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Behavioural adaptations in South African Galagos

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Figure 8. G. crassicaudatus with the tail marks used for field identification (the tail hair is dyed and clipped).

of new animals as well the re-marking of others when their tail marks had disappeared.

2.4 Radio Tracking

The focal animals were followed using a commercial radio telemetry system consisting of a portable radio receiver (type LA12, AVM instrument company, Champaign, Illinois). The system operated in the 148MHz region, which is the standard frequency used when tracking animals in Africa.

The transmitters were powered by 1,4V mercury cells (type RM630T2), which had a battery life of at least six weeks. One of these was attached to a transmitter and the two units were stuck on a narrow leather belt and covered with dental acrylic (Fig. 9). A lining of brightly coloured PVC was used to prevent rubbing when the collar was attached and it enabled the belt to be located easily if it came off the animal. The collar, which weighed about nine grammes when complete, was fastened around the bushbaby just above its hips (Fig. 10).

The receiver had twelve channels which, with high and low-pass filtering, allowed the use of twenty-four different transmitter frequencies. A three element yagi, which had a directional ability of $\pm 10^{\circ}$, was attached to the receiver. Distance from the collared bushbaby could be gauged by the signal strength which was shown on a meter and by the strength of an audio tone. The range of reception was about 300m. but could be more under favourable conditions.

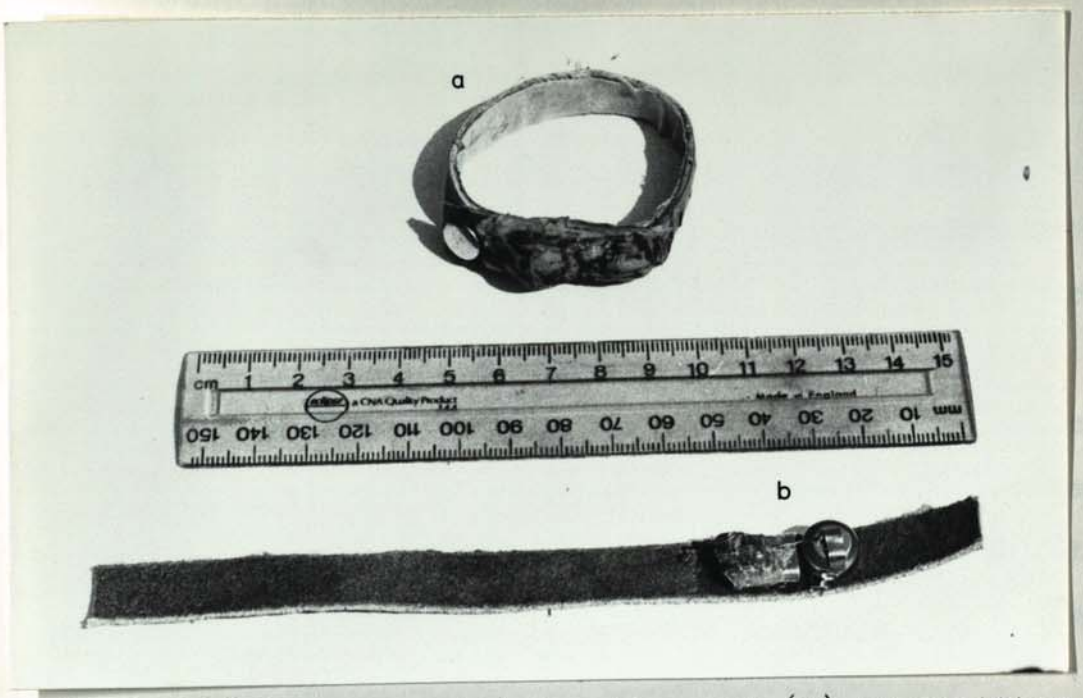

Figure 9. (a) The completed collar and (b) transmitter and battery prior to being covered with dental acrylic.



Figure 10. *G. senegalensis* wearing the radio belt.

2.5 Observations and Data Collection

The galagos were watched at night using a miner's head lamp powered by a six-volt accumulator, which could provide light for more than twelve hours of continuous observation. A celluloid filter was placed over the lamp glass to produce a red light as galagos are insensitive to that range of the spectrum. Southern (1955) described this method of watching nocturnal animals and it has since been successfully used by a number of people who have been observing prosimians at night (Bearder, 1969, 1975; Charles-Dominique, 1977; Clark, 1978).

Behavioural categories for both species were defined after fifty-five hours of preliminary observations in the semi-natural conditions (Doyle and Bekker, 1967) at the Primate Behaviour Research Group laboratory, University of the Witwatersrand. Activities were classified as feeding, foraging, travelling, moving, grooming, resting, playing, agonistic or marking behaviour (Appendix 6). The latter behaviours included urine-washing (Fig. 33), hind-foot rubbing, ano-genital and chin rubbing.

A further fifty hours of preliminary observations in the field allowed the above categories to be checked under natural conditions and additional ones added where necessary. In both species feeding behaviour was separated into two categories: 1) ingestion of gum and 2) ingestion of invertebrates. Similarly foraging was divided into searching for each of these resources (Appendix 6).

The two focal animals were studied for over 300 hours. In the two seasons, summer (November to February) and winter

(May to August), both galagos were followed throughout the night three times. The remaining hours were distributed over the other nights so that observations in each hour were repeated at least six times in each season.

An appropriate check sheet was designed during the initial field observations and practice data were collected on these for over thirty hours before the tracking equipment was obtained.

Once the focal animal had been located, using the radio tracking equipment, data on its activity were taken onto check sheets at one minute intervals. There were two techniques that could have been used to collect data from which the percentage time spent on each activity could be calculated:

1) a continuous recording of the animal's behaviour with time of transition from one activity to another;
2) instantaneous sampling (J. Altmann, 1974) where the individual's activity is recorded at pre-selected intervals.

The former method could not be used because keeping a continuous check on the time as well as on the bushbaby required two observers. Most authors (J. Altmann, 1974; Dunbar, 1976; Hinde, 1973) consider that point sampling of behaviours accurately reflects the proportion of time occupied by that activity. The length of the time interval used is obviously important as is the necessity of ensuring that data are taken exactly on the minute, rather than recording an interesting or conspicuous activity just before or after the minute. One minute intervals were chosen as they were realistic under field conditions and were short enough (Dunbar, 1976; Hinde,

1973) to give a true reflection of the percentage time spent on each behaviour.

The number and species of the tree and the height of the bushbaby in that tree were recorded each minute as well (heights were judged in feet so have been presented as such in the results in later chapters). Other observations, such as whether a tree was flowering, climatic conditions and type of prey caught, were also noted. The lengths of gum-feeding bouts were timed and any marking behaviour or social interactions that occurred between the point samples were recorded.

Data on sleeping sites, for example, tree species, height in tree and sleeping partners of the focal galagos and any others that could be found, were taken during the day.

2.6 Assessment of Prey Use

2.6.1 Stomach contents: A non-destructive method of sampling stomach contents (R. F. Kay, pers. comm.; Sheine and Kay, 1977) was tried. The bushbabies were immobilized by an intramuscular injection of Ketamine Hydrochloride (10mg/kg). A long, flexible tube (ERU feeding tube, size 2 for *G. senegalensis*, size 4 for *G. crassicaudatus*) was passed through the mouth into the stomach. A small volume of water was injected into the stomach via the tube and the stomach contents were then withdrawn by applying gentle suction with a syringe attached to the tube.

Stomach contents were extracted from *G. crassicaudatus* using this technique but attempts to stomach pump *G. senegalensis*

were not successful, possibly because the bore of the tube was too small. As this method required two people and considerable time it was discontinued after the summer observations.

2.6.2 Faecal Analysis: Faecal samples were collected and preserved in alcohol. They were most commonly found in traps but occasionally were picked up under sleeping sites.

Samples were weighed and then immersed in a five per cent solution of potassium hydroxide and heated in a water bath until the pellets broke up. Any invertebrate parts were removed from the sample and identified to their order, or further if possible. All vegetable matter was also removed and identified where able. Any of the invertebrate parts which could be used to estimate size and number of items taken were then mounted on slides in DPX. The minimum number of prey in each faecal sample was estimated by counting the number of body parts, (legs, heads, wings, etc.) and reconstructing the different prey items from these. Sizes were estimated by comparison with invertebrates from the same order as that of the specimen. When size and number of prey in each order had been estimated, these two variables were multiplied together to give an estimate of the contribution of each order to the galagos' diet. The figures were corrected for differences in the quantity of faecal material collected from each species in summer and winter.

3. FOOD SELECTION

3.1 Introduction

Body size is inversely related to metabolic rate (Kleiber, 1961) and protein requirement (Brody et al 1934). As a result the smallest species of primates (0,1 - 0,2kg) use invertebrate prey as their staple diet. This includes a maximum amount of fat and protein, which provides a maximum amount of energy (Hladik, 1979). Larger-bodied primates cannot catch enough insects to supply themselves with sufficient energy as the chances of finding a given prey item in a particular habitat are the same regardless of body size (Charles-Dominique, 1971, 1977; Hladik, 1979). Those species with a body size of 0,2 - 2,0kg have to use resources with a high carbohydrate content such as fruits and gums (Hladik, 1979; see Appendix 7 for an analysis of gum). They still have to eat some insects to increase the proportion of protein in their diet but a negative correlation is found between body weight and the proportion of animal protein ingested (Gautier-Hion, 1978). The largest prosimians have to include leaves in their diet.

The difference in nutritional requirements between different sized species enables primates to be classified into three grades (Hladik, 1975, 1979). Each grade is characterized by a major food type:

Grade 1: Insects (and/or other small prey)
Grade 2: Fruits (and/or seeds and gums)

Grade 3: Leaves (and/or shoots)

The biomass of a species gives an indication as to which grade it belongs. The smallest species have the lowest biomass and are found in grade one, while the largest species have the greatest biomass and are found in grade three.

In optimal foraging theory a number of mathematical models have been constructed which predict how an animal should forage in a particular environment (Pyke, Pulliam and Charnov, 1977). The primary assumption made in all the models is that the reproductive fitness of an animal is a function of the efficiency of its foraging, usually measured in terms of net energy gain (Schoener, 1971), and that natural selection has resulted in animals that forage so as to maximise this fitness. In order to maximise its energy gain per unit time an animal must be able to assess the energy available in its environment and modify its foraging strategy accordingly (Wilson, 1976). It has been suggested that if these assumptions are true then foraging behaviour can be used to deduce the energy available in an environment (Wilson, 1976). There are four aspects of feeding behaviour to which optimal foraging theory has been commonly applied:

1) an animal's choice of food type,
2) its choice of which patch to feed in,
3) optimal time to spend in the different patches and
4) optimal patterns of speed and movement between patches.

Of these, prey selection (1) and giving-up time at a resource (3) will be examined.

Optimal foraging theory suggests that the longer an animal spends in a particular patch the lower the energy per

unit time that it is gaining. The animal should cease feeding in a particular patch or on a particular item when the energy it is gaining is less than it would gain by further search and capture. It would be expected, therefore, that the giving-up time in an energy rich environment would be shorter than in an energy poor environment. This was found to be the case for two species of tiger beetle (Wilson, 1976).

Minimum acceptable prey size may also be of use in measuring energy availability. As food becomes scarce animals are less discriminating in what they eat (Emlen, 1966; Emlen and Emlen, 1975) and it is suggested that the size of prey taken will decrease as energy availibility decreases (Goss-Custard, 1977; Wilson, 1976). It was shown that blue-gill sunfish (Lepomis macrochirus) took large daphnia when these were abundant and small ones only when the bigger ones were scarce (Werner and Hall, 1974). Similarly insectivorous birds from a temperate climate have been shown to take smaller prey species in winter than in summer and this has been correlated with the lower energy availability in winter (Wilson, 1976). Another factor affecting prey size is the size of the predator, the bigger the predator the bigger the prey (Gibb, 1956; Hespenheide, 1975; Schoener, 1969; Storrer, 1966). The energy expended per prey item is considered to be fairly constant regardless of prey size (Emlen, 1973). Thus the value of any prey species, in terms of energy gain per unit time, increases with its size until it becomes so big that the predator has difficulty in catching or handling it.

A number of studies have shown that the same species of prosimian can adapt its foraging patterns and selection of

food items to use different resources in different habitats (Budnitz, 1978; Jolly, 1966b, Pollock, 1977; Richard, 1977) as well as changing the proportion of food types in its diet with seasonal changes in availability (Bearder, 1975). For the two study species, though they are considered to be in the same dietary grade (Hladik, 1979), the difference in their body size suggests that there will be a difference in the proportion of the food items (invertebrates and gum) in their diet and a difference in the size of prey taken, The optimal feeding strategy is predicted to vary between the two species.

3.2 Results

3.2.1 Gum-Feeding: *G. senegalensis* spent considerably longer each night licking at gum spots (Fig. 11a), mostly from *A. karroo* (Fig. 12), in winter than it did in summer. A mean of one hour licking per night was found in winter and a mean of only fifty seconds per night in summer. In winter the continuous time spent at a lick gum spot (bout length) ranged from one second to 805 seconds and in summer from one second to 260 seconds. However, the mean bout length was thirty-four seconds in both seasons. A chi-squared test showed no significant difference between seasons in the pattern of time spent licking gum at one spot ($X^2=219$, $df=4$).

Similarly in *G. crassicaudatus* more time was spent licking *A. karroo* gum (Fig. 11b) on a winter night than on a summer night. The mean time per night in winter was thirty eight minutes and the mean time in summer was forty seconds. A bout of gum licking at one spot in winter varied from one





Figure 11. Gum licking by (a) G. senegalensis and (b) G. crassicaudatus.



Figure 12. Gum exuded from an Acacia karroo tree.

second to 525 seconds with a mean of forty-four seconds and in summer from one second to 180 seconds with a mean of thirty seconds. A significant difference between the pattern of bout lengths was found (X^2 = 9,03, df = 3, $p < 0,05$) with the bushbabies tending to stay longer at licks in winter (Fig. 13).

A difference was found between the species and seasons in the ratio of time spent gum-feeding to time spent gum-foraging. For G. senegalensis in summer the ratio was 4,7 and in winter was 1,57. For G. crassicaudatus it was 2,43 in summer and 1,55 in winter. This indicates that in winter both species had to spend more time foraging for a given time spent feeding. The ratio was very similar between the species in winter but in summer G. senegalensis was spending half as long foraging as was G. crassicaudatus for the same time spent feeding.

3.2.2. Prey Selection: The types, sizes and numbers of insects, or other invertebrates, eaten by both species in the two seasons were compared. The percentage contribution of each invertebrate order to the galagos' diet was calculated (Table 1).

Table 1. Percentage contribution of each invertebrate order to the diet of G. senegalensis (Gs) and G. crassicaudatus (Gc) in summer (S) and winter (W).

	Gs Summer	Gs Winter	Gc Summer	Gc Winter
Coleoptera	44	22	19	19
Orthoptera	27	33	28	33
Hymenoptera	2	28	27	40
Odonata	13	0	4	0
Neuroptera	8	0	0	0
Lepidoptera	4	0	0,3	0
Hemiptera	2	1	2	2,5
Isoptera	0	15	4	0
Chilopoda	0	0	14	0
Diptera	0	0	2	2,5
Dictyoptera	0	0	0	2,5
Arachnida	0	0	0	1,3

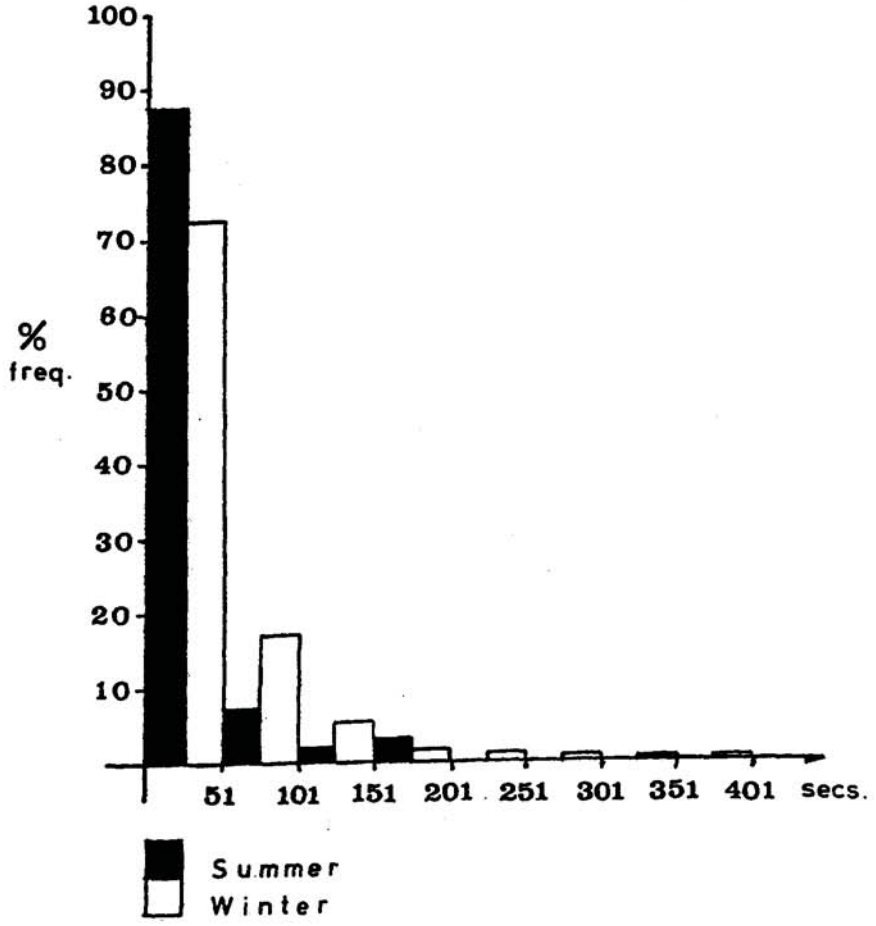

Figure 13. Pattern of gum-licking bout lengths in G. crassicaudatus.

The differences in percentage contribution of each order were significant between the seasons for each species (Gs X^2 = 32,6, df = 3, p<0,001; Gc X^2 = 13,83, df = 3, p<0,01) and in summer between the species (X^2 = 38,04, df = 3, p<0,001), but not in winter (X^2 = 5,54, df = 3).

Before analysing for differences in the size of prey taken all social insects (termintes and ants) were removed from the data. This was done as though each individual ant or termite is small in many cases one 'capture' will involve mumerous individuals. G. crassicaudatus was, indeed, seen licking up trails of either ants or termites on a number of occasions.

In both species larger prey was taken in summer than in winter (Gs X^2 = 13,75, df = 3, p<0,02; Gc X^2 = 8,43, df = 3, p<0,05). G. senegalensis took smaller insects than did G. crassicaudatus in summer (X^2 = 12,98, df = 3, p<0,05), but in winter the two species used the same size range of prey (X^2 = 0,86, df = 3). The actual quantity of insects taken by G. senegalensis varied little between seasons (Fig. 14) but there was a considerable decrease in winter in the number of insects taken by G. crassicaudatus (Fig. 15, and see chapter 4).

In addition to the prey species found in the faecal samples G. crassicaudatus was observed eating large millipedes (Diplopoda, 50-150mms long) on several occasions in summer. In a preliminary analysis of a faecal sample from G. senegalensis two small flies were found. These have not been included in the quantitative results as their sizes were not estimated nor was the sample that they came from weighed. A body louse found in a winter faecal sample of G. senegalensis was

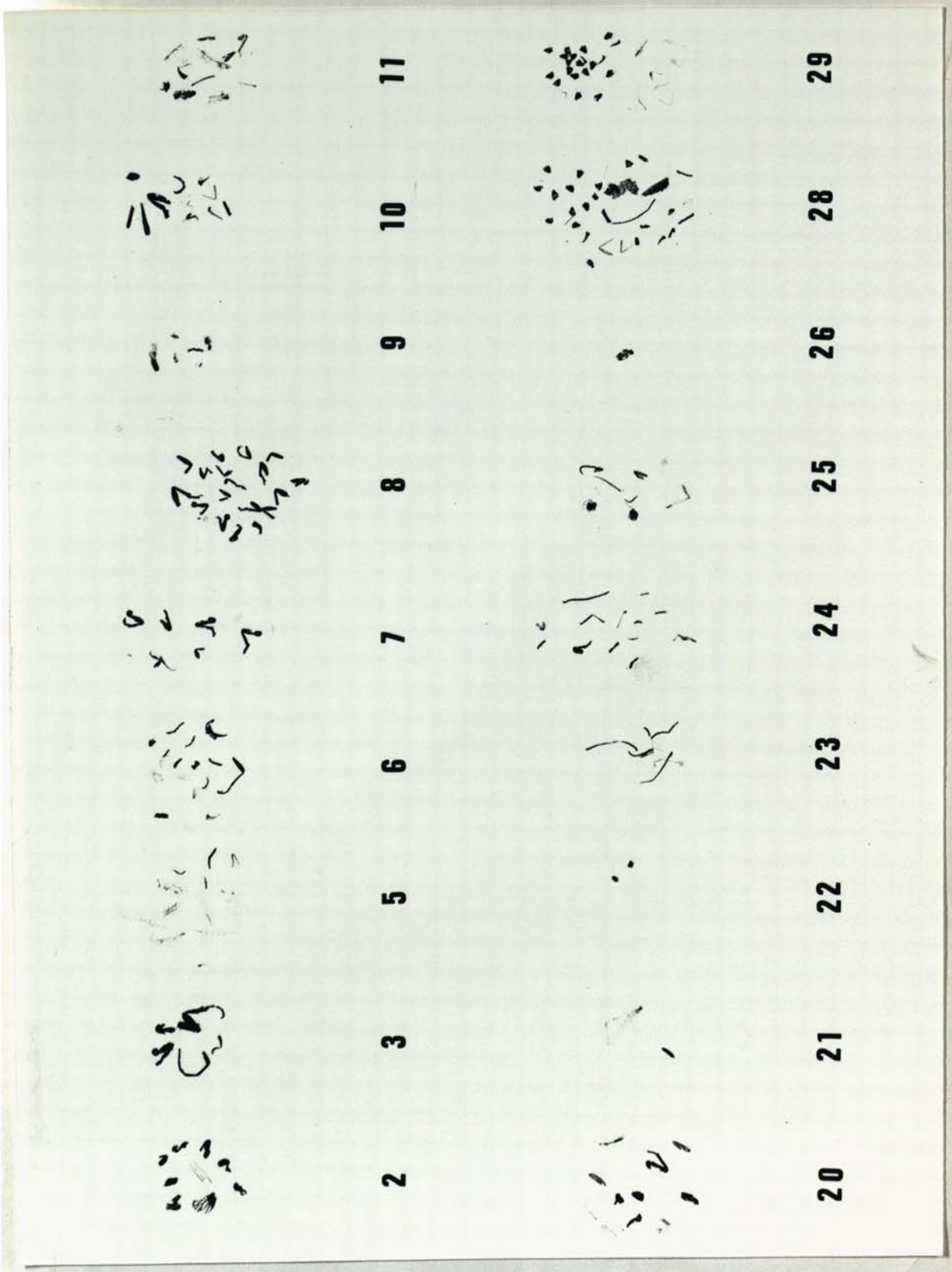

Figure 14. Body parts of invertebrates recovered from faeces of G. senegalensis in summer (2-11) and winter (20-29).

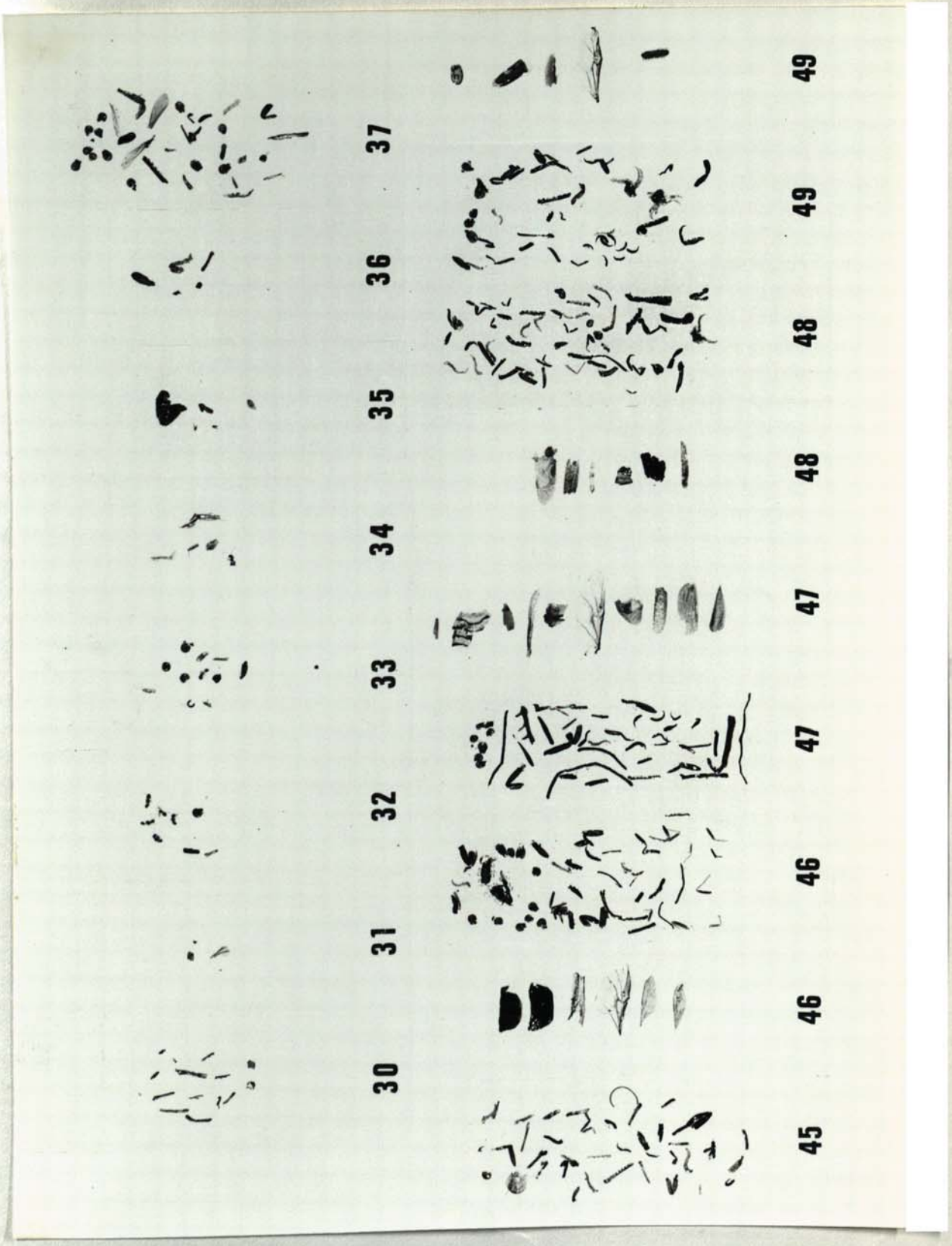

Figure 15. Body parts of invertebrates recovered from faeces of G. crassicaudatus in winter (30-37) and summer (45-49).

probably taken while the animal was grooming itself. The invertebrate species in the stomach contents of G. crassicaudatus were identified but no differences were found between these and those in the faecal samples. The results were not used in the analysis owing to small sample size and to the absence of comparable data in winter.

3.2.3 Vegetable Matter: Acacia leaflets, bits of bark and small pieces of unidentified material were found in the faecal samples of both species. Grewia sp. seeds were found in a winter faecal sample from G. crassicaudatus. Euclea sp. seeds, some Combretum sp. flowers and some unidentified seeds were found in one of the summer faecal samples from the same species. However, the focal thick-tailed bushbaby was never seen to eat anything other than invertebrates and gum except for two observations in May 1977 of this animal, and some others with her, spending short times feeding on the berries of Zizyphus mucronata (A. B. Clark, pers. comm.).

G. senegalensis probably took vegetable matter only incidental to feeding on gum (bark) and insects (Acacia leaflets), as it was never seen eating anything apart from these two resources.

3.3 Discussion

Data from the present study confirmed the earlier assignment of G. crassicaudatus to a grade two diet (Hladik, 1979) and this would be expected from its body weight. The high utilisation of insects throughout the year by

G. senegalensis indicated that it had a grade one diet but, particularly in winter, it tended towards a grade two diet. As the body weight of the sub-species in this study was on the border between the 0,1-0,2kg and the 0,2-0,5kg groupings of body size (Hladik, 1979) its diet could be expected to be intermediate between grades one and two. Other populations of G. crassicaudatus use different resources in different proportions (Bearder, 1975) to those used by the study population but this degree of variability has not been reported from observations of G. senegalensis in its natural state. Haddow and Ellice (1964) did report vegetable matter in the stomachs of about a quarter of the 103 lesser bushbabies that they disected but they did not identify it and it may well have been taken incidentally to feeding on gum and insects, as was considered to be the case in the present study.

Both species showed an increased use of gum in winter but in G. senegalensis this was not coupled with a very marked decrease in the number of invertebrates taken as it was in G. crassicaudatus. In the smaller species its higher metabolic rate did not allow it to conserve energy by inactivity in the winter. Instead, it had to take in more food as not only did it have to maintain its activity levels, it also had to expend more energy to keep warm. The increased use of gum by G. crassicaudatus in winter had to compensate for a greatly decreased use of insects in that season.

In this study G. senegalensis showed no difference in the pattern of its giving-up time at gum licks between the seasons. During the year there is no appreciable difference in the availability of gum (Bearder and Martin, in press). In

an earlier study on the same species a seasonal difference was found between the mean lengths of time spent gum-licking at one spot (Bearder, 1969), which is an indication that the pattern of gum-lick use also changed. These, apparently contradictory, results can be explained when the use of insects is taken into account. They will be returned to later.

An increase in the giving-up time at gum licks in winter was found in G. crassicaudatus. This is comparable to Bearder's results for G. senegalensis. This, too, will be returned to later.

In both seasons G. senegalensis spent longer feeding on gum each night than did G. crassicaudatus. However, time spent feeding does not reflect food intake (Hladik, 1977; Wyatt and Eltringham, 1974). The bigger species will almost certainly be taking more gum in a given licking time than will the smaller. For this reason a comparison of gum feeding bout lengths between the species would have been meaningless.

The changes in the ratio of time spent gum feeding to time spent foraging suggest that in winter both species were using smaller gum spots which they had to spend longer searching for. In summer G. senegalensis probably fed on the gum spots it encountered while foraging for insects and hardly spent any time actively searching for gum. G. crassi caudatus had to spend more time gum foraging in summer possibly because a lot of its insect foraging was on or near the ground where it was less likely to encounter gum.

The seasonal difference in percentage contribution of each invertebrate order in the diet of the two species can

probably be explained to a large extent by the life cycles of the prey species, many of them are likely to survive winter as eggs or pupae and be in places inaccessible to the galagos. Both species took smaller prey species in winter even though the amount of energy expended to catch them was the same as for bigger prey whereas the energy gain from the smaller species was less per item. This indicates that there was a reduction of energy available in both habitats in winter.

The difference between the species in the size of invertebrates taken in summer was due to the fact that the bigger predator (G. crassicaudatus) was taking larger prey species than the smaller predator (G. senegalensis). Differences in orders taken also reflected size differences, for example the millipedes were too large to be handled by G. senegalensis. As the species were in different habitats it is likely that there were environmental differences in the orders of invertebrate available which may explain some of the variation in type of insect taken. Another possibility is that one sort of invertebrate is easier to catch for one of the species than it is for the other (c.f. differences in the prey taken by the prosimian species studied by Charles-Dominique, 1977). In winter the convergence in prey size as well as prey type taken by the two species reflects the reduced availability of invertebrates in both habitats.

Insects are the more important component of the diet of G. senegalensis. Therefore its optimal foraging strategy was to search for insects in both seasons rather than to spend a long time at any one gum spot. It was however, acquiring less energy per unit time in winter when it was

feeding on small prey and so it had to take in more gum in this season. G. crassicaudatus would be gaining even less energy, proportional to its body weight, from small prey than would G. senegalensis so its optimal strategy was to spend longer at gum licks in winter rather than to hunt for invertebrates. These results are consistent with the predictions of optimal foraging theory but only to a certain extent. G. crassicaudatus did react in winter as optimal foraging theory predicts; prey size was decreased and gum-lick bout lengths (giving-up time) was increased as the overall energy in the environment fell. However, it appeared that G. senegalensis treated the two food types differently. Giving-up time at a gum spot was not increased as this, apparently, would not compensate for a decrease in insect feeding. Bearder (1969) did find a large decrease in the time spent insect feeding in winter and an increase in mean time spent at a gum lick by G. senegalensis. He, though, found a loss in physical condition in the bushbabies which was not the case in the present study. Evidently the severity of the winter in the earlier study forced the bushbabies to increase gum licking bout lengths to compensate for the drastic decrease in insect availability even though this was not a successful strategy as shown by the loss of weight. Insects will provide both energy, from the fats, and protein whereas there is little or no protein available in gum. The smaller species of bushbaby, with its higher metabolic rate, will be using comparatively more protein than the larger so cannot exist on gum alone.

It has been suggested that nutritional needs are not

important to the theory of optimal foraging (Schoener, 1971) but both the above results and those from a preliminary laboratory study of this question (Masters, 1977) suggest that this is not always true. In severe conditions an animal treats its environment as a one currency (energy) system and its overall foraging strategy is designed merely to maximise energy intake. However, in less severe conditions, its strategy is designed to maximise the different nutritional components of the diet. Thus the assumption of the maximization of a single currency by a foraging animal is true only under low energy conditions or where the animal concerned can obtain all its nutritional needs from a single food type. Under poor environmental conditions maximization of energy allows the animal to survive whereas at high energy levels it may maximize nutrient intake and so increase its reproductive fitness. This fits in well with laboratory studies showing specific dietary drives (Richter, Holt and Barelane, 1938; Rozin, 1976; Strangeways-Dixon, 1961).

In winter the use of large quantities of gum by both species as well as prey species of similar size and type will result in a considerable degree of dietary overlap. In a sympatric population there would be a high degree of competition as a result (Emlen, 1973). This would be reduced in summer when gum is no longer taken to any great extent and there is a difference between the size and species of prey taken due to differences in body size of the two predators species. The fact that the two species are found sympatrically, though the biomass of each is then reduced (Bearder, 1975), suggests that each species can modify its behaviour in the

presence of the other otherwise one would be excluded. The devices employed to avoid competition may be the use of smaller gum spots by G. senegalensis, G. crassicaudatus increasing the amount of fruit it eats, or both species exploiting different heights and slightly different foraging strategies.

4. USE OF TIME

4.1 Introduction

An animal has to use the time available to it in such a way as to maximise its chances of survival and reproductive fitness. At any time it has to decide whether to continue with its present activity or to change to some other form of behaviour (McFarland, 1976). This decision depends, ultimately, on the relative cost and benefit of the alternative behaviours. The cost and benefit of a behaviour alters with changes in the external and internal environment of the animal. As a result, the animal has to assess a wide variety of factors before it can make the necessary decisions about its activity. As it continues in one activity that activity will become less profitable until, after a certain length of time, depending on the external and internal factors, it will reap a greater benefit by switching to another behaviour.

The amount of time and energy expended on a particular activity will differ between taxa. Wilson (1975) considers that the time-energy budget of a species has evolved to fit times of greatest hardship. This 'principle of stringency' is contradicted by field studies on a number of mammals. The immediate surroundings of an animal such as prevailing weather conditions, can cause considerable variation in its

behaviour patterns from day to day (gorilla - Fossey and Harcourt, 1977; impala - Jarman and Jarman, 1973; gibbons - Raemaekers, 1977). Seasonal variation in time-energy budgets occur also (red colobus - Clutton-Brock, 1974; howler monkey - Smith, 1977; sifaka - Richard, 1977). The ability of a mammal to alter its time-energy budget in response to environmental conditions indicates that these budgets are a response to a fluctuating habitat rather than fixed to suit times of hardship. It is possible that the specific budgets are not what are selected for but rather the ability to vary time and energy allocation as necessary (King, 1977).

Regular patterns of activity throughout the twenty-four hours of each day and night have been reported for some species (impala - Jarman and Jarman, 1973; black and white colobus - Oates, 1977; spider monkey - Richard, 1977; elephant - Wyatt and Eltringham, 1974), but even within these species there are variations depending on the age and sex of the animals involved, the external conditions and hormonal influences. Early morning and late afternoon peaks of feeding are a common pattern in diurnal primates (brown lemur, ring-tailed lemur - Sussman, 1977; rhesus monkey - Lindburg, 1977; orang-utan - Rodman, 1977). In most species light is almost certainly the determinant of the twenty-four hour variation in behaviour (Jarman and Jarman, 1973; Kavanau, 1977; Park and Keller, 1932; Randolph, 1971). The functional significance of diurnal variation in activity patterns is not obvious in most cases, nor is its cause necessarily easy to determine. In some species, especially those with a midday rest period, the activity pattern may be an adaptation to

temperature variation. Early and late feeding peaks may serve to maximise the amount of food that can be digested per day (Clutton-Brock, 1977; Klein and Klein, 1977).

Field studies on nocturnal prosimians have suggested a bimodal activity pattern in some species (thick-tailed bushbaby - Bearder, 1975; dwarf bushbaby - Charles-Dominique, 1971; mongoose lemur - Tattersall and Sussman, 1975). In others no consistent pattern is reported (potto, angwantibo, Allen's bushbaby, needle-clawed bushbaby - Charles-Dominique, 1971, 1977; sportive lemur - Hladik and Charles-Dominique, 1974).

A variety of different activity patterns has been reported from studies on captive G. senegalensis and G. crassicaudatus. Activity has been measured in two very different ways: 1) by direct observation, recording time spent on particular behaviours through the night (Pinto, 1972; Pinto, Doyle and Bearder, 1974; Randolph, 1971; Sanderson, 1957; Sauer and Sauer, 1963), or 2) by mechanical recording of movement either in an aktograph cage (Haddow and Ellice, 1964) or by using phtoelectric cells (Ehrlich, 1968).

The patterns reported were not even consistent within these two methods of measurement. For G. crassicaudatus peaks of locomotion in the first and last hours of darkness and a peak of feeding in the first hour were reported and overall the activity pattern was biphasic (Pinto, 1972; Pinto et al, 1974). Sanderson, (1957) found a similar pattern though his animal did not begin its activity until two hours after sunset. The latter author did not report any statistical analyses to confirm his conclusions, nor did he report

how he collected his data. Randolph (1971) found that feeding was fairly constant throughout the dark period except for a significant reduction in the last hour of darkness. Locomotion increased to reach a peak in the eighth hour of darkness, this too was significantly reduced in the last hour. Use of the nest box was significantly increased only in the last hour. Haddow and Ellice (1964) reported a biphasic activity pattern, similar to that described by Pinto (1972), in the two female G. crassicaudatus that they studied. Their male had early-and mid-period peaks of activity with a rest period in between, then irregular activity until dawn. No statistical analyses were reported in this study. Ehrlich (1968) found great variation between individuals and from day to day. The only consistently significant difference between hours was a decrease in activity in the last hour of darkness. Studies on G. senegalensis have reported a unimodal pattern of activity with feeding and locomotion peaking early in the night (Pinto, 1972; Pinto et al, 1974), a biphasic activity pattern with early and late peaks of movement (Haddow and Ellice, 1964) and a triphasic pattern with a peak just before midnight as well as the early and late peaks (Sauer and Sauer, 1963).

Charles-Dominique (1977) found that the pattern of activity in some other nocturnal prosimians in the laboratory could be greatly altered by changing their feeding schedules.

In field studies where time use by the two South African species of bushbaby was considered (using distance travelled per hour as an indication of activity) a bimodal pattern of activity, with peaks of travelling early and late