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Daily Ranging Behavior of Red Colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda

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Abstract. Daily ranging behavior (DRB) of red colobus monkeys (*Colobus badius tephrosceles*) is examined to determine (1) what social and environmental variables are related to ranging patterns, and (2) how these variables are related to one another and to DRB. It is suggested that foraging constraints primarily determine variation in DRB but that other variables, i.e. rainfall and intra- and intergroup conflicts periodically influence DRB as well.

Introduction

I am concerned here with the relationship of daily ranging behavior (DRB) of red colobus monkeys (*Colobus badius tephrosceles*) to numerous social and environmental variables. Many variables affecting DRB in primates have been identified in the literature including food distribution and abundance [Clutton-Brock, 1977; Marsh, 1981; McKey, 1978; Milton, 1980; Raemakers, 1980; Rudran, 1978], habitat structure [Gautier-Hion et al., 1981; Kinzey and Gentry, 1979], group size [Waser, 1977], movements on previous days [Fossey and Harcourt, 1977], weather patterns [Chivers, 1969; Clutton-Brock, 1977; Curtin, 1982; McKey, 1978; Oates, 1974; Raemakers, 1980], intergroup social interactions [Rasmussen, 1979; Struhsaker, 1974; Struhsaker, 1975], position of sleeping trees [Rasmussen, 1979; Tenaza, 1975], and avoidance of internal parasites transmitted via fecal contamination of foods [Freeland, 1979]. In this paper, I use univariate

analyses to determine variables that are related significantly to DRB in red colobus and then examine these further with partial correlation analysis to detect relationships among variables and the directions of their relationships with DRB when covariance is controlled.

Methods

All data were collected from the Kanyawara study area of Kibale Forest in western Uganda (0°13' to 0°41' N and 30°19' to 30°32' E). Detailed descriptions may be found in Rudran [1978] and Struhsaker [1975].

One group of about 65 red colobus was studied for approximately 1,800 h from February 1980 through December 1981; most data presented here are limited to observations collected from January 1981 through October 1981 when occurrences of 'rapid quavers' (RQs), an adult male vocalization associated with intragroup conflicts [Struhsaker, 1975], were noted. Data presented here were usually gathered during 4-5 consecutive sample days every month on group movements, feeding behavior and social behavior.

Group Movements

For each day that the group was followed at least 11.5 h, points representing the estimated center of mass [Altmann and Altmann, 1970] of animals visible to me were plotted every 15 min on range maps (1:2,500) and the number of visible animals was recorded. Repeatedly sighted identifiable individuals among those visible confirmed that my position relative to the group was constant throughout the day. A grid of trails, intersecting one another at 50- to 100-m intervals, facilitated access to the group and served as landmarks to plot the points accurately. Locations of other groups were also plotted when they were detected up to 200 m from the main study group (B group).

Day range length (DRL) was calculated by summing straight-line distances between successive chronological points for each day. The group's home range was broken into 1-km quadrats [Struhsaker, 1975] and diversity of quadrat use was determined using the Shannon-Wiener index of diversity, H' [Wilson and Bossert, 1971].

Feeding Behavior

Methods follow those of Struhsaker [1975] for comparison except that when 1 animal fed on two separate trees of a single species within 1 h I recorded it as two feeding scores rather than one. The change in methodology was inconsequential; of 3,760 tree feeding observations recorded between November 1980 and October 1981, inclusive, only 6, or less than 0.2%, fell into the new category.

For each score, whenever possible, I noted the age, sex and identity of the feeding animal and the time, food species and food item.

Social Behavior

Social interactions, particularly those between adult males, were recorded as they occurred. These included fights and chases, supplantations, presents, mounts, social grooming and RQs.

Variables Examined

(1) Group size.

(2) Intergroup social interactions: Groups were considered to interact when proximity to one another was no more than 50 m. This distance is for comparison with Struhsaker [1975] only and does not imply biological significance.

(3) Intragroup conflicts between adult males: A significant correlation of RQs with monthly frequency of chases and fights between adult males in the main study group ($r_s = 0.769$, $0.01 > p > 0.001$, $n = 10$, d.f. = 8) (table I) supports Struhsaker [1975] impression that RQs are related to intragroup conflicts. Frequency of RQs was therefore used as an indirect quantitative measure of intragroup conflicts.

(4) Tree species richness in the diet: Measured as total number of tree species fed upon per day.

(5) Species-specific food item richness in the diet: Total number of plant parts per tree species fed upon per day. Food items included petioles of young leaves, young leaves, petioles of mature leaves, mature leaves, fruit and seeds, foliar and floral buds, and flowers.

(6) Dietetic diversity: The frequency and proportion of observations of each tree species in the daily diet.

(7) Percentage of young growth in the diet: Includes foliar and floral buds, which are often indistinguishable in the field, as well as young leaves and petioles of young leaves.

(8) Abundance of young growth in the forest: Monthly phenological data were collected on 130 individuals from 8 tree species which accounted for 56.7% of 3,760 total tree feeding observations from the B group (table II). 10 to 20 specimens of each species were monitored and ranked from 0 to 4 for abundance of buds and young leaves, with 4 denoting maximum abundance. These food items were tested because earlier studies [Clutton-

Table I. Relations of rapid-quaver (RQ) vocalizations to social and environmental variables in Red Colobus B group, Kibale Forest

Month 1981	RQs	Copulations	Chases and fights	Young growth abundance	% young growth in diet
Jan.	32.2 ^a	21.5 ^a	6.7 ^a	4.6 ^b	37.8
Feb.	0.0	4.3	1.1	5.0	47.3
Mar.	8.9	31.3	7.8	9.8	60.6
Apr.	135.6	22.8	15.2	8.0	58.1
May	4.8	10.9	0.0	4.4	33.1
June	11.4	7.6	5.1	3.0	12.7
July	5.1	12.8	1.3	2.8	20.2
Aug.	21.0	6.5	4.4	5.8	39.6
Sept.	8.5	29.0	10.2	5.6	27.0
Oct.	127.4	17.4	41.9	7.8	37.0

^a Number of occurrences/100 h.

^b Excluding *Diospyros abyssinica*; see text for methods of determining abundance values.

Brock, 1975; Struhsaker, 1975] showed red colobus feed primarily on young growth. Scores for buds and young leaves were classed together and monthly means for each species summed to give abundance values for young growth.

(9) Rainfall: Rainfall was measured every morning using a rain gauge located in a clearing on the forest edge less than 50 m from the boundary of the B group's home range.

(10) Habitat disturbance: Over half the B group's home range was located in an area that had been selectively felled in 1969 [Oates, 1977]. A logging road, which in no way impeded the group's movement, separated the disturbed portion of the home range from the undisturbed portion and also marked the boundary between two forestry compartments. I measured the effects of timber harvesting on DRB by comparing the B group's utilization of each compartment, i.e. habitat type, against compartmental representation by area within the home range and by comparing DRL between compartments.

Statistics

All univariate statistical tests are taken from Siegel [1956] and are 2-tailed unless otherwise noted. Sample size for all univariate correlation tests (Spearman rank correlation coefficient) is 45 unless otherwise noted and significance was set at the 0.05 level. Partial correlation analysis using the SPSS program [Nie et al., 1970] was conducted on variables that were significantly correlated with DRB under univariate tests. Rainfall was also included due to conflicting results. By varying the number and combination of variables mathematically held constant, spurious correlations can be detected and true correlations clarified. Partial correlations provide three interpretations after univariate analysis, if for example, variables A and C both are correlated with variable B: (1) a spurious correlation can exist between C and B due to a true correlation between A and C; (2) both A and C can be true predictors of B, and (3) A and C can actually covary with a third variable, D, that predicts B, and thus be falsely correlated with B. Alternatively, if A is not correlated with B after univariate analysis, other factors may obscure a true correlation through their relationships with A.

Table II. Importance in diet of Red Colobus B group of tree species monitored for phytophase, November 1980–October 1981

Species	% feeding observations (n = 3,760)
1) <i>Trema guiniensis</i>	16.3
2) <i>Markhamia platycalyx</i>	13.6
3) <i>Celtis africana</i>	9.7
4) <i>C. durandii</i>	8.1
5) <i>Strombosia scheffleri</i>	5.1
6) <i>Aningeria altissima</i>	3.2
7) <i>Teclea nobilis</i>	0.9
8) <i>Diospyros abyssinica</i>	0.0
	56.9

Results

Univariate Analysis

DRB was quantified by measuring DRL and the proportion of time spent in each quadrat, i.e., quadrat utilization diversity (QUD). Since DRL and QUD were highly correlated with one another ($p < 0.001$), DRL was used as the sole measure of DRB in most cases. As a check, QUD was tested with variables that were significantly correlated with DRL and the results were identical in the direction, if not the level, of statistical significance in all cases. 'DRB' thus includes both DRL and QUD.

Group size apparently has no effect on DRL in red colobus, although it may affect ranging patterns in other species [Struhsaker et al., in prepara-

Table III. Rates of travel of Red Colobus B group before and after proximity to 50 m of another group of Red Colobus

Before, m/h	After, m/h
58.0	40.8
46.0	140.0
25.0	27.0
30.3	15.0
99.3	67.3
48.8	52.7
46.9	57.4
37.4	90.0
58.5	86.7

Table IV. Utilization by Red Colobus B group vs. representation in home range of selectively logged and unfelled compartments

	Selectively logged	Unfelled
Observed	52.3	28.0
Expected	46.5	32.9

Observed values = Number of days red colobus B group spent in each compartment; expected values = % of red colobus B group home range within each compartment \times number of days sampled ($n = 81$).

tion]. The B group, with approximately 65 animals, was nearly four times the size of the 20 member CW group [Struhsaker, 1975] but mean DRL was actually less in the B group by 8.7%.

Frequency of intergroup encounters were not significantly correlated with either DRL or QUD ($r_s = 0.048$, $p > 0.05$; $r_s = 0.108$, $p > 0.05$, respectively). Rates of travel were determined by the distance traveled over total length of time before and after conflicts occurred. Rates of travel before and after proximity to 50 m were also not significantly different (Wilcoxon matched-pairs signed-ranks test, $T = 16$, $p > 0.05$, $n = 9$) (table III).

DRL in the felled compartment ($\bar{x} = 553.0$ m) was not significantly different from the unfelled compartment ($\bar{x} = 596.0$ m) (Mann-Whitney U test, $n_1 = 18$, $n_2 = 44$, $p > 0.05$). Moreover, time spent in the logged section of the home range (home range utilization) did not differ significantly from expected values (% home range representation by compartment $\times n$) ($\chi^2 = 0.478$, $p > 0.05$, $n = 81$, d.f. = 1) (table IV).

The effect of rainfall on DRL was tested in two ways. First, to control for seasonal differences in phenological phases that might covary with rain-

Table V. Mean day range length (DRL) of Red Colobus B group on dry vs. wet days within each month

Month ¹	\bar{X} DRL dry days, m	\bar{X} DRL wet days, m
May 1980	515.0	416.2
June	818.3	540.0
July	570.8	350.0
Aug.	640.0	550.0
Sept.	530.0	509.5
Oct.	648.8	710.0
Nov.	475.0	528.8
Jan. 1981	600.8	430.0
May	742.5	520.0
Apr.	740.0	975.8
June	632.5	497.5
July	587.5	601.2
Sept.	991.2	594.2
Oct.	1,050.0	835.0

¹ Months in which dry and wet days occurred during sampling period.

fall, mean DRL was tested on dry vs. wet days within each month and was found to be significantly lower on wet days (Wilcoxon matched-pairs signed-ranks test, $T = 20$, $n = 14$, $0.05 > p > 0.02$) (table V). However, as a second test, when total daily rainfall was examined with DRL irrespective of seasonality, no correlation existed (table VI).

Mean monthly DRL was not correlated with the phenological assessment of abundance of young growth in the forest ($r_s = 0.538$, $n = 12$, $p > 0.05$).

DRB was positively correlated with the following variables (table VI): (1) tree species richness in the diet; (2) food item richness in the diet; (3) dietetic diversity; (4) percentage of young growth in the diet; (5) frequency of RQs.

Multivariate Analysis

Tables VII–X show the results of first- and second-order partial correlations with both measures of DRB. Three variables, i.e. RQs, tree species richness in the diet, and dietetic diversity, correlate more strongly with DRB than with any other variable. The only real difference between factors affecting DRL and QUD lies in the relative importance of tree species richness in the diet and dietetic diversity: the former is a better predictor of

Table VI. Spearman rank correlation half-matrix of variables tested for their relations with daily ranging behavior in Red Colobus B group

	QUD	RQs	Spp. Rich.	FI Rich.	Dietetic diversity	Rainfall	Young growth in diet
DRL	<i>0.893</i>	<i>0.380</i>	<i>0.485</i>	<i>0.392</i>	<i>0.384</i>	-0.180	<i>0.352</i>
QUD		<i>0.398</i>	<i>0.429</i>	<i>0.420</i>	<i>0.578</i>	-0.212	<i>0.304</i>
RQs			0.166	-0.016	0.210	0.138	0.238
Spp. Rich.				<i>0.786</i>	<i>0.755</i>	-0.092	0.134
FI Rich.					<i>0.672</i>	0.004	0.043
Dietetic diversity						-0.087	0.253
Rainfall							-0.145

Italicized coefficients are significant at 0.05 level or less.

DRL = Day range length; QUD = quadrat utilization diversity; RQs = rapid quavers; Spp. Rich. = tree species richness in the diet; FI Rich. = food item richness in the diet.

DRL, whereas the latter is a better predictor of QUD. Food item richness in the diet is spuriously correlated with DRB due to its high covariance with tree species richness in the diet and dietetic diversity. Young growth in the diet is falsely correlated with DRB as well, due to its covariance with RQs. Finally, daily rainfall has no effect on DRB under any order partial correlation test.

Table VII. First-order partial correlation matrix: DRL as the dependent variable

Variable held constant	RQs	Spp. Rich.	FI Rich.	Dietetic diversity	Rainfall	Young growth in diet
RQs		<i>0.463</i>	<i>0.430</i>	<i>0.336</i>	-0.254	0.291
Spp. Rich.	<i>0.347</i>		0.200	0.031	-0.156	<i>0.331</i>
FI Rich.	<i>0.420</i>	<i>0.311</i>		0.177	-0.197	<i>0.365</i>
Dietetic diversity	<i>0.332</i>	<i>0.322</i>	0.196		-0.159	0.285
Rainfall	<i>0.416</i>	<i>0.478</i>	<i>0.399</i>	<i>0.376</i>		<i>0.355</i>
Young growth in diet	<i>0.326</i>	<i>0.472</i>	<i>0.403</i>	<i>0.326</i>	-0.139	

Italicized coefficients are significant at 0.05 level or less.

Abbreviations as in table VI.

Table VIII. First-order partial correlation matrix: QUD as the dependent variable

Variable held constant	RQs	Spp. Rich.	FI Rich.	Dietetic diversity	Rainfall	Young growth in diet
RQs		<i>0.401</i>	<i>0.465</i>	<i>0.551</i>	-0.294	0.234
Spp. Rich.	<i>0.367</i>		0.148	<i>0.429</i>	-0.192	0.275
FI Rich.	<i>0.446</i>	0.176		<i>0.440</i>	-0.236	<i>0.315</i>
Dietetic diversity	<i>0.347</i>	<i>0.429</i>	0.052		-0.199	0.199
Rainfall	<i>0.441</i>	-0.192	<i>0.431</i>	<i>0.575</i>		0.283
Young growth in diet	<i>0.352</i>	0.275	<i>0.428</i>	<i>0.544</i>	-0.178	

Italicized coefficients are significant at 0.05 level or less.

Abbreviations as in table VI.

Table IX. Second-order partial correlation matrix: DRL as the dependent variable

Variables held constant	RQs	Spp. Rich.	FI Rich.	Dietetic diversity	Rainfall	Young growth in diet
RQs and Spp. Rich.			0.114	-0.016	-0.226	0.278
RQs and FI Rich.		0.218		0.060	-0.284	0.300
RQs and dietetic diversity		<i>0.338</i>	0.291		-0.228	0.238
RQs and rainfall		<i>0.451</i>	<i>0.447</i>	<i>0.319</i>		0.257
RQs and young growth in diet		<i>0.456</i>	<i>0.436</i>	0.293	-0.213	
Spp. Rich. and FI Rich.	<i>0.363</i>			0.028	-0.159	<i>0.335</i>
Spp. Rich. and dietetic diversity	<i>0.346</i>		0.014		-0.155	<i>0.333</i>
Spp. Rich. and rainfall	<i>0.381</i>		0.040	0.027		<i>0.317</i>
Spp. Rich. and young growth in diet	0.298		0.057	-0.051	-0.119	
FI Rich. and dietetic diversity	<i>0.391</i>	0.261			-0.180	<i>0.332</i>
FI Rich. and rainfall	<i>0.461</i>	0.290		0.157		<i>0.346</i>
FI Rich. and young growth in diet	<i>0.368</i>	0.274		0.075	-0.157	
Dietetic diversity and rainfall	<i>0.367</i>	<i>0.320</i>	0.213			0.271
Dietetic diversity and young growth in diet	0.294	<i>0.364</i>	0.261		-0.129	
Rainfall and young growth in diet	<i>0.360</i>	<i>0.468</i>	<i>0.408</i>	<i>0.332</i>		

Italicized coefficients are significant at 0.05 level or less.
Abbreviations as in table VI.

Table X. Second-order partial correlation matrix: QUD as the dependent variable

Variables held constant	RQs	Spp. Rich.	FI Rich.	Dietetic diversity	Rainfall	Young growth in diet
RQs and Spp. Rich.			0.262	<i>0.413</i>	-0.271	0.214
RQs and FI Rich.		0.055		<i>0.360</i>	-0.335	-0.240
RQs and dietetic diversity		-0.019	0.139		-0.275	0.144
RQs and rainfall		<i>0.386</i>	<i>0.488</i>	<i>0.544</i>		0.192
RQs and young growth in diet		<i>0.391</i>	<i>0.467</i>	<i>0.528</i>	-0.262	
Spp. Rich. and FI Rich.	<i>0.419</i>			<i>0.413</i>	-0.214	0.295
Spp. Rich. and dietetic diversity	<i>0.347</i>		0.074		-0.200	0.199
Spp. Rich. and rainfall	<i>0.409</i>		0.177	<i>0.432</i>		0.257
Spp. Rich. and young growth in diet	<i>0.326</i>		0.184	<i>0.390</i>	-0.162	
FI Rich. and dietetic diversity	<i>0.367</i>	-0.054			-0.204	0.213
FI Rich. and rainfall	<i>0.497</i>	0.146		<i>0.427</i>		0.292
FI Rich. and young growth in diet	<i>0.402</i>	0.134		<i>0.381</i>	-0.202	
Dietetic diversity and rainfall	<i>0.391</i>	-0.022	0.071			0.180
Dietetic diversity and young growth in diet	<i>0.320</i>	0.004	0.091		-0.178	
Rainfall and young growth in diet	<i>0.397</i>	<i>0.406</i>	<i>0.436</i>	<i>0.544</i>		

Italicized coefficients are significant at 0.05 level or less.
Abbreviations as in table VI.

Discussion

The B group came to within 50 m of another group on 49% of 45 sample days, while overt conflicts, i.e. interactions involving chasing and loud vocalizations, occurred on only 6.5% of those days. In comparison, Struhsaker's CW group was proximal to other groups on 59% of 83 sample days; 36% of those days included conflicts [Struhsaker, 1975].

The question that arises is: Why should the CW group have nearly six times as many conflicts as the B group? Both groups occupy broadly comparable habitat where estimated densities of conspecific groups do not significantly differ [J.P. Skorupa, unpubl. data], and the criterion for determining conflicts was similar for both studies.

I would suggest that with about 20 animals, which is 30 less than the mean for red colobus at Kibale [Struhsaker, 1975], the CW group was a relatively recently formed group during Struhsaker's initial study and consequently intergroup relations were unstable. That the size of the CW group has not remained stable but has increased to 35 animals since the initial study [Struhsaker, personal commun.] lends support to this idea. The B group, on the other hand, consisted of about 65 animals and intergroup relations with all but one neighboring group were typically passive.

It should be noted here that due to different methods of determining QUD, comparisons between the B and CW groups are limited to DRL.

No correlation was found between DRL and daily rainfall but this may be a function of analyzing pooled data rather than a sample stratified *within* months. Analysis on a daily or monthly basis [Struhsaker, 1975] does not control for phenological effects that may obscure correlations; a difference in mean DRL between dry and wet days within same months is therefore more likely to be biologically significant than results from correlational tests with DRL. Reduced travel during rainy days is a common response among primates [Chivers, 1969; Clutton-Brock, 1977; Curtin, 1982; McKey, 1978; Oates, 1974; Raemakers, 1980; Rudran, 1978].

Despite habitat disruption due to logging in one compartment and an 11.5% decrease in total number of food tree species in the disturbed area, DRL was not significantly different between compartments. This may be because the average number of tree species fed upon each day was not noticeably different between compartments (9.2 vs. 10.0).

One drawback of correlation analysis is that causality is often difficult to assess. In the case of RQs and DRB it is intuitively obvious that conflicts within the group influence ranging patterns rather than vice versa. What

causes these conflicts is unclear, however. Competition for females might be a cause; indeed, Struhsaker [1975] noted that RQs are usually directed toward copulating pairs. The B group included 15–16 adult males, 49.7% higher than average for 8 known red colobus groups. In addition, 3 males changed or were changing from juvenile-subadult to adult status during the study. The juvenile and subadult stages are critical transition periods for males, during which the immature animal's presence in the group is often challenged by adult males [Struhsaker, 1975].

This possibility is clouded by the positive correlation between RQs and percentage of young growth in the diet. It is conceivable that a spurious correlation might arise between number of conflicts and abundance of young growth if breeding is concentrated during periods of young growth abundance. Yet, this is not supported by evidence. Neither RQs nor copulations are correlated with monthly phenological abundance of young growth ($r_s = 0.454$, $p > 0.05$; $r_s = 0.588$, $p > 0.05$, respectively, $n = 10$) (table I), although percentage of young growth in the diet is significantly correlated with abundance of young growth in the forest ($r_s = 0.745$, $0.02 > p > 0.01$, $n = 10$) (table I). Moreover, Struhsaker [personal commun.] has recorded in the CW group births occurring in nearly every month over a 12-year period.

Alternatively, young growth generally is of higher quality and is more limited in abundance than mature growth and the monkeys might therefore compete for it. This is not likely since I observed no supplantations or other direct conflicts over young growth. The relationship between RQs and young growth unfortunately remains obscure.

It has been suggested that red colobus are dependent upon diversity in the diet [Clutton-Brock, 1975; Struhsaker, 1974; Struhsaker and Oates, 1975]. Apparently, dietetic diversity and tree species richness are equally important in the red colobus diet. The importance of both variables may lie with obtaining sufficient nutrient mixing [Milton, 1980; Westoby, 1974].

It is not clear a priori whether ranging behavior influences, or is influenced by, foraging constraints. If it is suggested that foraging patterns are a result of DRB, then some variable(s) other than food availability and dietetic requirements must determine DRB. Species richness in the diet and dietetic diversity, both of which reflect food availability and dietetic requirements, would then be spuriously correlated with DRB via their true correlations with the other variable(s). Partial correlations are designed to uncover spurious correlations, yet these variables remained significantly correlated with DRB when covariance was controlled for other significant

variables identified to date. Therefore, barring any undiscovered factors affecting both diet and DRB, food availability and dietetic requirements would appear to be strong causal factors of red colobus DRB.

In conclusion, it appears that red colobus ranging patterns are primarily determined by foraging constraints but that in relatively undisturbed habitat at least, these constraints are flexible, thereby allowing red colobus to respond to other, more ephemeral pressures, such as intra- and intergroup interactions and rainfall, when they arise. This may help explain the conflicting results of Clutton-Brock [1975] and Struhsaker [1975]. Struhsaker found that only intergroup encounters affected ranging behavior in the CW group whereas Clutton-Brock, studying a group of 80 red colobus in Tanzania, found that intergroup conflicts were less frequent than the rate at which the CW group experienced conflicts and thus did not influence ranging, while food availability did affect group movements.

Summary

The ranging behavior of a group of red colobus was studied for more than 1,800 h in Kibale Forest, Uganda. Several variables were tested at both univariate and multivariate levels to determine (1) which variables affect daily ranging behavior (DRB), and (2) how those variables interact to influence DRB. Factors include: (1) intergroup social interactions; (2) intragroup conflicts between males; (3) rainfall; (4) group size; (5) timber harvesting; (6) abundance of young leaves and buds in the forest; (7) tree species richness in the diet; (8) species-specific food item richness in the diet; (9) dietetic diversity; (10) percentage of young leaves and buds in the diet.

Those factors which were significant at the univariate level, i.e., intragroup conflicts, rainfall, and all four parameters of diet, were then subjected to partial correlation analysis. Intragroup conflicts, dietetic diversity and tree species richness in the diet were significantly correlated with DRB. Food item richness in the diet was related to tree species richness in the diet and dietetic diversity rather than to DRB. The cause(s) of male-male conflicts in the group remains unclear but it is likely due to competition for females and/or competition for food. Rainfall, though not correlated with DRB on a daily basis, was a significant factor in determining DRB when phenological effects were eliminated. Red colobus monkeys are apparently sufficiently flexible in their ranging behavior that they are not overly restricted by foraging constraints in the face of more ephemeral pressures.

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