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

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19. SUMMARY

1. Observations of the behaviour and ecology of Thick-tailed Bushbabies (Galago crassicaudatus) have been carried out over a period of eighteen months between February 1970 and August 1971. Detailed information was collected during fifteen months in a single study area while comparative observations were made in two other widely separated localities. Individual bushbabies, or groups, were followed for long periods at night using red light from a headband torch and a strong beam of white light from a hand lantern when necessary. A total of 663 animal observation hours were made, concentrating on the evenings and mornings when the animals were most active. Eleven bushbabies were caught in traps, of which four were housed under semi-natural conditions and the remainder marked for easy identification prior to their release. The data which were obtained are compared with those for other nocturnal prosimians, particularly the Lesser Bushbaby (G. senegalensis), the only other prosimian in southern Africa, which is sympatric with the study species in some areas.

2. The distribution of G. crassicaudatus is outlined in comparison with that of G. senegalensis. Effective isolation of breeding populations appears to have resulted in a number of sub-species, but the classification remains unclear. Three populations of G. crassicaudatus, which are generally considered as separate sub-species, were studied in different habitat types: G.c. umbrosus Thos. in riverine bush of the North Eastern Transvaal; G.c. garnetti (Ogilby) in forest habitats of Zululand and G.c. lönnbergi Schwarz in open woodland of Eastern Rhodesia. Each study area is described in terms of its vegetation, topography and climate, with a list of other local primate species. A few size and weight measurements are presented for individuals of the first sub-species from the main study area.

3. G. crassicaudatus are found at various altitudes and show tolerance to marked seasonal and diurnal variations in temperature. The species occurs in relatively open habitats but it is typically confined to dense evergreen vegetation. Estimations of population densities indicate that G. crassicaudatus are most abundant in high rainfall, humid

forest areas where there are many trees bearing fleshy fruits. This contrasts with G. senegalensis which are most common in semi-arid acacia thornveld. The relatively high population densities of both species when compared with related forms in tropical forest habitats can be explained as a result of the few nocturnal arboreal competitors.

4. G. crassicaudatus are strictly nocturnal. They leave cover after sunset and return before sunrise at times which are dependent on the level of light intensity beneath the trees. Activity at night follows a broadly bimodal pattern, with periods of rest tending to increase towards midnight. Long spells spent in a single tree are often followed by sudden movement through several trees. This pattern is basically similar to that of G. senegalensis, although this species shows many short bursts of movement during each hour. The difference between the two species in this respect may be related to divergence in their feeding habits. The similarity of the circadian activity cycles of these prosimians in the wild and under artificial conditions in captivity suggests an 'internal clock' which governs the general level of activity at any one time.

5. Fruits and resins (gums) represent the staple diet of G. crassicaudatus in the main study area but seeds, nectar and insects are also consumed. Moisture may occasionally be licked from leaves but otherwise bushbabies have not been seen to drink. Gum is extremely important in the winter when soft fruits are not available. Particular gum licks are well known to the animals, they are visited regularly and appear to be remembered. Gum is obtained by licking, or by first biting and then licking, but not by scraping with the lower anterior teeth. A remarkable number of gum licking postures may be assumed which enable this species to reach gum which is unavailable to food competitors. Continuous exploration ensures that small new sources of food are not missed but large sources may be smelled from a distance. The animals return repeatedly to certain food trees for as long as they remain productive. Predation on birds and other small vertebrates has often been reported for G. crassicaudatus but evidence is presented to show that it is not a universal characteristic. It appears to be a local habit which may spread within a population while being absent from another nearby. G. senegalensis also eat gum, particularly during the winter, but otherwise they are predominantly insectivorous. They catch insects by means of a ritualized prey catching strike, which G. crassicaudatus lack, and

they are able to survive in the absence of free water.

6. The locomotory postures of G. crassicaudatus are described and illustrated and compared with those of G. senegalensis and other prosimians. The overall pattern of locomotion differs from that of other Galaginae and is in many ways similar to that of the Lorisinae. Despite the morphological specializations which suit an active leaping mode of progression, this species is behaviourally adapted to a slower quadrupedal gait. This may be interpreted as a relatively recent adaptation for obtaining food by stealth in a forest environment, which has not been matched by skeletal changes. Undoubtedly the ability to move quietly also enables bushbabies to avoid detection by potential predators but, nevertheless, they are still capable of rapid escape. Similarities between the locomotion of G. crassicaudatus and the slower moving Perodicticus potto are considered to be a result of convergent adaptation.

7. G. crassicaudatus make regular use of a number of sleeping places during the day which provide concealment and direct protection from predators and extremes of temperature. Nest building is rare but it has been seen during the breeding season when young infants may require a suitable support. The offspring may be afforded additional protection from predators at this time by their mothers' habit of moving them from one sleeping place to another. This behaviour is similar to that of G. senegalensis which, however, continue to build nests after they are no longer essential for the support of the young. Members of this species will sleep in exposed places, relying to a greater extent on their colouration for camouflage, and they will move in the face of a threatening stimulus or a change in weather conditions.

8. G. crassicaudatus have a restricted breeding season at least in the southern part of their range. All births occur within a single period of approximately three weeks at the start of the rainy season when food and dense cover is readily available. Twins are most common but triplets and a singleton have also been recorded. Mating is correspondingly restricted to a short period in mid-winter and it is accompanied by a general increase in the level of excitability within a population. G. senegalensis have two birth and mating periods during the year but, like G. crassicaudatus, practically all infants are weaned by the end of the wet summer months.

9. G. crassicaudatus sleep either alone or in small family groups of two to six animals which may include an adult male, an adult female

and the offspring of one or two generations. The male and maturing offspring will often sleep alone, while the female and her youngsters usually sleep together. An examination of the social dynamics and mother/offspring relationship within a single group has been used to illustrate the development of the young and the nature of associations between individuals. In contrast to most other nocturnal prosimians, in which the sleeping groups split up for much of the night, G. crassicaudatus are commonly found in small groups whose members forage together. It is the female and the young which move together as a cohesive unit. Even when the infants are too small to follow the mother she will carry them from place to place, either in her mouth, one at a time, or with them clinging to the fur of her back, or both. This close association continues until the offspring are at least sub-adult. The range of the adult male may coincide to a large extent with that of the maternal group but he generally remains alone. He occasionally joins the group and moves with it without any signs of serious hostility. Even larger groupings may be formed through attraction to a particular food source.

10. The movements and use of space of G. crassicaudatus are discussed with reference to night range and annual home range. Rapid movements between feeding trees are made by way of regular pathways but when moving slowly the animals make a variety of deviations which allow exploitation of food sources at different heights over a large area. There is evidence that sight and hearing coupled with a kinaesthetic sense are important aids to movement rather than scent trails through the trees. In the main study group the adult male moved over a wider range than the female and offspring which utilized an annual home range of seven hectares. The maternal group spent most time in a central core area containing many sleeping sites, food trees and resting places yet covering only 4% of the total range. The male made use of the same fixed points but he frequented a different core area. The use of fixed points varied during the year and seems to depend on custom and convenience as much as on their suitability. Seasonal changes in the focus of activity can be related to the productivity of favourite food trees. G. crassicaudatus, like many other primate species, show little in the way of active territorial defence but groups may remain attached to a single range for long periods, while much of their behaviour maintains internal cohesion and ensures the dispersal of maturing individuals and separation between groups. Differences in the pattern of movement in a variety of

habitats indicate that the height or density of the vegetation has little direct effect on the distribution of this species, although it is somewhat less versatile in its movements than the smaller G. senegalensis.

11. Various aspects of social behaviour in G. crassicaudatus are described and discussed in relation to the establishment and maintenance of social ties and the spacing mechanisms between conspecifics. Bushbabies are able to groom almost all parts of the body by autogrooming using the tongue, ventral anterior dentition, or tooth-scraper, and the toilet claws on the second pedal digits. Yet allogrooming is performed at a high frequency which suggests that it serves important social functions. The amount of time spent allogrooming in this species is greater than for G. senegalensis in which group members spend less time together. It appears to enhance intra-group harmony and it may aid friendly contact between compatible strangers. Play is considered as a second cohesive force which serves a number of other functions as well. G. crassicaudatus perform six marking and/or rubbing actions in a variety of situations. Particular places are marked repeatedly and these may act as information posts of significance in a territorial or social context, or they may merely reassure the marker. It is suggested that the complex ritualized pattern of urine washing was originally derived as an adaptation to help maintain an effective grip in small active primates following the loss of claws. A detailed comparison of the vocalizations of G. crassicaudatus and G. senegalensis shows up remarkable structural and functional similarities in their vocal repertoires, while the differences correlate with divergencies in group structure and the rearing of the young. Finally, agonistic behaviour is outlined and compared with similar interactions by bushbabies in captivity where the types of encounters are often unnatural. Antagonism between individuals is mediated by mutual recognition of the sex and status of a social fellow or rival. Intra-group tension is mild and spacing mechanisms ensure that fighting between strangers is rare. G. crassicaudatus has a basically similar social structure to other nocturnal prosimians which have been studied but it shows trends towards a better developed social way of life through increased social contact between the mother and her offspring.

12. Some potential predators of G. crassicaudatus are listed and their importance discussed briefly. A number of the behavioural characteristics of the species enable it to avoid detection in most cases. It

is particularly vulnerable on the ground and it is often reluctant to descend unless this is unavoidable. Bushbabies may interact with a number of non-predatory species and the nature of some relationships is noted.

13. In conclusion the similarities and differences between the ecology and behaviour of G. crassicaudatus and G. senegalensis are discussed and the important factors which bring about their ecological separation are outlined. By making comparisons with other closely related species it is possible to speculate on the probable condition of the ancestral species and on the ways in which the recent forms have become specialized.

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APPENDICES

Appendix 1. Mean temperatures (t,^{o}C), precipitation (p,mm) and relative humidity (h, %) for the study areas of a) G.c. umbrosus b) G.c. garnetti and c) G.c. lönnbergi

	Month	t,^{o}C Max.	Min.	p,mm	h,% 0800 hrs.
(a)	J	29.1	17.7	352	82
	F	28.6	17.7	307	85
	M	27.7	16.4	280	88
	A	26.8	13.4	95	87
	M	25.1	8.4	44	86
	J	23.2	5.1	20	85
	-				
	J	23.1	5.0	29	83
	A	24.8	6.8	28	79
	S	27.0	10.0	49	73
	O	28.8	13.4	109	73
	N	29.0	15.4	189	78
	D	29.8	16.8	266	80
	YEAR	26.8	12.2	1768	80

	Month	t, °C Max.	Min.	p, mm	h, % 0800 hrs.
(b)	J	27.7	17.6	127	79
	F	28.0	18.1	145	85
	M	26.6	17.3	203	88
	A	25.4	15.5	121	88
	M	23.9	13.3	103	85
	J	22.2	11.4	98	85
	-				
	J	22.0	11.0	75	84
	A	23.3	11.8	59	84
	S	24.2	13.2	63	85
	O	24.9	14.6	81	83
	N	25.9	15.9	106	81
	D	27.4	17.3	111	79
	YEAR	25.1	.2	1292	81
(c)	J	26.9	17.5	34	89
	F	26.1	16.1	23	89
	M	27.1	15.9	25	83
	A	26.6	14.5	19	83
	M	22.7	9.5	78	77
	J	20.6	8.0	05	79
	-				
	J	21.5	7.5	02	69
	A	24.3	10.0	11	68
	S	26.3	11.4	10	60
	O	26.6	14.5	05	70
	N	26.2	16.1	45	85
	D	27.5	16.6	41	83
	YEAR	25.2	13.1	298	78

Appendix 2. Scientific names for exotic trees and fruits referred to in the text. (For detailed descriptions and illustrations see Masefield et al., 1969 and Immelman et al., 1973.)

Common name(s)	Species
Anonaceous fruits - Custard apples	Anona spp.
Avocado pear	Persea americana
Banana	Musa spp.
Bluegum	Eucalyptus globulus
Cherry guava - Strawberry guava	Psidium cattleianum
Fig	Ficus carica
Grapevines	Vitis spp.
Guava	Psidium guajava
Indian mahogany	Cedrela toona
Jacaranda	Jacaranda mimosaefolia
Litchi	Litchi chinensis
Mango	Mangifera indica
Mulberry	Morus nigra
Papaya - Paw paw	Carica papaya
Passion fruit - Purple granadilla	Passiflora edulis
Pines	Pinus spp.
Wattle (Australian)	Acacia cyanophylla

Appendix 3. Predominant indigenous trees and climbers of the riparian bush in the North Eastern Transvaal showing known food trees (÷) and those bearing fleshy fruits (+).

Acacia ataxacantha ÷
Acacia karoo ÷
Adina microcephala
Albizia versicolor ÷
Andrachne ovalis
Annona senegalensis +
Antidesma venosum +
Apodytes dimidiata
Bauhinia galpini
Bequaertiodendron megalismontanum +
Brachylaena discolor
Bridelia micrantha ÷ +
Bridelia mollis +
Canthium ventosum +
Canthium mundianum +
Carissa bispinosa +
Cassia spp.
Catha edulis
Celtis agricana +
Cephalanthus natalensis +
Chaetachme aristata
Combretum kraussii
Combretum collinum
Combretum molle
Combretum zeyheri
Croton sylvestris
Cryptocarya liebertiana +
Curtisia dendata
Cussonia spicata +
Dalbergia armata
Diospyros mespiliformis ÷ +
Dombeya rotundifolia
Ekebergia capensis ÷ +
Encephalartos transvenosus +
Erythrina lysistemon
Fagara davyi
Ficus capensis ÷ +
Ficus ingens +
Ficus petersii +
Ficus sonderi +
Ficus stuhlmanni ÷ +
Ficus sycamorus ÷ +
Gardenia amoena +
Gardenia jovis-tonantis +
Gardenia spatulifolia +
Grewia occidentalis
Halleria lucida +
Harpephyllum caffrum +
Heteropyxis natalensis
Lannea discolor +
Lannea edulis +
Lonchocarpus capassa
Maesa lanceolata
Maytenus heterophylla
Mimusops zeyheri ÷ +
Mimusops obovata +
Ochna atropurpurea

Ochna holstii
Parinaria curatellifolia +
Pavetta scumanniana
Piliostigma thonningii
Protorhus longifolia +
Pterolobium exosum
Pterocarpus angolensis
Pterocarpus rotundifolius
Rapanea melanophloeos +
Rauvolfia caffra +
Rawsonia lucida +
Rhoicissus tomentosa +
Rhus chirindensis +
Rothmannia capensis +
Sclerocarya caffra +
Scolopia zeyheri +
Scotia brachypetala +
Scheffiera umbellifera +
Strychnos spinosa +
Strychnos innocua
Strychnos mitis +
Strychnos usambarensis +
Syzygium cordatum + +
Syzygium gerrardii +
Syzygium guineense +
Terminalia sericea
Tapiphylum parvifolium +
Trema orientalis +
Trichilia emetica
Vangueria infausta +
Ximenia caffra +

Ochna holstii
Parinaria curatellifolia +
Pavetta scumanniana
Piliostigma thonningii
Protorhus longifolia +
Pterolobium exosum
Pterocarpus angolensis
Pterocarpus rotundifolius
Rapanea melanophloeos +
Rauvolfia caffra +
Rawsonia lucida +
Rhoicissus tomentosa +
Rhus chirindensis +
Rothmannia capensis +
Sclerocarya caffra +
Scolopia zeyheri +
Scotia brachypetala +
Scheffiera umbellifera +
Strychnos spinosa +
Strychnos innocua
Strychnos mitis +
Strychnos usambarensis +
Syzygium cordatum + +
Syzygium gerrardii +
Syzygium guineense +
Terminalia sericea
Tapiphylum parvifolium +
Trema orientalis +
Trichilia emetica
Vangueria infausta +
Ximenia caffra +

Appendix 1. Predominant indigenous trees and climbers of the coastal dune forest at Mtunzini in Zululand showing plants bearing fleshy fruits or gum (+).

Acacia sieberiana +
Acokanthera oblongifolia +
Albizia adianthifolia
Albizia versicolor +
Aloe bainesii
Allophylus natalensis
Annona senegalensis +
Andidesma venosum +
Apodytes dimidiata +
Barringtonia racemosa
Bersama lucens
Brachylena discolor
Bridelia micrantha +
Burchellia bubalina
Calpurnia aurea
Canthium obovatum +
Canthium ventosum
Carissa bispinosa
Carissa macrocarpa
Cassine aethiopica
Cassine papillosa
Clausena anisata
Clerodendrum glabrum
Colpoon compressum
Cordia caffra
Cussonia chartacea
Cussonia kraussii
Cussonia spicata
Cyathea dregei
Dalbergia armata
Dalbergia obovata
Deinbollia oblongifolia
Dichrostachys cinerea
Dovyalis rhamnoides
Dovyalis zeyheri +
Drypetes natalensis
Ekebergia capensis +
Erythrina lysistemon
Euclea natalensis+
Eugenia zuluensis +
Fagara capensis+
Ficus capensis +
Ficus burtt-davyi +
Ficus hippopotami +
Ficus natalensis +
Grewia occidentalis
Halleria lucida +
Harpephyllum caffrum +
Hibiscua tiliaceus
Hyphaene crinita
Ilex mitis
Macaranga capensis
Maesa lanceolata
Maytenus heterophylla
Maytenus undata
Mimusops caffra +
Myrica serrata
Ochna arborea
Ochna natalita
Olea woodiana +

Passerina falcifolia +
Peddiea africana +
Phoenix reclinata +
Popowia obovata
Protorhus longifolia +
Psycnotria capensis +
Rapanea melanophloeos
Raphia australis
Rauvolfia caffra +
Rhus macowani
Sapium ellipticum
Sapium integerrimum
Scheffiera umbellifera
Sclerocarya caffra +
Scolopia zeyheri +
Scutia myrtina +
Sideroxylon inerme +
Strelitzia nicolai
Strychnos innocua +
Strychnos spinosa +
Syzygium cordatum +
Trema orientalis +
Tricalysia sonderiana
Trichilia dregeana +
Trimeria rotundifolia
Turraea floribunda
Vangueria infausta +
Vepris undulata +
Voacanga thouarsii
Xeromphis obovata
Ximenia caffra

Appendix 5. Predominant indigenous trees and shrubs of the woodlands near Umtali, Rhodesia.

Acacia abyssinca
Acacia campylacantha
Acacia karoo
Acacia sieberiana
Albizzia gummifera
Annona cuneata
Annona senegalensis
Antidesma venosum
Azanza garckeana
Bauhinia galpinii
Bauhinia petersiana
Bolusanthus speciosus
Bridelia micrantha
Calodendrum capense
Carissa edulis
Cassia capensis
Cassia floribunda
Celtis africana
Chaetacme aristata
Clerodendrum glabrum
Combretum mollii
Craibia brevicaudata
Cussonia kirkii
Cussonia natalensis
Cussonia spicata
Diospyros lycioides
Diospyros sericea
Encephalartos manikensis
Ficus capensis
Ficus sycomorus
Ficus quibeba
Fluggea microcarpa
Gardenia imperialis
Grewia caffra
Maytenus spp.
Mimusops zeyheri
Olea africana
Pavetta assimilis
Peltophorum africanum
Phoenix reclinata
Pittosporum viridiflorum
Rhus longipes
Rothmannia manganjae
Sapium ellipticum
Scheffiera umbellifera
Spathodea campanulata
Steganotaenia araliacea
Synadenium sp.
Syzigium cordatum
Teclea nobilis
Trichelea emetica
Vernonia amygdalina

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