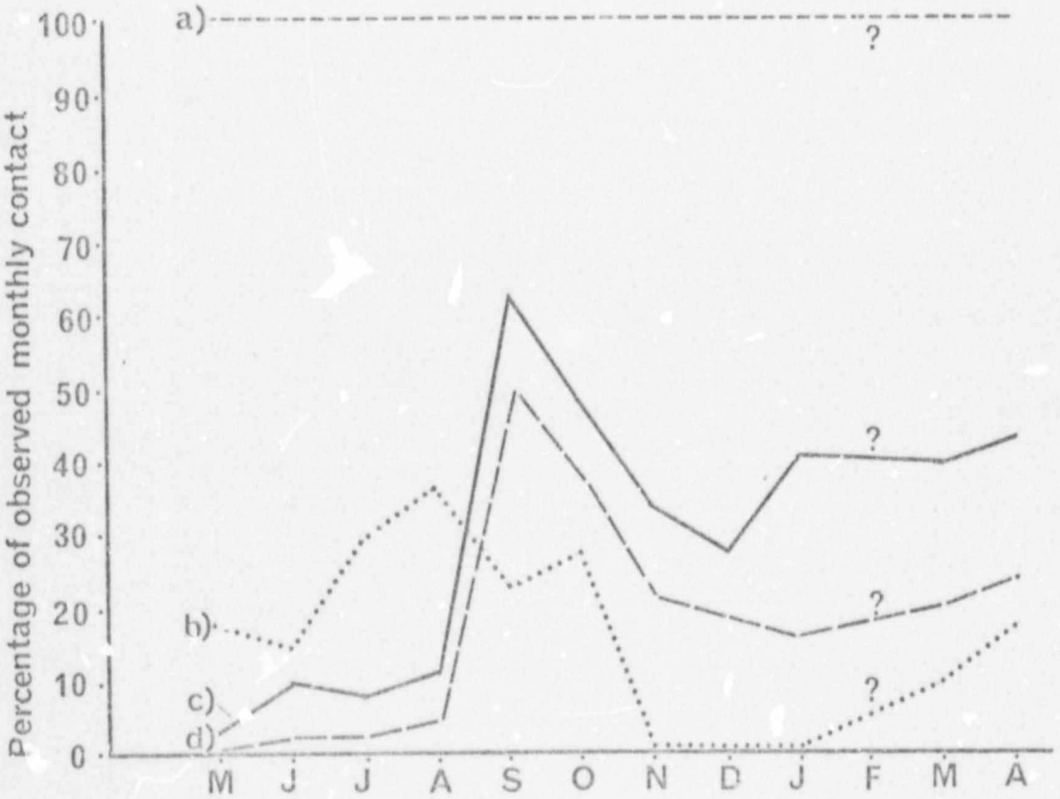

Figure 27. Graph to illustrate some aspects of the observed social contact within the main study group during one year. (a) Sleeping associations between mother and offspring. (b) Offspring sleeping alone. (c) Nocturnal associations between adult male and maternal group. (d) Sleeping associations between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

dominantly as they reached maturity. The adult male associated with the female and young to a greater or lesser extent on 33% of the observation nights, mainly in the evenings and early morning. Likewise he slept with members of the group, or nearby, on 32% of the days, in a pattern which followed that of social contact at night. An analysis of contact between the male and the group indicates that they spent 20% of the total observation time together, whereas the female and offspring were together for 90% of the time. This may be compared with the situation in G. senegalensis in which all individuals, regardless of their age or sex, spend approximately 70% of the night alone (Bearder, 1969).

4.3 The Mother/Offspring Relationship

Observations of the main study group provided information on the development of the mother/offspring relationship over a period of fourteen months. Additional data were gained from observations of eight other females with thirteen infants. Some indices of development are listed in table 8. The period from birth to maturity can be conveniently divided into six stages:

(i) Infants mainly confined to a 'nest'.
(ii) Infants transported by the mother.
(iii) Infants or juveniles follow the mother.
(iv) Juveniles begin independent movements but usually remain with the mother.
(v) Sub-adults move with the mother or independently.
(vi) Adults move independently from the mother.

Relatively little information could be gained concerning the infants during their first few days of life. The movements of a single female with two small infants were followed throughout one night. She left a nest forty minutes later than usual, after an extended period of grooming, carrying a struggling infant in her mouth. She moved away with the infant uttering squeaks, then rested and groomed and then returned to the sleeping tree, but did not go to the nest. Thereupon she retraced her steps and carried the infant further away from the nest, occasionally stopping to groom or suckle for up to thirty minutes at a time. Later she left the infant alone for one hour during which time it remained quiet and motionless. On returning she carried the infant back past the nest site, alternately moving and resting until just before dawn when she left it in a new sleeping place. She then retrieved the second infant from the nest where it had remained throughout the night.

It has been noted previously that lactating females could often be recognised by distinctive bald patches on the abdomen. Judging from this it appears that mothers left their infants hidden for much of the night since they were frequently seen alone. In addition these females used different sleeping places on successive nights which is reminiscent of the behaviour of G. senegalensis (Bearder, 1969; Doyle et al., 1969).

When the infants were approximately three weeks old the mother carried them with her at night although she occasionally left them on a

Table 8. Aspects of the mother/offspring relationship in G. crassicaudatus, including some indices of development. Data are drawn from observations of nine females with eighteen young in the main study area.

Behaviour observed		Approximate age of offspring in days
Infant behaviour		
Vocalizations - (see section 16.4)	Squeaks	3 to 9
	Clicks and Crackles	9 to 200
	Knocks	40 onwards
	Spits	40 onwards
Suckling		3 to 70
Struggling when carried		3 to 9
Clinging to fur of mother's back		25 to 70
Following the mother		25 to 120
Licking gum independently		32 onwards
Grooming each other or the mother		32 onwards
Playing with one another or the mother		32 onwards
Associating with adults apart from the mother		32 onwards
Moving between trees in absence of the mother		40 onwards
Maternal behaviour		
Vocalization - Clucks		32 to 65
Infants mainly confined to a nest		0 to 10
Grooming infants		3 onwards
Oral transport of infants, occasional 'parking'		3 to 70
Oral transport and/or transport of infants on the back		25 to 70
Juvenile behaviour		
Vocalization - Buzz		72 onwards (except adult males)
Following sub-adults or adults apart from mother		60 onwards
Moving on the ground		80 onwards
Leading group; independent forays; sleeping alone		120 onwards
Grooming adults apart from mother		120 onwards
Playing with adults apart from mother		126 until adult
Moving independently from mother or migrating to a new range		300 onwards

branch, or in a tree fork while she moved away to forage. At this stage a female was able to carry three infants at one time with one in her mouth and the others clinging to the fur of her back. Even encumbered in this way she could make small jumps or climb upside-down beneath a branch. The infants were able to follow the mother and to lick gum at an early age but they continued to be carried and suckled until approximately ten weeks old. During this period the mother made quiet vocalizations which ceased after ten weeks, while the offspring made clicks and crackles which persisted for longer. They began many activities which continued into adult life. They fed, allogroomed and played with one another or with the mother. Their locomotion became more and more efficient and they were able to make small jumps. They would even move from one tree to another in the absence of the mother and were observed to follow other adult or sub-adult bushbabies for short distances.

An example taken from field notes illustrates the behaviour of a female with triplets of this age:

> The group was initially observed in a gum tree (Acacia karoo) where the infants groomed and played on top of and around the mother. She then moved away slowly with the infants following, but they were unable to reach the next tree by the same route. She immediately returned and guided them to a higher branch where they could cross. Thereafter she picked up one infant in her mouth and the other two clambered onto her back. She carried all three for a short distance before one climbed off her back of its own accord and she jumped to the next tree with the others. She then returned alone to collect the third infant on her back. Movement continued slowly with the mother carrying one or two infants at a time while the other(s) followed behind, until they reached a fig tree (Ficus sycomorus). The infants were then left together while the mother fed.

When the offspring were between ten and sixteen weeks old they followed the mother at all times. If they were unable to move along exactly the same route they soon found an easier passage. At this stage they were observed to cross the ground between trees where the mother had made a jump. The female always initiated movement and she waited for the infants if they were slow to follow. When they were left behind they made clicks or buzzes and showed signs of agitation until they were able to rejoin the mother. The offspring were now extremely active and playful, especially when they were close to the mother and the group members spent long periods grooming together.

After sixteen weeks the juveniles were evidently familiar with certain parts of their range. They occasionally became separated from the mother and although they showed signs of agitation they nevertheless were able to move from one food tree to another, or to a sleeping place, of their own accord. Their movements, however, remained more limited than those of the adults. When moving with the group, one or other of the juveniles frequently led but the mother continued to control the timing and general direction of movement, the juveniles soon returning if she did not follow. In the less frequented parts of the range, movements of the group were more cohesive than in familiar regions where each individual utilized different routes and feeding places while moving in the same general direction. The juveniles continued to show a high level of activity and playfulness and they were observed to groom and play with the adult male.

Not until after the offspring were ten months old did they begin to make completely independent movements. The data on social dynamics cited earlier indicate that sub-adult males may move away from the range of the parents before the females, which may maintain a loose association with the mother until at least fourteen months old.

15. HOME RANGE MOVEMENTS

Primate territoriality and home range use are reviewed by Bates (1970). Whilst there is little evidence of territoriality in the classical sense, involving overt physical aggression in defence of an area against encroachment by conspecifics (Burt, 1943), most primate species restrict their activities to a measurable, circumscribed geographic area, and many appear to have behavioural mechanisms which keep groups apart (Jay, 1965; DeVore, 1963). To avoid confusion with the strict definition of a territory, most authors use the term 'home range'. The home range may be defined as 'the area over which an animal normally travels in pursuit of its routine activities' (Jewell, 1963). In the majority of primates the size of this area may be established by following the movements of a group, but since these movements may vary seasonally it is often more practical to consider the 'annual home range' (Jay, 1968) and the daily (or nightly) range (Mason, 1968). Many of the nocturnal prosimians, which may sleep in small groups during the day, move alone for much of the night and it is therefore often possible to establish the home ranges of individuals. These may overlap to a greater or lesser extent with those of other individuals (Charles-Dominique, 1971).

Several terms have been introduced which are useful in describing the movements and use of space of primates and many other mammals within their home ranges. The term 'core areas' indicates those parts of the home range which are used more frequently and regularly than other parts (Kaufmann, 1962). Core areas are usually exclusive to the group using them (Jay, 1965). They contain 'fixed points' such as sleeping trees, resting trees and food sources (Mason, 1968) which are usually connected by 'traditional pathways' along which the animals travel. Deviations may be made from these pathways in order to forage or explore (Jay, 1965). Continuous exploration of the home range is often extremely important in order to find new sources of food (Charles-Dominique, 1971).

15.1 Night Range

By following the movements of G. crassicaudatus in different areas it was possible to establish the basic pattern of nightly movement. The movements made while feeding and the 'stop-go' nature of activity have already been described in earlier chapters, but some other aspects of range movement are considered here. The main study group is taken as an example which is not atypical, but variations were found in each study area which can be related to ecological variables such as the availability of sleeping places and food sources and the height or density of the vegetation.

A feature of the activity of G. crassicaudatus, which has been noted, is that group members were often seen together in particular trees which were favoured over long periods. In some cases each individual reached these trees by a slightly different route, while at other times they followed regular pathways, using the same trees and the same branches of those trees on each occasion. Such pathways enabled bushbabies to move quickly from place to place, whereas the deviations ensured a thorough exploration of the available bush. The main pathways used by the maternal group during one year are shown in figure 28.

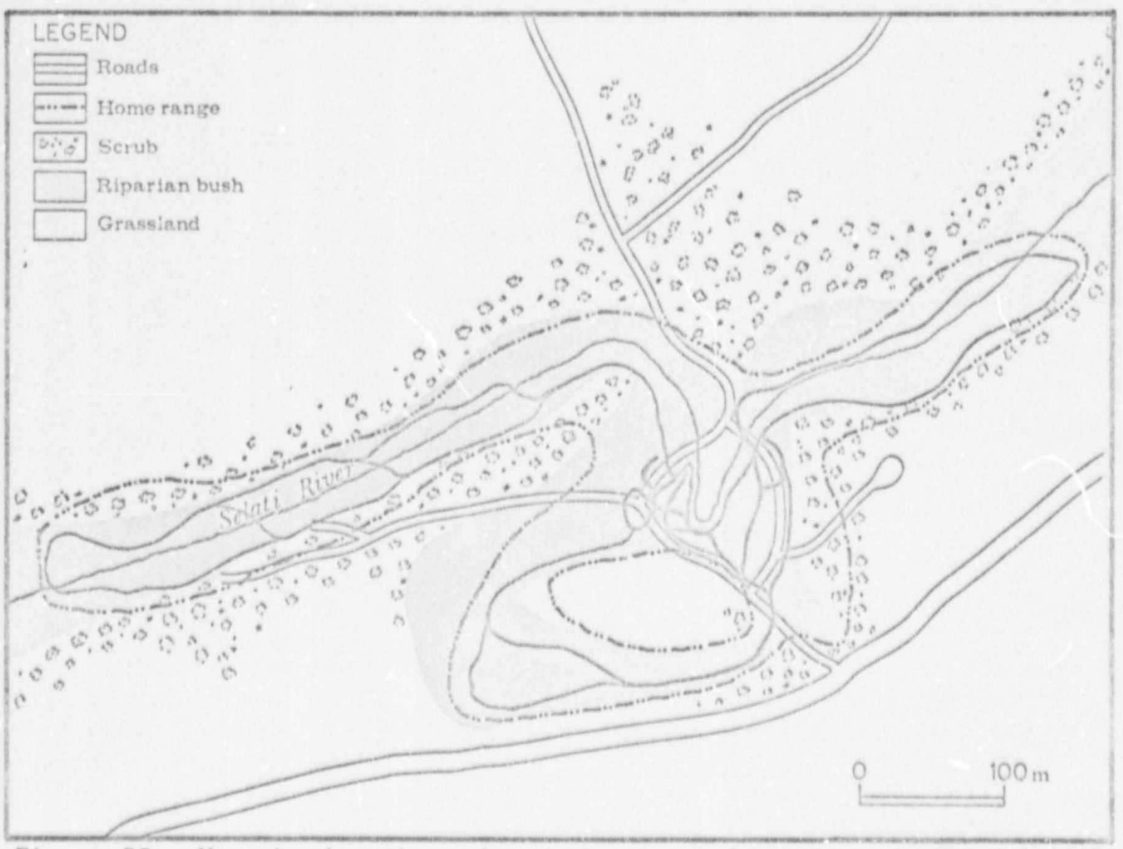

Figure 28. Map showing the major pathways used by the main study group within its annual home range (continuous heavy lines)

Some examples of nightly movements by different individuals are illustrated in figure 29. A distinction can be made between the distance travelled when measured from point to point and the 'path length', or total distance actually moved by each animal (Mason, 1968). Minor deviations were not measured during this study but the direct distances covered during a sample of 406 observation hours varied between 0 and 400 m per hour with an average of 84 m per hour. This represents a travel distance of approximately 1 km each night, but since the hours of observation were least common in the middle part of the night, when the animals were less active, it is likely that this represents an upper estimate of the normal distance of travel. One or more circular excursions were usually made so that the animals seldom retraced their steps, although they sometimes returned by the same route as used on the outward journey. The adult male tended to move further than the adult female

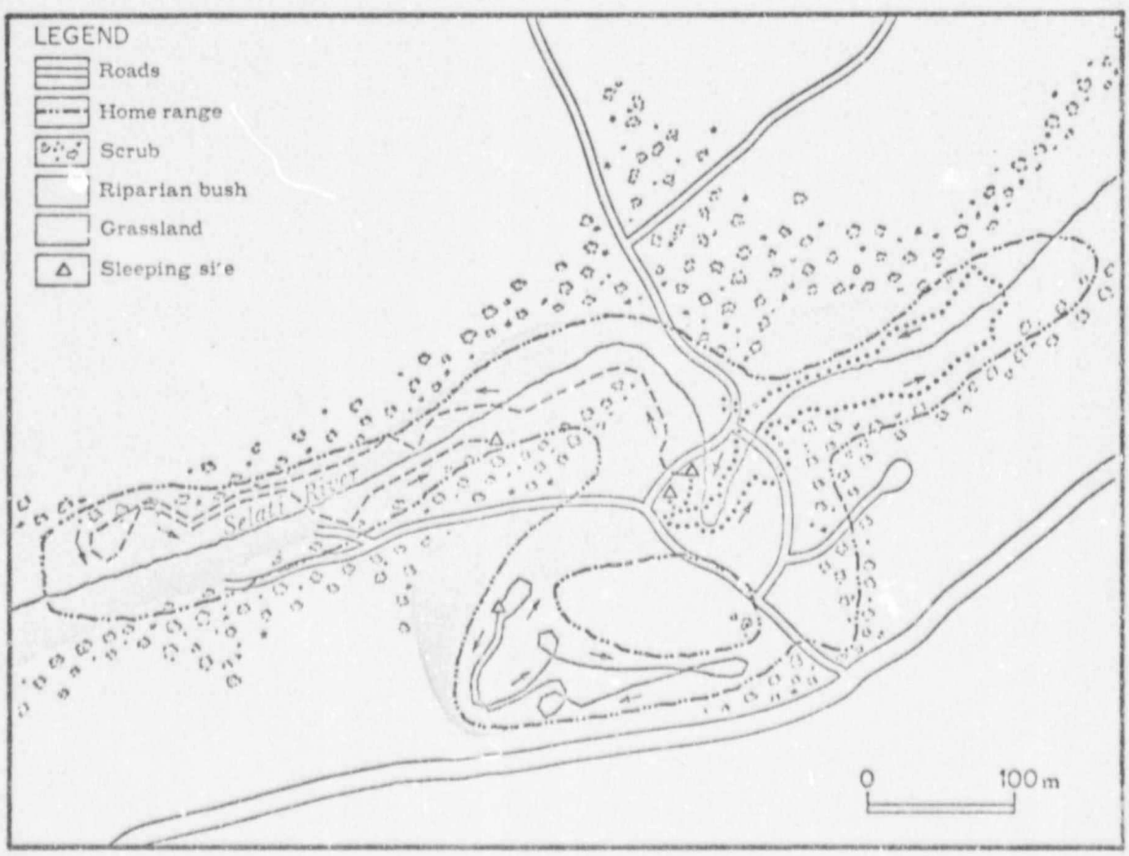

Figure 29. Map showing some examples of nightly routes taken by G. crassicaudatus: the maternal group = dotted lines; adult male = broken lines, and isolated juveniles = continuous lines

whose movements were probably somewhat restricted by the offspring, especially when they were small. In addition the juveniles did not travel very far if they had become separated from the mother. A third factor which evidently affected the distance covered was the spacing of food trees in relation to the sleeping site. When food was readily available in a small area the nightly movements were often short.

The relative importance of the senses in aiding movement may be judged from a number of observations. G. crassicaudatus often responded to the calls of their fellows or the noise of their movements, when travelling in the same general direction, which illustrates the significance of auditory clues. In addition there was evidently an interplay between vision and a kinesthetic sense. In one instance the adult male, which normally moved with assurance and economy, became hesitant and reluctant to make small jumps when following the maternal group in a less frequented part of his range. This occurred despite the fact that the female and juveniles had executed the same jumps with ease. On the other hand when bushbabies were deliberately prevented from following a regular pathway they soon found a different route if it was available. When all the routes were blocked in one place the animals often waited until the disturbance had ceased, or they made lengthy detours in order to continue in the same direction. Only when all else failed did they abandon their attempts to move in one direction and go elsewhere. During the course of movement bushbabies occasionally stopped to sniff at a branch or projection and the possible function of this is discussed in section 16.3.

15.2 Use of Space

At the beginning of the study, G. crassicaudatus were located at random by investigating wide areas where there was suitable habitat. It soon became obvious that bushbabies were found most easily by searching in those places where they had been seen previously and the search was often further reduced by first looking into particular trees. Regular observations of the main study group for more than a year confirmed the fact that there was a well-defined range of movement which remained stable over long periods. In order to examine the use of space in more detail the concept of annual home range has been employed. This is the area

enclosed by a line joining the peripheral points of movements which were observed during the year. In the case of the maternal group this area could be plotted with a fair degree of accuracy and it was found to be 7 ha (17,5 acres) in extent. The home range of the adult male was known to be larger, and it overlapped 80% of that of the maternal group, but its exact limit in one direction was never mapped (figure 30).

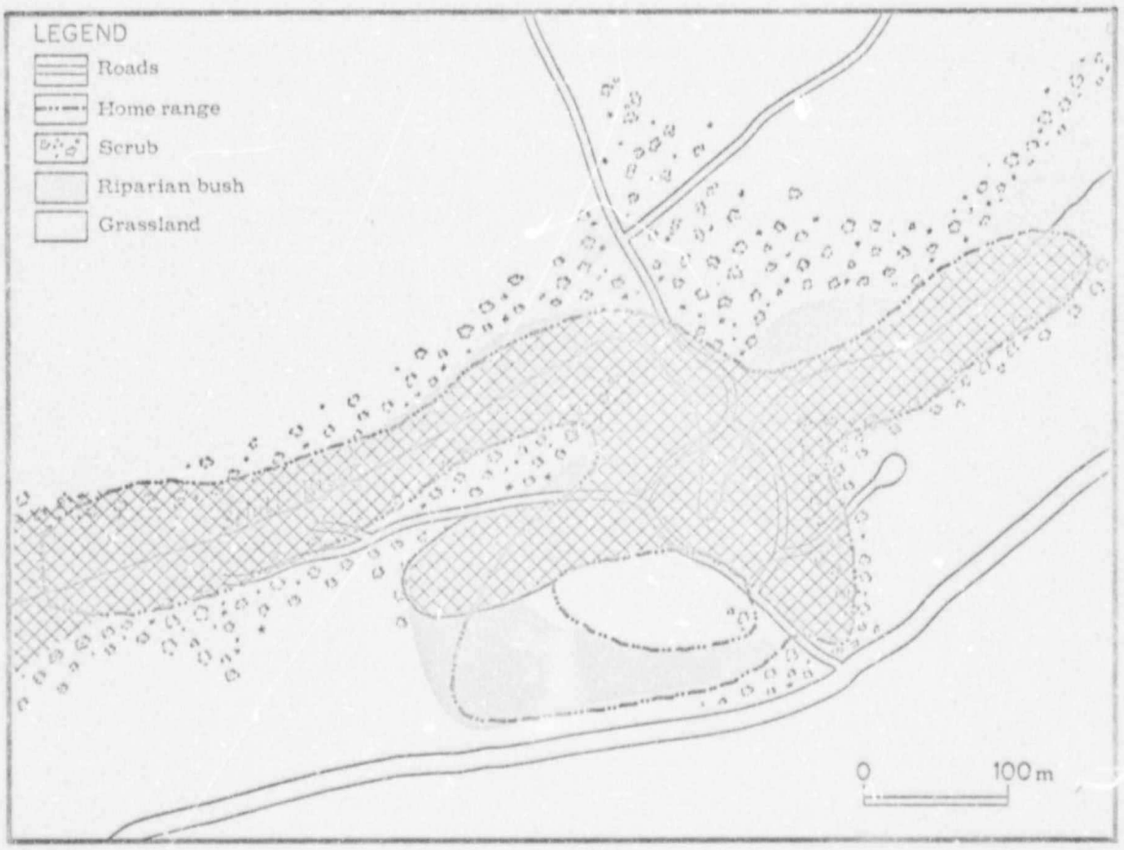

Figure 30. Map showing the annual home range of the adult male G. crassicaudatus (hatched) superimposed upon that of the maternal group in the main study area

Having established the size of the annual home range, two facts immediately became obvious, (a) its shape conformed very closely to that of the dense riverine vegetation within the study area and (b) if a bushbaby moved from the centre of the range to any point on the periphery it would always be able to return to the centre again in a single night. The significance of the centre was confirmed by mapping the size and shape of the area used by bushbabies on a monthly basis which showed that even

localized movements invariably encompassed the centre of the entire range. This may conveniently be termed the core area.

The use of different sectors of the home range is shown in figures 31 to 35 which represent those months in which the movements of the maternal group were well documented. On average only 45% of the annual home range was covered in any one month, varying between 36% in June 1970 and 55% in April 1971. These figures are somewhat arbitrary since no major changes occurred in the focus of activity during the months chosen. If, for example, the period between March and April 1971 had been illustrated, the movements of the group would have covered almost the entire home range. Nevertheless the maps point to two facts concerning the behaviour of G. crassicaudatus. First, that they made similar movements on consecutive nights over a period of days, weeks or even months, and second, that they would alter their movements quite suddenly in order to utilize a new sector of the range. The movements

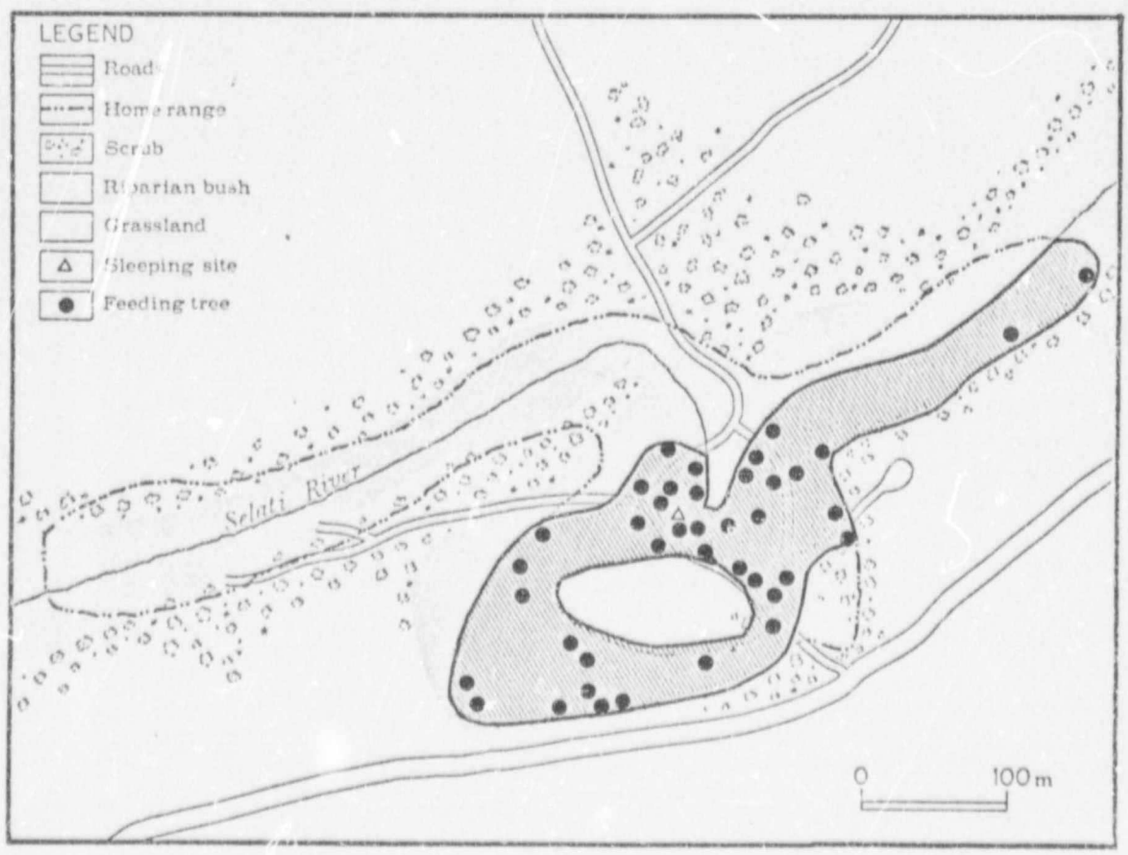

Figure 31. Map showing the range of the maternal group during April 1970

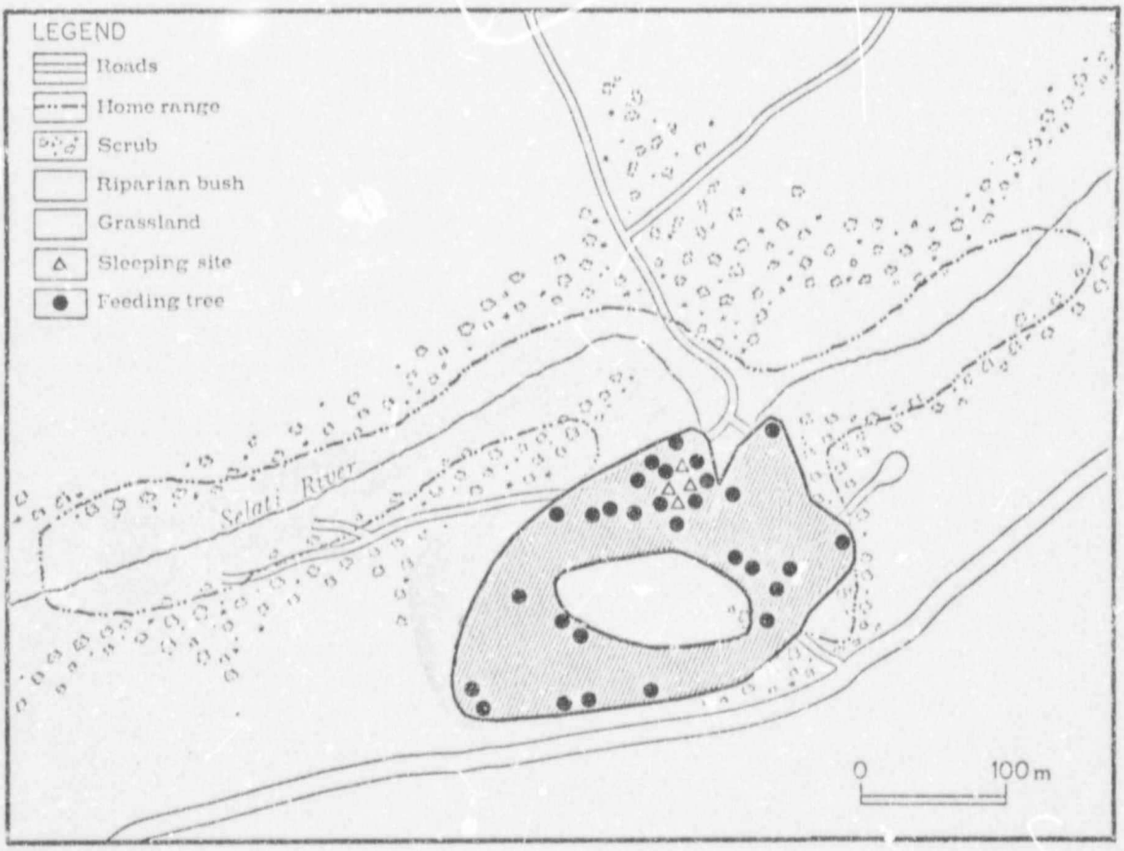

Figure 32. Map showing the range of the maternal group during June 1970

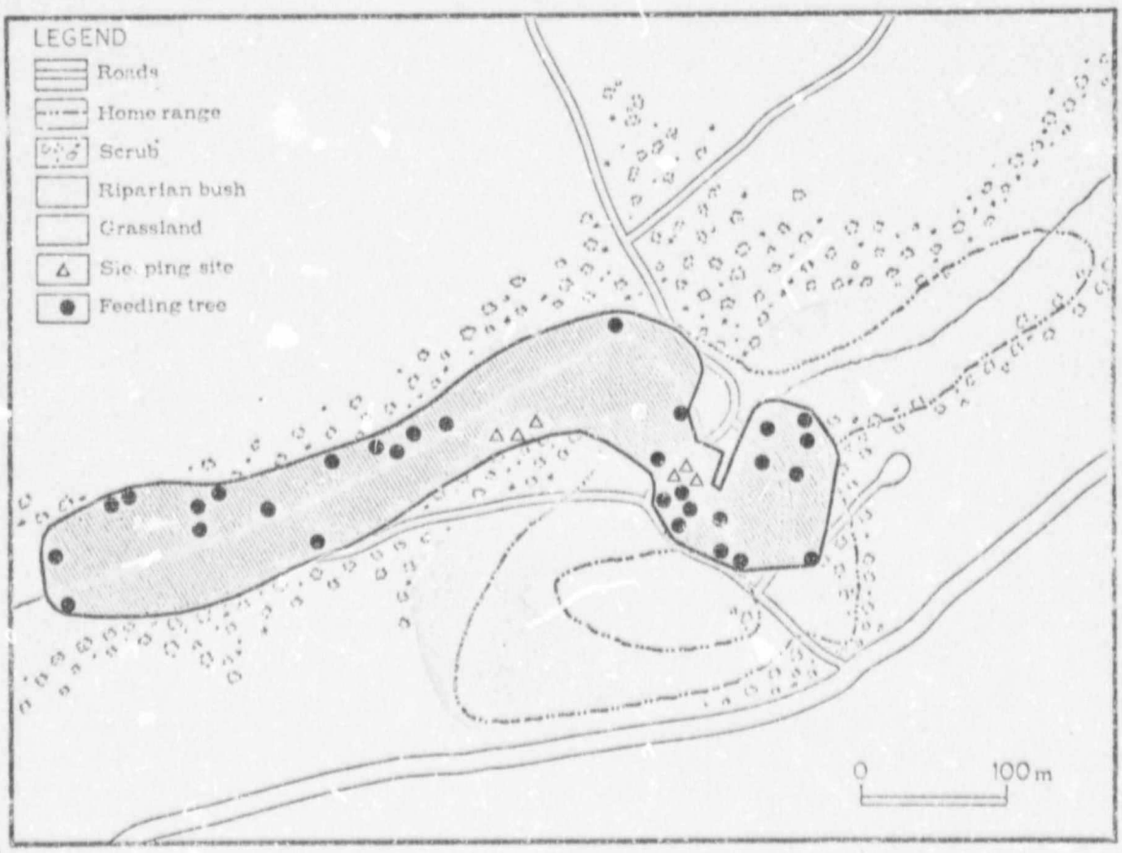

Figure 33. Map showing the range of the maternal group during September 1970

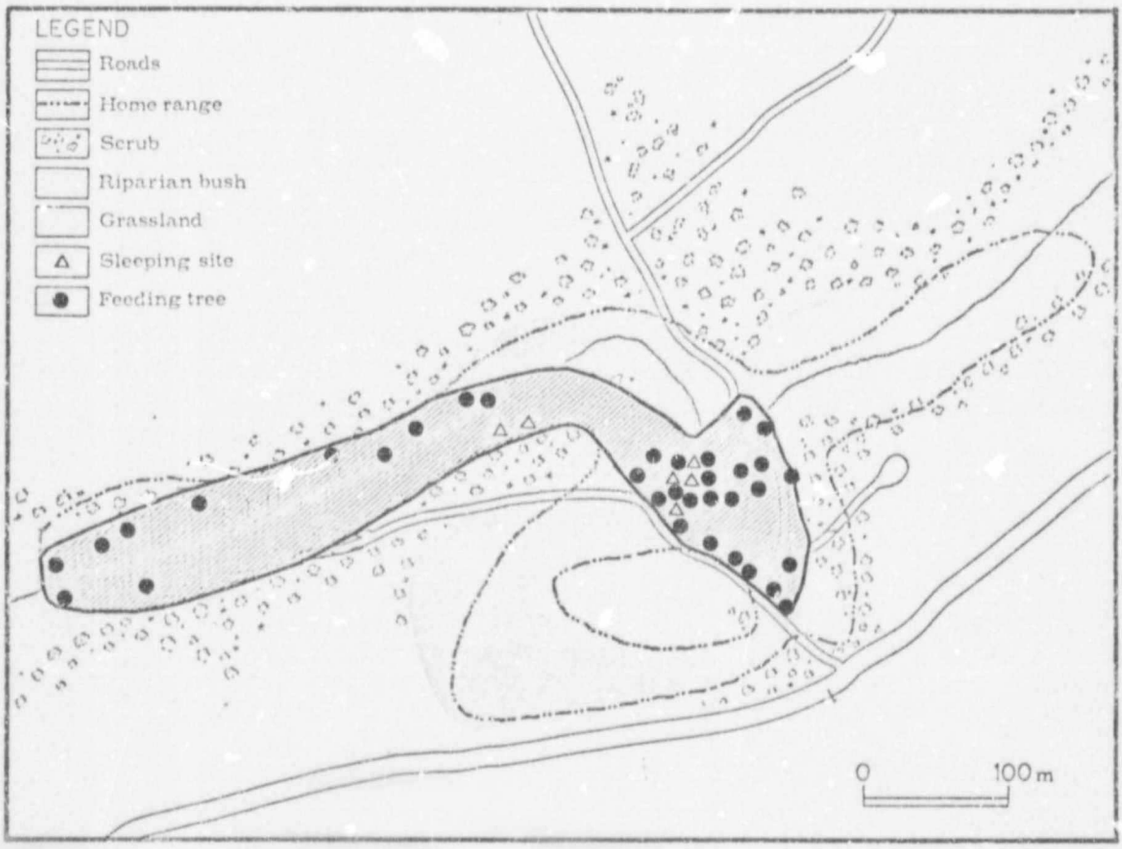

Figure 34. Map showing the range of the maternal group during March 1971

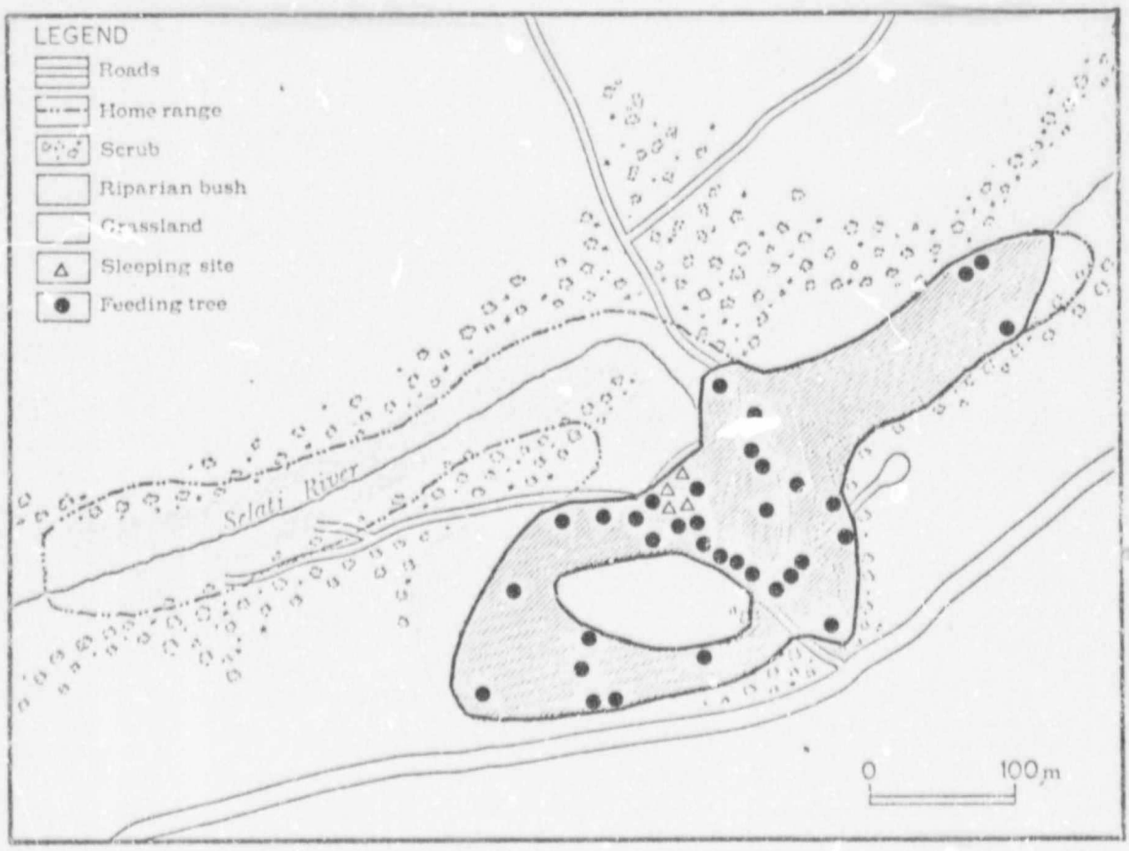

Figure 35. Map showing the range of the maternal group during April 1971

were related to the repeated use of regular sources of food in one area and to the use of new food trees in a different area almost as soon as they became productive. The change in focus of activity may have followed an exploratory excursion into the new area, but it is also possible that certain sectors of the range were used habitually at particular times of the year from one year to the next. The movements observed in April 1971 were almost identical to those seen one year previously.

The nature of range movements was further investigated by plotting the position of the maternal group during each hour of observation and calculating the percentage frequency of sightings in different parts of the range. On the basis of this, the annual home range was divided into five sections (A-E) showing a progressive decrease in their amount of use (figure 36 and table 9). The results are inevitably open to some degree of sampling error since comparatively few sightings were made in the middle of the night when the animals were often furthest away from their sleeping places. Thus the estimated use of sections C, D and E is probably lower than in reality.

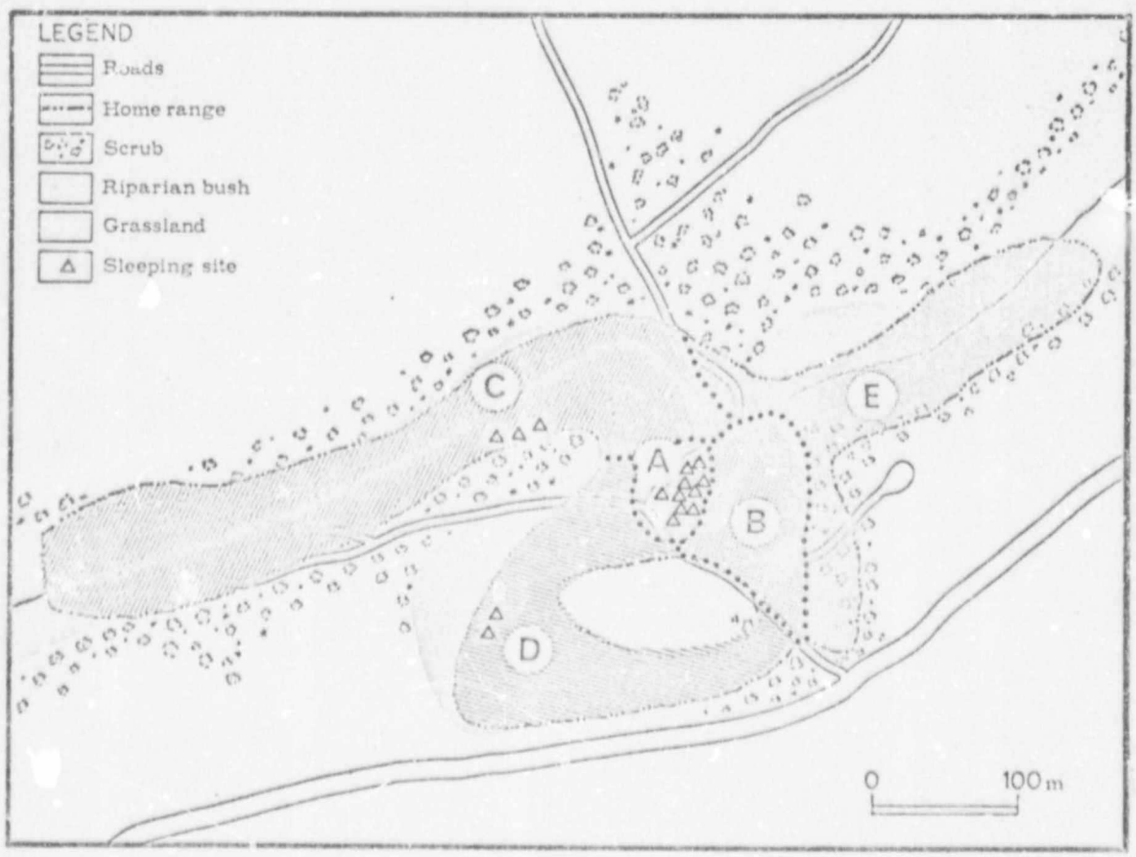

Figure 36. Map showing the division of the annual home range into five sections based on their relative frequency of use (see text). Section A has been termed the core area.

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 availability of sleeping places

Section	A	B	C	D	E	
Size compared with the total home range (%)	4	11	39	22	24	(N = 7 hectares)
Relative degree of use (%) *	43	37	12	5	3	(N = 411 sightings)
Proportion of sleeping places (%)	67	0	20	13	0	(N = 15)
Relative frequency of use (%)	83	0	14	3	0	(N = 158 days)

The central section A is considered as the core area, representing only 4% of the total range but accounting for 43% of the sightings of bushbabies. This was related to the fact that it contained 67% of the sleeping trees which were used on 83% of the days that observations were made. Several large trees were densely overgrown with climbers and they provided many suitable retreats where the animals could hide during the day. It has been noted that sleeping sites did not remain equally suitable throughout the year, which may partially explain their varied use (table 10). Otherwise this appeared to be largely a matter of custom and convenience since many suitable trees were available but not used. A similar tendency has been noted for Callicebus moloch (Mason, 1968).

Table 10. The frequency of use of different sleeping places by G. crassicaudatus within a single home range on 158 days during the study period

Number of the sleeping place	1	2	3	4	5	6	7	8	9	10
Percentage frequency of use										
Section A	16	11	2	21	8	2	3	3	14	3
Section C	8	5	1							
Section D	2	1								

* Range use is here based on the proportion of total hourly spot sightings in each section.

A second characteristic feature of the core area was that it contained several feeding trees which the group members used regularly and where they spent long periods of time. The main study group were frequently found in a large Acacia karoo which they used after leaving the sleeping place in the evening and before returning to it in the morning. When the movements of the adult male brought him into the range of the maternal group he visited the same 'fixed points' but his frequent absence indicated that he made use of a different core area.

The foregoing consideration of home range movements demonstrates that G. crassicaudatus may show a long-term attachment to a single geographic area. Despite the absence of other conspecifics nearby, the main study group confined its activities to a relatively small area for more than a year. In addition the maturing male eventually left the area covered by the home ranges of its parents, which indicates that dispersal mechanisms may have been at work. The behaviours which maintain group cohesion and inter-group separation are outlined and discussed in section 16.

15.3 Characteristics of Movement in Different Habitats

A final point of interest concerning the home range movements of G. crassicaudatus is that they varied in relation to differences in the habitat. A comparison has been made of the typical movements of this species in riverine bush (North Eastern Transvaal); forests (Zululand) and open woodland (Rhodesia), while at the same time they are compared with the characteristic movements of G. senegalensis in riverine bush (present study) and acacia thornveld savannah (Bearder, 1969).

Both species of bushbabies showed characteristic modes of locomotion which did not vary from one area to another and they were each active at all levels within their habitat. However the amount of activity at different levels varied between one habitat and another depending on the spacing of trees and the availability of food (figures 37 and 38). Those animals of both species which lived in open areas often descended to the ground in order to cross spaces of up to 100 m, or to forage, whereas in dense vegetation they descended only rarely, if at all. In the case of G. crassicaudatus 66% of all sightings on the ground were made in the open woodland of Rhodesia, despite the fact that only 10%

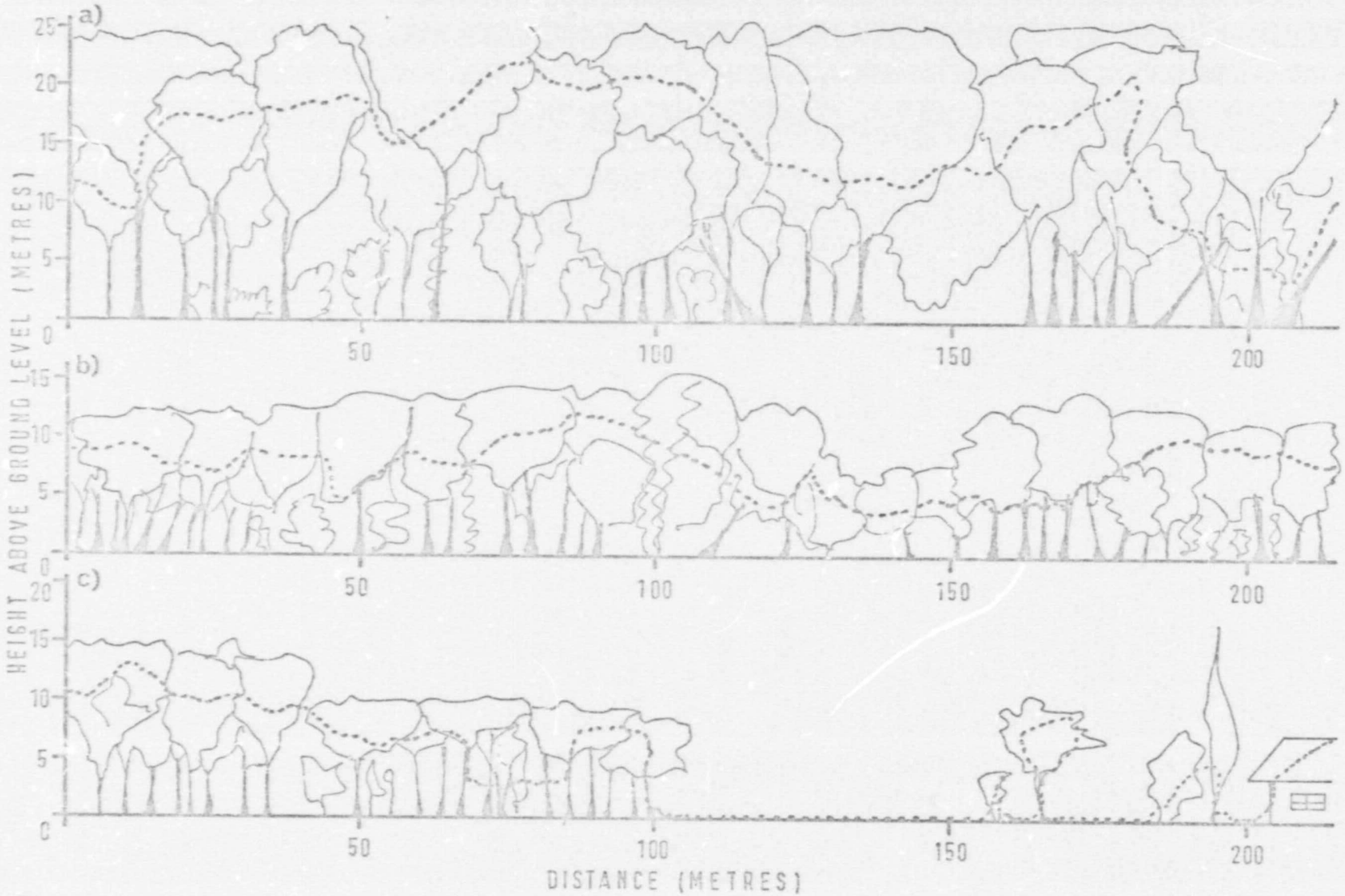

Figure 37. Diagram to illustrate the characteristic movements of G. crassicaudatus in different habitats. (a) Temperate forest. (b) Dune forest. (c) Open woodland and garden vegetation.

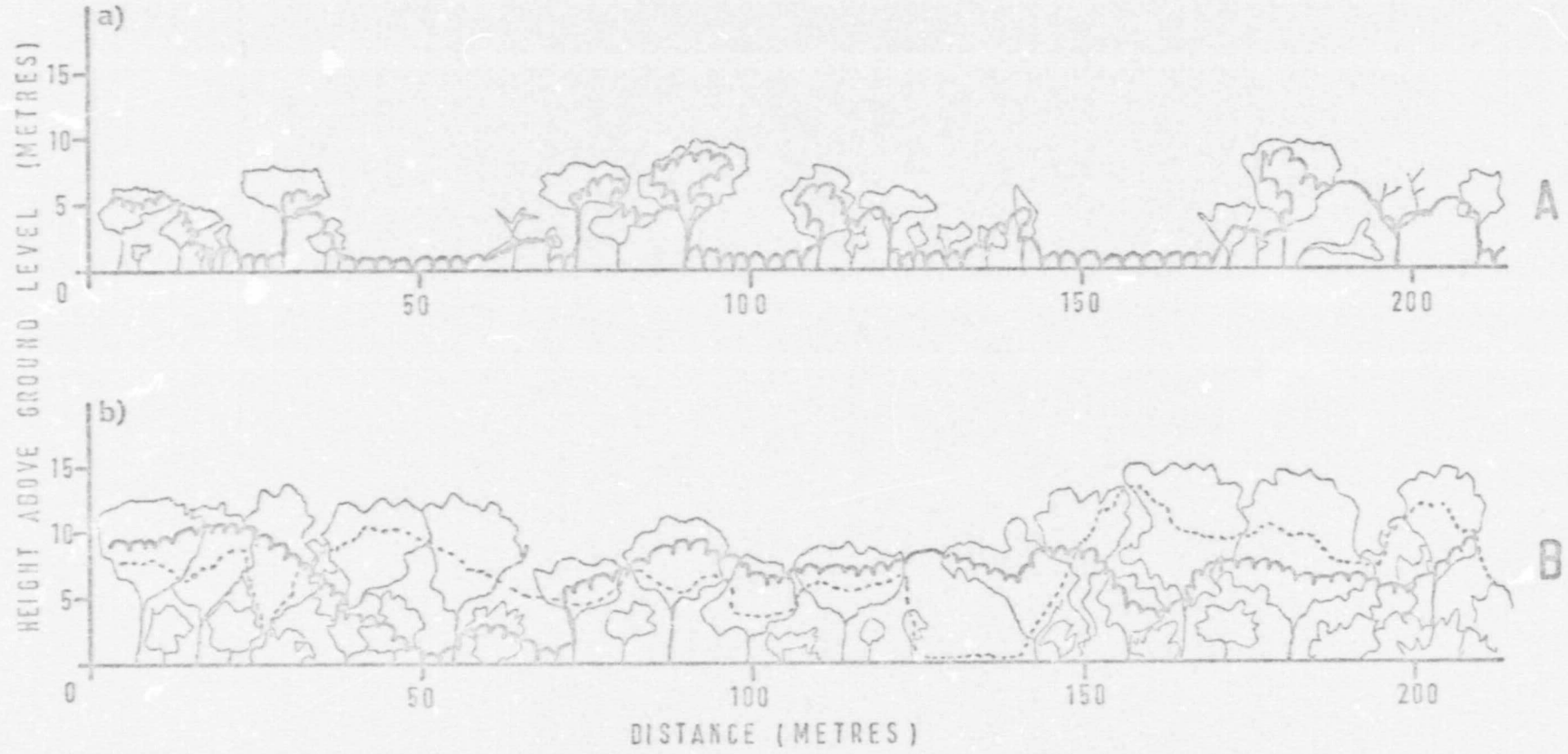

Figure 38. Diagram to illustrate the characteristic movements of G. crassicaudatus (broken line) and G. senegalensis (continuous line) in different habitats. (a) Acacia savannah. (b) Riparian bush.

of the observations were carried out in this area. This indicates that the chances of seeing a bushbaby on the ground were eighteen times greater than in the North Eastern Transvaal, while in Zululand bushbabies were seen on the ground only once following a fight. Observations of behaviour confirmed that those animals which did not often move on the ground were more cautious and reluctant to descend than those which did so regularly.

The nature of home range movements of G. crassicaudatus in an open area is further illustrated in figure 39, which shows some characteristics of a habitat where this species was sympatric with G. senegalensis. It can be seen that although G. crassicaudatus are often found in forest habitats, it is not necessarily the height or density of the vegetation which has a direct effect upon their distribution. G. crassicaudatus, like G. senegalensis, employed a variety of supports when moving within each habitat, but G. senegalensis owing to its small size was able to utilize fine, closely spaced and often highly thorny branches without difficulty, while in addition it required less cover for sleeping purposes (Bearder and Doyle, 1974a).

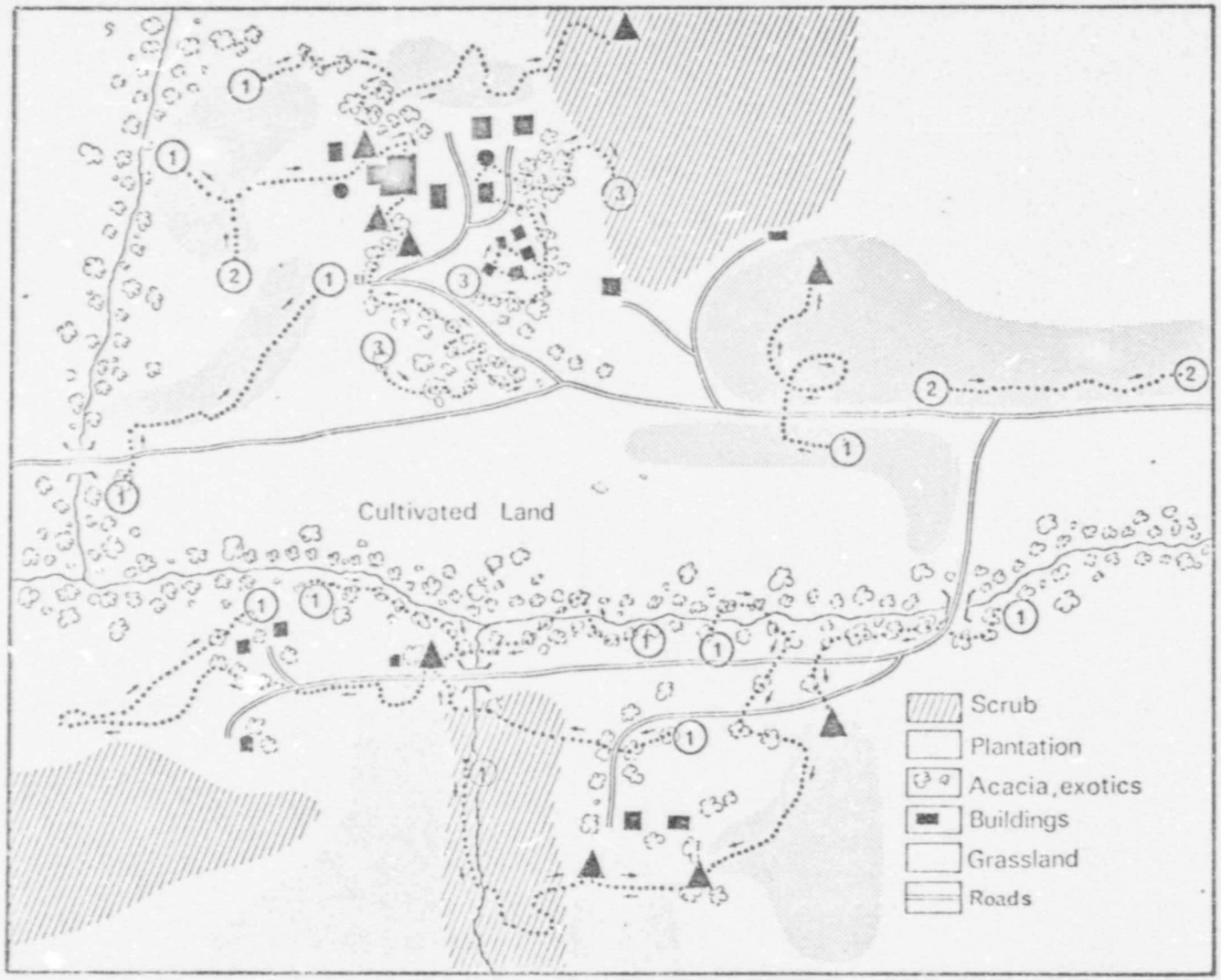

Figure 39. Map showing sightings of G. crassicaudatus, with the number of individuals (in circles) and their movements (dotted lines) in relation to sleeping sites (triangles) in an open habitat (E. Rhodesia).

16. SOCIAL BEHAVIOUR

A wide variety of behaviours which occurred within the context of intra-specific contact and communication are considered under the broad heading of social behaviour. Some related non-social acts are also included where applicable (autogrooming, non-social play). Several authors have focused on social behaviour as a communication process (see Altmann, 1967; Moynihan, 1967). Moynihan discusses the social behaviour of New World primates in terms of communicatory signals: any behaviour pattern which conveys information from one individual to another of the same species may be considered as a social signal, even if it has many other functions as well. He divides signal patterns into four main types based on the senses by which they are perceived, namely, tactile, olfactory, visual and acoustic. A number of these patterns have been recorded for G. crassicaudatus in the field.

One of the main difficulties in the interpretation of field observations on social behaviour is the lack of quantifiable data obtained on a systematic basis. During the course of observation the animals were lost for short periods or temporarily hidden from view, while some details of behaviour were difficult to see. For example, it was often hard to determine whether a bushbaby was using the procumbent 'tooth-comb' while grooming, or merely licking the fur with its tongue. Furthermore, even if the behaviour of particular individuals had been followed in detail for a long period on one night, it was not always possible to find them at the same time on the following night. Consequently a general approach has been adopted by recording as much information as possible on many different types of behaviour during each hour of observation and the quantitative data which are presented often give only a general picture of the frequency and duration of the patterns described. Certain types of behaviour, however, lend themselves to a more detailed analysis owing to the relative ease with which they are recorded. Vocalizations are described in detail and compared to the well-documented calls of G. senegalensis (Andersson, 1969).

16.1 Grooming

Grooming was one of the most frequent and conspicuous behaviour patterns of G. crassicaudatus. Although autogrooming cannot be regarded as a social act, it is considered here in comparison with allogrooming to indicate the relative frequency of the two types of behaviour and the relationship between them.

Unlike the monkeys and apes which groom predominantly with their hands, most prosimians lick themselves and 'comb' or scrape their fur with the procumbent lower incisors and canines with upward movements of the head (Buettner-Janusch and Andrew, 1962). Hair which becomes lodged between the teeth may be freed by the cartilagenous sub-lingula which is specially adapted to this end (Hill, 1953). It is then swallowed and passes out with the faeces. The toilet claw on the second pedal digit is occasionally employed to clean and scratch certain areas such as the insides of the ears and the back of the head, after which the claw is often licked clean. Some species, for example G. senegalensis (Lowther, 1939), Nycticebus coucang (Rosenblum et al., 1966; Tenaza et al., 1969), and G. crassicaudatus (Pinto, 1972) have been observed to wipe the face and head with the arms or hands after they have been licked. Otherwise the hands are only used to grip the fur or hold a part of the body in order to make an area of fur more accessible to the mouth (but see Doyle, 1974).

Grooming postures in G. crassicaudatus were extremely varied and nearly all of the body could be groomed, in a similar way to G. senegalensis (Lowther, 1939, figure 40). During allogrooming the toilet claw was not utilized and the licking or scraping was usually confined to the anterior of the body, above the eyes, behind the ears, the cheeks and chin, the neck, shoulders and behind the arms. Allogrooming of the anogenital region was not observed. Allogrooming was usually reciprocal, one animal being groomed before it groomed the other, although one sometimes groomed for much longer. It was initiated by approach and grooming of a fellow; by approach and presentation of part of the head to be groomed; or by adopting a playful attitude (most social play was accompanied by allogrooming). The eyes were frequently half closed and the ears flattened against the head. Andrew (1964) notes that once allogrooming has begun, an individual will respond to a touch on the side of the face by turning the head to one side to present a new area to be

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