sniff and chirp, which were heard only rarely from adults. Several parts of the series were given together with agonistic contact calls (spits, screams) in a similar way to equivalent calls in G. senegalensis (Andersson, 1969) and this is discussed in section 16.4.4.

Call No 7, Chatter (figure 48a): An extremely rapid series of monkey-like chattering notes which did not last for longer than five seconds at a time. The chatter was intimately linked with high-intensity calls of the mobbing sequence without grading into them. It interrupted bouts of whistled-yaps or occasionally squawks. The behaviour of the caller indicated that it was intensely excited but the significance of the call is unclear. It was heard only occasionally at different times of the year and may be compared with the caw of G. senegalensis (Andersson, 1969).

Call No 8, Moan (figure 48b): A quiet, low-pitched numming sound, not unlike a drawn-out growl (Jolly, 1966a). The moan was uttered once or it was repeated at intervals of a few seconds. Moans often accompanied knocks and they were heard in association with sniffs, creaks, chirps, spits and screams. It was a common call given by adults and juveniles of both sexes throughout the year.

Moans were evoked in many potentially dangerous situations, by strange animals or objects or during social encounters with other bushbabies. The caller showed signs of wariness, approaching hesitantly, staring or moving away from the stimulus. During social encounters moans were usually made by the individual which was being approached, irrespective of its relative size, age or sex, with the exception of adult males which occasionally moaned as they approached a female. When used in a social context the call was often followed by allogrooming and it was most common when a male rejoined a group after a long period of separation. The moan appears to represent a mood of mild anxiety which may act as a qualifier for other anxiety/alarm calls or those involved in agonistic contact. The call compares with the explosive-cough of G. senegalensis which is given under similar circumstances (Bearder, 1969).

16.4.3 Calls associated with Agonistic Contact

G. crassicaudatus gave four discrete calls directed towards a conspecific or another species during, or prior to, bouts of physical contact.

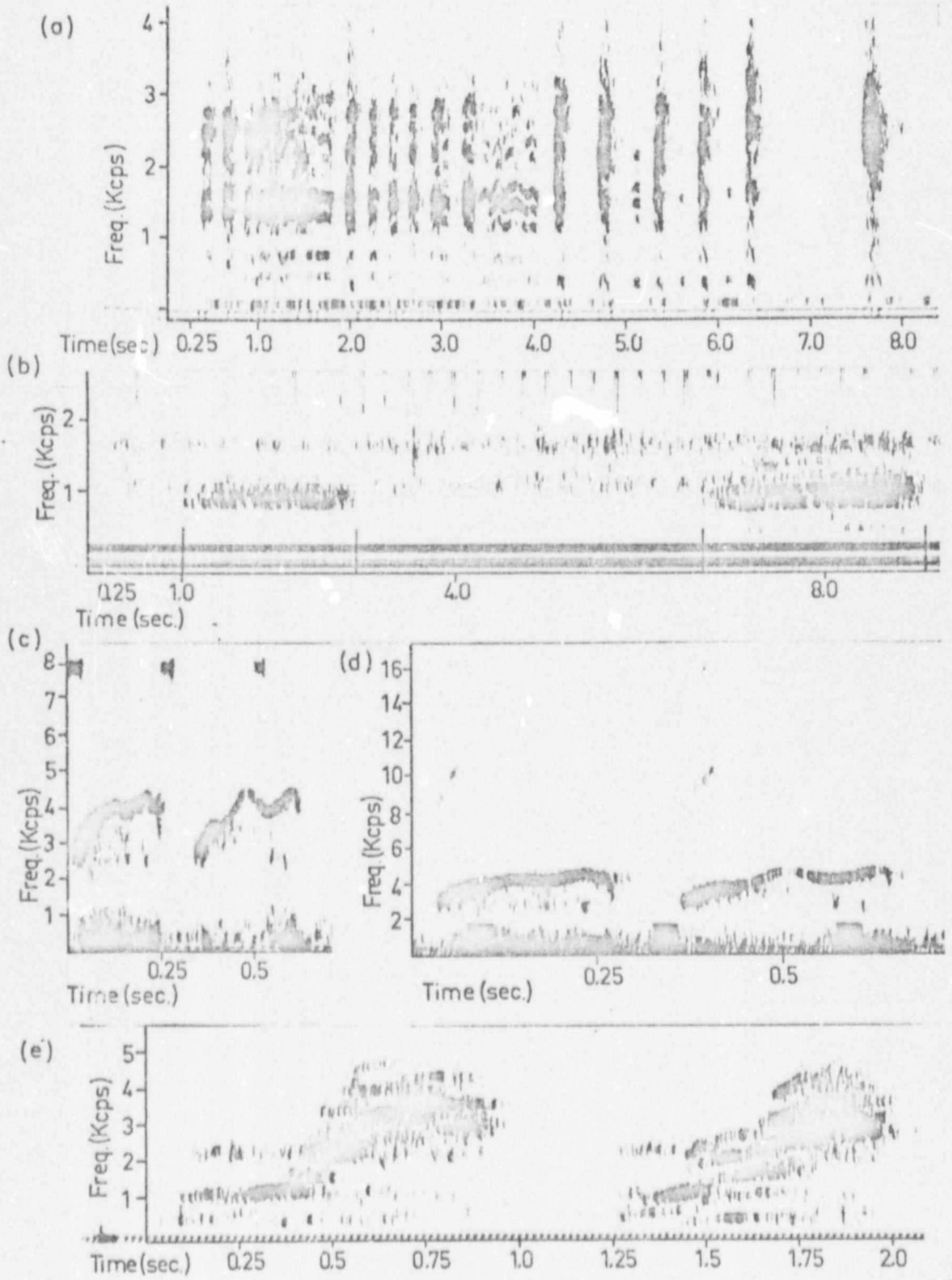

Figure 48. Spectrogram of various calls in G. crassicaudatus. (a) Chatter, (b) Moan, (c) & (d) Screams, (e) Yell.

Call No 9, Hack: A faint coughing or gasping sound which was made spontaneously by juveniles or adults when they were startled by the sudden approach of another animal such as a swooping owl. The caller retreated hastily and then remained tense and alert. The same call was made during contact between bushbabies while grooming or playing. No equivalent call has been recorded for G. senegalensis.

Call No 10, Spit: An explosive sound which is uttered at various intensities with the mouth open. Spits were given by all age classes throughout the year in association with knocks, moans and occasionally, screams. Spitting occurred in situations of contact between bushbabies or with another species. It was accompanied by lunging or cuffing at the protagonist or by retreat of the caller and it usually averted, or at least subdued, the approach of another animal. Similar sounds are made by a number of primate species including G. senegalensis (Andrew, 1963a; Andersson, 1969).

Call No 11, Scream (figure 48c & d): A brief, high-pitched screech which was associated with spits, knocks, moans and squawks. The scream was particularly common during the mating season when it was often preceded or followed by a cry. Screams occurred during agonistic contact between bushbabies involving a skirmish or fight. In one instance an adult female screamed when merely held by a male after which the animals sat quietly together. A similar scream has been reported for G. senegalensis (Andersson, 1969).

Call No 12, Yell (figure 48e): A very loud and distinctive two-tone call, rising in pitch at the end of each unit, which was repeated several times while the bushbaby was in the grip of a predator (dog) or when it was handled after being trapped. Jolly (1966a) notes that this call may provoke a mobbing bark (squawk), or even attack, by other members of a group but no indications of attack were witnessed in the present study. It appears that G. senegalensis does not give a separate call under the same circumstances.

16.4.4 Discussion of Vocalizations

The vocal repertoire of G. crassicaudatus has been divided into eleven discrete calls and one continuous call. Discrete calls are relatively distinct and separable while the parts of a continuous call more or less grade into one another without a break (Hockett, 1960; Marler,

1961). There appears to be disagreement between authors as to which calls constitute a continuous series and which are discrete. Rowell (1962) shows for the rhesus monkey (Macacca mulatta) that some calls, which at first appear separate, actually constitute one continuous system linked by a series of intermediates. Jolly (1966a) lumps a number of vocal patterns of G. crassicaudatus under one name, while Andersson (1969) considers a similar series in G. senegalensis to be several discrete calls. The difficulty in making the separation is that most calls show a certain amount of intra-specific variability which is to be expected in any biological system that is relatively successful from an evolutionary standpoint (Struhsaker, 1967a). But, in addition to structural variation (syntactic), continuous patterns also have functional variation (pragmatic) and it is this which is often difficult to demonstrate. Altmann (1962; 1965; 1967) emphasizes that the ethological approach of dividing up a continuum of action is only valid if it reflects natural units of social behaviour as indicated by differences in the response of other animals in a social group, since otherwise the signalling function of an isolated pattern can only be supposed.

It has been noted that the mobbing call of G. crassicaudatus can be subdivided into seven parts which reflect syntactic and pragmatic variation. Each part shows differences in loudness, quality, pitch and speed of repetition of the constituent units which denote changes in the situation, the behaviour of the caller and the behaviour of other bushbabies which hear the call. The most common associations between calls of this series and related discrete calls are shown in figure 49. Andersson (1969) has arranged the calls which occur in 'anxiety' or 'alarm' situations in G. senegalensis into an ascending scale corresponding to an increase in the seriousness of the stimulus situation and she notes that calls using a similar type of basic unit, or used in similar types of situations, may be lumped together. Andersson's calls have been regrouped from field data (personal observations, see appendix 6) in a way which is shown in figure 50. Two continuous groups of calls are indicated, the elements of which are related on the basis of similarities in structure and the existence of intermediates between them.

The combination of discrete and graded vocal patterns in G. crassicaudatus and G. senegalensis is not entirely expected. Moynihan (1964,

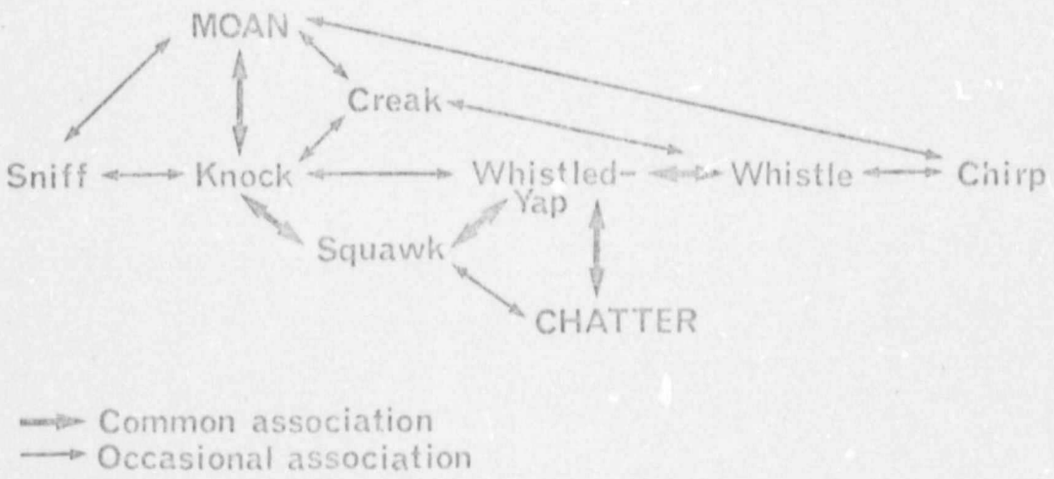

Figure 49. Diagram to show the most common relationships between calls of the continuous 'anxiety/alarm' series in G. crassicaudatus and associated discrete calls.

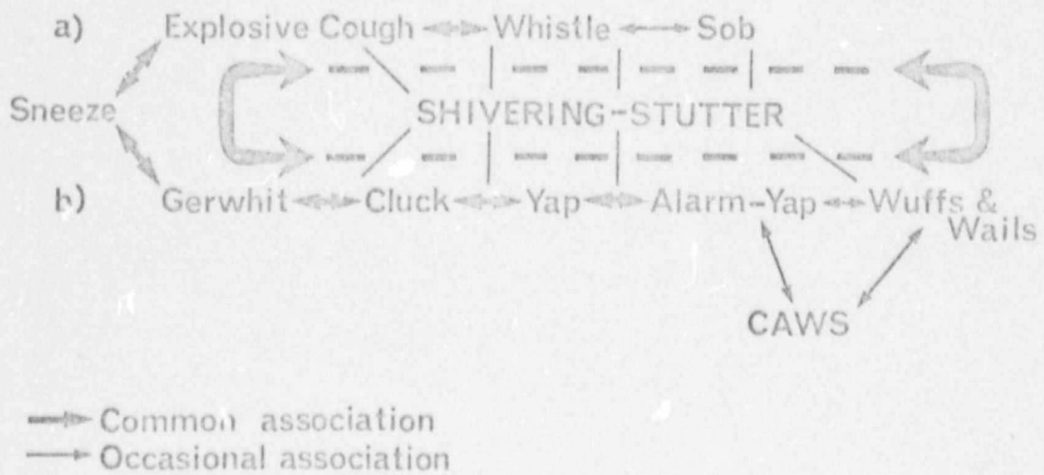

Figure 50. Diagram to show the most common relationships between calls of two continuous 'anxiety/alarm' series in G. senegalensis and associated discrete calls.
(Personal observations.)

1967) notes that the night monkey (Aotus trivirgatus) uses a series of relatively discrete calls when motived by a complex combination of tendencies, each of which expresses only one or two tendencies. He suggests, in accordance with Marler (1965; 1967) and Altmann (1967) that this may be partly an adaptation to a nocturnal and arboreal way of life so as to avoid ambiguity. Andersson (1969), notes that G. senegalensis appears to show a compromise between the necessity for discrete signals and the necessity of expressing fine differences in mood intensity when contacting conspecifics, which is more easily achieved by a continuous type of signal repertoire. In this species certain calls which may convey a single message when given on their own are often combined with units of other calls in a rapidly changing series, particularly during agonistic encounters, in which case they may convey a number of other mood messages.

Moynihan (1964) suggests that graded calls may be more common where they are supplemented by tactile or visual signals. He found that infant Aotus trivirgatus which remained close to their parents had a repertoire which included relatively more intermediate notes. This is also true of the repertoire of G. crassicaudatus when compared with that of G. senegalensis and likewise it may be explained by differences in intra-group contact between the two species. In G. crassicaudatus group members were often close enough to see either the caller or the stimulus which had evoked the call.

Many of the calls which were associated with 'anxiety' or 'alarm' situations were not only given when a bushbaby was confronted by a potentially dangerous situation, but also during intra-specific agonistic encounters, which may lead to confusion between the two catetories. These calls did not stand for particular elements in the environment as, for example, the predator alarm calls of vervets (Cercopithecus aethiops: Struhsaker, 1967a) but they seemed to reflect the motivational state or degree of arousal of the caller. Marler (1965) and Lancaster (1968) note that this is a common tendency for the calls of non-human primates. Thus G. crassicaudatus did not necessarily give calls at the mere presence of a potential predator but only if it came in the way of normal activity. The degree of arousal of the bushbaby, as judged by its behaviour, was reflected by the type and intensity of its vocalizations. The extent to which this motivational state can be communicated depends on the nature

of the signals and the ability of other animals to interpret them (Lancaster, 1968). Some of the loud calls in the mobbing series (whistled-yaps and whistles) often persisted for long after the danger had passed and they may well have alerted several bushbabies in the vicinity to the presence of a potential danger. Calls which were directed towards a predator may also have indicated the exact position of the source of danger.

When considering the functional significance of vocalizations it is useful to adopt the approach of Marler (1968). He underlines the importance of communication signals in maintaining patterns of spatial distribution in primates and he postulates four categories: distance-increasing signals; distance-maintenance signals; distance-reducing signals; and proximity-maintenance signals. The classification of calls into these categories can be made by observing the responses of other animals which hear the call and by noting whether or not the call appears to be directed towards a conspecific or another species (table 14).

Calls are directed, or addressed, towards another animal by means of a variety of qualifiers (Altmann, 1967). In G. crassicaudatus the cry generally appeared to be undirected but it may have been directed by carrying information concerning the identity of the caller which would enable group members or rivals to respond appropriately. Most calls of the mobbing sequence were directed towards the threatening stimulus by the proximity of the caller, which faced the source of danger, while at other times these calls appeared to be undirected. Rival bushbabies could direct their calls by staring at, and answering, one another and evidently the context of the call was most important. Table 14 shows, for example, that clicks were used by infant G. crassicaudatus to attract the mother in one instance or to maintain contact with her, as she led them through the trees, in another. Spits, screams and hacks were directed by the close contact of the animals during agonistic encounters. They acted as distance-increasing signals and may have been derived from protective responses (Andrew, 1963a; 1963b; 1964).

The vocal repertoire of G. crassicaudatus shows extensive similarities with that of G. senegalensis (table 15) including six calls which appear to be analagous in significance and eight calls which are possibly homologous. Despite differences in structure the two call systems carry a comparable load in terms of message content. The 'anxiety/alarm' calls

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

Call	Directed to a conspecific	Directed to another species	Undirected	Distance-increasing signals	Distance-maintenance signals	Distance-reducing signals	Proximity-maintenance signals
CRY	X		X	X	X	X	
BUZZ	X				X	X	
CLUCK	X		X			X	X
CLICK	X		X			X	X
SQUEAK	X		X			X	X
SNIFF		X			X		
KNOCK	X	X	X	X	X		
CREAK	X	X	X	X	X		
SQUAWK	X	X	X	X	X		
WHISTLED-YAP	X	X	X	X	X		
WHISTLE	X	X	X	X	X		
CHIRP		X	X	X	X		
CHATTER			X				
MOAN	X	X	X	X	X	X	
HACK		X		X			
SPIT	X	X		X			
SCREAM	X			X			
YELL		X		X			

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

G. crassicaudatus	G. senegalensis	Homologous (H) or Analagous (A)
SOCIAL COHESION CALLS		
Cry	Bark	A
Buzz	Hoot	-
Cluck	Coo	A
Click	Click	H
Squeak	Squeak	H
'ANXIETY' or 'ALARM' CALLS		
Sniff	Sneeze	-
Knock	Shivering-stutter	A
Creak	Gerwhit/Cluck	H
Squawk	Whistle & variants	A
Whistled-yap	Yap	H
Whistle	Yap-alarm	H
Chirp	Wuff/Wail	H
Chatter	Caw	A
Moan	Explosive Cough	A
---	Sob/Moan	-
AGONISTIC CONTACT CALLS		
Hack	Grunt	
Spit	Spit/Spit-grunt	H
Scream	Scream/Fighting chatter	H
Yell	Rasp	-

of G. crassicaudatus have the potential of giving a continuously varying array of mood messages while those of G. senegalensis are better adapted for mixed unit messages. The few cases in which a call in one species is not matched by an equivalent call in the other may be explained by the differences in the rearing of the young and the structure of the foraging groups at night. The list of calls which have been described for G. crassicaudatus remains open for modification in the light of additional data. A thirteenth call named the rattle was heard from an adult female with small infants but its exact nature and context were insufficiently clear for it to be classified. In addition the variability of calls, such as the chirp, indicates that G. crassicaudatus are capable of producing an extensive variety of noises, many of which have not become stereotyped in order to serve as social signals.

16.5 Agonistic Behaviour

Agonistic interactions are yet another reflection of the social structure of a species. In studies of captive animals there is often a tendency to place a number of unrelated individuals in a cage and thereafter consider them as a natural group. Meaningful interactions are only witnessed if the animals are allowed to associate in a way which stimulates the situation in the wild. Gartlan (1968) points out that in several primate species, agonistic behaviour is more common in captivity than in the wild and that it may be further increased by crowding. For some prosimians, however, it is sometimes possible to build up unnaturally large groupings with few signs of aggression. Doyle and Bekker (1967) and Manley (1966) have shown for G. senegalensis that this is best achieved by housing the animals in family units of a single male and female with their offspring. Subsequent infants are then perfectly integrated into this 'group' and they usually remain so even when mature. If, however, strangers are introduced to one another the situation is quite different. Agonistic interactions are common and fighting may break out which can lead to serious injury and death. Fighting under these conditions has been reported for G. senegalensis (Bishop, 1964; Bearder, 1969), Perodicticus potto (Walker, 1970; Blackwell and Menzies, 1968), Loris tardigradus (Rahaman and Parthasarathy, 1970) and Nycticebus coucang (Ehrlich, 1969). It is apparent that as long as the animals remain familiar with one another their relative dominance is fixed and the unit is stable.

Agonistic behaviour has been described for G. crassicaudatus in captivity by Jolly (1966a); Drews (1971) and Roberts (1971). It involves threatening, chasing and sometimes fighting, accompanied by a variety of vocalizations and an increase of marking and rubbing behaviour. It is always followed by at least temporary avoidance on the part of one animal. In the wild, dominance interactions and aggressive encounters were rare and their nature seemed to depend on the frequency with which the animals came into contact. They were observed on fifty occasions during the study of which over 70% were mild intra-group encounters (44% within the maternal group and 33% between the maternal group and the adult male). The remaining 23% were aggressive episodes between comparative strangers. These data were drawn from all study areas but it must be remembered that most observations were made on relatively isolated groups in an area of low population density. There were indications that aggression was more common in areas of high population density, particularly during the mating season.

Jolly (1966a) notes that, even between familiar individuals, social encounters may have an element of tension about them, particularly those which involve close physical contact. Quarrelling was observed between group members during play, allogrooming and at dawn when individuals came together to sleep in a huddle. In these cases one animal grabbed, cuffed or lunged at the partner while vocalizing. Agonistic behaviour between the male and the maternal group usually took the form of the male chasing the female. She would vocalize and cuff as he approached, but thereafter the two usually groomed together. Chasing of the male by the female was not observed.

Drews (1971) found that food competition tests in the laboratory failed to show up dominance relationships in G. crassicaudatus. In the wild there were occasional squabbles over food which resulted in one animal being displaced (figure 51). This is unlike the behaviour of G. senegalensis, in which even food stealing by the youngsters is not followed by reprisal (Doyle et al., 1969). The difference between the two species in this respect may be a natural outcome of their different feeding habits. In G. crassicaudatus, group foraging at night may inevitably lead to some competition for the same food sources, although this remains at a minimum.

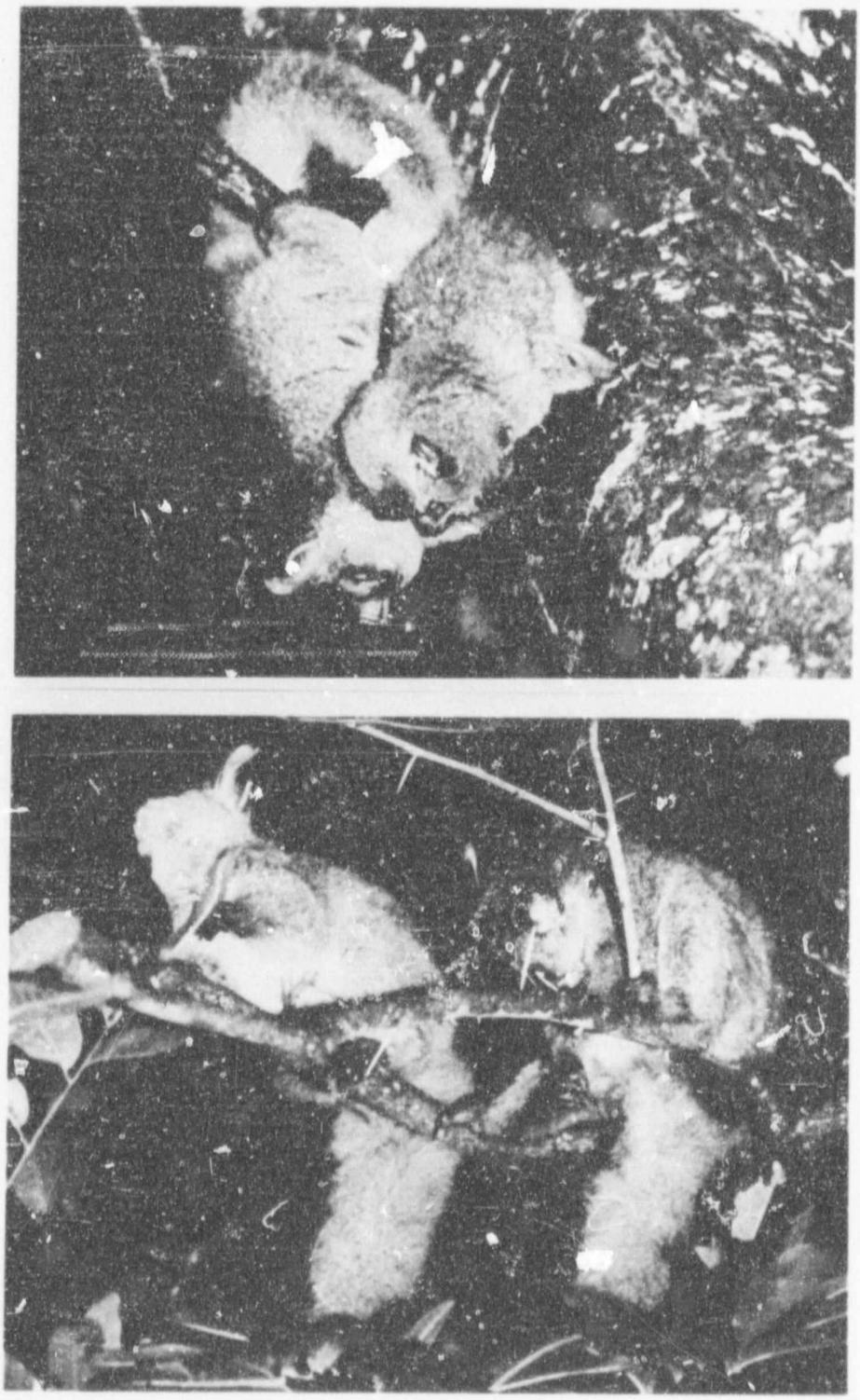

Figure 51. Photographs depicting aspects of social contact in G. crassicaudatus. (a) Agonistic behaviour between juveniles at a gum lick. (b) Association between juveniles while grooming.

Aggressive encounters, including grappling, fighting and high intensity vocalizations, were witnessed on a few occasions, particularly in Zululand. As in captivity (Drews, 1971), fighting sometimes continued after the animals had fallen to the ground and chasing took place either along the ground (in Rhodesia) or through the trees. There are reports of bushbabies being approached by man and even handled when fighting on the ground (J. Wylie, personal communication). Fights were usually brief, followed by rapid retreat of the loser. Astley-Maberly (1967) judged from vocalizations that bushbabies in the montane forests of the North Eastern Transvaal were particularly quarrellsome at certain times of the year.

The somewhat scant information presented above indicates that dominance interactions are rare within a group of familiar individuals where there is evidently a stable hierarchy. Contact between comparative strangers on the other hand may lead to fighting. It sometimes happens that two bushbabies will pass one another without any obvious greeting or hostility, which indicates that mutual recognition has already been achieved at a distance.

Recognition may be made possible by a variety of clues which are difficult to evaluate in a field study. Laboratory observations and experiments on G. senegalensis, however, indicate that olfaction is extremely important (Bearder and Doyle, 1974b). Naso-nasal and/or naso-genital sniffing always accompanies greeting and strangers which are timid of one another may sniff at those places where the other has just been sitting. The motivation of a subordinate to smell a dominant animal is high, even if it results in antagonism. When a stranger is introduced into a stable group, or an individual returned after a period of absence, there is a period of olfactory checking of the newcomer and also between members of the group. It is known that recognition can be achieved in the absence of visual clues. Adult males will attempt to fight one another through small cracks in an opaque partition separating their home cages, causing damage to their fingers. If one of these males is allowed to enter the cage of the other they fight almost immediately following mutual approach, irrespective of the relative size of the other animals present and in the absence of auditory signals. In addition members of either sex respond to one another appropriately although there is no marked sexual dimorphism. Even the age of a stranger may be recognised

through olfaction since there is a differential response by an adult towards a sub-adult, even though the sub-adult may be larger.

Other factors may be equally important in affecting the outcome of agonistic encounters. In G. senegalensis, for example, it has been demonstrated that although the nature of interactions between particular age/sex classes is usually quite predictable, they are influenced to some extent by the 'moods' of the animals concerned. The initial position of dominance between strangers (as indicated by displacement following agonistic interactions) can be reversed, given sufficient time, as the newcomer becomes more settled and familiar with the environment. An individual may be sub-dominant in a strange cage but dominant over the same animal in its home cage. Finally, it soon becomes obvious that certain individuals are particularly aggressive while others are unusually timid (Bearder, 1969).

16.6 Discussion of Social Behaviour

One of the most important characteristics of primates is their social nature. They usually live in social groups which remain stable over long periods and within which the individual learns much of the behaviour which adapts it to life in a particular environment and social setting. Some of the advantages of a social way of life are described by Dolhinow and Bishop (1970). The youngster can learn the subtleties of communication, food habits, which paths are used for travelling from one place to another, which trees provide suitable sleeping places and which animals are dangerous. Social behaviour also enables individuals to become familiar with other members of the community in which they live. Dolhinow and Bishop (1970) point out that within a group of primates there are adjustments in social interaction patterns and changes of membership over the years. In social troops which include members of successive generations there may be long traditions of interaction and relationship, the nature of which varies considerably between species. Jolly (1966a) stresses that bushbabies (G. crassicaudatus and G. senegalensis) have a far less integrated group and less well-differentiated individual roles in the group than even caged lemurs, let alone a wild lemur troop, and that social interactions are therefore relatively uncomplicated.

The patterns of social groupings in nocturnal prosimians have been reviewed by Doyle (1974). Detailed information is available for Lepilemur mustelinus (Charles-Dominique and Hladik, 1971), Microcebus murinus (Martin, 1972a), G. demidovii (Charles-Dominique, 1971, 1972) and G. senegalensis (Bearder, 1969). Each of these species has a basically similar system of social organization consisting of a spatial pattern of individual relationships. Social contact occurs between particular adult males (central males) and adult females (central females) over a long period which cannot be related to the short oestrus of the females. Population 'nuclei' seem to exist, which may be separated from one another to a greater or lesser extent. Within each nucleus there are a number of central males with adjacent home ranges (or territories) each of which overlap that of one (or more) central female(s). Other adult males are found at the periphery. Such 'peripheral' males may migrate between the population nuclei or possibly replace the central males in certain circumstances.

There is every indication that the same basic type of social structure exists in G. alleni, Euoticus elegantulus, Perodicticus potto (Charles-Dominique, 1971) and in G. crassicaudatus. Evidence from the wild and in captivity suggests that the Galaginae exhibit a greater tendency to form social aggregations than the Lorisinae (Doyle, 1974; Martin, 1972b) and this is accompanied by differences in their social behaviour, for example, in their range of vocalizations (Vincent, 1969). Martin (1972b) suggests that the genera Microcebus and Galago probably exhibit specialization of a primitive, more solitary Strepsirhine pattern of social organization developed through enhanced association between females which have contact with a single adult male.

It appears that the gregarious social way of life which is seen in most diurnal primates, in which the adults remain associated together for much or all of their lives, has developed from the comparatively solitary existence of the nocturnal prosimians, which are nonetheless social animals. Their family groups may be defined as comprising those animals whose individual ranges coincide or overlap to a large extent and who will share the same sleeping places, at least on occasions. Group members may meet one another or move together at night, when they display a variety of social acts.

Andrew (1964) points out that most of the displays necessary for life in social groups have evolved, either by extension of the periods of association between the adult male and female for breeding, or by an increased association between parent and offspring, or both. 'The main change in such displays after the appearance of societies is probably an increase in the ease with which they are elicited' (Andrew, 1964).

G. crassicaudatus shows several trends towards a better developed social way of life than any other nocturnal prosimian species which has been studied. The structure of the group during the period of nocturnal activity seems to be unique among the Lorisidae while among the lemurs, only Avahi is reported to be found in small groups at night (Martin, 1972b). Examination of the social dynamics and mother/offspring relationship in G. crassicaudatus show that strong ties exist between individuals which are maintained over long periods. The amicable social interactions between the adult male and other members of the group (play, grooming, etc.) are indications of a thorough familiarity with one another (figure 51). Such individual recognition is probably one of the most important factors in social organization in all group-living primates. Andrew (1964) notes that contact-vocalizations are extremely important where there is increased social contact between the mother and her infants. These vocalizations are found in Microcebus murinus, G. demidovii (Charles-Dominique and Martin, 1970) and in G. senegalensis (Andersson, 1969) and they are carried a stage further in G. crassicaudatus.

17. OTHER ASSOCIATED SPECIES

17.1 Predators

Predation on G. crassicaudatus was not witnessed during the present study but there are reports of bushbabies being included in the diet of leopards (Panthera pardus: Turnbull-Kemp, 1967) and, as noted previously, the black eagle (Aquila verreauxi: H.D. Jackson, personal communication). Most evidence of injury came from Rhodesia where the animals often had to descend to the ground in order to move between trees. Two bushbabies were found with damaged limbs and others were known to have been knocked down by cars on the roads or killed by domestic dogs (J. Wylie, personal communication). Astley-Maberly (1967) records that they are sometimes caught and killed on the ground by dogs in the North Eastern Transvaal. It seems likely that G. crassicaudatus is liable to predation from a number of carnivores when it descends to the ground. Lions (Panthera leo), hyaenas (Crocuta crocuta) and jackals (Canis mesomelas) were absent from the study areas but they represent a potential threat in the game reserves and other protected regions.

Raptorial birds were a source of danger during the day should the bushbabies sleep in exposed positions or, for some reason, return late to the sleeping place. Apart from the black eagle, the martial eagle (Polemaetus bellicosus) and the crowned eagle (Stephanoaëtus coronatus) were seen in the study areas where they preyed upon young monkeys (Cercopithecus aethiops), rock hyraxes (Procavia capensis) and small species of antelope.

Snakes were potentially harmful to bushbabies while they were asleep during the day. The violent reaction shown by a bushbaby towards a snake at night has already been recorded. Of the many species of snakes in the study areas, four may be mentioned as being particularly dangerous to bushbabies: the Egyptian cobra (Naja naja); the black-necked spitting cobra (Naja nigricollis); the black mamba (Dendroaspis polylepis) and the python (Python sebae). The latter is now somewhat rare due to exploitation for its valuable skin but the others were encountered frequently.

G. crassicaudatus is occasionally caught by man for food but it usually goes undetected. Unlike G. senegalensis it is rarely caught and sold as a pet. There is a superstitious belief that the loud cries and whistles made by bushbabies emanate from a large, multi-coloured snake which is said to attack and kill people at night by pecking a neat hole in their heads (Astley-Maberly, 1967). Even today this legend results in some degree of protection for the species which is generally avoided at night.

The reactions of bushbabies to the observer serve to illustrate their response to a potentially dangerous species. They usually retreated to a vantage point from which they stared or they approached hesitantly making a number of characteristic calls. Continued disturbance caused them to move higher into the tree or to move away. If they were then followed they moved in circles, or changed direction repeatedly, until they were invariably lost. Vervet monkeys (Cercopithecus aethiops) observed by Struhsaker (1967b) in the Ambroseli reserve, Kenya, took two weeks before they allowed his close approach. Bushbabies, on the other hand, became habituated to the observer within two hours following a quiet approach. They subsequently continued their activities undisturbed to the extent of going onto the ground only a few metres away. There was, however, a differential response to the observer in different habitats. G. crassicaudatus reacted most strongly and was more inquisitive of the observer in the forests of Zululand where it was presumably least liable to predation by a large, terrestrial animal. This may be explained as an effect of novelty, or stimulus contrast, since contact with man in these areas was minimal. An alternative explanation is that the observations in Zululand were made at the time of mating when there may have been a general increase in the excitability of bushbabies. This is supported by the fact that they even showed an alarm reaction towards bushpigs (Potamochoerus porcus) in the undergrowth.

It appears that G. crassicaudatus normally learns quickly which animals to fear and it ignores those which cause no harm. In Rhodesia an individual foraged on the ground near two bushbuck (Tragulapus scriptus) but it moved rapidly into a tree at the approach of a domestic cat. In the North Eastern Transvaal four bushbabies were watched while they fed on guavas (see appendix 2) in a garden which adjoined natural bush. The

owner of the garden had often chased them away and when he chanced to walk by the animals moved off into the bush making soft calls characteristic of anxiety. After he had gone the bushbabies soon returned to feed, showing no fear of the approach or presence of the observer.

Predation-pressure is probably indirectly responsible for a number of behavioural characteristics in G. crassicaudatus. The animals usually spent the day in hidden sleeping places which they did not leave until after sunset and at night they remained in the safety of trees for most of the time. They were cautious before descending onto the ground and could escape quite rapidly if danger threatened, but when moving quietly they could often pass undetected. A number of vocalizations warned conspecifics of the presence, position and even the seriousness of a potential danger. Bushbabies are sufficiently large when adult to be unperturbed by owls or small carnivores such as genets (Genetta tigrina) and they have behavioural mechanisms to protect the infants which were otherwise most vulnerable. The structure of the group probably ensured that the offspring learned from the mother which species to avoid and, finally, they usually returned to cover well before sunrise so as to avoid diurnal predators.

17.2 Primates

All five of the indigenous non-human primates were found in the North Eastern Transvaal and the Eastern Highlands of Rhodesia, namely, chacma baboons (Papio urinus), vervet monkeys (Cercopithecus aethiops), samango monkeys (Cercopithecus mitis), lesser bushbabies (G. senegalensis) and the study species. In the main study area the success of primates was indicated by the relative lack of other mammal species which had disappeared in the face of trapping and hunting by the local people and their dogs.

There was a varying degree of niche separation between the five species. Baboons generally remained in the higher regions on mountain ledges and open slopes. They slept along cliff faces and rarely descended to the valley floor. Samango monkeys occupied the dense forested regions at the heads of mountain streams, extending downstream to where the dense vegetation narrowed to a strip bordering the watercourses. Each main branch of the valley appeared to be utilized by a single group of samangos.

Further downstream, where riparian bush adjoined more sparce vegetation and farmland, vervet monkeys were found. Their range overlapped that of the samangos but they were not seen together. Struhsaker (1967b) recorded that C. mitis are confined to the denser regions along the Tsavo river in Kenya, while C. aethiops are found in greater numbers in more open areas. He observed intermingling of the two species without any aggression.

A similar separation existed between G. crassicaudatus and G. senegalensis. The former were mainly confined to dense vegetation throughout the length of the valley while G. senegalensis were absent from the forest regions at the top and were typically found in open vegetation lower down. Encounters between the two species were not uncommon. They were seen in the same trees feeding on the same type of food but, apart from briefly staring, they ignored one another completely.

Vervet monkeys occasionally used the same trees as G. crassicaudatus for sleeping purposes and they were seen together in the mornings and evenings. On one occasion two young monkeys approached an adult bushbaby which took no notice until they came to within one metre. It then spat at them and they retreated rapidly. At night a bushbaby seemed to be disturbed by sleeping monkeys, which blocked its line of movement, and it uttered alarm vocalizations (squawks). No interactions were witnessed between G. crassicaudatus and samango monkeys or baboons.

17.3 Viverridae

The most numerous of all inter-specific interactions which were witnessed were those between bushbabies and genets (Genetta tigrina). The adults of these two species were approximately the same size and they had several ecological characteristics in common. It may be said that they showed a mutual respect for one another and although the bushbabies displaced genets in most cases their relationship was a complex one. Each species was seen to spit growl and lunge at the other on occasions with the females being particularly intolerant when they had young. A female bushbaby left her infants to chase a genet which rapidly descended the tree and escaped along the ground while making a guttural rumbling sound and sharp hisses. Similarly a female genet made a mock attack on a large male bushbaby as she left an arboreal sleeping place with her infants.

The bushbaby did not retreat and the genet continued to hiss and growl as she moved away. At other times the two species slept peaceably in the same trees or rested and groomed close by at night and they were seen to feed together in a fig tree. The approach of a genet occasionally induced mild intensity alarm vocalizations from bushbabies, similar to those evoked by a cat.

The nocturnal marsh mongoose (Atilax paludinosus) was also encountered by bushbabies and its movements occasionally provoked a startle reaction, but this was the typical response to any sudden noise including the sound of jumping by conspecifics.

17.4 Birds, Bats and Rodents

Interactions between G. crassicaudatus and owls were observed in which the former showed little sign of fear. On four occasions a wood owl (Ciccaba woodfordii) swooped down on a bushbaby which merely jumped away at the last minute making a brief, low-intensity call (hack). Two juvenile bushbabies were seen to approach a barn owl (Tyto alba) which craned its neck and extended its wings forward before flying away. Eagle owls (Bubo africanus) were common in the main study area but they did not appear to cause G. crassicaudatus any alarm, unlike the smaller G. senegalensis which reacted strongly to these owls (personal observation).

The possible predatory habits of G. crassicaudatus have been discussed in connection with its diet. It may be mentioned here that fruit bats (Epomophorus wahlbergi) and various species of mice were common food competitors of bushbabies at night but they were always ignored. An interesting phenomenon was observed in which two fruit bats flapped around a resting wood owl, approaching to within a few centimetres of the owl for some minutes. This may be interpreted as a mobbing response towards a potential predator which was not shown towards bushbabies.

18. DISCUSSION

The foregoing consideration of ecology and behaviour in G. crassicaudatus is based upon those data which were most easily obtained by observation and limited experimentation in the field, supplemented by occasional observations on animals housed in the laboratory. The nocturnal habits of bushbabies and the dense nature of their preferred habitats often made it impossible to structure the study in a way which would ease the analysis of data. Thus an emphasis has been placed on description and illustration of aspects of behaviour and ecology followed by comparisons with closely related species as an aid to understanding the functional significance and survival value of these adaptations. This in turn helps clarify the exact taxonomic relationships between species which have been classified with reference to other criteria. A particular comparison is made with G. senegalensis which is allopatric or sympatric to G. crassicaudatus throughout a large part of Africa. These species remain morphologically conservative but they have probably become specialized following divergence from a common ancestry with the remaining lorisids and lemurs. Striking similarities and differences are revealed between the two, some of which have been discussed separately under the relevant headings. A broad comparison prompts the following questions: In what way are the two species similar to one another? Do they share common characteristics with other related forms which may reflect the ancestral condition? In what important ways have they probably become specialized and diverged from each other? Finally, what are the significant factors which bring about their ecological separation?

Apart from differences in size, G. crassicaudatus are morphologically extremely similar to G. senegalensis and in addition the two species have a remarkable number of behavioural and ecological characteristics in common. They are nocturnal and have a broadly bimodal pattern of activity each night. In captivity the two species are more or less omnivorous and in the wild their feeding habits overlap to some extent. Both will take insects and flower secretions and they make extensive use of gum, particularly in the dry winter season. Gum-licking postures are almost

tical. Both may build nests and they breed during the wet summer months when food and cover are readily available. They give birth to a small number of offspring which are weaned before the end of the wet season. The mothers frequently move their young infants from one retreat to another, carrying them one at a time in the mouth. Later they may be left clinging to a branch while the mother moves away alone in order to forage, but they are always retrieved before day-break to sleep with the mother.

There are certain basic similarities in group structure, home range and use of space. Both species have family groups in which the adults show possible territorial behaviour in the form of olfactory marking, vocal advertisement and aggression towards rival conspecifics. The movements of the males are separate from those of the females, although familiar pairs come into regular contact and they may sleep together in a huddle. There appear to be bonds between certain individuals which may be established and enhanced through allogrooming. Both species utilize all levels within their habitats and they are wary before descending to the ground. A comparison of various social behaviours, grooming, play and particularly vocalizations, shows up remarkable similarities between the two. The adaptability of both species is indicated by their occurrence in a variety of habitats, which may even include human dwellings.

Many of the characteristics listed above clearly resemble the common features of G. demidovii and Microcebus murinus, a fact which supports the findings of Charles-Dominique and Martin (1970) that there are many similarities between the Cheirogaleinae and the Galaginae in general. Following the proposal of these authors that this is probably a reflection of ancestral primate characteristics it is possible to elaborate on the suggestions of Martin (1972b) concerning the ancestral condition.

Martin's interpretation is that the common ancestor of the lemurs and lorises was probably a small omnivorous form, feeding primarily on insects, fruit and gum. He suggests that the gum was gathered by using the 'tooth-scraper' in the lower anterior dentition. There was probably a weakly developed spatial system of social organization, with central males of a population nucleus each having access to a small number of females, while peripheral males lived on the fringe of each population. He points out that competition between males and migration of peripheral males between nuclei would ensure selective mating and exogamy. Following

Walker (1967a), he shows that the ancestral form probably exhibited hind-limb dominated locomotion. Evidence points to the fact that it was nest living and gave birth to a small number of well-developed infants after a relatively long period of gestation. The infants matured fairly slowly and were cared for by the mother. Finally, Martin indicates that this form was possibly nocturnal and most likely had a well-developed seasonal pattern of activity with a limited breeding season and the ability of store fat reserves which ensured survival during periods of food scarcity.

Further interspecific comparisons indicate that the common ancestor was probably agile and active, having fairly generalized locomotor abilities which included vertical-clinging-and-leaping. Hind-limb dominated locomotion and the extensive grasping action of the feet may have freed the hands to a greater extent for the manipulation of food items. These developments were apparently accompanied by the loss of claws. It is possible that urine washing developed at the same time as an aid to good grip. Further morphological specializations of the hands and feet, or adaptations for slower movement, may have made such an action redundant in some descendant species. The widespread occurrence of gum-licking amongst the Lorisidae and some Lemuridae indicates that gum may have represented an extremely important food source when high-energy nutrients were in short supply. It also seems likely, judging from present-day species, that the early individuals foraged alone. This could be related to a predominantly insectivorous diet, since the foraging patterns demand a solitary technique (Charles-Dominique, 1971). Such a diet might explain the existence of stereotyped predatory patterns in G. senegalensis, G. demidovii and Microcebus murinus (Bishop, 1962; Charles-Dominique and Martin, 1970). Independent movements may also result in part from nocturnal habits (Eisenberg et al., 1972).

The ancestral form probably exhibited social grooming and play similar to that of modern species, using the 'tooth-scraper' as a grooming implement and gripping the fur with the hands. It may also have been quite vocal, correlated with its nocturnal habits and an ability to escape danger rapidly. Small size and agility may have precluded the infants from gripping onto the mother's fur and they were thus probably carried one at a time in the mouth.

The large G. crassicaudatus differ from other Galagines in several ways which have been enumerated in earlier chapters. The most obvious are

the differences in locomotion and group structure, which may in fact be interrelated. Examination of locomotory postures indicates that there has been a secondary behavioural adaptation away from the more typical Galagine pattern of vertical-clinging-and-leaping, towards slower stealthy movement, which is not matched by corresponding skeletal changes. Decreased reliance on leaping may be correlated with an increase in body size. One advantage of slow movement and large size could have been that the female was able to carry more than one infant at a time and this possibly led to the change in social group structure.

It has been shown that after an initial period of oral transport alone, the infant G. crassicaudatus may also be carried while gripping onto the fur of the mother's back. Riding on the mother was originally reported for this species by Haagner (1920) and Shortridge (1934), although subsequently it was not generally accepted. Buettner-Janusch (1964), for example, considered it unlikely that the infants would ride while their mothers leaped through the trees, despite the fact that he observed infant G.c. argentatus clinging to the mother in captivity. In fact wild G. crassicaudatus seldom leap through the trees, although the females may indeed make small jumps while carrying their infants on the fur.

Fur-clinging is almost a universal characteristic of primates and it has several adaptive advantages, not least of which is the greater degree of protection afforded to the infants. It has not been reported for any other galago species, but it is usual among the Lorisinae. The lorises, however, have a single infant which clings to the mother's belly and which does not appear to be picked up or carried in the mouth. G. crassicaudatus on the other hand usually have two and may have three infants which cling to the fur of the mother's back or are carried in her mouth with almost equal frequency. The infants have not been observed to cling to the belly in the wild. It therefore seems likely that this method of infant transport has developed from the pattern of oral transport seen in other Galaginae following an adaptation for slower movement and an increase in body size. (G. crassicaudatus infants are relatively tiny compared with those of G. senegalensis.) An active leaping mode of progression is unlikely to be favourable for infant carriage on the fur and, although both adaptations occur together in some lemurs (Lepilemur and Hapalemur), it must be remembered that these species evolved in the comparative absence of rigorous selection pressures. There are indications

that this habit may result in high infant mortality in the face of recent disturbances by man (J.-J. Petter, personal communication).

Infant 'parking' is a characteristic of galagos and lorises which enables the mother to continue her activities unencumbered. As a possible consequence of fur-clinging, infant parking in G. crassicaudatus is the exception rather than the rule. Unlike G. senegalensis, in which contact between the mother and her infants at night is minimal after the first few days of life, the young G. crassicaudatus are first carried from place to place and later follow the mother until they are mature. There is relatively more grooming and play between individuals and the system of auditory communication shows adaptations for use in a group context.

Eisenberg et al., (1972) discuss the space utilization patterns of some selected mammals and show hypothetical evolutionary pathways from one pattern to another. They distinguish between a 'solitary' pattern in which adult males and females have separate centres of activity and encounter infrequently (G. demidovii; Microcebus murinus) and a parental family pattern which is characterized in its extreme form by a bonded pair of adults and their immature dependants (Callithrix, Hylobates, Callicebus, Aotus). The term 'bond' implies that there are social relationships between specific individuals based on the performance of mutually reinforcing activities (grooming, huddling) in addition to mating behaviours. The spacing pattern of G. crassicaudatus appears to be a variation of the solitary pattern which closely approaches the family group structure and it may be thought of as an intermediate stage between the two. It is interesting to note that those species which are organized into parental family groups tend to be frugivorous rather than insectivorous, which is also true of G. crassicaudatus.

Despite extensive similarities between G. crassicaudatus and G. senegalensis they are best adapted for life in different habitat types for which they show a distinct preference. In general the smaller G. senegalensis are found in a greater variety of habitats at higher population densities than G. crassicaudatus. They breed more rapidly, require less food of a type which is widespread in its occurrence and have a smaller home range. In addition they have greater agility, less stereotyped movements, fewer requirements for dense cover and are able to make use of smaller branches than G. crassicaudatus.

Where the two species live sympatrically, the population densities of one or both are lower than for those regions in which they are found alone. This may be a result of interspecific competition, or because the vegetation does not represent an optimum habitat. In fact competition appears to be minimal. No antagonism or fear was seen during interspecific encounters. Each species typically occupied different parts of a shared habitat. G. senegalensis spent more time in the open 'orchard' bush or at the periphery of the riparian bush or forest which was most utilized by G. crassicaudatus. Only in Rhodesia, where G. crassicaudatus had adapted to a more open environment than elsewhere, were there indications of some competition for food and here the population density of G. senegalensis was surprisingly low.

The highest population densities of G. crassicaudatus were found in dense sub-tropical evergreen forest, while G. senegalensis are most abundant in open acacia thornveld savannah. It is possible that individuals of the smaller species are least liable to predation in open areas where they are able to spot danger from a distance and react appropriately. The larger and slower G. crassicaudatus on the other hand have greater requirements for cover while sleeping during the day. Their relatively quiet movements in dense vegetation may not only enable them to avoid detection, but also ensure that they are not taken by surprise. Arboreal predators are more abundant and better concealed in forest areas than in open woodland. The fact that G. crassicaudatus may also be found in open regions, however, indicates that their type of movement is not a major factor which limits their distribution. Given sufficient cover for a daytime retreat the most important ecological factor which influences distribution patterns appears to be the availability of trees bearing edible fruits. Where bushbabies are absent from suitable habitats which are not separated by major physical barriers, their present distribution may partially be explained by considering the influence of disease epidemics, veld fires or the destruction of natural vegetation for development schemes, which may be disastrous in their effects.

Walker (1974) suggests that given the apparently stable conditions of the equatorial forest belt of Africa since before the Miocene, the ancestors of East African lorisids are likely to be found in East Africa and those of West African species in West Africa. He considers that adaptation to a more arid environment could have been caused by a forest

species colonizing the peripheral areas, or by adaptation of one species to the changing conditions of the peripheral areas as the forest contracted. Whichever is the case, it is evident that the ancestors of G. crassicaudatus and G. senegalensis underwent specializations which allowed them to spread into more open areas away from the equatorial forest belt. These have been carried to an extreme in G. senegalensis which may be found in semi-arid environments far from forests or riparian bush. G. crassicaudatus seems to represent a reversion to forest life, with a result that it is more restricted in its distribution. Similarities between the behaviour of G. crassicaudatus and members of the Lorisinae are probably the result of convergent adaptation to a similar ecological niche.