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Ecology and Population Dynamics of *Colobus guereza* in Ethiopia

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Abstract. The ecology of *Colobus guereza* in Ethiopia is described. Data on group size from a number of localities are given, and groups are typically found to be one-male groups of 5–8 animals. The dynamics of one population are discussed with particular reference to birth and death rates and immigration and emigration. Daily activity patterns and use of home ranges are described. The ecological determinants of population density, group size and home range size are investigated.

Key Words
C. guereza
Population dynamics
Diet
Range use
Density

The colobines of Asia *(Presbytis* spp.) have been extensively studied during the past 10 years. Those of Africa *(Colobus* spp.) have, however, been relatively little studied, although this imbalance is currently being rectified. The black and white colobus, *Colobus guereza*, has been the subject of several field studies in East Africa (VON ULLRICH, 1961; SCHENKEL and SCHENKEL-HULLIGER, 1967; LESKES and ACHESON, 1971; MARLER, 1972; J. F. OATES, personal commun.]. However, with the exception of OATES' study, these studies have been concerned primarily with social behaviour and communication.

The present study reports on the ecology of *C. guereza* groups in Ethiopia in an attempt to provide quantitative data for comparison with the East African studies.

Methods

The main study was carried out in the Bole Valley (9° 25′ N,38° 33′ E). A preliminary 10-day study was made in May 1971, and the bulk of the datawas collected between May and September 1972. Colobus groups were under observation for a total of 192 h,

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with observation distances varying from 10 to 300 m. In addition, a number of other localities was visited for periods of 2–3 days, with a view to assessing group sizes in different areas and the range of habitats occupied by *C. guereza* in Ethiopia. Figure 1 shows the locations of the study sites, together with other areas where colobus are known to occur.

The Bole Valley is a box canyon, some 600 m deep, the river bed being at an altitude of 1,700 m. A narrow gallery forest lined the river bed, consisting mainly of *Ficus* spp., *Albizia grandibracteata*, *Celtis ?africana*, *Syzigium guineense* and *Podocarpus gracilior* with a dense undergrowth. The canopy reached a maximum height of 30 m. In two sections, the undergrowth had been cleared and coffee planted beneath the canopy. In one section, the forest trees had been replaced by imported *Grevillea* sp. The forest

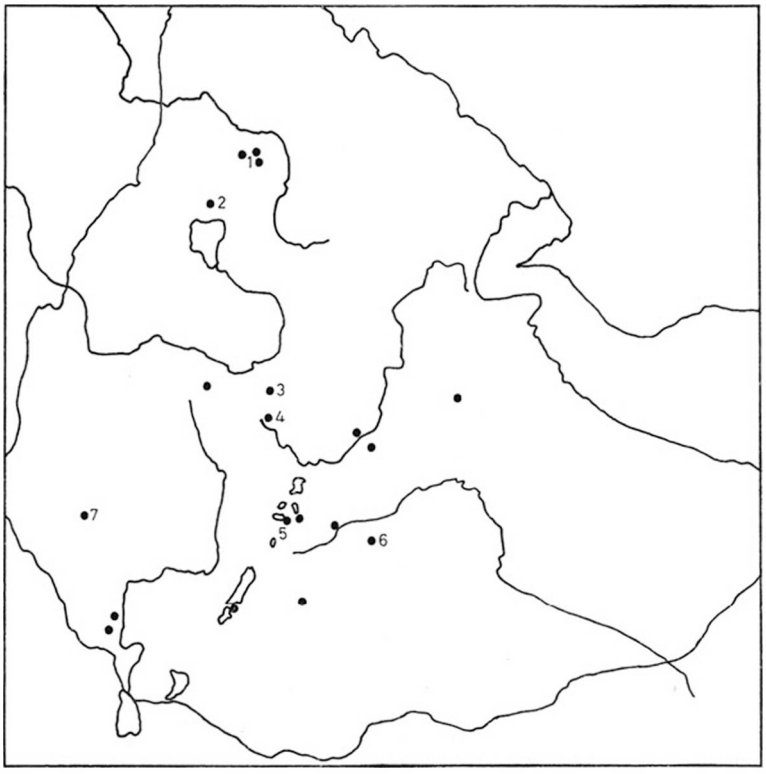


Fig. 1. Distribution of *Colobus guereza* in Ethiopia, showing study areas and other sites where colobus were observed or are reported to occur. 1 = Simien Mountains; 2 = Gondar; 3 = Bole Valley; 4 = Mt. Wochacha; 5 = Lake Shalla; 6 = Mt. Gaysay; 7 = Godare.

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was bounded by sheer sandstone cliffs up to 60 m in height. Above these, the lower, flatter slopes of the valley were covered by a dense mass of vegetation up to 5 m in height, consisting mainly of *Olea ?africana*, *Acokanthera schimperi*, *Combretum glaucescens* and *Rhus* sp. This area was dissected by deep gullies, in the heads of which dense patches of forest occurred round natural springs. The steep upper slopes of the valley are covered by grass, with scattered *Olea* and other bushes. A more detailed description of the study area is given elsewhere [DUNBAR and DUNBAR, in press].

Activity counts of all visible animals [*vide* CROOK and ALDRICH-BLAKE, 1968] were carried out at 10-min intervals throughout periods of observation during May–June.

Criteria for sexing individuals were identical to those used by MARLER [1972]; in addition, the male's penis and the female's teats were often clearly visible and provided clear means of identification at close quarters. The age-sex classes used in this study are listed in table I.

Results

Group Size and Composition

Table II gives the sizes and compositions of the 18 groups of colobus living in the valley. The compositions are given as of May 1972. The 17 groups whose compositions are completely determined have an average size of 6.7 individuals, a figure slightly lower than that of 8 given by MARLER [1972] for colobus groups in the Budongo forest, Uganda. However, the

Table I. Age-sex classes

Class	Approximate age[1]	Description
Adult	♂ 5 years + ♀ 3 years +	full size, ♂ slightly larger than ♀; teats clearly visible in ♀, penis visible in ♂
Subadult	♂ 2–5 years ♀ 2–3 years	smaller than adult; ♂ slightly larger than ♀; teats not visible in ♀; canines small in ♂, penis long
Juvenile	1–2 years	up to ca. half adult size; ♂'s penis small (not pendulous as in adults and subadults); completely independent of mother
Black and white infant	5–12 months	small; adult colouration; dependent on mother, but will move away on own; always carried by mother during progressions
White infant	0–4 months	all white in colour; totally dependent on mother

[1] Age estimates are based on those provided by J. F. OATES [personal commun.], since his categories seem to be identical to ours.

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Table II. Group sizes and compositions in the Bole Valley as of May 1972

Group	♂	♀	?ad	M	F	?S	J♂	J♀	?J	I	B	Total
I	1	2	–	–	2	–	–	1	–	–	1	7
II	1	1	–	–	1	–	–	–	–	–	–	3
IIIa	1	3	–	–	–	–	2	1	–	1	1	9
IIIb	1	2	–	1	–	1	–	1	1	–	–	7
IV	3	2	–	1	1	–	2	1	–	–	–	10
V	1	2	–	1	–	–	–	1	–	–	1	6
VI	3	3	–	1	1	–	2	–	–	–	–	10
VII	1	1	1	1	–	–	–	–	3	?	–	8
VIII	1	3	–	1	1	–	4	–	–	–	1	11
IX	1	2	1	1	–	–	1	–	1	1	–	8
X	–	2	–	1	–	–	1	–	–	–	–	4
XI	1	1	1	–	–	–	–	–	1	–	–	4
XII	1	1	–	–	–	–	–	–	1	–	1	4
XIII	1	2	1	–	1	1	2	–	–	–	1	9
XIV	–	–	4	–	–	–	–	–	1	–	–	5
XV	1	1	1	–	–	–	–	–	1	1	1	6
XVI	1	1	1	–	–	–	–	–	1	–	–	4
XVII	1	1	–	–	–	–	–	–	2	–	–	4+

♂ = Adult ♂♂; ♀ = adult ♀♀; ?ad = unsexed adults; M = subadult ♂♂; F = subadult ♀♀; ?S = unsexed subadults; J♂ = juvenile ♂♂; J♀ = juvenile ♀♀; ?J = unsexed juveniles; I = black and white infants; B = white infants.

range of group size in the two areas is similar (3–11 at Bole, 2–13 at Budongo), and the Bole groups are not significantly smaller (Mann Whitney U test, $p > 0.10$).

All except 3 of the groups were one-male groups. MARLER [1972] found a similar ratio of one-male:multi-male groups both at Budongo and the Queen Elizabeth II National Park, though KOFORD [quoted in MARLER, 1972] found a higher porportion of multi-male groups in the Kibale Forest, Uganda.

Group sizes were also sampled in a number of other areas in Ethiopia: in mixed *Ficus* and *Acacia tortilis* lake-side forest at Lake Shalla (1,500 m); in *Ficus* and *Hagenia* forest on the Simien Mountains escarpment face (ca. 3,000 m); in *Juniperus* forest on Mt. Wochacha (Menegasha Forest Reserve, 2,500 m) and at Gondar (2,200 m); and in *Hagenia abyssinica* forest on Mt. Gaysay (Bale National Park, 3,300 m). 6 groups were located and counted at Shalla; these had an average size of 6.8 (range 4–10). 4 of these were

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one-male groups, the remaining 2 each having 2 adult males. In the Simien, we counted groups of 7 and 11 below Sankaber, and on the Wolkefit Pass (30 km to the west), 10 groups were counted with an average of 5.6 individuals (range 3–8). On Mt. Wochacha, groups of 8, 5 and 3 were counted, and at Gondar, a single group of 4 was observed in relict *Juniperus* forest in a monastery compound, all of these 4 groups being one-male groups. A single group of 2 adults was observed on Mt. Gaysay. BROWN and URBAN [1970] counted groups of 6, 4, 4, and 3 at Bagadur near Godare in the south-west forests *(Cordia abyssinica* and *Ficus* spp. at 950 m altitude).

As MARLER [1972] notes, one-male groups of between 6 and 10 in size would appear to be typical of the species. The largest group so far recorded was one of 15 by SCHENKEL and SCHENKEL-HULLIGER [1967], and this would seem to be the upper limit for group size.

Population Dynamics

In May 1971, we were able to obtain accurate counts of 5 groups in the Bole Valley river bed, and it proved possible to trace changes in composition of these groups over the succeeding 17 months. These changes are shown in table III. Since we did not visit the valley between May 1971 and May 1972, it is possible that some changes might have occurred which we are unable to detect: an adult male might have died, for instance, and been replaced by one from another group. We are confident, however, that no such changes occurred, and we are able to account for all the juveniles and infants which were present in 1971. It is, however, possible that more infants might have been born during the year we were absent, but died before we returned to the study area. At most, however, only two such cases could have occurred (see below).

In May 1971, the 5 groups comprised a total of 37 individuals. By May 1972, 6 births and 1 disappearance (an adult female) brought the total at the end of 12 months to 42, an increase of 5 (13.5%). In the succeeding 5 months (May–September 1972 inclusive), a further 2 births occurred, 3 infants died, and 1 subadult male immigrated into the subpopulation, resulting in no further increases in the size of the population by the end of September 1972. Assuming that there is no birth peak, this would give an annual rate of increase of 9.5%. However, since the valley was a more or less closed population, an immigration into one group must be counterbalanced by an emigration from another, and immigrations should consequently be discounted: this would give an annual rate of increase of 7.6% *per annum* based on a 17-month period.

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Table III. Changes in group composition over 17 months

Group	1.5. 1971		1.5. 1972		31.5. 1972	30.6. 1972	31.7. 1972	31.8. 1972	30.9. 1972
I	♂♀♀J♀ J♀I	(6)	♂♀♀FFJ♀ B	(7)	x	x	x	(B = I)	x (7)
II	♂♀♀J♀	(4)	♂♀F	(3)	x	+B	x	(B = I)	x (4)
III	♂♂M♀♀♀♀♀J♂ J♀ JI	(12)	a ♂♀♀♀J♂ J♂ J♀IB	(9)	x	x	−B + M (J♀ = F)	x	(I = J♀) (9)
			b ♂MS♀♀JJ♀	(7)	x	x	x	x	x (7)
IV	♂♂♂M♀♀FJ♂ J♂ J♀	(10)	no change		+B −B	x	(J♀ = F)	x	x (10)
V	♂M♀♀J♀	(5)	♂M♀♀J♀B	(6)	x	−B	x	x	x (5)
VIII	uncertain		♂M♀♀♀FJ♂ J♂ J♂ J♂B	(11)	x	x	x	−F (B = I)	x (10)

Symbols for age-sex classes are as for table II. Subsequent changes in composition are indicated as follows: + = birth or immigration; − = death or emigration; changes in the ages of individuals are indicated as, for example, (B = I); x = no change in composition.

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One group (group III) underwent fission between May 1971 and May 1972. In May 1971, this group was frequently observed split into two or three distinct sections up to 50 m apart. The other groups in the area were invariably more compact than this, and it seems likely that the fission process had begun some time before. By May 1972, the two subgroups had separated completely, the smaller section (IIIb) moving into a new home range up one of the gullies. They were observed intermittently until the end of the study in the gallery forest at the base of the gulley, where they once joined group IIIa for a morning. If this represents a constant rate of fission for 5 groups over 17 months, then a fission rate of 0.14 divisions/group/year is suggested. This would imply that each group undergoes fission once in every 7 years.

During the 12-month period May 1971 to May 1972, 6 infants were born to the 12 females in the population, giving an average of 0.5 births/year/female, or 1 birth every 2 years. (The female who disappeared from group II has been discounted from this calculation.) It is considered unlikely that any of the other females in the population gave birth to, but lost, an infant during the year, since 2 of these gave birth in May 1972, and 2 already had young infants in May 1971; the remaining 2 females both belonged to group IV which had 3 adult males, and the tensions in the group may have interferred with the group's breeding efficiency. If these 2 females did give birth but lost their infants, the minimum inter-birth interval would be 18 months.

The death-rate among infants is high: 3 infants died before colour change was complete out of 8 born during the study (37.5%). Deaths after the colour change were less common. 1 adult female disappeared from group II during the year we were away, and 1 subadult female disappeared from group VIII during August 1972. Since the groups were well known by this time, and the latter female was clearly identifiable, yet could not be located, it may be presumed that she at least died. This gives a total of 2 deaths in 724 animal-months (0.036 deaths/animal/year) or 3.6% *per annum* for the subpopulation of 47 animals. This is approximately one third of the annual death rate for pre-colour-change infants (10%).

Although no emigrations took place from the subpopulation, a subadult male immigrated into group IIIa in July 1972, giving an immigration rate of 0.017/animal/year, or 1.9% *per annum* for the subpopulation of 37 animals.

Daily Activity Pattern and Use of Habitat

Colobus are essentially sedentary animals, spending much of their time in the trees in inactivity. A period of inactivity is generally followed by movement, then feeding, followed again by inactivity. This cycle is repeated three

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times during the day, as illustrated by the activity count data in figure 2. The figure shows 3 peaks of feeding: a small one around 08.00 h, and two major peaks around midday and late in the afternoon. These data are, of course, primarily for the dry season, and the pattern might well change during the rains. The pattern is, however, typical of many other forest monkeys in the dry season, e.g. *Cercocebus albigena* [CHALMERS, 1968] or *Cercopithecus mitis* [ALDRICH-BLAKE, 1970].

The colobus seldom travelled more than 200–300 m during the course of a day; indeed, sometimes groups remained within the same *hectare* of ground throughout the day. An analysis of 29 days on which a group's day range was known gives an average distance travelled of 260 m (range 75–500 m). Most of this movement takes place in 2 brief periods of travel, 1 midmorning (usually between 09.00 and 11.00 h) and 1 later in the afternoon when the animals return to their sleeping trees.

Although territory sizes were small (see below, fig. 3), a tendency for groups to use the various parts of their ranges differentially was noted. This can be illustrated in the case of two neighbouring groups, IV and VIII. The locations of these two ranges is shown in figure 3.

Group IV's range fell partly in the gallery forest in the river bed and partly in one of the gullies leading up into the zone above, where they also

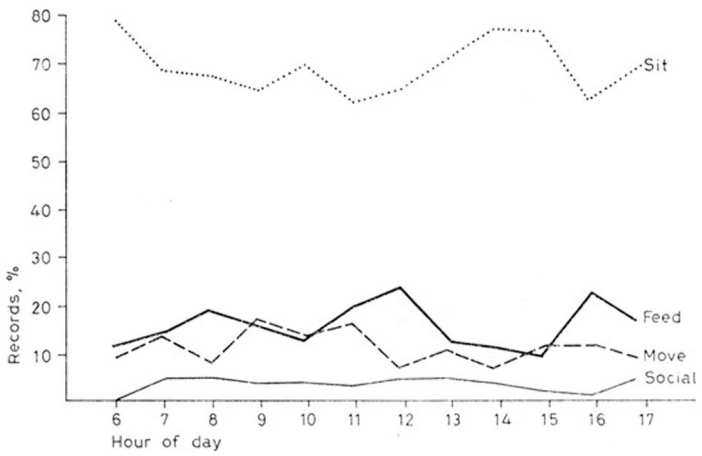


Fig. 2. Activity patterns of colobus monkeys in the Bole Valley, based on sweep samples at 10-minute intervals.

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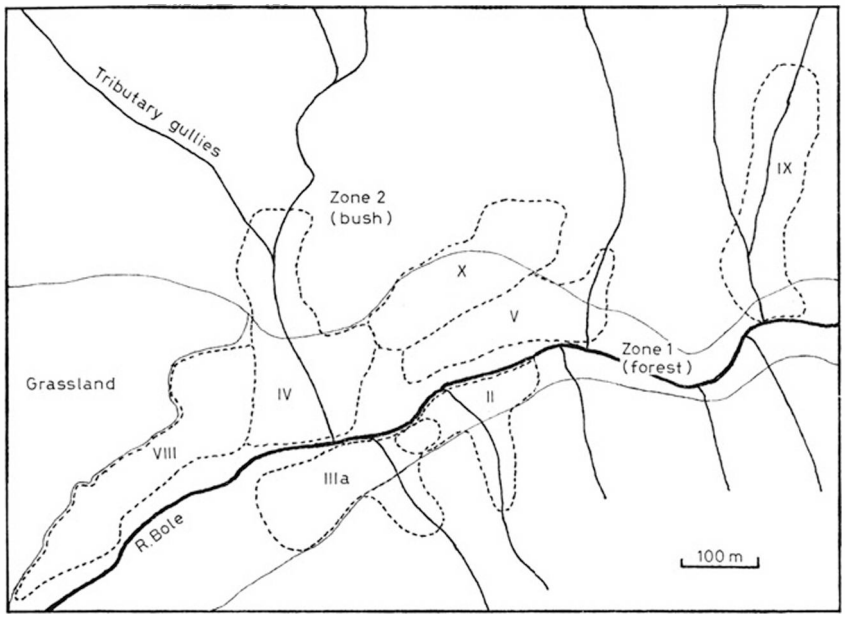


Fig. 3. Home ranges of the 7 most intensively studied colobus groups in the Bole Valley.

made use of the dense bush. These two areas were about equal in size. On 74 days, it was possible to determine whether the group was in the lower or upper part of its range (either by direct observation or by a systematic search of one half of the range). On 37 days (50%), they were in the gallery forest. On 22 occasions, it was possible to estimate the average length of stay in each half of the range. On 13 occasions, they stayed for only 1 complete day, 7 times for 2 days and twice for 3 days. These give an average of 1.5 days, with a median of 1. Thus, the group tended on the whole to alternate occupancy of each half of its range, despite the fact that the upper part was qualitatively poorer than the lower part. A similar analysis can be made for group VIII. Group VIII's range lay immediately downstream from group IV's, but, unlike the latter's, their home range lay entirely within the confines of the riverine forest and did not extend up into the bush zone above. Group VIII spent 51 of the 74 days (68.9%) in the downstream half of their range (i.e., on the side away from group IV's range). This part of their range,

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Table IV. Use of richer (A) and poorer (B) halves of home range by 2 groups at Bole

	Group IV			Group VIII		
	May–June	July–September	total	May–June	July–September	total
A	21(17.5)	16(19.5)	37	17(10.9)	6(12.1)	23
B	14(17.5)	23(19.5)	37	18(24.1)	33(26.9)	51
	35	39	74	35	39	74

Group IV: $\chi^2 = 1.952$; $p > 0.10$; df = 1. Group VIII: $\chi^2 = 7.936$; $p < 0.01$; df = 1. Expected values derived from marginal totals are given in parentheses.

Table V. Diet breakdown for Bole Valley colobus

Species	Type	Leaves, %	Fruits, %	Total
Acokanthera schimperi	bush/tree	–	11.8	11.8
sp. indet. No. 2 (Sapotaceae)	tree	5.9	9.7	15.6
Ficus (F. platyphylla, F. vallis-chaudae, F. sycamorous)	tree	2.2	26.9	29.1
Celtis ?africana	tree	12.4	–	12.4
Combretum spp.	bush/tree	10.8	–	10.8
Albizia grandibracteata	tree	0.5	–	0.5
Podocarpus gracilior	tree	1.1	–	1.1
Olea africana	tree	1.6	–	1.6
Salix subserrata	shrub	0.5	–	0.5
Syzigium guineense	tree	–	1.1	1.1
sp. indet. No. 21	tree	–	1.6	1.6
spp. indet.	creeper	1.6	–	1.6
spp. indet.	bush/tree	10.2	2.2	12.4
Ficus salicifolia	tree	eaten	–	–
sp. indet. No. 13	bush/tree	eaten	–	–
Calpurnia subdecendera	bush	eaten	–	–
Coffee (cultivated)	bush	eaten	–	–
Total		46.8	53.3	

Based on samples taken at 10-min intervals.

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however, was qualitatively the poorer half, having fewer large trees and proportionately more bush. Both groups showed a seasonal tendency to use the richer central parts of their ranges more than the bushed parts, though only in the case of group VIII was the difference statistically significant (table IV). Such an alternating use of parts of the home range has been reported for *Colobus badius* [CLUTTON-BROCK, 1972].

Although the colobus are essentially arboreal, they spent a good deal of time on the ground. Use of the ground was of two major kinds: resting on the rock faces bordering the gallery forest and moving on the ground from one clump of trees and bushes to another in the bush zones above the gallery forest. Of the 3,251 animals recorded in the activity counts, 302 (9.3%) were on the ground. Colobus, however, rarely fed on the ground. Of the 218 animals recorded as feeding, only 8 (3.5%) were doing so while on the ground. BROWN and URBAN [1970] recorded colobus moving (and 'fighting') on the ground in rain forest near Godare, and we also observed them moving along the ground in both areas in Simien.

This ability to move on the ground when necessary would seem to be important in allowing the colobus to colonize the variety of habitats in which they occur in Ethiopia. On the Simien escarpment face below Sankaber, for instance, there were few trees, and the vegetation was mainly low scrubby bush. In order to colonize such a habitat, it is necessary for them to move on the ground since even a small territory would not support enough vegetation in a single clump to support a typical group. Groups are thus forced to cross more or less open ground from clump to clump.

Diet

During all activity counts we attempted to record what each feeding animal was eating. Table V gives a breakdown of these data by species and part eaten. These data apply primarily to the period May–June. Colobus fed predominantly on relatively few species. 80% of their diet is accounted for by only 7 species: *Acokanthera schimperi*, *Ficus platyphylla*, *F. vallis-chaudae*, *F. sycamorus*, *Celtis ?africana*, *Combretum* sp. and the Sapotaceae sp. indet. No. 2. Fruits predominated slightly at this time of year (53.3% of all records), these being almost exclusively those of the *Ficus* spp., the Sapotaceae and *Acokanthera schimperi*. The leaves of rather more species were eaten, *Celtis* and *Combretum* being especially important in this respect. During the non-fruiting seasons, leaves almost certainly made up the bulk of the colobus' diet: in May 1971, for instance, the *Ficus* and Sapotaceae species had not yet come into fruit, and *Ficus* leaves were the most commonly eaten items.

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Ficus and *Celtis* species are also the most important food species for *Colobus guereza* in the Kibale forest in Uganda [J. F. OATES, personal commun.; CLUTTON-BROCK, 1972].

On Mt. Wochacha, the colobus were observed feeding on the fruits of *Juniperus procera* as late as October, and at Gondar, it is doubtful whether any other species contributed much to their diet. On Mt. Gaysay, on the other hand, the predominant edible tree species was *Hagenia abyssinica*, and this probably contributed the bulk of their diet in this locality. *(Erica arborea* was also abundant in this locality, but it is unlikely that the colobus fed on it to any extent.)

Determinants of Population Density

One obvious feature of the environment which might affect population density is the quality of the habitat. The locations of the ranges of all the Bole Valley groups are shown in figure 4. Of the 18 groups in the valley, 11 were based on the gallery forest in the river bed. The ranges of these groups covered an overall area of 55 ha, giving an average density of 1.4 animals/ha. The 7 groups whose ranges lay exclusively outside the gallery

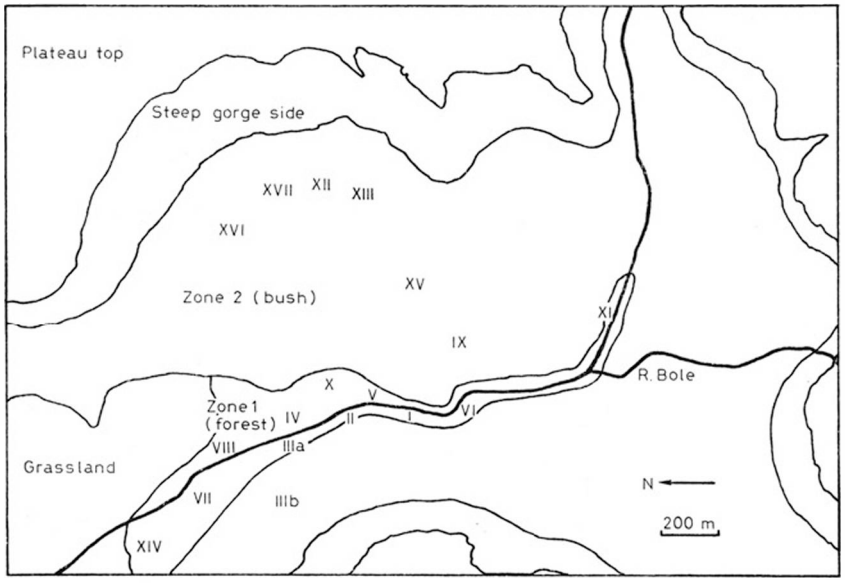


Fig. 4. Distribution of colobus groups in the Bole Valley.

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Table VI. Relationships between population density and vegetation cover in two sections of the Bole Valley

	Number of animals	Area, ha	Density/ha	Mean % ground cover[1]	Number of plots with bush cover	Number of plots with tree cover	Number of plots sampled
Lower level (zone 1)	78	55	1.4	44.0	9(90 %)	7(70 %)	10
Upper level (zone 2)	42	90	0.5	42.8	34(89.5 %)	5(13.2 %)	38

Vegetation cover based on m^2-plots sampled at 15-meter intervals along a transect.
[1] Mean of % cover in all plots.

Table VII. Relationships between population density and habitat in 6 localities in Ethiopia

Locality	Altitude m	Commonest tree species	Number of groups	Number of animals	Area surveyed ha	Density/ha	Ranked degree of forestation	Ranked food tree density
Bole (zone 1)	1,700	*Ficus, Albizia, Celtis*	11	77	55	1.4	1	1
Lake Shalla	1,500	*Ficus, Acacia*	6	41	30	1.4	3	2
Bole (zone 2)	1,900	*Olea, Rhus, Ficus, Albizia*	7	43	90	0.5	6	3
Wolkefit Pass	2,700	*Ficus, Hagenia*	10	56	100	0.6	4	4
Mt. Wochacha	2,500	*Juniperus, Olea, Hagenia*	3	16	50	0.3	2	5
Mt. Gaysay	3,300	*Hagenia, Hypericum, Erica*	1	2	10	0.2	5	6

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forest, were distributed over an area of 90 ha, giving an average density of 0.5 animals/ha. Thus, the gallery forest and its environs supported three times as many colobus as the poorer thicket zone. This difference is statistically significant ($\chi^2 = 36.996$; $p < 0.001$; $df = 1$). The relevant data are given in table VI, which also gives vegetational data for the two zones based on m^2-plots sampled at 15-meter intervals along a compass bearing. It can be seen that, while the upper bush zone has the same proportions of ground and bush level cover as the gallery forest, it has significantly less tree cover ($\chi^2 = 10.778$; $p < 0.01$; $df = 1$). Thus, the density of monkeys appears to be closely related to the amount of tree cover available.

An alternative test of this hypothesis can be made by comparing habitat quality with population density in the various localities visited during the general survey. Although neither the density of monkeys nor the habitat quality was directly quantified in any of the localities visited except the Bole Valley, the areas can be ranked on both these criteria. The density of colobus in each area can be estimated fairly closely from a knowledge of the number of different groups located and their compositions in the area surveyed. The relative quality of the habitat cannot be estimated so easily, but each locality represented a markedly different biotope, and these can be ranked in terms of (a) the amount of forest present and (b) the number of preferred food trees available. Both at Bole and the Kibale forest [CLUTTON-BROCK, 1972; J. F. OATES, personal commun.], the preferred trees were of the *Ficus* and *Celtis* genera, and the prevalence of these trees in each habitat was used in estimating (b).

The relevant data for 6 habitats are given in table VII. Comparison of the ranks for population density and for preferred food tree availability gives $r_s = 0.928$ ($p < 0.05$; $n = 6$), suggesting a close relationship between them. On the other hand, the correlation between population density and degree of forestation (irrespective of species) is poor ($r_s = 0.493$; $p > 0.10$), suggesting that the genera of trees available are more important than the degree of forestation.

Determinants of Home Range Size and Group Size

Figure 3 shows the ranges of the 7 groups studied in detail in the gallery forest. These have an average of 2.01 ha (range 1.6–2.5 ha). These ranges are, of course, representative only of a 6-month period, and the annual range size could be larger. Three lines of evidence, however, suggest that, in the present case, they are unlikely to be very much larger, if at all. Firstly, any marked increase in size would necessitate extensive overlap of the ranges of

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neighbouring groups; on the whole, the ranges of the groups overlapped relatively little, and groups did appear to defend their ranges from incursion. Secondly, the ranges of the groups in May 1971 corresponded precisely to those based on the longer period of observation in 1972. This would suggest a considerable stability of ranges over time. Furthermore, there was no marked variation in the areas used from month to month in 1972. Although some variation was observed in the *extent* to which groups used different parts of their ranges (see p. 198), all parts of the range were visited at least once in any given month. Finally, the fact that the 1972 observation period covered both the dry season and the wet season should reflect the most marked changes in the annual availability of food items and, hence, should include the extremes of range size.

These ranges are thus considerably smaller than those given by MARLER [1972] for colobus groups in the Budongo forest, Uganda (mean of 5 ranges = 13.7 ha), and by VON ULLRICH [1961] for one group on Mt. Kilimanjaro

Table VIII. Group size, range size and range quality for 7 groups at Bole

Species	Number of large trees in range of group						
	VIII	IV	IIIa	IX	V	X	II
Ficus spp.	26	24	10	10	29	8	7
F. salicifolia	9	4	5	–	7	–	3
Albizia grandibracteata	17	10	22	8	5	2	2
sp. indet. No. 2 (Sapotaceae)	36	17	1	12	23	13	5
Syzigium guineense	33	12	16	4	3	13	10
sp. indet. No. 21	8	4	–	–	1	2	–
Celtis ?africana	4	9	3	2	–	1	1
sp. indet. No. 13	3	–	2	–	–	–	1
Podocarpus gracilior	–	4	3	3	1	–	1
Olea africana	–	1	2	6	–	–	–
Grevillea sp.	–	–	–	–	2	14	–
Maytenus undatus	–	–	8	–	–	–	6
Acacia spp.	–	1	–	–	–	1	1
spp. indet.	3	5	12	5	2	1	7
Number of trees	139	91	84	50	73	55	44
Range size, ha	2.50	1.75	2.25	1.75	1.70	2.50	1.60
Trees/ha	55.6	52.0	37.3	28.6	42.9	22.0	27.5
Group size	11	10	9	8	6	4	3
Trees/individual	12.6	9.1	9.3	6.3	12.2	13.8	14.7

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(15 ha), but are of the same order of size as those estimated by MARLER [1972] for the groups observed by SCHENKEL and SCHENKEL-HULLIGER [1967] near Limuru, Kenya (mean 2.02 ha, range 1.03–3.51 ha).

MARLER [1972] suggests that home range size may be related to the size of the resident group, though he has insufficient data to demonstrate the point statistically. On the other hand, the foregoing discussion indicates that population density in Ethiopia is closely related to the quality of the habitat, and this suggests that the local abundance of food might be important in determining home range size.

These two possibilities are examined in table VIII which gives the group size, range size and an estimate of the food abundance for each of the 7 groups shown in figure 3. Since the colobus fed predominantly in trees, the relative abundance of food in each range was estimated by counting all the trees which were greater than 30 cm in diameter at a height of 30 cm above the ground. The numbers of trees of each species are given in each case.

The correlation between group size and range size is poor ($r_s = 0.491$; n.s.) as is the correlation between range size and the number of large trees ($r_s = 0.546$). Group size, however, correlates well with the number of trees ($r_s = 0.893$; $p = 0.01$; l-tailed), the fit being considerably better if *Grevillea* (a species the colobus rarely entered and certainly never ate) are excluded ($r_s = 0.964$; $p < 0.005$; l-tailed). Thus, at least at Bole, group size would seem to be closely related to the amount of food available in the group's range, as estimated by the relative abundance of large trees.

If this is the case, what might account for the difference which apparently exists between Budongo and Bole, assuming that MARLER's [1972] suggestion of a relationship between group size and range size is correct despite the small size of his sample? The likelihood that this is attributable to quality differences between the two habitats can presumably be disregarded, since mature rain forest may be assumed to be more productive than riverine forest. One possible answer might lie in the relative densities of colobus in the two areas. MARLER's data for Budongo suggest an average of 0.5 animals/ha, compared with a density of 3.7/ha at Bole (calculated on the basis of group sizes and home range sizes in each area, and assuming minimal overlap between ranges of neighbouring groups).

It seems likely that, at high densities, range size will be reduced to a minimum. Where the density is low, on the other hand, there is presumably room for expansion as increases in group size necessitate. Thus, while range size might well correlate with group size at Budongo, range size would

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appear to be more or less fixed at Bole, and group size is, in consequence, limited by the size of the range (or, more precisely, by the amount of food available in the range). SCHENKEL and SCHENKEL-HULLIGER's [1967] data are in line with this. From their sketch-map, 4 groups totalling 39 animals occupied 7.8 ha of forest, giving a density of about 5 animals/ha. The estimated average home range size for the 5 groups, for which complete ranges are shown, is 2.02 ha. The situation in their study area would thus seem to be comparable to that at Bole. A comparable situation is known to occur in the langur, *Presbytis entellus*, in India. In low density areas at Orcha and Kaukori, home ranges averaged some 384 and 768 ha respectively, but, at Dharwar, where the population density was some 30 times higher, ranges averaged only 18.4 ha [YOSHIBA, 1968].

Thus, at Budongo, increases in group size could be compensated for by increases in the size of the range, but at Bole, range size is limited, and increases in group size above the maximum carrying capacity of the home range can only be compensated for by the group splitting and one part of it moving into a new range in the less densely populated, but poorer, bush zone above the gallery forest. This happened in the case of group III which underwent fission between May 1971 and May 1972. The smaller half (group IIIb) moved up into the bush zone along one of the gullies, although it still used a small part of the gallery forest at one end of group III's former range. In May 1971, group III had an average of 6.5 large trees/individual, a figure well below the average for all 7 groups in 1972 (11.1 trees/individual). Only one group had as few trees per individual as this (group IX which had an average of 6.3 trees/individual). Although group IX showed no tendencies to split, this may well have been due to the fact that it had only one adult male. It is suggested that when the subadult male matures in 1974–1975, the group will undergo fission, and it is hoped that a return visit will be possible at this time to test the hypothesis.

Relations with Other Species

Predators. Potential predators of arboreal monkeys in Bole Valley included leopard, at least one other species of small felid, Crowned-hawk eagles, Verraux's eagles, Black-chested harrier eagles and Man. Although colobus are hunted in many parts of Ethiopia, those in the Bole Valley have been protected since the 1930s [Mrs. D. A. SANDFORD, personal commun.]. The colobus were observed to react with 'roaring' and rapid descent from the canopy in response to Crowned-hawk eagle and Black-chested harrier eagle,

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and birds of prey probably constituted the major predators in their case. No actual cases of predation, however, were observed.

Other primates. Other primates in the valley included *Cercopithecus aethiops*, *Papio anubis* and *Theropithecus gelada*. *Galago senegalensis* were also to be found in the gallery forest but, being nocturnal, they probably rarely came into contact with the colobus. Colobus are clearly differentiated from the other primate species in diet, and probably little competition exists between them. However, the colobus would often move out of trees if the anubis baboons moved into them, and some interference with the colobus' feeding efficiency could result from their presence. During all periods of observation, samples were taken at 10-minute intervals to determine whether the colobus groups were alone or in mixed-species parties with other primates. (Two species were defined as being in a mixed-species party if the distance separating the two nearest members of the different species was less than the greatest distance separating any two adjacent members of the same species.) Out of a total of 1,283 samples, colobus groups were alone in 1,145 (89.3%). They were in mixed-species parties with gelada in only 7, anubis in 28 and with vervets in 103 samples. Thus, the amount of potential interference from the large baboons is insignificant, most of their associations being with the smaller vervets.

The actual amount of contact between any one colobus group and a vervet group was, however, limited by the fact that the home ranges of the vervet groups were considerably larger than those of the colobus (mean of 30.4 ha for two vervet groups), and their greater rate of movement tended to carry the vervets beyond the range of any given colobus group after a relatively short period of time. In several cases, however, the colobus groups followed the vervets until the latter had moved beyond the limits of their home range. Actual interaction between members of the two species in such parties, however, was rare. Only 5 interactions were observed in a total of 23 mixed parties: individual vervets 3 times moved away when approached by individual colobus, and colobus twice moved away from approaching vervets. Only one of these involved a direct social interaction: an adult male colobus ran at a small group of juvenile vervets who immediately moved away. Colobus and vervets did respond to each other's alarm calls on a number of occasions, with the vervets usually being the first to detect the danger source. The close presence of vervet groups may be advantageous to the colobus in that the presence of several adult males in vervet groups to act as 'look-outs' [GARTLAN, 1968] may improve the predator-detecting efficiency of the colobus groups with their single adult male. This might

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account for the tendency for colobus groups to follow vervet groups so long as they remained within their home ranges.

Conclusions

In view of their marked preference for a relatively small number of tree species, the variety of habitats in which black and white colobus occur in Ethiopia is surprisingly wide. The preferred food trees are those of the *Ficus* and *Celtis* genera, yet in Ethiopia, colobus have been able to colonize areas where these genera are rare or even entirely absent.

Their density in any given locality does, however, seem to depend on the abundance of these species. It is, therefore, surprising to find that in 3 of the 4 areas where colobus have been studied in East Africa, the density is low despite the fact that the areas all support primary rain forest with an abundance of *Ficus* and *Celtis* spp. Only in the SCHENKEL and SCHENKEL-HULLIGER's [1967] study area at Limuru was the density of colobus comparable to that at Bole, and the home ranges in these two areas were of the same order of size.

One possible explanation for this difference might be in the relative sizes of the forest blocks in each area. At Bole, Lake Shalla and the SCHENKEL's study area, the forest was extremely small, whereas at Budongo, Kibale and on Mt. Kilimanjaro, the forest blocks are extensive and cover several thousand km^2. It might be argued that in the latter areas, the new groups formed by fission are able to move into those parts of the forest that are relatively little used. At Bole, on the other hand, the limited amount of optimal (forest) habitat results firstly in a reduction in range size as the number of groups increases, then, when the density reaches the maximum carrying capacity, an expansion into the less suitable habitat on the slopes above the river bed. Thus, the density in the gallery forest is likely to remain high at all times, while the less suitable thicket parts of the valley act as buffer zones for the absorption of the excess population. However, since the habitat there is by comparison poor, the density will always be low, although probably close to the ceiling for that type of habitat. We might argue that the poorer habitat results in a higher mortality rate in these areas, but the data are inadequate for a test of this hypothesis.

Presumably, periodic epidemics or other population catastrophes decimate the population in all areas from time to time, but it would take proportionately longer for the population density to reach the theoretical ceiling

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in large forest blocks than it would in the small forests surveyed in Ethiopia. Consequently, while high densities would rapidly and repeatedly be achieved in the Bole Valley, the population density in areas like the Budongo forest might never approach their theoretical maxima. High densities, therefore, would be found only rarely in such areas.

Summary

Colobus guereza groups in Ethiopia typically consist of 6–8 animals. Although one male groups predominate, some groups may contain up to 3 adult males. Changes in a small population over a 17-month period indicate an annual growth rate of about 10%. The death rate is high for infants before the colour-change, but low thereafter. It is estimated that groups undergo fission approximately every 7 years. The inter-birth interval for females is approximately 1.5–2 years.

Colobus are relatively sedentary, rarely travelling more than 300 m in a day. Travel along the ground was observed where clumps of trees were separated by relatively open ground. During the fruiting season, figs and other soft fruits were an important feature of the colobus' diet but, at other times of the year, leaves predominate.

Home ranges in the main study area were small, averaging some 2.01 ha. Group size correlated positively with the number of large trees present, indicating that in this area, habitat quality determines the numbers of animals that can occupy a given range. Home ranges appear to be stable over time due to the high density of animals, and cannot expand to compensate for increases in group size. It seems likely that in areas of low population density, range size correlates more closely with group size. Comparison of population density with habitat quality in a number of localities in Ethiopia suggests that these are closely linked, the density of preferred food trees (*Ficus* and *Celtis* spp.) apparently being the critical factor. It is suggested that in areas where forest blocks are small in size, population density is generally high: home ranges are consequently small, and group size determined by the quality of the micro-habitat. In contrast, where the forest block is extensive, population density is more generally low, and range sizes are larger and can expand and contract in response to changes in group size.

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