food. The female thick-tailed bushbaby, though staying with other galagos for less of her time, allogroomed for longer in winter. This was due mainly to the change in her relationship with her offspring; though she was with them for shorter periods as they grew older she was meeting them more often and grooming with them more frequently. Grooming, rather than continual contact, was maintaining their bonds by this time. Young offspring of other females were also old enough to wander alone, meet and be groomed by the focal female.

Though *G. crassicaudatus* was more sociable during its active period than *G. senegalensis* the latter slept with other bushbabies more often than the former. This may have been due to the lesser bushbaby being the more selective species where sleeping sites were concerned. *Acacia mellifera*, which was not very common at Mosdene, was used as a sleeping tree by *G. senegalensis* 80% of the time and only seventeen different trees were ever used on the seventy-two occasions that the sleeping sites of the focal galago were found. In contrast, *G. crassicaudatus* regularly used *Combretum erythrophyllum* and *Acacia karroo* as sleeping trees, both of which were very numerous at Wallacedale, and a total of thirty-five different trees were used on the sixty-two times that the female was found. The larger galago would have fewer potential predators than the smaller and this is likely to be an important factor in the former's apparent lack of concern as to where it slept. However, in different habitats the size of sleeping groups may well change. *G. crassicaudatus* is usually reported to sleep in larger groups than *G. senegalensis*. A female's number of offspring will also
obviously affect the size of sleeping group found. In both species sleeping in groups had certain advantages: bonds between individuals using the same area were maintained; some allogrooming took place in the sleeping site before the galagos became active in the evening or after settling for the night. This would be particularly important for the lesser bushbaby which was alone for most of the night. Allogrooming enabled parasites to be removed from places that could not be reached when autogrooming. In addition, there is a suggestion that sleeping in groups may be an adaptation to avoid insect-borne diseases, each animal in the group having less chance of being bitten by an infected insect than if it were alone (Freeland, 1976). Similarly it may be an adaptation for escaping predation. Sleeping alone is more frequent in winter but this is probably due just to the absence of young offspring.

Bearder's (1969, 1975) figures for the time each species spent in contact with other galagos, though different from those reported in the present study, showed a similar degree of difference between the two species: G. senegalensis spending about 40% more of its time alone than G. crassicaudatus. There was a variety of factors that could have contributed to the intraspecific differences found in the studies. The most obvious was different methods of observation. Most of Bearder's observations on G. senegalensis were in the early morning and evening when the bushbabies tended to be together more than at any other time of the night (Bearder, 1969). For both species it is possible that groups of galagos were easier to find than solitary animals which may have biased
Bearder's figures towards less frequent sightings of individuals. This could not have occurred where data were based on follows of individuals rather than sightings. Differences in habitat could also have contributed to the variation in results. This is likely to be an important factor for *G. crassicaudatus* in particular, as the two populations of this species were using different resources. In Bearder's study (1975) fruits, seeds and flower secretions made up 33% of the galagos' diet during the year whereas they played little or no part in the present study (chapter 3). These resources were probably clumped, widely dispersed and unpredictable so that they would have attracted a number of bushbabies to them. Solitary foraging techniques would not be necessary for these resources so several galagos could feed at one time and then possibly remain grooming and resting together before moving away to forage elsewhere. Population density may have been different in the study areas; higher densities could increase time in contact between individuals. Another difference between the present study and those of Bearder was that the data for this study were collected from follows of females alone instead of from both sexes. However, females would be expected to spend more time with other galagos than would adult males and if a "group" exists at all it is that of mother and offspring. Therefore including males in the study should decrease time in contact with other animals not increase it.

There is evidently a basic social structure found in all the galagos but sociality can show a wide variation depending, essentially, on body size and resource distribution, the
latter causing seasonal variation within a population as well as differences between populations of the same species.
7. SUMMARY

Two nocturnal prosimians, Galago senegalensis and Galago crassicaudatus, were observed at two sites in the Northern Transvaal in South Africa. Detailed behavioural data were collected from a radio collared female of each species. Other bushbabies were trapped and marked to provide information on the social organisation and condition of the population. Faecal samples from a number of bushbabies were collected and analysed to obtain data on the diet of the species. The diet and behaviour, including social organisation, of the two species were compared in summer and winter.

Both species were found to use similar food resources, gum and arthropods. However, different proportions of each were used. The smaller bushbaby, G. senegalensis, used insects as its main food resource in both seasons though gum was used to quite a considerable degree in winter. The larger bushbaby, G. crassicaudatus, took mainly insects in summer but in winter these were replaced almost entirely by gum. In summer the size of arthropod prey taken depended on predator size. When environmental energy was low, as in winter, both species tended to take the same size range of prey items and this was smaller than that taken in summer. Dietary differences between species were explained by body size and consequent differences in metabolic rate. Optimal foraging theory was used to explain the seasonal and, to a certain extent, the species differences in diet.

There was no significant difference in the percentage
time devoted to each activity in each hour through the night by *G. senegalensis* in either season. For *G. crassicaudatus* the proportion of time in each hour devoted to insect foraging differed in summer and that devoted to gum feeding differed in winter. The total time devoted to each activity was dependent on the season and the species. The differences could mostly be explained in terms of animals of a different body size having different time-energy budgets which changed in response to changes in temperature and resource abundance. The distance travelled by both species was not constant in each hour in either season. The differences were probably due to differences in the ambient light levels.

Home range size was found to depend on body size to a certain extent but *G. crassicaudatus* had a heavily used area within its range which was similar in size to the whole area used by *G. senegalensis*. Different activities occurred in relatively discrete patches. These patches were spatially related to feeding patches. A semi-Markov model was used to explain the co-occurrence of feeding and non-feeding behaviours. However, some types of activity were excluded from particular types of feeding patch and it is probable that a hierarchical model of behaviour may be better used to explain the distribution of behaviours in space. Differences in the heights at which feeding behaviour occurred was related to the use of different resources.

The social structure of the two species was very similar. Adult females had either exclusive use of a territory or shared it with one or more related females. Adult males were divided into two social classes; they were either dominant
Central A' males or subordinate 'Central B' animals. 'Central A' males had territories overlapping those of several females in which the non-territorial 'Central B' males were tolerated. Sociality was found to be different between the species. G. crassicaudatus met and groomed more conspecifics and spent less time alone during the night than did G. senegalensis. This was related to the length of time offspring stayed with their mother (a consequence of body size) and to the different foraging strategies adopted by the two species. Both frequently slept with other animals during the day though G. senegalensis was alone slightly less often than G. crassicaudatus. This was suggested to be due to the comparative lack of suitable safe sleeping sites for the lesser bushbaby.

In the present study the behavioural adaptations of South African galagos were related to body size and resource abundance.
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Appendix I

Indigenous Species of the Acacia Thornveld at Mosdene

Acacia hebaclada
Acacia karroo
Acacia luederitzii
Acacia mellifera
Acacia nilotica
Acacia robusta
Acacia tortilis
Burkea africana
Boscia foetida
Boscia albitrunca
Carissa bispinosa
Combretum hereroense
Dichrostachys cinerea
Diospyros lycoides
Euclea undulata
Faurea saligna
Grewia spp.
Maytenus heterophylla
Peltophorum africanum
Rhus lanceolata
Rhus pyroides
Securidaca longipedunculata
Spirostachys africana
Strychnos sp.
Terminalia sericea
Zizyphus mucronata
Appendix 2

Indigenous Species of the Riparian Bush at Wallacedale

Acacia ataxacantha
Acacia karroo
Acacia nilotica
Acacia tortilis
Acacia woodii
Asalypha glabrata
Cassia abbreviata
Combretum erythrophyllum
Combretum hereroense
Combretum spp.
Dichrostachys cinerea
Diospyros Lyoides

Dorvalis zevheri
Ehretia rigida
Euclea sp.
Grewia flavescens
Lonchocarpus capassa
Plectoniella armata
Peltophorum africanum
Rhus pyroides
Rhus rehmanni
Securinega virosa
Zizyphus mucronata
Appendix 3

Weights of adult *Galago senegalensis* trapped in the study site at Kosdene.

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F = Female  
M = Male

Bearder (1969) classified adult females as being 200+ days old and weighing between 150-260gm. Adult males were classified as being 300+ days and weighing 180-300gm.
## Appendix A

**Weights of Adult Galago crassicaudatus Trapped in the Study Site at Wallacedale**

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**F = Female**

**M = Male**

Females of 1½ years and over and males of 2 years and over were considered as adult animals in this species.
Appendix H

Weights of Adult *Galago crassicaudatus* Trapped in the Study Site at Wallacedale

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</tr>
<tr>
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<td></td>
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<td>1200g</td>
<td></td>
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<td>JUN '78</td>
<td>1800g</td>
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</tbody>
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F = Female
M = Male

Females of 1½ years and over and males of 2 years and over were considered as adult animals in this species.
Appendix 5

Single subject research

Experimental design in the behavioural sciences normally requires the use of a number of subjects to provide an estimate of behavioural variability in the population. The use of estimates of variability based on between subject differences is appropriate only when the experimental situation is controlled in such a way as to provide a uniform set of independent variables for each subject. The use of between subject estimates of behavioural variability would require the assumption of an identical environment for each subject and this criterion cannot be met in field studies.

In the place of the usual multiple subject approach to data collection the present study used repeated observations of a single animal to provide estimates of variability in a particular environment. The use of single subject repeated measures designs violates a number of assumptions that are important in many statistical tests, particularly the assumption of independence. However, the violation of this assumption is most likely to lead to type II errors (the acceptance of the null hypothesis when it is false, Snedecor and Cochran, 1967) so any significant differences found in the results will be made more, and not less, valid. Ideally a second female in each species should have been used as a replication in the study but still the data would have been analysed separately for the two animals within a species.

Studying sympatric populations of the two species would have provided a more similar environment in terms of resource
availability but in this situation the way the animals used
the resources would be different due to competition and the
resultant niche divergence. The allopatric populations
chosen were as similar as possible in terms of food resources
used as this was thought to be a very important factor in
structuring behaviour. The individuals selected were also
as similar as possible; both were multiparous females that
were known to have been in the area for several years.
Neither area was isolated so there was no reason why abnormal
social organisations should have been found.
Appendix 6

The definitions of behavioural categories are listed below. Only those behaviours observed in the field are defined.

FEEDING: The actual ingestion of a particular resource. In the case of insect-feeding, handling time was included in this category.

FORAGING: The searching for resources.

INSECT-FORAGING: If the animal was looking up and around and grabbing at objects, often at the end of branches, or if it was searching through the grass or dead leaves on the ground.

GUM-FORAGING: When the animal was moving fairly slowly, looking down at or sniffing along a branch.

TRAVEL: Fairly rapid, directed movement, usually between trees.

MOVING: A relatively slow progression over a short distance, usually within one tree.

GROOMING: Scraping with the teeth or licking at fur. In contrast to many other primates, hands are not used for grooming by galagos.

AUTOGROOMING: Self-directed grooming (Fig. 32).

ALLOGROOMING: Other galagos groomed or were groomed by the focal animal (Fig. 32).

RESTING: Sitting motionless, sometimes with the eyes closed.

PLAYING: The animals would chase each other over short distances or wrestle together but the interactions were always silent. Partners in these bouts were usually infants, juveniles or infants and juveniles, though older animals would
Figure 32. (a) Autogrooming and (b) allogrooming by *G. crassicaudatus* (in the laboratory).
play with younger ones occasionally.

**AGONISTIC INTERACTIONS:** Both fights and chases were seen. These were distinguished from play bouts by the aggressive calls (Andersson, 1969; Bearder, 1975) which accompanied the interactions. Fierce fighting as described by Andersson (1969) was never seen.

**MARKING BEHAVIOUR**

**Urine-washing:** The hand and foot on one side of the body are raised simultaneously. The hand is cupped beneath the ano-genital region and a few drops of urine discharged onto it. The hand then rubs or grasps the sole of the foot. This may be repeated using the other hand and foot.

**Hind-foot Rubbing:** Rapid scraping of the under surface of the hind foot along a branch or tree trunk. Only *G. crassicaudatus* was seen to behave in this way.

**Chest Rubbing:** The bushbaby lowers its chest to a branch and pushes backwards and forwards with a sliding movement, wrapping both arms round the branch where necessary to keep itself in position. It has been reported in both species (Andersson, 1969; Bearder, 1975; Katsir, 1979) but was observed only in *G. crassicaudatus* in this study.

**Chin Rubbing:** Rubbing the chin, side of the mouth or other parts of this face on a surface, usually the end of a branch. Andersson (1969) reports this in *G. senegalensis* but it was only seen in the thick-tailed bushbaby in the present study.

**Ano-genital Rubbing:** Both male and female *G. crassicaudatus* were seen to lower their hindquarters and rub their ano-genital regions against or along a branch. This has not been reported to occur in *G. senegalensis*. 
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Figure 33. *G. senegalensis* urine-washing.
### Analysis of *Acacia karroo* gum

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Analysed by A. S. Wehmeyer  
National Food Research Institute  
C.S.I.R., South Africa.