Socioecology of the Blue Monkeys *(Cercopithecus mitis stuhlmanni)* of the Kibale Forest, Uganda

RASANAYAGAM RUDRAN

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 249

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world cf science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 249

Socioecology of the Blue Monkeys *(Cercopithecus mitis stuhlmanni)* of the Kibale Forest, Uganda

Rasanayagam Rudran

SMITHSONIAN INSTITUTION PRESS
City of Washington
1978

ABSTRACT

Rasanayagam Rudran. Socioecology of the Blue Monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology*, number 249, 88 pages, 34 figures, 58 tables, 1978.—This study was conducted between December 1972 and November 1974 and included some 2100 hours of observation. Blue monkeys usually lived in "one-adult male" social groups that included 13 to 27 animals ($\bar{X} = 20.8$). The large disparity in the adult sex ratio of these groups was partly accounted for by the emigration of young males that lived as solitary individuals at least for a short period after leaving their parental groups.

Blue monkeys frequently formed large mixed-species groupings with one or more of the other primates living in the study area and these associations probably functioned in the avoidance of predation. Associations with the folivorous red colobus (*Colobus badius*) probably enhanced the acquisition of invertebrate food, while other types of associations, particularly with redtails (*Cercopithecus ascanius*), may have resulted in efficient location of food resources. Polyspecific associations seemed to be avoided during the times blue monkeys fed on plant foods.

Blue monkeys exploited a large number of food plants but tended to be selective feeders. Fruits were usually the most frequently used plant component, but foliar foods and invertebrates were periodically used at high frequencies. Spearman rank correlation tests indicated (1) a significant negative correlation between the frequency of use of fruits and indices of diet diversity computed on the basis of the Shannon-Wiener equation, and (2) a significant positive correlation between the frequency of use of foliar foods and indices of diet diversity. The use of food resources showed considerable intermonthly variations and depended on availability, relative abundance, and the dietary preferences of the blue monkeys. The frequency of food intake and the composition of the diet of four age/sex classes were found to differ. The adult male seemed to adopt a "time minimizing" feeding strategy and exploited a larger proportion of fruits and a smaller proportion of invertebrates than adult females, subadults, and juveniles.

Blue monkeys of the Kibale Forest occupied relatively large home ranges. On a daily basis, however, they used only a small portion of their home range and the size of daily ranges varied appreciably during different sample periods. Overlaps in areas used on different days of a sample period were usually small. Thus on the average less than 5% of the area used during a sample period was used on all five days of the sample period, while about 66% was visited on only one day of the sample period.

Phenological data collected during the study suggested that differential use of the home range was affected by variations in food abundance. Spearman rank correlation tests showed that ranging patterns were related to the location and exploitation of abundant food resources. In addition the ranging patterns appeared to be partially affected by climatic factors and the location of areas used for night resting.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Rudran, Rasanayagam
Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda.
(Smithsonian contributions to zoology ; no. 249)
Bibliography: p.
1. *Cercopithecus mitis*—Behavior. 2. Social behavior in animals. 3. Animals, Food habits of. 4. Mammals—Ecology. 5. Mammals—Uganda—Kibale Forest Reserve. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology ; no. 249.
QL1.854 no. 249 [QL737.P93] 591'.08s [599'.82] 76-608404

Contents

Page

Introduction 1
  Purpose of the Study 1
  Description of the Blue Monkey 1
  Description of the Study Area 3
  General Field Procedures 5
  Acknowledgments 5
Aspects of the Social Organization and Dynamics of Blue Monkey Groups.. 6
 Methods 6
 Results 7
  Group Size and Composition 7
  Changes in Group Composition 7
  Mortality Factors 7
  Periodicity of Births 8
  Solitary Monkeys 8
  Intragroup Social Structure 8
  Intergroup Relations 12
  Interspecific Relations 13
  Polyspecific Associations 14
 Discussion 16
Food Habits of Blue Monkeys 18
 Methods and Definitions 18
 Results 19
  Plant Diet of Group I during an Annual Cycle 19
  Selection Ratios 19
  Important Components of Total Diet during an Annual Cycle 20
  Food Plants Used by Blue Monkeys during the Entire Study Period.. 20
  Patterns of Use of Food Resources: Intermonthly Variations 21
  Patterns of Use of Food Resources: Intermonthly Similarities 22
  Factors Affecting the Patterns of Use of Food Resources 24
  Intramonthly Variations in Diet 27
  Diet Overlap 29
  Diet Diversity 29
  Invertebrate Component of the Diet of Blue Monkeys 31
  Monthly Importance of Plant Species and Microhabitats in Providing Invertebrate Food Items 31
  Feeding Motor Patterns Employed in the Capture and Ingestion of Probable Invertebrate Food Items 32
  Investigative Activities Related to the Ingestion of Probable Invertebrate Food 32
  Fruits as a Source of Invertebrate Food 34
  Water Requirements of the Blue Monkeys 35
  Vertebrate Food Eaten by Blue Monkeys 35

Page

- Intraspecific Food Niche Separation 35
- Intergroup Dietary Differences 36
- Discussion 40
  - Blue Monkey Feeding Patterns and Adaptive Significance of Diet 40
  - Intraspecific Food Niche Separation 42
  - Food Niche Separation between Sympatric Cercopithecines 42
  - Intergroup Dietary Differences 43
  - Interpopulational Comparisons of Blue Monkey Diet 44

The Ranging Patterns of Blue Monkeys 45

- Methods 45
- Results 45
  - Home Range Size 45
  - Areas Used during Different Sample Periods 46
  - Range Overlap between Sample Periods 48
  - Daily Range 51
  - Range Overlap between Days of the Same Sample Period 52
  - Distribution of Time in Space 53
  - Differential Use of Quadrats and Food Abundance 59
  - Group Spread 64
  - Group Movements 64
  - Effect of Climatic Factors on Group Movements 65
  - Areas and Trees Used for Night Resting 69
  - Quadrat Utilization Diversity 72
  - Intergroup Home Range Overlap 73
- Discussion 74
  - Home Range Size 74
  - Factors Affecting Ranging Patterns 75
  - Comparison with Other Studies 77

Summary and Conclusions 77

Appendix 79

- Table A.—Group I, percent of frequency of use of specific food items 79
- Table B.—List of food plants exploited by the blue monkeys 80
- Table C.—Group I, rank order (I–V) and percent of frequency of use of top five food plants 81
- Table D.—Percent of frequency of ingestion of probable invertebrates from specific microhabitats (I–XI) 82
- Table E.—*Cercopithecus mitis,* Groups I and II, frequency of use of different motor patterns 83
- Table F.—Group I, percent of use of specific plant food items 84
- Table G.—Group II, percent of use of specific plant food items 85

Literature Cited 86

Socioecology of the Blue Monkeys *(Cercopithecus mitis stuhlmanni)* of the Kibale Forest, Uganda

Rasanayagam Rudran

Introduction

Purpose of the Study.—Although monkey species living in rain forests vastly outnumber those dwelling in the savannah, the paucity of information on these species proves to be the most serious shortcoming in clarifying the relation between the ecology and social organization of primates. In fact early theories on the socioecology of primates (De Vore, 1963; Crook and Gartlan, 1966) are considered untenable mainly because they are based primarily on field studies of savannah-dwelling forms. Sometimes even more recent hypotheses (Struhsaker, 1969; Crook, 1970; Eisenberg et al., 1972) are found to be deficient in explaining the social organization of forest-dwelling primates. These problems not only highlight the dearth of information available from rain-forest monkeys, but also serve to show the importance of studying them in order to fully understand the relation between the ecology and social organization of primates. Therefore, I conducted a field study of an African rain-forest primate, the blue monkey (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, western Uganda.

Prior to and during my study of the blue monkeys, T. T. Struhsaker, J. F. Oates, and P. M. Waser completed field investigations of other primates that lived in the Kibale Forest. We used similar methods in our studies so that detailed and meaningful interspecific comparisons could be made in order to elucidate niche separation between closely related sympatric species. Such comparisons were one of the prime objectives of our investigations in the Kibale Forest. The comparison between the red colobus (*Colobus badius tephrosceles*) and the black and white colobus (*Colobus guereza*) has already been made (Struhsaker and Oates, 1975), while the comparisons of blue monkeys with red-tailed monkeys (*Cercopithecus ascanius schmidtii*) and mangabeys (*Cercocebus albigena johnstonii*), respectively, are in progress.

Although I collected data on many aspects of the ecology and behavior of blue monkeys, in the following sections I mainly evaluate the premise that space utilization patterns resulting from the peculiarities of food dispersion affected the social organization of primates (Eisenberg et al., 1972). Therefore, after a brief description of the study area, I describe the social structure of the blue monkeys. Following this I report their diet and their ranging patterns and examine the relationship between these aspects of the life-style of the blue monkeys.

Description of the Blue Monkey.—The blue monkey is also called the diademed monkey (Dorst and Dandelot, 1970) because it has a prominent row of forward pointing white fur just above its brow line (Figure 1). The upper parts of its body and tail are frosty gray in color while its limbs are somewhat darker in appearance. It has whitish whiskers that are particularly well developed in adult males. The

---

Rasanayagam Rudran, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.

FIGURE 1.—A blue monkey (*Cercopithecus mitis stuhlmanni*).

throat and underparts of the body are gray white. Some young animals have indistinct russet-colored rump patches, which I have not seen in adults. The naked parts of the body, such as face, hands, and feet, are black in individuals that are above two or three weeks of age. In infants below this age, these areas are pink. Adult males of this species weigh over 6 kg (Kingdon, 1971) and an infant male that I "collected" weighed 360 gm a few hours after its birth.

The blue monkey is an extremely arboreal animal that rarely descends to the ground. This distribution of this monkey is patchy and restricted to certain parts of Zaire, Uganda, and Rwanda. Related subspecies, however, are to be found in central and east Africa, in Mozambique, and parts of South Africa (Dorst and Dandelot, 1970; Rahm, 1970).

DESCRIPTION OF THE STUDY AREA.—The Kibale Forest study area (0° 34′ N; 30° 21′ E) is situated close to the Kanyawara Forestry Station, which is about 25 km east of the Ruwenzori mountains. It is located on undulating terrain at an elevation of approximately 1500 m and is about 3 km^2 in extent. The study site is bounded by grassland on its eastern and western sides while it is continuous with more forest on the other two sides. Within this area there are over 40 km of foot trails that facilitated monkey observations but in no way altered the character of the habitat. Due to selective felling conducted in 1969 for the removal of certain commercially valuable species, however, about a third of the study site (referred to as Compartment 14) remains somewhat disturbed. The rest of the study site (Compartment 30) consists of undisturbed mature forest.

In this area the climate is cool and temperatures are relatively moderate. The mean minimum and maximum temperatures are 12.7° and 25.5°C (Struhsaker, 1975). The mean annual rainfall of 1475 mm is relatively well dispersed throughout the year but some months of the year are wetter than others (Kingston, 1967). Typically, March and April and September through November are considered wet months.

Within the study area the forest is tall, and some emergents such as *Parinari excelsa* and *Aningeria altissima* reach heights of over 45 m. The tree canopy layer that usually lies between 10 and 30 m above ground level is dense, and more or less continuous except in the selectively felled area. The vegetation is both complex and heterogeneous. On the undulating terrain of the study area relatively small trees (e.g., *Chaetachme aristata, Dombeya mukole,* and *Diospyros abyssinica*) predominate the well-drained upper slopes, while large species (e.g., *Parinari excelsa* and *Mimusops bagshawei*) are found most often on the lower slopes. In the water-logged valley bottom, trees, such as *Smyphonia globulifera* and *Neoboutonia macrocalyx,* and semi-woody vegetation are most common. Thus, many of the tree species within the study area exhibit a clumped distribution (Oates, 1974; Struhsaker, 1975). The shrub vegetation is thick, particularly in the swampy areas and in Compartment 14, where selective felling had created some large openings in the tree canopy layer.

The phenological activity of this forest is extremely complex. In general, species differ considerably in the pattern and timing of their phytophasic activity. For example, *Balanites wilsoniana* produce young leaves only once each year during a short period between January and March, while *Celtis durandii* and *Celtis africana* flush throughout the year with peaks of flush production occurring in April–May and October–November in both species (Oates, 1974). *Olea welwitschii* also produces flush throughout the year, but does not have a peak period of flush production. Similarly, different tree species also show variability in their reproductive activity. The patterns of flowering activity of *B. wilsoniana, C. durandii,* and *C. africana* are the same as their leafing activity, but *O. welwitschii* produces blossoms on a biannual basis. *Pancovia turbinata* and *Teclea nobilis* are seasonal in their fruiting activity, but they produce fruits at different times of the year; in February–March and July–November, respectively (Figure 2). In contrast, *C. durandii, C. africana,* and *Ficus exasperata* produce fruits almost throughout the year. On the other hand, *Parinari excelsa* produces fruits with superannual periodicity. This species produced fruits in 1973 after a lapse of nearly three years (Struhsaker, pers. comm.). Furthermore, considerable interindividual variations in phenological activity may be noted within many species.

Due to the complex patterns of phenological activity all phytophases are available during many months of the year but are more abundant during certain times than during others. For instance,

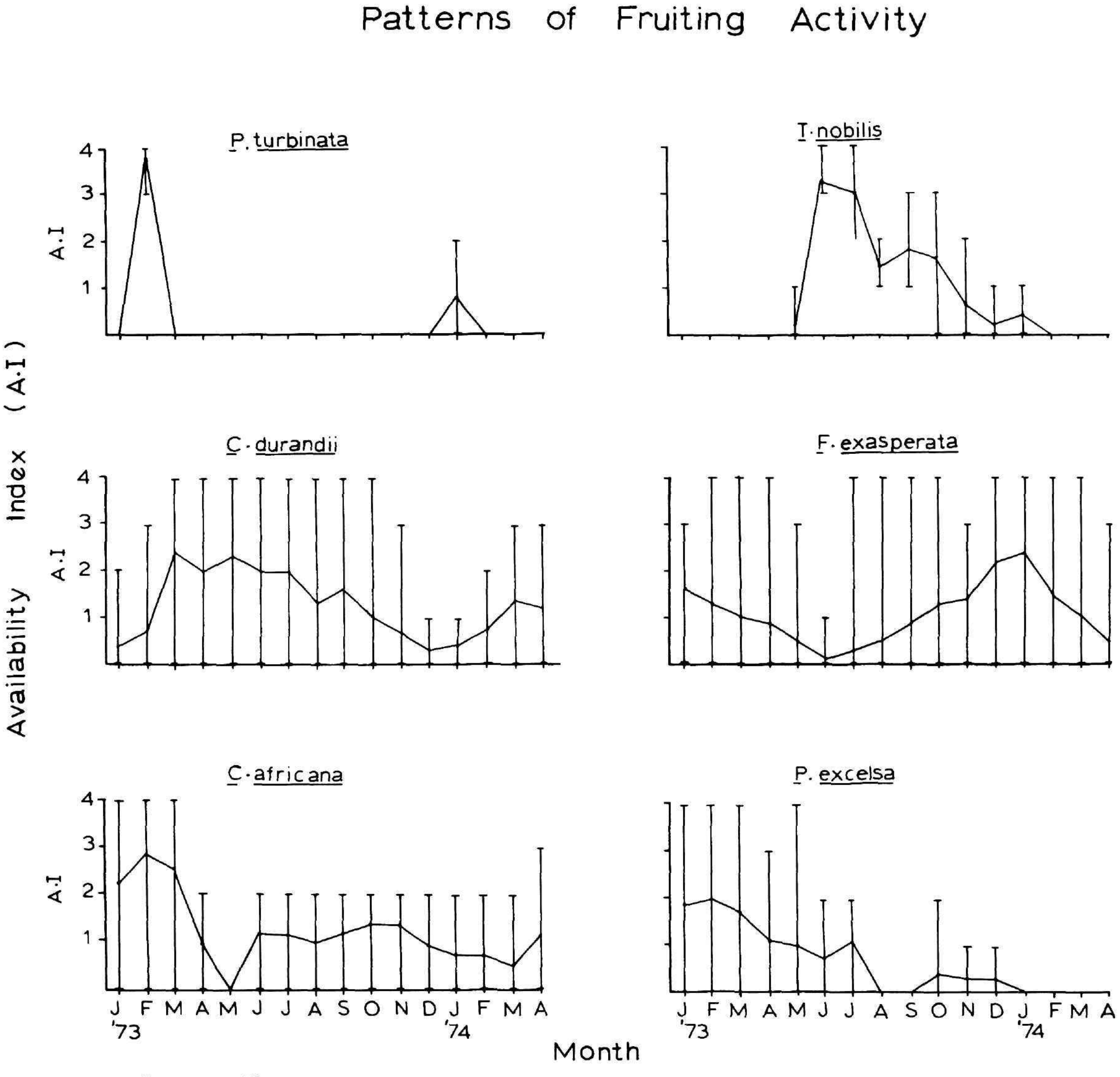


FIGURE 2.—The mean and the range of monthly availability of fruits on selected blue monkey food plants illustrating variations in their patterns of phenological activity. The availability index (AI) is a subjective assessment of the abundance of fruits (based on a 0–4 scale) on trees included in the phenological sample. Data for *T. nobilis*, *C. durandii*, *C. africana*, and *P. excelsa* from Struhsaker (pers. comm.).

peaks of leaf and flower production occur about one month after rainfall that follows a dry period (Oates, 1974; see also Struhsaker, in press). Therefore, blue monkey foods can be highly variable in their temporal as well as spatial abundance.

The faunal complement of the Kibale Forest Study Area is quite diverse. Two hundred and seventy-six bird species are to be found within and around the Kibale Forest (Friedmann and Williams, 1970, quoted in Struhsaker, 1975). Mammals that are commonly found in this area are the bush buck (*Tragelaphus scriptus*), Harvey's red duiker (*Cephalophus harveyi*), the blue duiker (*C. monticola*), the bush pig (*Potamochoerus porcus*), and the African civet (*Viverra civetta*). Less common are the elephant (*Loxodonta africana*), the buffalo (*Syncerus cafer*), the ratel (*Mellivora capensis*), the crested porcupine (*Hystrix sp.*), the flying squirrel (*Anomalurus sp.*), the serval cat (*Felis serval*), and several viverrid species. Other parts of the same forest contain the lion (*Panthera leo*), the leopard (*Panthera pardus*), the golden cat (*Felis aurata*), the giant forest hog (*Hylochoerus meinertzhageni*), the warthog (*Phacochoerus aethipicus*), and hippopotamus (*Hippopotamus amphibius*).

By far the most conspicuous members of the mammalian fauna of the Kibale Forest study area are the primates. These include the black and white colobus (*Colobus guereza occidentalis*), the red colobus (*Colobus badius tephoroscles*), the blue monkey (*Cercopithecus mitis stuhlmanni*), the red-tailed monkey (*C. ascanius schmidtii*), the lhoest's monkey (*C. l. lhoesti*), the mangabey (*Cercocebus albigena johnstoni*), and the chimpanzee (*Pan t. troglodytes*). Sometimes, the olive baboon (*Papio anubis*) may be seen within the study area. Other primate species found here are the small nocturnal forms, such as the potto (*Perodicticus potto*), the dwarf galago (*Galago demidovi*), and a larger galago believed to be *G. inustus*.

General Field Procedures.—My study of the blue monkeys of the Kibale Forest began in December 1972 and ended in November 1974. During the first two months of my investigations, I conducted a pilot study in order to (1) become familiar with the fauna and flora of the area and (2) standardize my methods of data collection with those used in the investigations of other primate species found in the Kibale Forest. From February 1973, I began intensive data collection from two groups of blue monkeys (i.e., Group I and Group II). I collected these data on a monthly basis during five consecutive days of dawn to dusk observations of each group. During some months each of these groups was observed for two 5-day periods (in the following text I refer to each 5-day period as a sample period). Thus, Group I, which was investigated for 16 months, was contacted during 23 sample periods, and Group II, which was observed during 18 months, was contacted during 20 sample periods (Table 1). Three other groups were also periodically contacted during the study.

I have given the details of the methods of collection of socioecological data in the appropriate sections. In general, however, methods of data collection were by and large predicated by the generally poor visibility conditions within the forest. Because of this it was usually not possible to keep all or even one member of a group under continuous surveillance for more than a few minutes. This precluded the possibility of conducting longitudinal sampling of the group. Therefore, much of the data were collected either in a systematic manner by sampling group activities during predetermined 10-minute periods of observations or on an opportunistic basis. The 10-minute periods of systematic observations (referred to as scan periods) were centered at the hour, at the half hour, at a quarter to, and a quarter past the hour.

Acknowledgments.—I acknowledge the financial support given me by the New York Zoological Society, the National Institutes of Mental Health of the United States (Grant No. 1 RO1 MH23008-01 awarded to Dr. Thomas T. Struhsaker), and the Smithsonian Institution. I also thank the President's Office of Uganda and the Uganda Forestry Department for permission to conduct my research in Uganda and in the Kibale Forest. The National Research Council of Uganda is thanked for acting as my local sponsor during my stay in Uganda.

Several people helped me in many ways during various stages of my research on the blue monkeys. I am most grateful to all of them. As in the past, Dr. John F. Eisenberg, my adviser, inspired and encouraged me through all stages of my project. Through him I met Dr. Thomas T. Struhsaker, who gave me the opportunity to conduct field research in Uganda and shared with me the fruits of his field experiences. To these two people I

TABLE 1.—Monthly schedule of fieldwork in Kanyawara in sample periods of usually five consecutive days of observations

Schedule			Contact with Group I			Contact with Group II			
Month and year	Number of days	Number of hours	Number of sample periods	Hours during sample periods	Hours during other times	Number of sample periods	Hours during sample periods	Hours during other times	Contact (hours) with other groups
Jan 73	13	114	-	-	21.00	-	-	12.50	36.50
Feb 73	19	169	1	46.25	-	1	43.75	1.00	30.75
Mar 73	21	215	2	95.25	2.00	1	50.50	1.50	3.75
Apr 73	21	206	2	94.00	2.00	1	46.50	2.00	-
May 73	19	190	2	91.75	-	1	47.75	1.50	-
Jun 73	21	203	2	97.50	1.00	1	48.25	6.75	-
Jul 73	17	153	2	117.50	2.00	-	-	0.75	-
Aug 73	21	193	2	115.25	2.50	1	39.75	6.00	-
Sep 73	14	133	1	51.25	2.50	1	59.25	2.50	-
Oct 73	13	129	1	54.75	-	1	55.00	2.00	-
Nov 73	22	206	2	114.50	5.00	1	49.75	2.00	-
Dec 73	18	162	1	60.50	1.50	1	59.75	1.50	5.50
Jan 74	13	123	1	56.00	1.25	1	51.50	-	-
Feb 74	14	125	1	56.50	0.50	1	43.00	0.75	-
Mar 74	11	85	1	20.75	-	1	36.75	-	-
Apr 74	21	128	1	25.50	13.75	1	52.50	-	14.75
May 74	11	55	1	18.00	-	-	-	-	19.25
Jun 74	7	38	-	-	-	1	14.75	2.00	-
Jul 74	1	16	-	-	-	-	-	-	6.00
Aug 74	9	83	-	-	-	1	50.00	9.25	-
Sep 74	18	120	-	-	-	2	82.75	12.50	4.00
Oct 74	20	128	-	-	-	2	53.00	1.25	33.50
Total	344	2974	23	1118.25	55.00	20	884.25	67.75	154.00

owe an immense debt of gratitude for helping me mold my professional career.

The members of my committee, Drs. Ed Buchler, John Eisenberg, Douglas Gill, Douglass Morse, Eugene Morton, and Jane Potter, and my colleagues Drs. Wolfgang Dittus, John Oates, John Seidensticker, Tom Struhsaker, and Peter Waser read part or all of several drafts of the manuscript. Their coments, which vastly improved the quality of this dissertation, are gratefully acknowledged.

The Nairobi Museum and Mr. A. B. Katende of the Makerere University Herbarium are thanked for identification of plant specimens. Dr. Charles Roberts of the Smithsonian Institution is thanked for helping me with statistical analyses. Mrs. Wyotta Holden typed the final draft of this paper. I am extremely grateful to her for this and for her competence and kindness. Thanks are also due to Mr. Chris Triolo, who helped in the final preparation of the manuscript.

I also wish to thank Mr. and Mrs. Bruno Illi, Dr. and Mrs. Lance Tickell, and Dr. Peter White for their warm hospitality, which made visits to Kampala extremely pleasant, and the people of Kanyawara, who made my East African sojourn a memorable one. Lastly, but by no means the least, I wish to note my appreciation to my wife, Ranji, and to Bobby. I am indebted to Ranji, who endured the hardships of a bush life for two years, for her patience, understanding, and secretarial help and to Bobby for his companionship.

In Appendix Table B, Metcalfe and Chalk (1950), Eggeling and Dale (1951), Lawrence (1951), Struhsaker (1975), A. B. Katende of the Department of Botany, Makerere University, and S. P. Kibuwa of the East African Herbarium, Nairobi, were consulted for the identification and nomenclature of the listed food plants.

Aspects of the Social Organization and Dynamics of Blue Monkey Groups

METHODS

I used interindividual distances between group members as a way of illustrating the social structure of blue monkeys. These distances were obtained by successively considering each group member who was visible during a scan period as a focal animal and noting its neighbors. Neighbors were operationally defined as animals within 10 m of the focal animal, with whom their spatial relationship remained unaltered for at least five seconds. Intraspecific and interspecific social interactions were recorded throughout the day.

Polyspecific associations formed by blue monkey groups were defined using the following criteria. I considered a blue monkey group to be in association with another primate species if during a scan period (1) a single blue monkey was 5 m or less away from an individual of another species, or (2) when three individuals of different species (including at least one blue monkey) were no more than 10 m from each other, or (3) when four or more individuals of different species (including at least one blue monkey) were no more than 20 m of each other.

The first criterion can be used only to define two-species associations, while the other two criteria can be used to define associations involving two or more species.

RESULTS

GROUP SIZE AND COMPOSITION.—Table 2 presents the size and composition of five blue monkey groups on the first day complete counts were obtained from them. Since immature individuals were extremely difficult to sex, I have distinguished them only on the basis of age classes. Four of the groups contained a single adult male each, while the fifth group included two adult males. Thus the "one-male group" was the most predominant social structure of these blue monkey groups. The sizes of these groups, however, were highly variable (range 13–27; $\bar{X} = 20.8$), because each group contained between 4 and 12 adult females and 7 to 16 immature animals.

The mean ratio of adult males to adult females in these bisexual groups (i.e., the socionomic sex ratio) was 1 : 6.8. The large disparity in adult sex ratio was at least partly caused by emigration of young males from bisexual groups and also by the slower rate of maturity of males. Due to the difficulty in sexing immature animals, I was unable to ascertain whether an unequal sex ratio at birth contributed to the disparity in adult sex ratio but there was no evidence to suggest that differential mortality among the sexes could have caused this situation.

CHANGES IN GROUP COMPOSITION.—Changes in the composition of blue monkey groups were usually minor and were caused by (1) births, (2) recruitment of young animals into older age classes and, (3) the "disappearance" of individuals, which in most cases may have been due to deaths. One of my study groups (i.e., Group II) also underwent an important social change when an adult male joined this group and took its leadership from the resident adult male (Rudran, in prep.). The details of the changes in composition of the two groups that I studied most intensively (Groups I and II) are given in Table 3.

MORTALITY FACTORS.—The reason for the disappearance of the two adult females from Group I (Table 3) was unknown. In Group II, RLT's infant died after being abandoned by its mother when she was attacked by other group members. Intragroup aggression may also have been the cause of the disappearance of Bulb (and her infant), who was frequently harassed by other group members just before she disappeared. Adult female M may have succumbed to the wounds she had

TABLE 2.—Composition of five bisexual groups on the first day that complete group counts were obtained

Group	Date	Adult males	Adult females	Sub-adults	Juveniles	Infants	Total
I..........	4 Feb 73	1	11	3	5	4	24
II.........	25 Jan 73	1	5	2	4	1	13
III........	22 Jan 73	1	12	3	8	3	27
IV.........	19 Apr 73	1	4	1	6	1	13
V..........	25 Dec 73	2	9	4	8	4	27
Total....		6	41	13	30	13	104
Percent..		5.8	39.8	12.6	29.1	12.6	

TABLE 3.—Changes in group composition in Groups I and II (AM = adult male, AF = adult female, SA = subadult, J = juvenile, I = infant)

Group and date	Age/sex class						Comments
	AM	AF	SA	J	I	Total	
GROUP I							
Feb 73....	1	11	3	5	4	24	
Jun 73....	1	9	3	9	2	24	Recruitment of 4 infants into juvenile age class; birth of 2 infants; loss of 2 adult females
Nov 73....	1	9	3	10	1	24	Recruitment of 1 infant into juvenile age class
Feb 74....	1	9	3	11	4	28	Recruitment of 1 infant into juvenile age class; birth of 4 infants; composition unchanged in May 74
GROUP II							
Jan 73....	1	5	2	4	1	13	
Jun 73....	1	4	2	5	-	12	Loss of adult female M; recruitment of M's infant into juvenile age class
Sep 73....	1	4	2	4	-	11	Loss of M's offspring (a small juvenile)
Jan 74....	1	4	2	4	2	13	Birth of 2 infants (to females LLT and Bulb)
Jan 74....	1	3	2	4	1	11	Loss of Bulb and her infant
Feb 74....	1	3	2	4	2	12	Birth of infant (to RLT)
Feb 74....	1	3	2	4	1	11	Loss of RLT's infant
Aug 74....	1	3	2	5	-	11	Recruitment of LLT's infant into juvenile age class
Sep 74....	2	3	2	5	-	12	Addition of 1 adult male; composition unchanged in October 74

just prior to her disappearance. She may have sustained these wounds either during intragroup or intergroup aggressive encounters. Female M's offspring disappeared due to unknown causes. During the study, I did not find any evidence to suggest that disease or predation was an important mortality factor. Aerial predation of young blue monkeys by large raptors may have been an infrequent cause of mortality. Occasionally, I saw crowned hawkeagles (*Staphaeonatus coronatus*) attempt to catch these monkeys.

PERIODICITY OF BIRTHS.—Just prior to the beginning of and during the study, 14 infants were born into Groups I and II. Their estimated birth dates showed that in two successive years there were a total of six births in December, four births in January, two births in February, one birth in March, and another in May. This shows that blue monkey births occurred seasonally, and the above data suggests that there was either a long birth season between December and May or two shorter seasons separated by the month of April. None of the identifiable adult females carried infants during successive December–May periods, which indicates that interbirth interval was longer than one year.

SOLITARY MONKEYS.—Solitary blue monkeys were infrequently seen, which may have been partly because they were less conspicuous than social groups. Throughout the entire study, I saw no more than eight solitary animals. Six of these were adult males and two were unsexed subadults. Adult females or juveniles were not seen as solitary individuals. Solitary animals seemed to be transients and did not appear to stay for more than three weeks in any particular area. They were usually evicted from the home ranges of bisexual groups by the adult males of these groups.

Just before my study began an easily identifiable subadult male that disappeared from Group III was located as a lone individual within the home range of Group I (M. S. and P. Waser, pers. comm.). This suggests that males nearing adulthood emigrate from their parental groups and live as solitary animals. The social change that took place in Group II tends to show that these males may reenter bisexual groups as adults.

INTRAGROUP SOCIAL STRUCTURE.—Intragroup social structure may be elucidated by considering spatial relationships within the group. The social structure of blue monkey groups was relatively stable but, in order to illustrate variations in spatial relationships due to changes in group composition, I have considered data collected from Group I during April 1973 as well as October 1973.

In April 1973, the proportion of sightings of adult females with neighbors was nearly twice as large as in October 1973 (Table 4). This was because Group I contained a greater number of young infants in April 1973 than in October 1973 and these infants were always neighbors to their mothers. Also, in October 1973, small juveniles spent proportionately greater amounts of time with neighbors than in April 1973, which was probably related to the age difference between individuals that belonged to the small juvenile class during these two months. The small juveniles of October 1973 were between 6–10 months of age (born during the 1972–1973 birth season), while the small juveniles of April 1973 were 11 months or older (probably born during the 1971–1972 birth season). Therefore, it appeared that as infants matured they progressively spent less time in the company of neighbors. Large juveniles and older age classes (except adult females with infants) spent a greater proportion of time without neighbors than with them, but these proportions were relatively constant between the two months. Thus, it would seem that spatial relationships were affected by births of infants and their early development. Other factors, such as the estrous condition of females, may also have affected the social structure, but in the field I was unable to assess the sexual state of blue monkey females.

TABLE 4.—Group I, percent of sightings of different age/sex classes with neighbors within 10 m, April 1973 and October 1973

Age/sex class	Group composition		Frequency of sightings		Percent of sightings with neighbors	
	Apr 73	Oct 73	Apr 73	Oct 73	Apr 73	Oct 73
Adult male.......	1	1	48	52	27.1	27.0
Adult female.....	11	9	404	388	59.2	30.7
Subadult.........	3	3	156	177	27.6	33.4
Large juvenile...	2	5	109	160	30.4	36.2
Small juvenile...	3	5	152	112	55.4	74.1
Infant...........	4	1	133	31	100.0	96.8

For any pair combination of age/sex class, a set of two interindividual distances were obtained because an animal was considered as a focal animal as well as a neighbor to other focal animals. Due to changes in the spatial relationships between animals, these two distances were not necessarily the same but they did not differ greatly. For example, the mean interindividual distance between the adult male and adult females was 2.0 m when the adult male was considered as the focal animal, and 2.2 m when the adult females were considered as focal animals. Thus, I obtained the mean of these two distances in order to simplify the presentation of results (Table 5). I have also combined the data from April 1973 and October 1973 since interindividual distances did not vary appreciably between these two months.

TABLE 5.—Group I, mean interindividual distances (m) between different age/sex classes computed from data collected in April 1973 and October 1973 (N = 1329 observations; small juveniles and adult males were not recorded as neighbors within 10 m of each other)

Age/sex class	AM	AF	SA	LJ	SJ	I
Adult male......	-	2.1	3.6	4.6	-	2.5
Adult female....	-	2.6	2.4	2.3	1.3	0.5
Subadult........	-	-	1.6	1.9	1.5	1.8
Large juvenile..	-	-	-	1.6	1.5	2.6
Small juvenile..	-	-	-	-	1.0	1.4
Infant..........	-	-	-	-	-	1.2

Spatial relationships between different age/sex classes show the following:

1. The adult male was in closer proximity to adult females than to other age classes.

2. Adult females were nearest to infants, and adult female to adult male distance was shorter than adult female to adult female distance.

3. Subadults were in closest proximity to each other or to small juveniles and farthest away from the adult male. The spatial relations of large juveniles were similar to those of subadults.

4. Small juveniles were closest to each other, and of all age/sex classes were farthest from the adult male.

5. Infants were closest to their mothers and they were closer to each other than would be predicted by distances between adult females. This suggests that adult females with infants were in closer proximity to each other than to adult females who did not carry infants.

Intragroup social structure can be further clarified by considering the frequencies with which each age/sex class was nearest neighbor to other classes. As indicated earlier, for each pair combination of age/sex class, a set of two nearest neighbor values was obtained since each animal was considered as a focal animal as well as a neighbor (Table 6). Observed frequencies of nearest neighbors were compared to frequencies expected from a random model, which were computed in the following manner. Since the mean group count for April 1973 and October 1973 was 24 each, a focal animal could have 23 pair combinations of nearest neighbors. Therefore, all 24 animals (each considered as a focal animal) could have (23 × 24) 552 pair combinations of nearest neighbors and the probability of observing any particular pair combination was 1/552 (= 0.0018). Considering the adult male and adult females, the probability of the adult male having one of the 10 adult females as nearest neighbor was 10/552 (= 0.018). Therefore, of 983 nearest neighbor records, the frequency of adult females as nearest neighbors to adult male would be 17.8 (0.18 × 938). The frequency of the adult male as nearest neighbor to adult females would also be the same. Similarly, the frequency of 10 focal adult females having one of the other nine adult females as nearest neighbors in 983 records would be (1/552 × 9 × 10 × 983) 160.3.

The frequencies with which different age/sex classes had nearest neighbors differed significantly from expected ($\chi^2 = 59.95$, df = 5, $p<0.005$). Large juveniles and older age classes had less than the expected number of nearest neighbors while small juveniles and infants had greater than the expected number of nearest neighbors (Table 6).

Indices of association between different age/sex classes can be obtained by computing the ratio of observed frequency of nearest neighbors to the expected frequency (Table 7). The magnitude of this ratio indicates the degree of association between age/sex classes and a ratio of one shows that the association was as expected from the random model. The indices of association between age/sex classes substantiate the points made earlier using interindividual distances. They also show that associations between two age/sex classes were not always equally strong in both directions. For example, the indices of association between the adult male and adult females were 0.8 and 1.2 depending on which sex class was considered as focal (Table 7). This was because while the adult male had adult females as his nearest neighbors, the adult females sometimes had other age/sex classes as their nearest neighbors (Table 6).

In order to understand the effect of the strong association between adult females and infants on the social structure of the group, adult females

TABLE 6.—Group I, observed and expected frequencies of nearest neighbors of each age/sex class (mean number of animals in each age/sex class is given within parentheses; focal animals in left vertical column, nearest neighbors in top horizontal row)

Age/sex class	AM(1)	AF(10)	SA(3)	LJ(3.5)	SJ(4)	I(2.5)	Total
Adult male							
observed.......	0	22.0	5.0	1.0	0	4.0	32.0
expected.......	0	17.8	5.4	6.2	7.1	4.5	41.0
Adult female							
observed.......	14.0	80.0	31.0	21.0	79.0	156.0	381.0
expected.......	17.8	160.3	53.4	62.3	71.2	44.5	409.5
Subadult							
observed.......	4.0	33.0	22.0	13.0	23.0	9.0	104.0
expected.......	5.4	53.4	10.6	18.7	21.4	13.4	122.9
Large juvenile							
observed.......	3.0	33.0	15.0	26.0	23.0	5.0	105.0
expected.......	6.2	62.3	18.7	15.6	24.9	15.6	143.3
Small juvenile							
observed.......	0	86.0	17.0	17.0	64.0	14.0	198.0
expected.......	7.1	71.2	21.4	24.9	21.4	17.8	163.8
Infant							
observed.......	1.0	142.0	1.0	2.0	5.0	12.0	163.0
expected.......	4.5	44.5	13.4	15.6	17.8	6.7	102.5
Total							
observed.......	22.0	396.0	91.0	80.0	194.0	200.0	983.0
expected.......	41.0	409.5	122.9	143.3	163.8	102.5	983.0

with infants and those without infants were considered separately. The mean interindividual distances and indices of association of these two adult female classes with other age classes indicate the following:

1. Adult females without infants were in closer proximity to the adult male than adult females with infants (Table 8).

2. The closest association among adult females was between those that had infants, and associations within each adult female class were greater than associations between them (Table 9).

TABLE 7.—Group I, indices of association between age/sex classes computed on the basis of observed and expected frequencies of nearest neighbors (focal animals in left vertical column, nearest neighbors in top horizontal row)

Age/sex class	AM	AF	SA	LJ	SJ	I	Total
Adult male......	0	1.2	0.9	0.2	0	0.9	0.78
Adult female....	0.8	0.5	0.6	0.3	1.1	3.5	0.93
Subadult........	0.7	0.6	2.1	0.7	1.1	0.7	0.85
Large juvenile..	0.5	0.5	0.8	1.7	0.9	0.3	0.73
Small juvenile..	0	1.2	0.8	0.7	3.0	0.8	1.20
Infant..........	0.2	3.2	0.1	0.1	0.3	1.8	1.60

TABLE 8.—Group I, mean distances between adult females (with and without infants) and other age classes

Age/sex class	AM	AF	AF+I	SA	LJ	SJ
Adult female......	1.9	2.6	3.4	2.4	2.3	1.4
Adult female plus infant......	2.9	3.1	1.7	2.4	2.7	1.5

TABLE 9.—Group I, observed and expected frequencies of nearest neighbors of adult females (with and without infants) and the indices of association with other age/sex classes (focal animals in left vertical column, nearest neighbors in top horizontal row)

Age/sex class	AM	AF	AF+I	SA	LJ	SJ	Total
Adult female							
observed........	15.0	74.0	14.0	33.0	21.0	86.0	243.0
expected........	11.1	72.1	27.7	33.3	38.8	44.3	227.2
Adult female plus infant							
observed........	6.0	14.0	9.0	7.0	5.0	19.0	60.0
expected........	3.7	27.7	5.5	11.1	12.9	14.8	75.7
Total							
observed........	21.0	88.0	23.0	40.0	26.0	105.0	303.0
expected........	14.8	99.8	33.2	44.4	51.7	59.1	303.0
	Indices of association						
Adult female.....	1.4	1.0	0.5	1.0	0.5	1.9	1.1
Adult female plus infant.....	1.6	0.5	1.6	0.6	0.4	1.3	0.8

3. Adult females without infants associated more closely with subadults and juveniles than adult females with infants.

4. Adult females without infants most closely associated with small juveniles, while the closest association of adult females with infants was with other females with infants.

From the above it can be seen that, within the group, adult females with infants formed subgroups, and, unlike the other adult females, they had less than the expected number of nearest neighbors ($\chi^2 = 4.36$, df = 1, $p < 0.05$).

An understanding of intragroup social structure may also be gained by considering the directionality and frequencies of aggressive encounters. In Group I, I observed only 99 aggressive interactions in over 1100 hours of group contact (Table 10), which may have been partly because my observations were hampered by poor visibility within the forest. The observed and expected frequencies (computed in the same manner as before) of aggressive interactions show that the adult male and subadults were the only animals that aggressed more frequently than expected. Also these two classes and large juveniles were aggressees more often than expected. The adult male who had the highest overall index of aggression (Table 11) aggressed far more frequently than expected against subadults and large juveniles. These age classes also aggressed against the adult male more frequently than expected. Moreover, the indices of aggression within and between subadult and large juvenile

TABLE 10.—Group I, observed and expected frequencies of aggressive interactions between different age/sex classes (mean number of individuals within each age/sex class in parentheses; aggressee in top horizontal row)

Aggressor	AM(1)	AF(10)	SA(3)	LJ(3.5)	SJ(4)	I(2.5)	Total
Adult male							
observed.......	0	2.0	6.0	9.0	1.0	0	18.0
expected.......	0	1.8	0.5	0.6	0.7	0.4	4.0
Adult female							
observed.......	3.0	1.3	13.0	5.0	2.0	1.0	37.0
expected.......	1.8	16.1	5.4	6.3	7.2	4.5	41.3
Subadult							
observed.......	3.0	13.0	4.0	10.0	3.0	0	33.0
expected.......	0.5	5.4	1.1	1.9	2.2	1.3	12.4
Large juvenile							
observed.......	2.0	1.0	2.0	5.0	0	0	10.0
expected.......	0.6	6.3	1.9	1.6	2.5	1.6	14.5
Small juvenile							
observed.......	0	1.0	0	0	0	0	1.0
expected.......	0.7	7.2	2.2	2.5	2.2	1.8	16.6
Infant							
observed.......	0	0	0	0	0	0	0
expected.......	0.4	4.5	1.3	1.6	1.8	0.7	10.3
Total							
observed.......	8.0	30.0	25.0	29.0	6.0	1.0	99.0
expected.......	4.0	41.3	12.4	14.5	16.6	10.3	99.0

TABLE 11.—Indices of aggression between age/sex classes (mean number of individuals in each age/sex class in parentheses; aggressee in top horizontal row)

Aggressor	AM(1)	AF(10)	SA(3)	LJ(3.5)	SJ(4)	I(2.5)	Total
Adult male......	-	1.1	12.0	15.0	1.4	0	4.5
Adult female....	1.6	0.8	2.4	0.8	0.3	0.2	0.9
Subadult........	6.0	2.4	3.6	5.3	1.4	0	2.7
Large juvenile..	3.3	0.2	1.1	3.1	0	0	0.7
Small juvenile..	0	0.1	0	0	0	0	0.1
Infant..........	0	0	0	0	0	0	0
Total.........	2.0	0.7	2.0	2.0	0.4	0.1	

age classes were high. Unfortunately, the sex of immature individuals was not known, but the data indicate that aggression, particularly by the adult male, may have been the cause of the emigration or eviction of young males from bisexual groups.

The contexts of nearly 60% of the aggressive encounters were known and in these encounters 61% were conflicts over food (Table 12). About 67% of the interactions at feeding sites were considered to be high intensity aggressive encounters. High intensity aggression included prolonged chases and physical contact, such as biting, while low intensity aggression was those interactions without body contact. High intensity aggressive interactions were greater in a feeding context than in other contexts, which suggests that group members fought most frequently and most violently over food.

INTERGROUP RELATIONS.—Aggressive interactions between groups were infrequent and I observed only 13 of these interactions during my entire study. This was probably due to the fact that blue monkey groups lived in home ranges that did not overlap greatly with those of their neighbors. Intergroup interactions normally took the form of prolonged chases and counter chases accompanied by threat vocalizations. Although I did not observe physical contact between animals, I suspected that the high incidence of injuries in Group II during April 1974 was due to the unusually high frequency of intergroup conflicts (four in five days of observations) that this group was involved in during this period. Adults of both sexes as well as subadults and juveniles took part in intergroup interactions, and each group seemed to have priority of access to different parts of the areas of range overlaps. For example, the area of overlap between the home range of Groups II and III lay to north and south of a track that ran through the study area. Group II always evicted Group III from areas to the north of this track, while Group III displaced Group II every time these two groups interacted in areas to the south of this track. Thus, blue monkey groups appeared to hold territories although they sometimes ranged outside these areas. Seven of 10 encounters between Groups II and III were at fruiting *Ficus* trees, which were important food sources of these monkeys. This suggests that (as in the case of intragroup conflicts) food was the major cause of intergroup conflicts.

TABLE 12.—Group I, contexts and frequencies of low and high intensity aggressive encounters (March 1973 to February 1974, all sample periods)

Context	Low intensity aggression	High intensity aggression	Total
Feeding..........	12	24	36
Sitting, play, grooming, etc...	13	10	23
Uncertain........	14	26	40
Total..........	39	60	99

Blue monkey groups reacted to loud calls such as the "Ka" train and "Pyow" (terminology from Marler, 1973) of their neighbors. The "Ka" train was an alarm vocalization most frequently given by the adult male, but I also heard other group members emitting this call. Analysis of 531 hours of observation of Groups I and II showed that these groups responded immediately to 6 of 10 extra-group "Ka" train sequences. Their responses were either "Ka" trains or chirps, which were also alarm vocalizations. During the same time period 7 of 14 extra-group "Pyows" also evoked calls in Groups I and II. The immediate responses to extra-group "Pyows" were usually chirps and sometimes phrased grunts (that were intragroup contact calls) or trills (that usually served a submissive function), but never calls in kind. In fact, of a total of 141 "Pyows" emitted by the adult males of Groups I and II (during 531 hours of group contact), none were immediately followed or preceded by similar calls from neighboring groups. Thus, there was no evidence for counter calling between adult males, although Aldrich-Blake (1970a) found this to be the case in the blue monkeys of the Budongo forest.

INTERSPECIFIC RELATIONS.—Blue monkeys interacted with all five resident monkey species, but seemed to avoid chimpanzees, which have been reported to prey on blue monkeys (Sugiyama, 1968; Teleki, 1973). On one occasion, a group of blue monkeys chirped and hastily evacuated a fruit-laden *Ficus* tree as soon as a solitary and transient adult male baboon (*Papio anubis*) climbed into it.

Throughout the study I observed a total of 201 interspecific encounters, of which nearly 88% were aggressive encounters. In comparing the frequency of interactions between blue monkeys and other species, the density of these species within the study area was taken into account. These comparisons showed that blue monkeys interacted more frequently than expected with redtails (*Cercopithecus ascanius*) and mangabeys (*Cercocebus albigena*) and less frequently than expected with the red colobus (*Colobus badius*), black and white colobus (*Colobus guereza*), and *Cercopithecus lhoesti* (Table 13). It may be noted that mangabeys and redtails were arboreal and had much in common in terms of diet with blue monkeys while the two colobines were folivorous and *C. lhoesti* was a predominantly terrestrial species.

In about 92% of the aggressive interactions with the smaller redtails, blue monkeys were aggressors. Sometimes these aggressive encounters were bidirectional with redtails retaliating to harassment by blue monkeys. Normally, aggressive interactions between these two species were bipartite, but blue monkeys sometimes formed temporary coalitions of two or three animals against redtails. Blue monkeys were also more frequently the aggressors than aggressees against the larger mangabeys and black and white colobus, but, against the larger red colobus, they were more frequently the aggressees (Table 13). In aggressive encounters against these species, blue monkeys normally formed coalitions of up to four animals and against mangabeys the adult male blue monkey was frequently involved in these coalitions. In general, however, subadults and large juveniles aggressed much more frequently than expected against other species (Table 14).

The contexts of 67 aggressive encounters were known and 79% of these were conflicts over food. About 80% of the conflicts over food were with redtails, whose diet had the greatest similarity to that of blue monkeys (Struhsaker and Rudran, in prep.).

Interspecific affiliative encounters included play and grooming. Participants of play were always young animals and the duration of play was less than 15 minutes. Grooming also usually involved young animals and was unidirectional. On one occasion, however, a solitary adult male blue monkey was groomed by a subadult red colobus. Adult female blue monkeys ignored interspecific solicitation for grooming on four occasions.

In addition to the above types of encounters, the primates of the Kibale Forest interacted with each

TABLE 13.—Groups I and II, total frequency of interspecific aggressive and affiliative interactions during all 5-day periods of observation (expected frequencies of interactions between blue monkeys and other species were computed on the basis of species densities from Struhsaker, 1975, and Oates, 1974)

	Percent of aggressive interactions		Percent of affiliative interactions			Total interactions	
Interactions with—	With *Mitis* as aggressor	With other species as aggressor	Play	Grooming	Solicit grooming	Observed	Expected
C. ascanius.........	121	10	9	1*	3	144	31.9
C. badius...........	2	16	6	2**	-	26	148.0
C. albigena.........	14	5	2	-	-	21	4.1
C. guereza..........	5	4	-	-	-	9	15.1
C. lhoesti..........	-	-	-	-	1	1	1.9
Total.............	142	35	17	3	4	201	201.0

* *C. mitis* was groomer

** *C. mitis* were groomees

TABLE 14.—Observed and expected frequencies of each age/sex class of blue monkeys as aggressor against other species (data from Groups I and II combined)

Age/sex class	Observed	Expected
Adult male......	7	7.4
Adult female....	29	50.7
Subadult........	50	18.3
Large juvenile..	38	28.2
Small juvenile..	3	22.4
Total.........	127	127.0

other through calls given during alarm situations. Of 32 blue monkey "Ka" trains recorded during 531 hours of observation of Groups I and II, 22 (i.e., 69%) were either immediately followed or preceded by the calls of one or several of the other primate species. Blue monkeys also frequently reacted to the alarm calls of other mammals, such as the sun squirrel (*Heliosciurus rufobrachium*), the red duiker (*Cephalophus harveyi*), and the bushbuck (*Tragelaphus scriptus*), and to the calls of birds like the great blue touraco (*Corythaeola cristata*) and the hornbill (*Bycanistes subcylindricus*). These calls usually evoked loud chirps from blue monkeys and sometimes also "Pyows" from the adult male. Distant calls of aerial predators, such as the crowned hawk eagle (*Staphaeonatus coronatus*), were accompanied by geckers and chirps. When these predators flew overhead, blue monkeys emitted the "Ka" train and frequently sought cover in the shrub vegetation. Perhaps the most remarkable interspecific vocal interaction was that between adult male blue monkeys and adult male redtails. About 50% of the "Pyow" sequence given by the adult males of Groups I and II (N = 141 sequences) evoked hack calls from adult male redtails. The hack calls of redtails, however, were never followed by "Pyow" sequences of blue monkeys.

POLYSPECIFIC ASSOCIATIONS.—An interesting aspect of the interspecific relations of blue monkeys was their involvement in mixed groupings consisting of two or more primate species. Blue monkey associations with the black and white colobus, the mangabey, and *C. lhoesti* were usually transitory in nature but their associations with redtails and red colobus sometimes lasted for six to seven hours of a day.

Blue monkeys simultaneously associated with a maximum of three other species, but these types of associations were extremely infrequent. Most frequently blue monkeys associated with one other species. Of a total of 815 associations recorded during 20 sample periods of observations of Group I about 85% were associations with one other species. About 64% of the two-species associations and 68% of all associations included the redtails. The frequencies with which different monkey species associated with blue monkeys did not appear to be solely related to their population density (Table 15). Redtails and mangabeys associated with blue monkeys proportionately more frequently than the two colobines and *C. lhoesti*. Considering this and diets of blue monkeys, redtails and mangabeys, it would appear that polyspecific associations were biologically significant rather than random groupings.

Group I formed polyspecific associations during all sample periods they were observed and spent an average of 19% of the scan periods in mixed groupings (Table 16). Most consistently blue monkeys were associated in either two- or three-species associations with redtails and red colobus; however, the frequency with which Group I associated with other species varied between sample periods. In order to assess the significance of these variations, Spearman rank correlation values (r_s) were computed considering the percentage frequencies of associations during sample periods and various aspects of blue monkey time budget, diet, and ranging patterns (Table 17). Since blue monkeys associated with mangabeys, black and white colobus, and *C. lhoesti* rather infrequently, these associations were not considered separately in these tests.

The above tests showed that there were significant negative correlations between the percentage of time Group I apportioned to feeding on plant material during sample periods, and the percentage frequency with which they formed (1) polyspecific associations with all species, (2) three-species associations including redtails and red colobus, and (3) two-species associations with red colobus. On the other hand, the percentage of time blue monkeys spent in searching and feeding on probable invertebrate foods was positively and significantly correlated with the percentage frequency with which they formed two-species associations with

TABLE 15.—Group I, frequency of different types of polyspecific associations recorded between February 1973 and February 1974, inclusive

Associations with—	Polyspecific associations 2-species	 3-species	 4-species	Total Observed	 Expected
Redtail................	445	110	2	557	157.1
Red Colobus............	229	108	2	337	716.6
Mangabey...............	18	6	0	24	22.0
Black-and-white Colobus	3	5	1	9	25.3
L'hoest's monkey.......	2	3	1	6	12.0
Total................				933	933.0

TABLE 16.—Group I, percent of frequency of polyspecific associations during different sample periods

Sample period	2-species associations With *C. ascanius*	 With *C. badius*	 With other species	3-species associations With *C. ascanius* and *C. badius*	 With *C. ascanius* and one other species	 With *C. badius* and one other species	Number of scans with association	Total number of scans recorded	Percent of scans with associations
Feb 74 (I)....	2.1	2.1	-	-	-	-	8	187	4.2
Mar 74 (I)....	-	0.5	-	-	-	-	1	223	0.5
Mar 74 (II)...	8.9	7.1	-	5.4	-	-	36	168	21.4
Apr 74 (I)....	11.1	6.5	0.9 (*C. albigena*)	3.2	-	0.5 (*C. guereza*) 0.5 (*C. lhoesti*)	49	216	22.7
Apr 74 (II)...	22.2	7.0	-	4.1	0.6 (*C. guereza*) 0.6 (*C. albigena*)	-	59	171	34.5
May 74 (I)....	8.2	7.1	0.5 (*C. guereza*)	1.1	1.1 (*C. lhoesti*)	-	33	184	17.9
May 74 (II)...	22.6	3.6	-	6.7	-	-	65*	195	33.3
Jun 74 (I)....	16.3	9.0	-	6.4	-	-	74	233	31.8
Jun 74 (II)...	9.5	5.6	0.6 (*C. albigena*)	2.2	0.6 (*C. guereza*)	-	34	179	19.0
Jul 74 (I)....	5.7	3.3	0.4 (*C. guereza*)	-	-	0.4 (*C. guereza*)	25**	245	10.2
Jul 74 (II)...	14.0	3.4	0.4 (*C. lhoesti*)	1.7	-	-	46	235	19.6
Aug 74 (I)....	7.0	5.2	-	1.3	-	-	31	229	13.5
Aug 74 (II)...	9.9	5.4	-	0.8	-	-	39	242	16.1
Sep 74 (I)....	16.7	7.6	0.5 (*C. lhoesti*) 0.5 (*C. guereza*)	5.2	0.5 (*C. albigena*)	0.5 (*C. albigena*)	66	210	31.4
Oct 74 (I)....	13.4	9.4	1.3 (*C. albigena*)	2.2	0.5 (*C. albigena*)	-	60	224	26.8
Nov 74 (I)....	11.2	5.4	0.9 (*C. albigena*)	2.2	-	0.5 (*C. guereza*) 0.5 (*C. albigena*)	46	224	20.5
Nov 74 (II)...	6.2	6.6	2.0 (*C. albigena*)	1.2	-	-	39	244	16.0
Dec 74 (I)....	10.1	5.3	-	3.6	0.4 (*C. albigena*)	-	48	247	19.4
Jan 74 (I)....	3.1	4.4	1.3 (*C. albigena*)	-	-	-	20	229	8.7
Feb 74 (I)....	10.6	2.5	-	1.3	-	-	34	236	14.4
Mean........	10.4	5.4	0.5	2.4	0.2	0.1	813+2	4321	19.0

*One four-species association (i.e., 0.4% frequency) between blues, redtails, red colobus, and *C. lhoesti* was recorded.

**One four-species association (i.e., 0.4% frequency) between blues, redtails, red colobus, and black and white colobus was recorded.

the extremely folivorous red colobus monkey. There were also significant positive correlations between the mean distance moved by Group I during a sample period and the percentage frequency of all four types of associations considered in these tests (Table 17).

TABLE 17.—The r_s values of Spearman rank correlation tests between percent of frequency of polyspecific associations during different sample periods and aspects of time budget, diet, and ranging patterns of Group I

Correlation with--	Degrees of freedom	r_s values for polyspecific association with--			All species
		C. ascanius only	*C. badius* only	*C. ascanius* and *C. badius*	
		2-species association		3-species association	
Percent of time plant feeding..	17	-0.253	-0.456*	-0.565*	-0.484*
Percent of time invertebrate feeding......................	17	0.126	0.457*	0.288	0.325
Percent of time moving.........	17	0.419	0.438	0.212	0.433
Percent of time resting........	17	-0.337	-0.404	-0.169	-0.368
Percent of fruits in diet......	18	-0.091	0.091	0.190	0.101
Percent of foliar food.........	18	0.244	0.044	-0.013	0.050
Percent of invertebrates.......	18	0.340	0.401	0.409	0.435
Food diversity.................	18	-0.041	-0.079	-0.270	-0.229
Ranging diversity (Mar 73-Jun 73)..............	6	-0.298	0.673	0.070	-0.024
Ranging diversity (Jul 73-Feb 74)..............	9	0.472	0.389	0.277	0.527
Mean distance moved............	16	0.571*	0.791**	0.529*	0.672**

*Indicates r_s values significant at the 0.05 level
**Indicates r_s values significant at the 0.01 level

Discussion

Blue monkeys of the Kibale Forest normally lived in one-male social groupings and thus exhibited the typical social structure of many rain forest cercopithecines (Struhsaker, 1969). One-male groups of blue monkeys were also the most common in the Budongo Forest, although some two-male groups were to be found (Aldrich-Blake, 1970a). In the Budongo Forest, however, group sizes were somewhat smaller and less variable than in the Kibale Forest. Two of my study groups that contained the smallest number of animals (Groups II and IV) occupied home ranges in the selectively felled area, while the other three lived in the undisturbed part of the study area. Felling operations, which undoubtedly led to a decrease in blue monkey foods, may have caused the apparent reduction in size of the groups living in selectively felled areas. Thus, the normal variation in blue monkey group sizes may have been exaggerated within the Kibale study area.

The emigration of young males from their parental groups provides a means by which the integrity of the one-male group structure could be maintained in this species. Peripheralization of young males was probably caused by the high frequency of adult male aggression directed against subadults and large juveniles (Table 11). This mechanism, however, does not prevent the possibility of inbreeding inherent in a one-male social structure. The social change that occurred in Group II through the addition of an adult male (Table 3) suggests a means by which outbreeding may be enhanced in these social groupings. Shortly after an extra-group adult male took over the leadership of the Group II, all adult females of this group became sexually receptive and copulated only with the new leader (Rudran, in prep.). This type of social change was in some ways similar to those seen in the Asiatic langurs (Sugiyama, 1965; Mohnot, 1971; Rudran, 1973; Hrdy, 1975).

The low frequency with which several age classes were seen with neighbors (Table 4) may be partially attributable to the poor conditions of visibility within the forest, but it was also due to relatively large intragroup dispersion. The median value of the spread of Group I was 50 m, while the maximum was about 120 m. Dispersion over large areas was probably necessary for the efficient exploitation of the largely frugivorous diet of blue monkeys (see Eisenberg et al., 1972). Nevertheless, blue monkeys of the Kibale Forest lived in cohesive social groupings. In this respect these social groupings may have differed greatly from those of the Budongo Forest, which apparently broke up into "parties" (Aldrich-Blake, 1970a). The term "party" as defined by Aldrich-Blake was an aggregation of animals of uncertain social status; for example, a party might be a small portion of a group or two groups combined. My own observations of the Budongo Forest blue monkeys, however, indicated that the social structure of both populations was quite similar. Interinvestigator variability in the ability to maintain group contact was probably one factor that was responsible for our different views on the social structure of blue monkeys. Even in the absence of these biases, however, the social organizations of different primate populations have been found to be variable (Rowell, 1969; Gartlan and Brain, 1968).

During relaxed movements phrased grunts emitted by juveniles and older age classes (except the adult male) probably served to maintain group cohesion (Marler, 1973; Rudran, unpubl.). When the group was widely dispersed the loud "Pyow" call (given only by the adult male) also probably served the same function. "Pyows" of different males were quite distinctive and therefore revealed the location as well as the identity of the caller. Furthermore, nearly 65% of "Ka" trains and other alarm calls discussed in this paper were followed by "Pyows." This suggests that the "Pyow" functions as a rally call that restores group cohesion after a period of disruption. Struhsaker (1970) and Gautier (1969) stress the rallying function of the loud calls of west African cerecopithecines closely related to the blue monkey, but Aldrich-Blake (1970a) suggests that the "Pyow" of the blue monkey serves in intergroup spacing.

In a relatively dense and compact population, such as the one studied by Aldrich-Blake, "Pyow" counter calls may function in intergroup spacing, but at the same time they can serve to rally widely dispersed members of neighboring groups in order to maintain each group's integrity. On the other hand, in the Kibale Forest where the population was less dense and groups occupied home ranges that were nearly 7 to 14 times larger than in the Budongo Forest the lack of counter calling suggests that the "Pyow" was ineffective in its possible intergroup spacing function. Using sonographic analyses of blue monkey vocalizations, Waser and Waser (in press) argue that the characteristics of the "boom" call of the adult male makes it a more effective intergroup spacing call than the "Pyow."

Intragroup, intergroup, and interspecific aggressive interactions of the blue monkeys frequently took place in a feeding context. Some important plant foods of blue monkeys were also important in the diet of one or more sympatric primate species (see Struhsaker, 1975; Waser, 1975); however, interspecific conflicts for plant foods appeared to be reduced by avoiding polyspecific associations when these foods were being eaten (Table 17). Intragroup conflicts for food were probably minimized by different age/sex classes concentrating on different aspects of the dietary spectrum of the species, and intergroup conflicts for food may have been largely averted through territoriality.

While avoidance of polyspecific associations seemed beneficial in acquiring plant foods, the formation of these associations with red colobus appeared to enhance the acquisition of invertebrates by blue monkeys. The exact nature of how this may occur was unclear, but two explanations may be offered. While moving in large mixed groupings with the red colobus, a larger number of invertebrates may have been flushed (due to the greater disturbance to invertebrate microhabitats) than when moving in smaller monospecific groups. This may happen in other types of mixed groupings as well, but in these associations blue monkeys may have had to share invertebrate foods with other species (such as redtails and mangabeys) in whose diets these foods were important (Struhsaker, 1975; Waser, 1975). Thus, in associations with red colobus, blue monkeys may have accrued the same advantages that some birds were suggested to derive from mixed flocks (Neave, 1910). The increased exploitation of invertebrates by blue monkeys when in the company of red colobus may have been due to the reduction in the dangers of predator attacks in these associations (see below). The red colobus rarely indulged in invertebrate feeding (which was an intent activity) and were, therefore, probably more alert to the dangers of predators than blue monkeys. As such, blue monkeys may have been most efficient in acquiring invertebrates when in the company of the red colobus (see also Willis, 1972). Thus, as in the case of mixed-species bird flocks studied by Morse (1970), blue monkey-red colobus associations may have served a multipurpose function (i.e., predator avoidance and invertebrate food acquisition).

Other types of associations of the blue monkeys did not appear to enhance significantly their exploitation of invertebrate food. Among birds, Moynihan (1962) pointed out that the functions of different flocks could be quite variable; however, the fact that member species of all types of associations responded to each other's alarm calls strongly suggests that predator avoidance was an important function of these mixed groupings. Gartlan and Struhsaker (1972) suggest that avoidance of predapators was one of the functions of the associations of cercopithecines in the Cameroon.

The direct relation between blue monkey movements and frequency of associations suggests another advantage that blue monkeys may have derived from polyspecific associations, particularly with redtails with whom they shared many dietary similarities (Struhsaker and Rudran, in prep.). The home ranges of blue monkeys were relatively large and encompassed several home ranges of redtails. Unlike blue monkeys, the redtails moved through almost their entire range within a few days (Struhsaker, pers. comm.). Therefore, they were probably more attuned to local abundances of food than were blue monkeys. Thus, by moving with the redtails, blue monkeys probably used the redtails as "information centers" (Ward and Zahavi, 1973; Krebs, 1974) to efficiently locate areas of food abundance. Once food resources were located, however, interspecific conflict was probably avoided by temporal separation of feeding activities. For example, the redtails usually began feeding earlier in the morning and continued this activity until later in the evening than blue monkeys (Struhsaker, pers. comm.). It has been suggested that associations of other primate species also function in food location and efficient exploitation of the environment (Gartlan and Struhsaker, 1972; Gautier-Hion and Gautier, 1975).

Food Habits of Blue Monkeys

METHODS AND DEFINITIONS

During the 5-day periods of contact with each group, I used a systematic method of scoring feeding observations. These observations were operationally distinguished by using the following criteria. Thirty minutes must elapse before an individual monkey M_1 scored for feeding on a particular food item I_1 from a particular food plant species S_1 was scored again for the same specific food item. During this 30-minute period, however, other feeding scores may be obtained if (1) individual M_1 utilized any other food item I_2 to I_x from the same plant species S_1, or (2) individual M_1 utilized any food item I_1 to I_x from food plants S_2 to S_x, or (3) another individual M_2 utilized food items I_1 to I_x from food plants S_1 to S_x.

A change in the plant species, food item, or feeding individual would lead to a score but 30 minutes must elapse before the same combination was scored again.

I also recorded the frequency of exploitation of probable invertebrate food using the same criteria. Observations of invertebrate feeding were scored taking into account the 30-minute interval criterion, the tree species, and the substrate from which the item was taken, and the motor pattern employed in the capture and ingestion of the food item. In most cases, I was unable to distinguish these food items, which were small, but the type of motor patterns employed in exploitation of these food items and the substrate (such as moss-covered branches) from which they were taken did suggest that these were invertebrate food items. Due to my inability to distinguish the type of invertebrate foods used, I restricted the dietary analyses that required species distinction to plant foods. Invertebrate foods were included only in the analyses of nonspecific food items.

I analyzed all feeding data collected from Group I (during 23 sample periods) and from Group II (during 20 sample periods), but in order to avoid unnecessary duplication of results, I have reviewed only the diet of Group I in detail. The feeding data for Group II are presented mainly by way of intergroup comparison and to illustrate intragroup food niche separation.

I computed intergroup overlaps in diet between comparable sample periods on the basis of the percentage of use of specific food items exploited by both groups (Holmes and Pitelka, 1968). The sum of the shared percentages of mutually exploited specific food items yielded the total overlap in diet. In other words, if during a sample period, the diet of Group I consisted of 40% of a specific food item, 30% of another, 20% of a third, and 10% of a fourth, and the extents of exploitation of the same specific food items by Group II during the most comparable sample period were 20%, 20%, 30%, and 30% respectively, the total overlap in diet would be 70%. Using this method, I also computed the intermonthly overlaps in the diet of Group I. Indices of monthly diet diversity were calculated using the Shannon-Wiener diversity equation $H' = -\Sigma\, p_i \log_e p_i$ (Pielou, 1966) where H′ was the measure of diversity and p_i was the proportion of the frequency of use of the i^{th} specific food item.

In the initial analyses of the diet of Group I, I have considered only one (the first) sample period of each month through an annual cycle from February 1973 to January 1974. This was done in order to overcome the biases introduced by unequal number of days of monthly observations and by the seasonal use of certain food plants. In the later analyses, I have considered feeding data through all sample periods.

RESULTS

Blue monkeys exploited a relatively wide variety of plant species and food items. In addition, they actively searched and preyed upon invertebrates that constituted an appreciable proportion of their diet.

PLANT DIET OF GROUP I DURING AN ANNUAL CYCLE.—During the sample periods considered for the annual cycle, 2068 feeding observations were scored from the use of 59 plant species and 101 specific food items (Appendix Table A). Fifty-five of these food plants were identified. Three of the four unidentified species were mushrooms and the other was a liana. Although Group I exploited a wide variety of food plants, they concentrated their feeding activity on a small number of food plants. About 66% of the feeding observations were recorded from the top 10 food plants and nearly 87% were from the top 20 food plants. *Diospyros abyssinica* was the most frequently used food plant with a 10.7% frequency of use. This species occupied top rank because Group I used it for as many as three important food items (i.e., its young leaves, fruits, and blossoms), while it usually exploited other food plants intensively for single food items. Thus, when specific food items were considered, the fruits of *Celtis africana* were the most important in the diet of Group I while the food items of *D. abyssinica* occupied 7th, 9th, and 12th rank orders (Table 18). The top 10 rank orders of specific food items constituted 55.3% and the top 20 made up 75.2% of their diet. When the use of plant food items regardless of species was considered, fruits were the most important food items and constituted 52.6% of the total plant diet used by Group I (Appendix Table A).

TABLE 18.—Group I, rank order and percent of frequency of use of top 20 specific food items exploited during first 5-day periods of observations from February 1973 to January 1974, inclusive

Rank order of specific food item	Frequency of use	Percent of frequency of use
1. *Celtis africana*, fruits................	170	8.22
2. *Pancovia turbinata*, fruits.............	169	8.17
3. *Teclea nobilis*, fruits................	135	6.53
Uvariopsis congensis, fruits...........	135	6.53
4. *Premna angolensis*, blossoms...........	110	5.32
5. *Celtis durandii*, fruits................	105	5.07
6. *Diospyros abyssinica*, young leaves.....	95	4.59
7. *Ficus exasperata*, fruits...............	93	4.49
8. *Diospyros abyssinica*, fruits...........	68	3.29
9. *Mimusops bagshawei*, fruits.............	63	3.05
10. *Funtumia latifolia*, seeds............	57	2.76
11. *Diospyros abyssinica*, blossoms........	55	2.65
12. *Markhamia platycalyx*, petioles........	50	2.42
13. *Parinari excelsa*, fruits..............	44	2.13
14. *Vangueria apiculata*, mature leaves.....	39	1.89
15. *Illigera pentaphylla*, mature leaves....	37	1.79
16. *Monodora myristica*, leaf buds.........	33	1.60
Neoboutonia macrocalyx, mature leaves..	33	1.60
17. *Teclea nobilis*, mature leaves.........	32	1.55
Dombeya mukole, young leaves..........	32	1.55

SELECTION RATIOS.—The variable frequencies of use of food plants suggest that blue monkeys were selective feeders. The use of food plants, however, may have been affected by differences in their densities and also possibly their canopy sizes (i.e., their potential food-producing areas). Thus, the frequency of use of a food plant was divided by the product of its density and canopy size (called the cover index*) in order to obtain a standardized measure of its use. This ratio, termed the selection ratio, was computed for certain food plants used by Group I (Table 19). Estimates of canopy sizes (except those of *U. congensis* and *P. turbinata*) and

---

[*] Since tree canopies assume irregular shapes, the size of a canopy cannot be easily measured in terms of its volume or surface area. Therefore, Struhsaker (1975) obtained an index of mean canopy size of a species by summing the mean depth and the mean spread of several individuals. He has also shown that the sum of these parameters was significantly correlated to their product ($r_s = 0.98$; $p < 0.01$), which may be considered a better measure of canopy size.

TABLE 19.—Selection ratios of some food plants exploited by Group I during first sample periods of months from February 1973 to January 1974, inclusive

Species	Percent of frequency of use	Density /ha	Canopy size	Cover index	Selection ratio X 100	Visibility class
D. abyssinica	10.7	65.7	19.3	1268.0	0.9	III
C. africana	9.0	2.1	26.4	55.4	16.3	II*
P. turbinata	8.4	6.3	19.1	120.3	7.0	IV
T. nobilis	8.2	21.0	19.1	401.1	2.1	IV
U. congensis	6.7	25.2	19.1	481.3	1.4	IV
C. durandii	5.2	22.8	34.3	782.0	0.7	I*
M. bagshawei	3.8	2.1	31.7	66.6	5.7	II
M. platycalyx	3.1	5.8	19.2	1113.6	0.3	II
B. phoberos	3.0	2.8	18.6	52.1	5.7	II
F. latifolia	2.8	14.7	13.9	204.3	1.4	III
P. excelsa	2.2	10.5	41.3	433.6	0.5	I
A. altissima	1.1	0.7	29.7	20.8	5.3	II*

*Average of visibility in the least foliated and completely foliated stages

species densities were obtained from Struhsaker (1975). Canopy sizes of *U. congensis* and *P. turbinata* were assumed to be similar to that of *T. nobilis* (whose canopy size was estimated in the field) to which they bear a close physiognomic resemblance.

Selection ratios indicate that the frequency of use of food plants was affected by their density and canopy size. For example, the use of *D. abyssinica* (which was the most frequently exploited food plant) was apparently due to its very high density of occurrence. In terms of selection ratios, eight species listed in Table 19 were more preferred than *D. abyssinica*. *C. africana* was the most preferred food plant and *M. bagshawei, B. phoberos,* and *A. altissima* were more preferred than indicated by their frequency of use.

The frequency of use of food plants may also have been affected by how visible monkeys were to the observer when they were within the canopies of different species, although a half-hour interval between feeding observations was used to minimize the effect of this variable. Since selection ratios were computed without taking this possible source of bias into account, comparisons are most meaningful between species whose canopies afford similar visibility. Struhsaker (1975) classified visibility conditions within the canopies of different species on a I (excellent) to IV (poor) scale (Table 19). Some semideciduous species (e.g., *C. africana, C. durandii,* and *A. altissima*), which afforded a variety of visibility conditions depending on their physiological state, were assigned an average of the conditions of visibility within their canopies in their completely foliated and least foliated stages.

IMPORTANT COMPONENTS OF TOTAL DIET DURING AN ANNUAL CYCLE.—Four hundred and ninety-eight scores of invertebrate feeding were recorded between February 1973 and January 1974 inclusive. Thus during an annual cycle, invertebrate feeding constituted nearly 20% of the total of 2566 feeding observations on plant and invertebrate matter (Table 20). The frequency of use of invertebrates was second only to the use of fruits, which constituted 42.7% of the total feeding observations; however, the sum of the frequencies of use of foliar food (i.e., leaf buds, young leaves, mature leaves, dry leaves, and petioles) was greater than the frequency of use of invertebrates.

The importance of foliar food was also indicated by the fact that Group I used 9 food plants among the top 20 (namely *P. angolensis, M. platycalyx, D. mukole, M. myristica, V. apiculata, N. macrocalyx, Clausena anistata, I. pentaphylla,* and *M. dura*) solely for foliar food or more frequently for these than for fruits (see Appendix Table A). Moreover, as indicated in Figure 7, foliar foods occupied top rank for three successive months (from March 1974 to May 1974), when they comprised 41% to 64% of the monthly feeding scores. This suggests that foliar foods were periodically important food resources, perhaps when fruits were scarce. Floral items were also periodically important and occupied top rank in July 1973 and February 1974.

FOOD PLANTS USED BY BLUE MONKEYS DURING THE ENTIRE STUDY PERIOD.—During the sample periods that were not included in the annual cycle, a total of 1841 feeding observations were recorded from Group I. Of these observations 1752 were distributed among the 59 species used during the sample periods considered for the annual cycle, and 89 were scored from use of 18 other species (Table 21). Thus the total number of food plants exploited by Group I was 77 (70 identified and 7 unidentified). The food plant list of blue monkeys increased further when the diet of Group II was considered. During the 20 sample periods of observations of this group, 3127 feeding scores were recorded from the use of 60 plant species. Forty-four (41 identified and 3 unidentified) of these were used by Group I also, and 16 were used exclusively by Group II (Table 22). The total number of food plants used by both groups was therefore 93 (Appendix Table B). Species acquisition curves (Figure 3) for the two groups suggest that in both groups some infrequently used food plants may have been discovered with further observations.

PATTERNS OF USE OF FOOD RESOURCES: INTERMONTHLY VARIATIONS.—Intermonthly variations in the diet of Group I are indicated by the high coefficients of variation computed for the top 10 food plants (Table 23). *Diospyros abyssinica,* which was the top-ranking food plant of Group I, had the lowest coefficient of variation, indicating that it was the least variable in its monthly use, while *P. turbinata* had the greatest coefficient of variation and was the most variable in its monthly use. The relatively large range of monthly frequency of use of these food plants also indicates appreciable intermonthly variations in diet.

Intermonthly variations in the diet of Group I can also be shown by comparing the monthly rank orders and frequencies of use of food plants and specific food items. Usually there were striking changes in the frequency of use of food plants (and specific food items), with almost a monthly change in the occupancy of top rank (Appendix Table C). In March 1973, Group I used *P. turbinata* at a very

TABLE 20.—Group I, mean percent of frequency of use of plant and invertebrate food items during first 5-day periods of observations from February 1973 to January 1974, inclusive (N = 2566 observations)

Food item	Mean percent of frequency of use	Food item	Mean percent of frequency of use
Leaf buds................	2.79	Blossoms..................	10.44
Young leaves..............	9.45	Fruits....................	42.70
Mature leaves.............	6.77	Seeds.....................	2.43
Dry leaves................	0.11	Nectar....................	0.74
Petioles..................	1.91	Galls.....................	0.58
Stems.....................	0.26	Unidentified plant items..	0.68
Flower buds...............	1.31	Invertebrates.............	19.83

TABLE 21.—Group I, frequency of use of specific food items exploited only outside the first 5-day periods of observations from February 1973 to January 1974, inclusive

Species	Leaf buds	Young leaves	Mature leaves	Petioles	Blossoms	Fruits	Unidentified items	Total frequency
_Ficus dawei_*...............	-	-	-	-	-	46	-	46
_Tarenna pavettoides_*........	-	-	-	-	10	-	-	10
Loxogramme lanceolata.......	-	6	2	-	-	-	-	8
_Apodytes dimidiata_*.........	-	-	-	-	2	-	-	2
_Pleiocarpa pycnantha_*.......	-	2	-	-	-	-	-	2
_Scolopia rhamniphylla_*......	-	-	-	-	1	1	-	2
_Acalypha bipatita_*..........	-	-	1	-	-	-	-	1
_Carapa grandiflora_*.........	-	-	-	1	-	-	-	1
_Cassipourea ruwensorensis_*..	-	-	-	-	1	-	-	1
_Cissus oliveriana_*..........	-	-	-	-	1	-	-	1
_Dovyalis macrocalyx_*........	-	-	-	-	1	-	-	1
_Euclinia longiflora_*........	1	-	-	-	-	-	-	1
Glyphaea lateriflora........	-	1	-	-	-	-	-	1
Pyrenacantha sp.*...........	-	-	-	-	-	1	-	1
Ritchia albersii............	-	-	-	-	-	-	1	1
Unidentified species (3)....	-	-	1	-	-	6	1	8
Total.....................								89

*Food plants not used by Group II

TABLE 22.—Frequency of use of specific food items exploited only by Group II between February 1973 and October 1974, inclusive

Species	Leaf buds	Young leaves	Mature leaves	Flower buds	Blossoms	Fruits	Total frequency
Angraecum distichum	-	-	2	-	-	-	2
Brachystephanus africanus	-	-	1	-	-	-	1
Basella alba	-	-	-	-	1	-	1
Brillantasia nitens	-	-	-	-	1	-	1
Chlorodendrum schweinfurthii	-	-	2	-	-	-	2
Canthium sp.	-	-	-	5	-	-	5
Drypetes battiscombei	-	-	2	-	-	-	2
Ficus stipulifera	-	-	-	-	-	18	18
Ficus congensis	-	-	-	-	-	1	1
Fagara mildbraedii	-	1	-	-	-	-	1
Lepisanthes senegalensis	-	-	-	-	-	3	3
Mimulopsis solmsii	-	1	-	-	-	-	1
Paulinia pinnata	-	1	-	-	-	-	1
Strychnos mitis	6	3	-	-	-	-	9
Tabernaemontana usamberensis	-	-	-	-	1	-	1
Tabernaemontana odoratissima	-	-	-	1	1	-	2
Total							51

high frequency (85.6%), but during the next month they did not use it at all when *C. africana* constituted 53.3% of their diet. In May 1973, the frequency of use of *C. africana* dropped to about 3.0%, while *C. gorungosanum* occupied top rank with a 16.1% frequency of use; *C. gorungosanum* and *Clausena anistata* were used only during the periods that they occupied top rank. Thus their use not only caused relatively large intermonthly variations in diet, but also showed the periodic importance of uncommon food plants.

When the rank orders of important food items (regardless of species) were considered, intermonthly variability in diet was less apparent than in the case of food plants and specific food items (Table 24). This was largely due to the fact that fruits often occupied top rank. Even when fruits were top-ranking food items, however, the range of their frequency of use was quite large (23.8%–75.5% in January 1974 and March 1973, respectively). Group I concentrated on fruits during certain months but used several food items more equitably during other months.

Intermonthly variations in the diet of Group I can also be demonstrated by considering temporal changes in the frequency of use of a selection of food plants and specific food items. These are illustrated in Figures 4, 5, and 6 for the food items that Group I used from its top 10 food plants and *P. excelsa* and *A. altissima*.

During each month, Group I usually concentrated its feeding activity on one or two specific food items which were not used during many of the other months. For example, the fruits of *P. turbinata*, *T. nobilis*, and *U. congensis* constituted over 40% of the feeding scores collected during some months; but the fruits of the first two species were used during five months and the fruits of the third were used only for four of the 16 months of observations (Figures 4, 5). Thus, intermonthly differences in diet were caused by variability in the frequency of use as well as restricted periods of use of specific food items. This pattern of exploitation holds true for species also except that the periods of use were extended for some food plants that were used for more than one food item, e.g., *D. abyssinica* and *P. angolensis*. The pattern of use of food items shows that the intermonthly variations in diet were largely due to differences in their frequency of use (Figure 7).

PATTERNS OF USE OF FOOD RESOURCES: INTERMONTHLY SIMILARITIES.—The patterns of use of food resources also showed certain similarities in monthly diet. For example, Group I exploited the fruits of *F. exasperata*, the mature leaves of *T. nobilis*, and the petioles of *M. platycalyx* more or less continuously throughout the study, although they used these resources at variable frequencies (Figures 5, 6). Hence, their use produced some similarities in the diet during different months. Similarly, fruits, foliar food, and invertebrates were regularly exploited food resources of Group I (Figure 7).

Dietary similarities were sometimes produced by seasonal use of specific food items. Since feeding

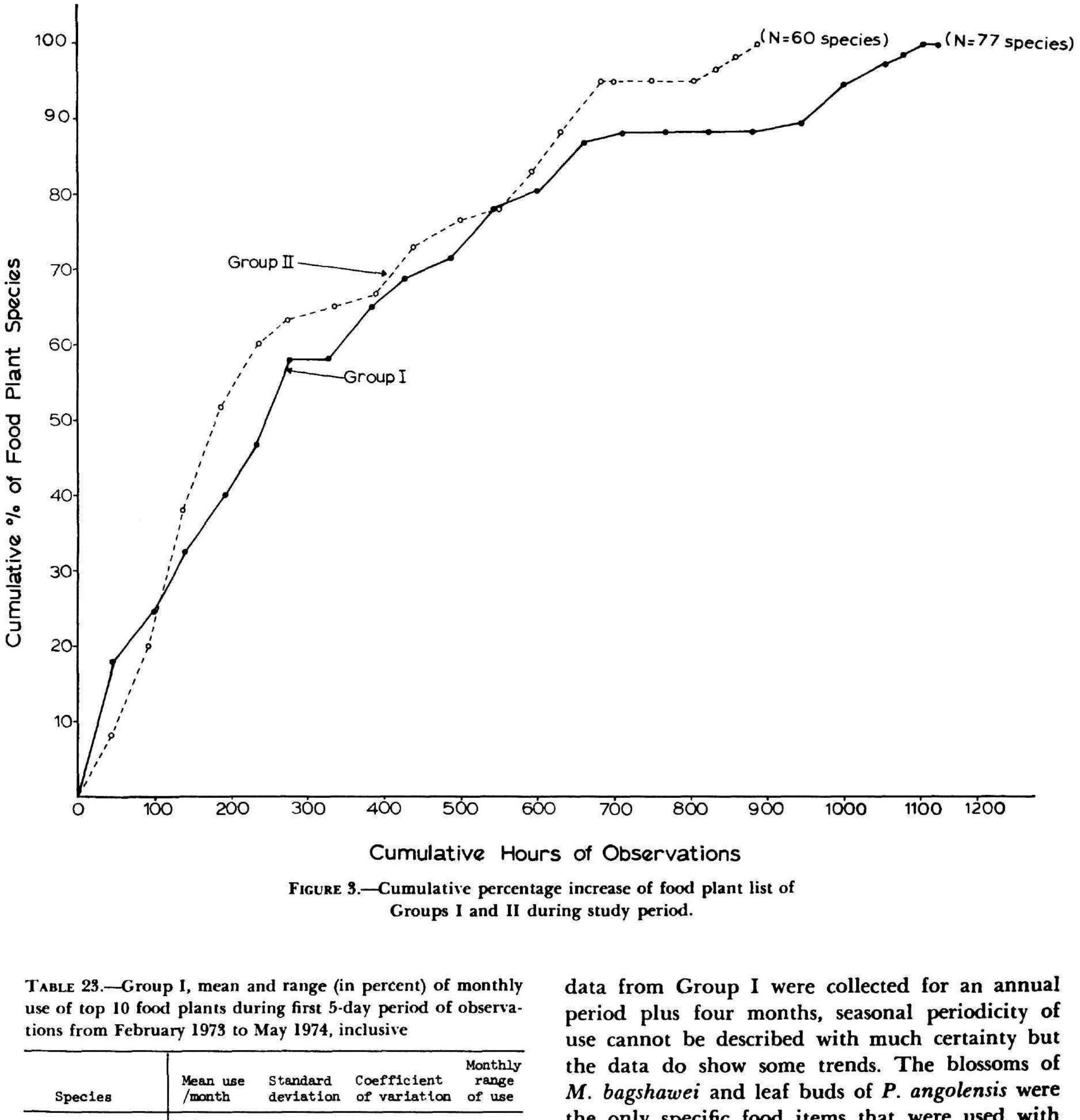


FIGURE 3.—Cumulative percentage increase of food plant list of Groups I and II during study period.

TABLE 23.—Group I, mean and range (in percent) of monthly use of top 10 food plants during first 5-day period of observations from February 1973 to May 1974, inclusive

Species	Mean use /month	Standard deviation	Coefficient of variation	Monthly range of use
D. abyssinica....	8.95	10.07	112.51	0-29.13
C. africana......	8.66	13.16	151.96	0-53.33
P. turbinata.....	6.64	21.33	321.23	0-85.56
T. nobilis.......	8.16	14.68	179.90	0-57.89
U. congensis.....	4.08	10.99	269.36	0-43.54
P. angolensis....	5.35	7.43	138.88	0-23.62
C. durandii......	4.78	9.07	189.75	0-28.15
F. exasperata....	4.54	5.85	128.85	0-21.48
M. bagshawei.....	5.62	9.38	166.90	0-34.00
M. platycalyx....	2.01	3.63	180.60	0-13.71

data from Group I were collected for an annual period plus four months, seasonal periodicity of use cannot be described with much certainty but the data do show some trends. The blossoms of *M. bagshawei* and leaf buds of *P. angolensis* were the only specific food items that were used with a truly annual periodicity, being used in April and May of 1973 and 1974 (Figure 6). If one or two months leeway in use is assumed to be within the normal range of variation of use of specific food items, then a few more can be considered to be used seasonally on an annual basis, e.g., the fruits of *P. turbinata* and the fruits and blossoms of *D. abyssinica.*

Some of the other specific food items showed annual peaks of use that brought about greater dietary similarity during these periods than others. The major peaks of use of *F. exasperata* fruits occurred nearly one year apart. When data from Groups I and II were considered, the fruits of *C. durandii* also showed a similar pattern of use. Consideration of the diets of both groups also indicated that the use of *U. congensis* fruits may bring about intermonthly similarities on a biannual basis. The use of the blossoms of *A. altissima* produced dietary similarities on a triannual basis, but the greatest similarities resulting from their use occurred on an annual basis.

Dietary similarities brought about by the patterns of use of food plants, such as *U. congensis, C. durandii, P. excelsa, F. exasperata,* and *A. altissima,* remain much the same as described for food items used from them. For some of the other species, the patterns of use changed from those described for each of their food items. *P. angolensis* showed a less than annual periodicity of use and the use of *D. abyssinica* suggests an extended period of use from December to August (Figure 6). The exploitation of *P. turbinata* and *M. bagshawei* indicates that they may bring about dietary similarities on a biannual basis.

Some food items (regardless of species) also showed regular peaks of use (Figure 7). The peak frequency of use of blossoms occurred in February 1973, May 1973, July 1973, and February 1974; in May 1974 flower buds were used at high frequency. This suggests a triannual periodicity of intensive use of floral items. The frequency of use of leaf buds suggests a biannual periodicity of intensive use in April–May and December. Thus, certain aspects of the diet of Group I may be said to show intermonthly similarities. Dietary similarities, however, are to be found mainly in respect to the periods of use rather than the frequency of use of food resources. In fact, intermonthly variations in the diet of Group I appear to be more conspicuous than similarities.

FACTORS AFFECTING THE PATTERNS OF USE OF FOOD RESOURCES.—The patterns of use of food resources were intimately related to the phenological activity of food plants. For instance, the patterns of use and availability of *P. turbinata* fruits were the same. However, the patterns of use of specific food items do not always follow their patterns of availability (Figures 4–6). For example, *C. africana* fruits were used at a low frequency in March 1973 when their availability had reached a peak (Figure 5). During the same month the availability of *P. turbinata* fruits had also peaked, and they were extensively exploited (Figure 4). This suggests that the fre-

TABLE 24.—Group I, rank order (I-V) and percent of frequency of use of top five food items during the first 5-day period of observations from February 1973 to May 1974, inclusive

	I		II		III		IV		V	
Sample period	Food item	Percent	Food item	Percent	Food item	Percent	Food item	Percent	Food item	Percent
Feb 73 (I)....	Fruits	57.23	Blossoms	27.04	Invertebrates	6.29	Young leaves	4.40	Unidentified	3.14
Mar 73 (I)....	Fruits	75.52	Invertebrates	18.14	Young leaves	2.95	Mature leaves	2.53	Blossoms, unidentified	0.42
Apr 73 (I)....	Fruits	66.93	Invertebrates	15.32	Petioles	6.45	Blossoms	5.24	Young leaves	2.02
May 73 (I)....	Invertebrates	28.32	Fruits	17.34	Blossoms, mature leaves	15.61	-	-	Leaf buds	9.25
Jun 73 (I)....	Fruits	41.67	Invertebrates	20.83	Young leaves	12.88	Blossoms	8.33	Mature leaves	6.44
Jul 73 (I)....	Blossoms	36.72	Fruits	21.31	Invertebrates	16.72	Mature leaves	12.13	Young leaves	9.18
Aug 73 (I)....	Fruits	22.03	Young leaves	21.15	Blossoms	20.26	Invertebrates	18.50	Mature leaves	13.22
Sep 73 (I)....	Invertebrates	33.70	Young leaves	25.00	Fruits	22.83	Petioles	4.89	Mature leaves	3.26
Oct 73 (I)....	Fruits	50.00	Invertebrates	21.51	Young leaves	15.70	Blossoms, nectar	3.49	-	-
Nov 73 (I)....	Fruits	71.50	Invertebrates	24.00	Young leaves	1.50	Mature leaves	1.00	Leaf buds, petioles, flower buds, unidentified	0.50
Dec 73 (I)....	Fruits	42.17	Invertebrates	25.30	Seeds	12.65	Leaf buds	10.24	Mature leaves	3.01
Jan 74 (I)....	Fruits	23.81	Mature leaves	22.08	Young leaves	15.15	Seeds	11.69	Invertebrates	9.09
Feb 74 (I)....	Blossoms	27.99	Fruits	25.75	Mature leaves	13.06	Young leaves	10.82	Invertebrates	10.07
Mar 74 (I)....	Invertebrates	30.71	Petioles	15.75	Young leaves, fruits	14.96	-	-	Mature leaves	14.17
Apr 74 (I)....	Young leaves	30.12	Mature leaves	16.87	Flower buds	12.05	Leaf buds	10.84	Fruits, invertebrates	8.43
May 74 (I)....	Flower buds	23.48	Petioles	17.39	Young leaves	16.52	Invertebrates	13.04	Fruits	11.30

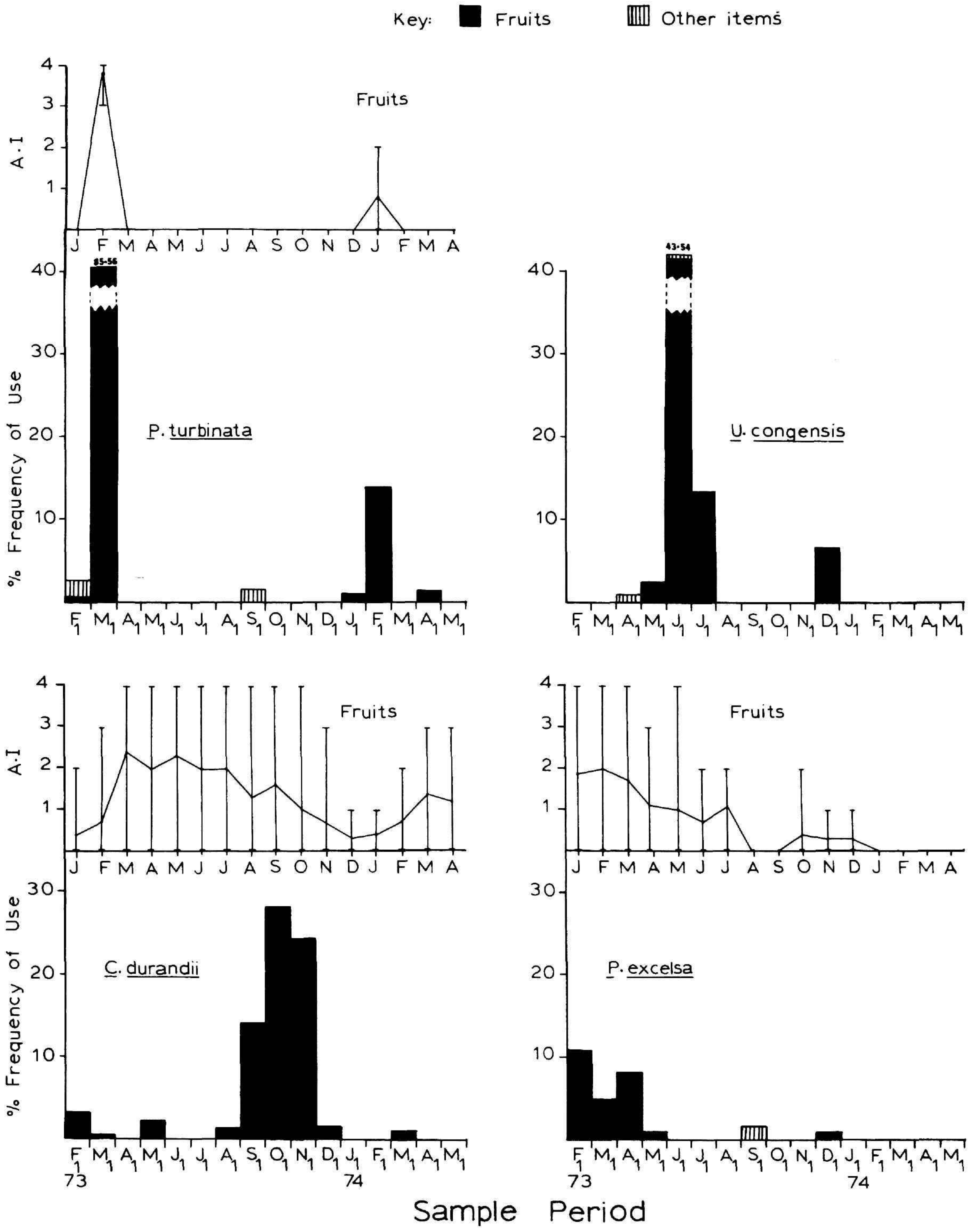


FIGURE 4.—Patterns of use of food plants and specific food items by Group I and availability indices (AI) of selected specific food items.

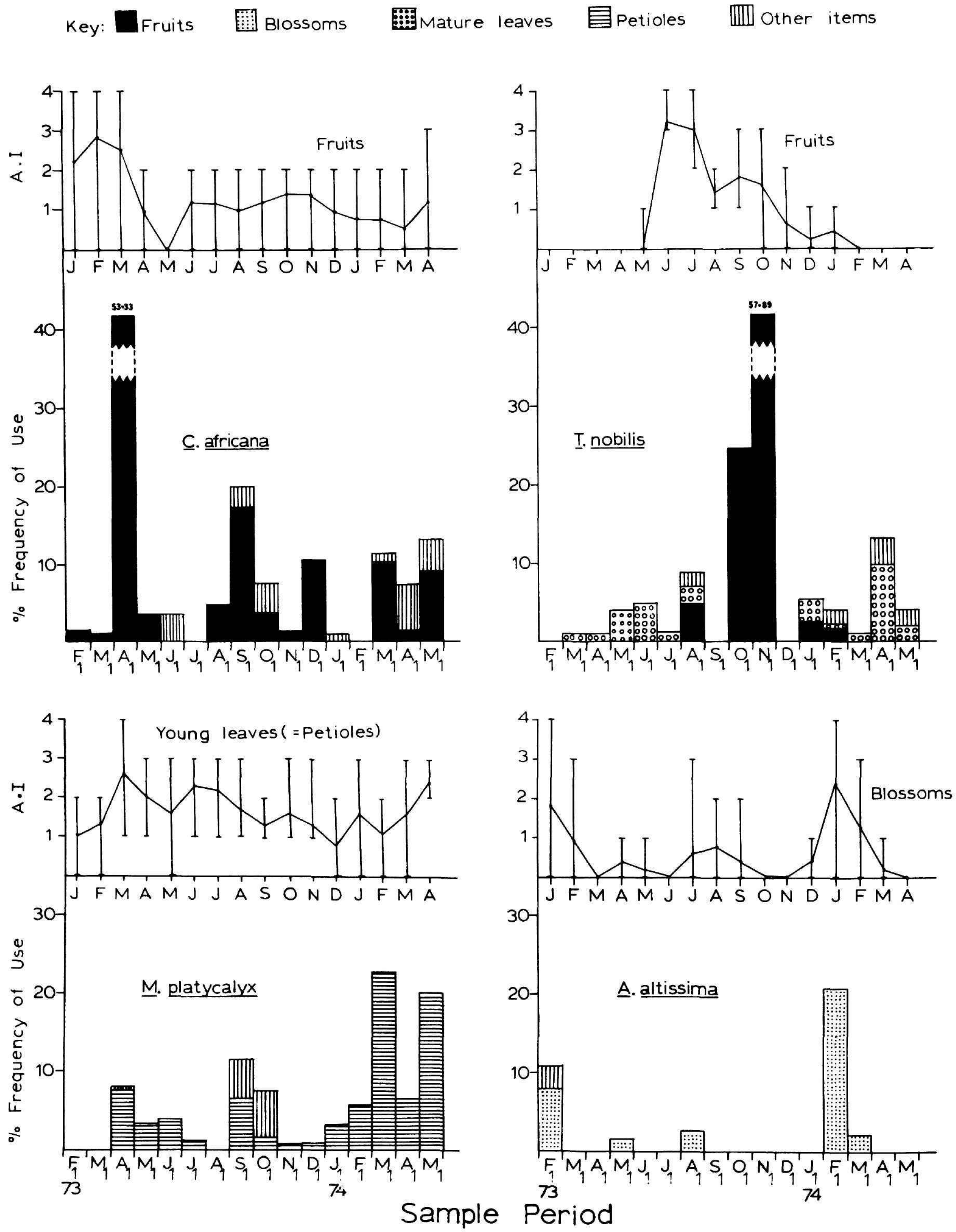


FIGURE 5.—Patterns of use of food plants and specific food items by Group I and availability indices (AI) of selected specific food items.

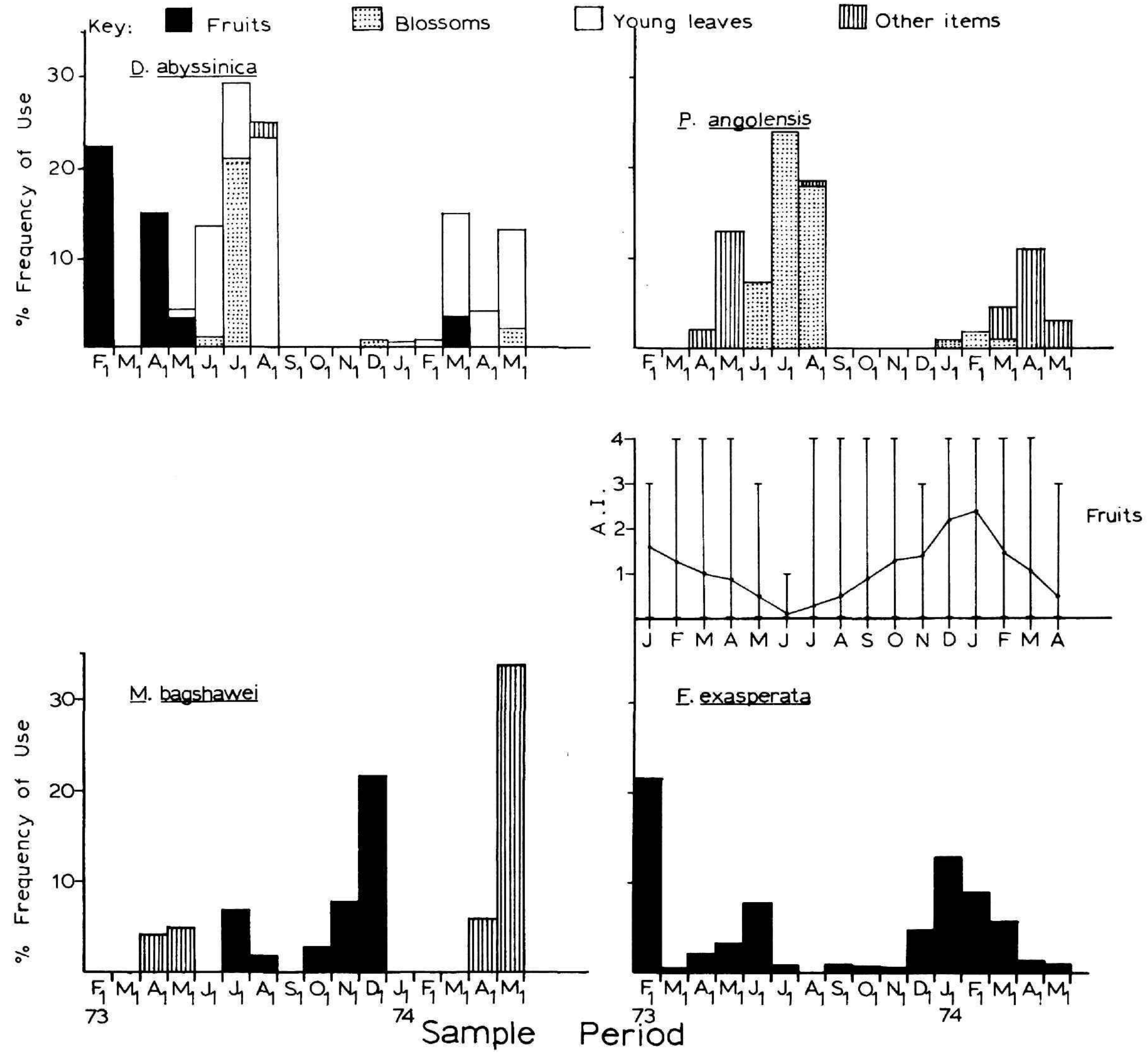


FIGURE 6.—Patterns of use of food plants and specific food items by Group I and availability indices (AI) of selected specific food items.

quency of use of specific food items was dependent on factors such as relative abundance and food preference as well as their availability.

INTRAMONTHLY VARIATIONS IN DIET.—The relatively large intermonthly differences in diet suggest that these variations may even occur over a time span shorter than a month. Data collected during seven months (from March 1973 to August 1973 inclusive, and November 1973) when two 5-day periods of observations were made each month tend to support this view. The diet during the two 5-day periods of each month was never identical although the intervals between observation periods were relatively short. In May and June the 5-day periods of observations were conducted over a 10-day period without a break in data collection. In

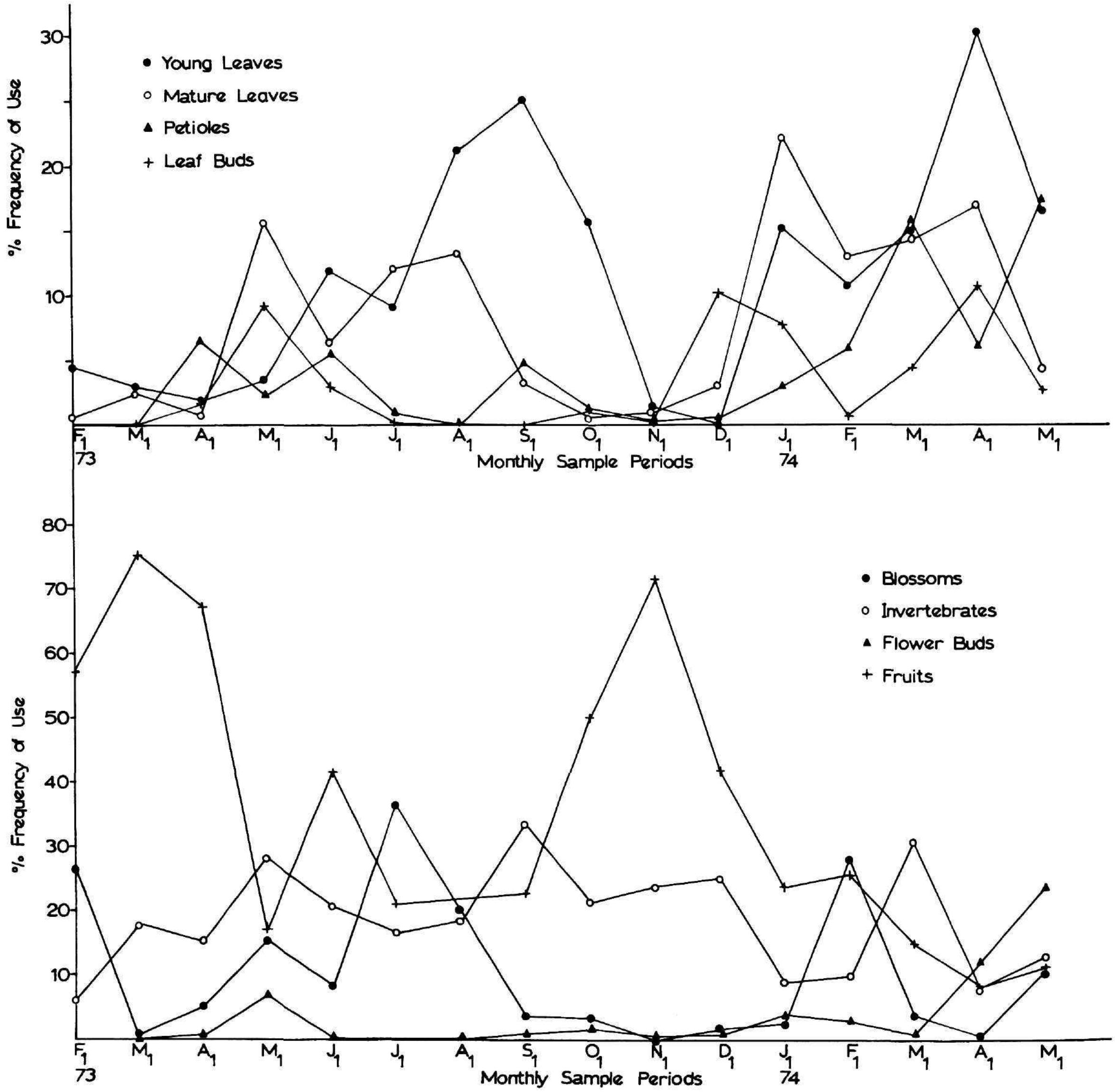


FIGURE 7.—Patterns of use of food items (regardless of species) by Group I.

April, July, and November there were 2-day intervals between sample periods and in March and August there were 7- and 3-day intervals respectively.

Of the seven months considered above, intramonthly differences in diet were greatest between the two sample periods of March and May (Table 25). In March, only two among the top five specific food items (i.e., fruits of *P. turbinata* and *C. africana*) were used during both sample periods and these were used at extremely variable frequencies. In May, the leaf buds of *P. angolensis* were the only specific food item among the top five that were used during both 5-day periods. Both in March and in May, the top-ranking specific food

TABLE 25.—Group I, rank order (I-V) and percent of frequency of use of top five specific food items of both 5-day periods of observations conducted from March 1973 to August 1973 and in November 1973

	I		II		III		IV		V		
Sample period	Food item	Percent	Food item	Percent	Food item	Percent	Food item	Percent	Food item	Percent	N
Mar 73 (I)....	*P. turbinata*, fruits	85.57	*P. excelsa*, fruits	4.64	*D. mukole*, young leaves	1.55	*A. gummifera*, young leaves *B. unijugata*, young leaves *T. nobilis*, mature leaves *C. africana*, fruits	1.03	-	-	194
Mar 73 (II)...	*C. africana*, fruits	30.00	*P. turbinata*, fruits	20.67	*D. abyssinica*, fruits	14.67	*C. durandii*, fruits	10.00	*M. platycalyx*, petioles	6.67	150
Apr 73 (I)....	*C. africana*, fruits	53.33	*D. abyssinica*, fruits	14.76	*P. excelsa*, fruits	8.10	*M. platycalyx*, petioles	7.62	*M. bagshawei*, blossoms	4.29	210
Apr 73 (II)...	*C. africana*, fruits	43.89	*D. abyssinica*, fruits	11.11	*M. platycalyx*, petioles	7.78	*P. angolensis*, leaf buds	7.22	*O. welwitschii*, flower buds	4.44	180
May 73 (I)....	*C. gorungosanum*, blossoms	16.13	*P. angolensis*, leaf buds	12.90	*N. macrocalyx*, mature leaves	6.45	*O. welwitschii*, flower buds	4.84	*T. nobilis*, mature leaves	4.03	124
May 73 (II)...	*F. dawei*, fruits	34.65	*P. angolensis*, leaf buds	19.69	*F. exasperata*, fruits	11.81	*D. abyssinica*, young leaves	11.02	*M. platycalyx*, petioles	7.09	127
Jun 73 (I)....	*U. congensis*, fruits	43.06	*D. abyssinica*, young leaves	13.40	*F. exasperata*, fruits	7.66	*P. angolensis*, blossoms	7.17	*T. nobilis*, mature leaves	4.78	209
Jun 73 (II)...	*U. congensis*, fruits	69.49	*F. exasperata*, fruits	9.04	*F. angolensis*, fruits	4.52	*M. platycalyx*, petioles	3.39	*P. angolensis*, blossoms	2.26	177
Jul 73 (I)....	*P. angolensis*, blossoms	23.62	*D. abyssinica*, blossoms	20.47	*U. congensis*, fruits	13.38	*D. abyssinica*, young leaves	8.66	*M. bagshawei*, fruits	6.69	254
Jul 73 (II)...	*P. angolensis*, blossoms	26.95	*D. abyssinica*, young leaves	15.65	*D. abyssinica*, blossoms *M. bagshawei*, fruits	6.52	-	-	*F. latifolia*, seeds *M. platycalyx*, petioles	4.78	230
Aug 73 (I)....	*D. abyssinica*, young leaves	23.24	*P. angolensis*, blossoms	17.83	*I. pentaphylla*, mature leaves	8.65	*P. microcarpa*, fruits	8.11	*T. nobilis*, fruits	4.86	185
Aug 73 (II)...	*D. abyssinica*, young leaves	15.42	*T. nobilis*, fruits	9.35	*F. latifolia*, seeds	8.76	*C. durandii*, fruits	8.41	*V. apiculata*, mature leaves	6.07	214
Nov 73 (I)....	*T. nobilis*, fruits	57.89	*C. durandii*, fruits	24.34	*M. bagshawei*, fruits	7.89	*F. angolensis*, fruits *C. africana*, fruits *I. pentaphylla*, mature leaves	1.32	-	-	152
Nov 73 (II)...	*T. nobilis*, fruits	56.04	*M. bagshawei*, fruits	8.79	*C. durandii*, fruits *F. latifolia*, seeds	6.59	-	-	*D. mukole*, young leaves	6.04	182

items of the two sample periods of each month were different, indicating that at least some of the important specific food items had very short periods of use. The fruits of *F. dawei*, which occupied top rank in May II 1973, are another example of an important resource that was exploited only during one sample period.

DIET OVERLAP.—Intramonthly as well as intermonthly variations in diet can also be shown by computing the total overlap in diet between the relevant pair combinations of the 23 sample periods recorded from Group I (Table 26). The mean overlap in diet between the 15 pair combinations of the first sample periods of adjacent months was 26.88% and the range was from 7.14% (between March 1973 and April 1973) to 55.88% (between October 1973 and November 1973). The mean overlap in diet between pair combinations of sample periods recorded during the same months was 52.83% (range 25.5%–73.80% in March 1973 and April 1973, respectively). Although intermonthly variations in diet were usually greater than intramonthly variations, this analysis shows the relatively rapid temporal changes in the diet of Group I.

DIET DIVERSITY.—Diet diversity indices, calculated using the Shannon-Wiener equation, also indicate variations in intermonthly and intramonthly diet of Group I (Figure 8). When the first sample periods of each month were considered, diet diversity indices range from 0.73 in March 1973 to 3.13 in May 1973. Between sample periods of the

TABLE 26.—Group I, total percent of overlap of specific food items in diet between different pair combinations of all 5-day periods of observations from February 1973 to May 1974, inclusive (N = 253, $\overline{X}$ = 15.96, standard deviation = ±12.61, range = 0.52–73.80)

Sample period	1973 Mar (I)	Mar (II)	Apr (I)	Apr (II)	May (I)	May (II)	Jun (I)	Jun (II)	Jul (I)	Jul (II)	Aug (I)	Aug (II)	Sep (I)	Oct (I)	Nov (I)	Nov (II)	Dec (I)	1974 Jan (I)	Feb (I)	Mar (I)	Apr (I)	May (I)
Feb 73 (I)....	7.88	23.44	26.09	17.99	12.64	13.39	8.62	9.04	2.12	1.77	7.82	9.82	12.06	4.74	5.38	6.08	9.94	14.87	19.19	13.84	3.29	2.34
Mar 73 (I)....	-	25.58	7.14	7.02	5.72	2.11	1.55	0.52	3.34	1.76	2.58	4.58	3.90	3.10	2.73	3.65	2.88	4.00	16.28	5.65	6.15	2.58
Mar 73 (II)...	-	-	57.63	55.11	19.08	14.52	4.98	3.95	1.84	5.87	6.60	17.49	33.77	19.18	11.38	10.39	13.71	4.76	20.60	27.78	16.56	21.33
Apr 73 (I)....	-	-	-	73.80	17.38	12.21	7.17	5.29	3.41	6.07	6.31	9.87	23.77	6.68	2.04	4.35	14.00	6.68	8.52	27.59	12.58	24.80
Apr 73 (II)...	-	-	-	-	32.87	18.47	17.65	7.32	6.26	8.79	10.32	13.60	24.87	5.78	2.64	4.95	18.78	9.70	8.73	25.94	19.69	28.14
May 73 (I)....	-	-	-	-	-	28.17	17.10	11.14	17.04	14.40	15.59	22.90	16.30	9.44	5.10	10.78	20.92	14.31	12.50	24.70	29.60	21.67
May 73 (II)...	-	-	-	-	-	-	28.22	16.92	16.14	18.26	11.81	19.01	8.14	5.37	1.51	3.18	11.96	16.91	16.56	28.70	25.86	25.68
Jun 73 (I)....	-	-	-	-	-	-	-	60.58	35.45	35.34	25.85	28.12	5.46	2.68	1.92	2.61	17.58	21.05	20.15	24.24	17.58	20.68
Jun 73 (II)...	-	-	-	-	-	-	-	-	21.62	12.04	5.05	8.74	4.21	2.08	3.15	1.70	16.02	16.63	15.78	10.76	7.23	6.08
Jul 73 (I)....	-	-	-	-	-	-	-	-	-	60.72	36.65	30.40	7.70	4.93	9.12	11.89	21.50	12.19	10.90	16.07	10.63	14.19
Jul 73 (II)...	-	-	-	-	-	-	-	-	-	-	45.55	44.71	10.54	6.27	9.73	14.68	16.61	19.37	18.34	20.27	18.25	21.64
Aug 73 (I)....	-	-	-	-	-	-	-	-	-	-	-	47.37	15.08	14.66	10.20	11.91	11.39	15.00	11.15	23.88	13.86	19.48
Aug 73 (II)...	-	-	-	-	-	-	-	-	-	-	-	-	23.39	27.18	24.19	30.22	21.68	34.69	25.91	30.77	20.77	24.42
Sep 73 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	33.42	16.79	16.75	17.84	8.37	10.31	22.16	20.35	18.88
Oct 73 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	55.88	46.63	11.18	5.86	5.52	12.63	18.59	8.68
Nov 73 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	73.56	13.05	7.12	6.20	3.84	4.74	2.04
Nov 73 (II)...	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24.60	11.22	8.44	8.90	10.59	5.45
Dec 73 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24.89	10.96	17.83	6.20	14.03
Jan 74 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	43.68	13.22	18.65	11.21
Feb 74 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18.71	20.44	14.25
Mar 74 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28.41	45.88
Apr 74 (I)....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	45.45

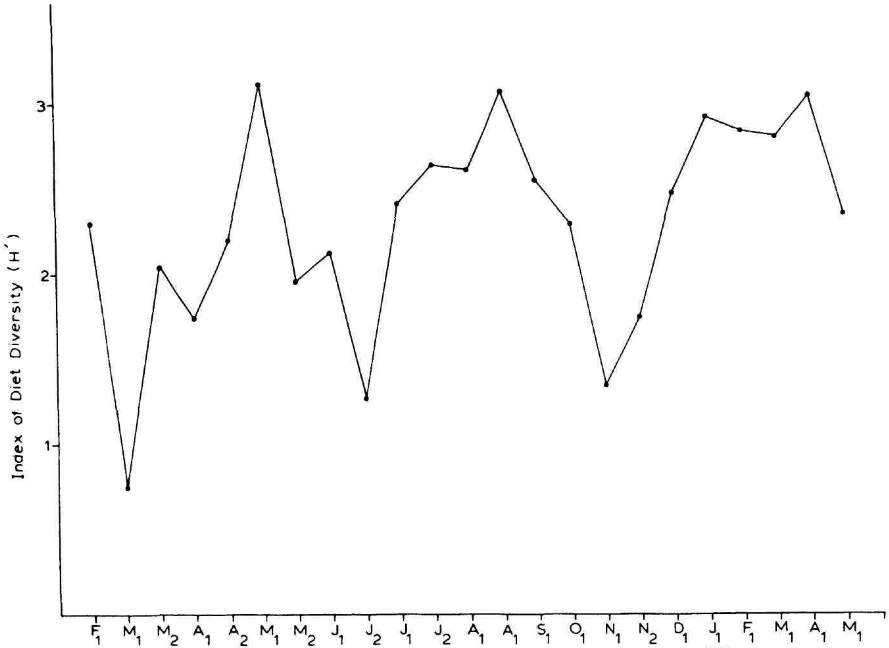


FIGURE 8.—Diversity indices of the diet of Group I.

same months, the greatest variation in diet diversity was found in March 1973 (0.73 to 2.04). During this month Group I used the same number of specific food items during both sample periods, but during the first sample period *P. turbinata* fruits formed an extremely high proportion (85.5%) of its diet. During the second sample period, the frequency of use of this resource decreased greatly (to 20.67%) and several specific food items were used more equitably.

Spearman rank correlation tests (Snedecor and Cochran, 1969) showed significant negative correlations between the frequency of use of fruits during a sample period and (1) the number of food plants exploited ($r_s = -0.570$, $p < 0.01$) and (2) diet diversity ($r_s = -0.860$, $p < 0.01$). There was also a significant positive correlation between the frequency of use of foliar foods and specific food items diversity ($r_s = 0.809$, $p < 0.01$).

INVERTEBRATE COMPONENT OF THE DIET OF BLUE MONKEYS.—As mentioned earlier invertebrate food items were usually indistinguishable even at relatively close quarters. The rare observations when these food items were clearly seen include feeding on a butterfly, a grasshopper, and some ants (two observations). On three occasions cocoons that probably contained immobile insect pupae were also eaten. Invertebrate food constituted nearly 20% of the feeding scores recorded from Group I (Table 20). They were eaten during all months of the study and were the most frequently used food item in May 1973, September 1973, and March 1974 (Table 24). About 81% of the total scores of ingestion of probable invertebrate food items were recorded from 29 identified plant species and 11 different microhabitats and 19% of the scores were recorded from several unidentified plants (Appendix Table D).

Considering microhabitats alone, invertebrate prey was taken most frequently from the surfaces of leaves, which accounted for 38.75% of the total scores of invertebrate feeding (Appendix Table D). Nearly 74% of the scores of ingestion of invertebrates were recorded from leaf surfaces, moss-covered branches and lichen-covered branches. Considering plant species, invertebrates were most commonly captured and eaten from *P. excelsa* (17.6%) and *S. scheffleri* (11.45%). Considering specific microhabitats, invertebrates were most frequently taken from the moss-covered branches of *P. excelsa* (7.43%) and the leaf surfaces of *S. scheffleri* (6.02%) (Table 27).

TABLE 27.—Group I, percent of frequency of ingestion of probable invertebrates from 15 specific microhabitats most commonly used for this purpose during first 5-day periods of observations from February 1973 to January 1974, inclusive (N = 498 observations)

Specific microhabitat	Percent of frequency of ingestion of invertebrates
P. excelsa, moss-covered branches........	7.43
S. scheffleri, foliage..................	6.02
D. abyssinica, foliage..................	5.62
P. excelsa, foliage.....................	4.61
S. scheffleri, moss-covered branches.....	2.61
P. excelsa, lichen-covered branches......	2.41
D. abyssinica, lichen-covered branches...	2.21
C. durandii, foliage....................	1.81
B. wilsoniana, lichen-covered branches...	
T. nobilis, foliage.....................	
M. platycalyx, dry leaves................	1.61
P. turbinata, foliage...................	
O. welwitschii, lichen-covered branches..	1.41
U. congensis, foliage...................	
P. excelsa, epiphyte-covered branches....	1.20
Total................................	36.94

MONTHLY IMPORTANCE OF PLANT SPECIES AND MICROHABITATS IN PROVIDING INVERTEBRATE FOOD ITEMS.—Table 28 presents the five plants most frequently used for the acquisition of invertebrates during each month. Almost every month, either *P. excelsa* or *S. scheffleri* provided the greatest amount of invertebrate prey, although neither of these species was exploited frequently for plant foods (see Appendix Table C). It is therefore possible that the distribution of *P. excelsa* and *S. scheffleri* within the home range of Group I affected the ranging patterns of this group, especially during those months when they exploited invertebrate food items at relatively high frequencies.

When the monthly frequency of ingestion of invertebrates from different microhabitats was considered, it was found that during a majority of the months of study, Group I took invertebrate prey most often from the surfaces of leaves (Table 29). Lichen-covered branches provided the greatest amount of invertebrate prey in one month (October 1973), and moss-covered branches provided the greatest amount of the same in three months (May 1973, September 1973 and March 1974). Peak frequencies of invertebrate feeding from moss-covered branches usually coincided with peaks in monthly rainfall (Figure 9). This may have been due to an

TABLE 28.—Group I, monthly percent of frequency of ingestion of invertebrates from five species most commonly used for this purpose during first sample periods between February 1973 to May 1974, inclusive

Month/year	I		II		III		IV		V		N
	Species	Percent	Species	Percent	Species	Percent	Species	Percent	Species	Percent	
Feb 73.....	*S. scheffleri*	20.0	*F. latifolia* *D. abyssinica*	10.0	-	-	-	-	-	-	10
Mar 73.....	*S. scheffleri*	11.6	*P. excelsa*	9.3	*S. globulifera* *C. durandii*	4.6	-	-	*N. buchanani* *F. dawei*	2.3	43
Apr 73.....	*P. excelsa*	15.7	*S. scheffleri* *M. bagshawei*	7.8	-	-	*C. gorungosanum* *U. congensis*	5.2	-	-	38
May 73.....	*P. excelsa*	36.7	*M. platycalyx*	12.2	*S. scheffleri*	6.1	-	-	*N. buchanani* *B. phoberos* *B. wilsoniana* *C. durandii*	4.0	49
Jun 73.....	*P. excelsa*	20.0	*D. abyssinica*	18.1	*S. scheffleri*	10.9	*A. altissima*	7.2	*B. wilsoniana*	5.4	55
Jul 73.....	*D. abyssinica*	13.7	*S. scheffleri* *P. excelsa*	11.7	-	-	*M. platycalyx*	9.8	*C. durandii*	7.8	51
Aug 73.....	*S. scheffleri*	21.4	*D. abyssinica*	14.2	*O. welwitschii*	9.5	*T. nobilis*	7.1	*P. excelsa* *B. wilsoniana* *P. angolensis* *P. turbinata*	4.7	42
Sep 73.....	*P. excelsa*	33.8	*D. abyssinica*	12.9	*M. platycalyx*	8.0	*C. durandii*	6.4	*T. nobilis* *A. altissima*	4.8	62
Oct 73.....	*P. excelsa*	18.9	*D. abyssinica*	16.2	*C. africana*	10.8	*C. durandii*	8.1	*T. nobilis* *B. wilsoniana*	5.4	37
Nov 73.....	*P. excelsa*	20.8	*D. abyssinica*	18.7	*B. wilsoniana*	8.3	*N. buchanani*	6.2	*C. africana* *C. durandii* *U. congensis* *S. scheffleri* *F. brachylepis* *T. nobilis*	4.1	48
Dec 73.....	*S. scheffleri*	33.3	*P. turbinata*	14.2	*D. abyssinica*	9.5	*P. excelsa* *M. dura* *T. nobilis*	7.1	-	-	42
Jan 74.....	*S. scheffleri*	23.8	*M. platycalyx*	9.5	*C. aristata* *U. congensis* *T. splendida*	4.7	-	-	-	-	21
Feb 74.....	*S. scheffleri* *T. nobilis* *C. durandii*	11.1	-	-	-	-	*P. excelsa* *P. turbinata* *D. abyssinica* *P. angolensis*	7.4	-	-	27
Mar 74.....	*P. excelsa*	46.1	*D. abyssinica*	30.7	*N. buchanani*	7.6	*C. durandii* *D. mukole* *U. congensis*	2.5	-	-	39
Apr 74.....	*S. scheffleri*	21.4	*D. abyssinica*	14.2	*P. excelsa* *C. aristata* *D. mukole* *M. platycalyx* *B. phoberos* *T. nobilis* *C. durandii*	7.1	-	-	-	-	14
May 74.....	*C. africana*	26.6	*P. excelsa*	20.0	*F. latifolia*	13.3	*D. mukole* *C. durandii* *F. kisantuensis*	6.6	-	-	15

increase in abundance of this substrate and/or its invertebrate inhabitants during the rainy season.

FEEDING MOTOR PATTERNS EMPLOYED IN THE CAPTURE AND INGESTION OF PROBABLE INVERTEBRATE FOOD ITEMS.—In this section, I have included feeding motor patterns (employed in the capture and ingestion of probable invertebrate food) recorded from both groups through all 5-day periods of observations because some motor patterns that occurred at low frequency in Group I were not recorded in Group II and vice versa. The complete catalog of motor patterns employed in the capture of probable invertebrates by both groups is given in Appendix Table E. In both groups, a very high percentage (over 90%) of the motor patterns employed in the capture and ingestion of probable invertebrate food items was slow motor patterns. This suggests that both groups concentrated their invertebrate feeding activity on slow-moving or immobile forms rather than on fast-moving forms, such as winged insects.

INVESTIGATIVE ACTIVITIES RELATED TO THE INGESTION OF PROBABLE INVERTEBRATE FOOD.—Invertebrate feeding was usually preceded by a considerable

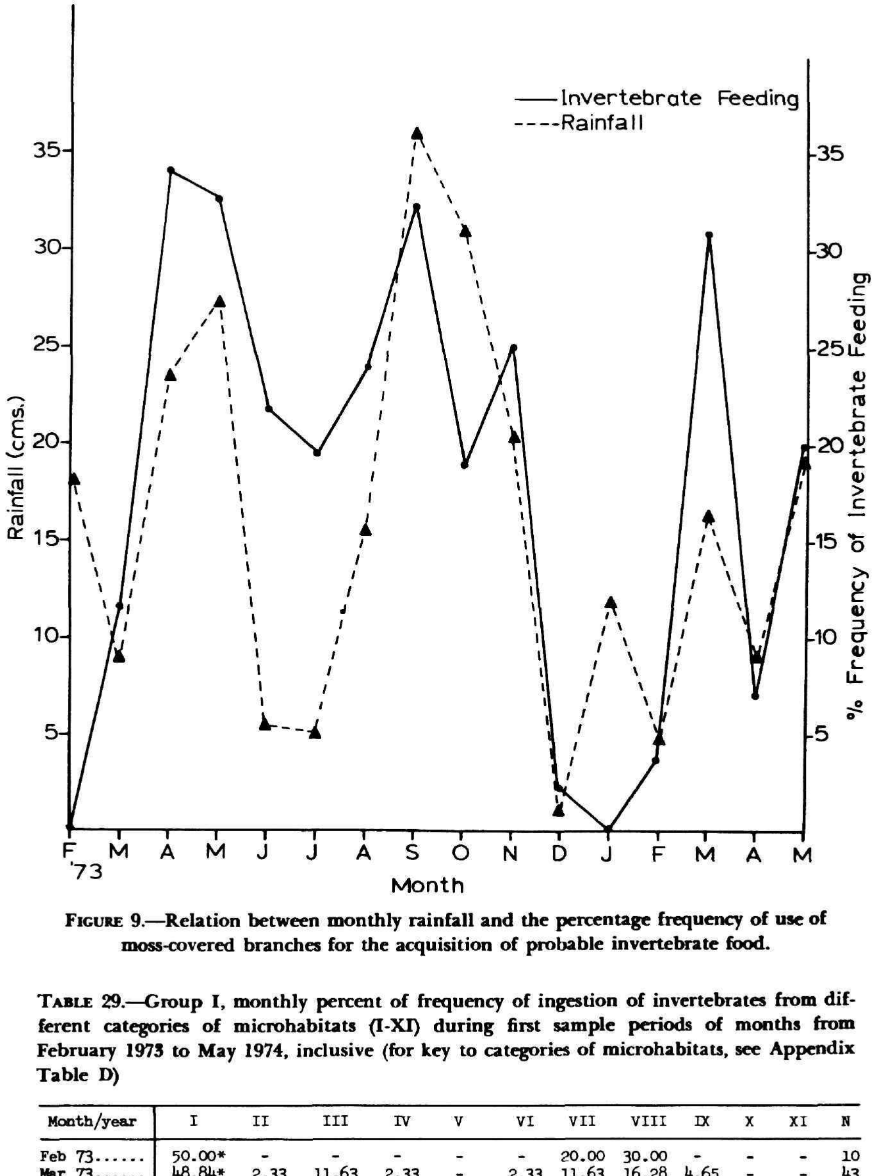


FIGURE 9.—Relation between monthly rainfall and the percentage frequency of use of moss-covered branches for the acquisition of probable invertebrate food.

TABLE 29.—Group I, monthly percent of frequency of ingestion of invertebrates from different categories of microhabitats (I-XI) during first sample periods of months from February 1973 to May 1974, inclusive (for key to categories of microhabitats, see Appendix Table D)

Month/year	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	N
Feb 73......	50.00*	-	-	-	-	-	20.00	30.00	-	-	-	10
Mar 73......	48.84*	2.33	11.63	2.33	-	2.33	11.63	16.28	4.65	-	-	43
Apr 73......	36.84*	10.53	34.21	2.63	5.26	-	2.63	5.26	2.63	-	-	38
May 73......	28.57	18.37	32.65*	-	2.04	8.16	2.04	8.16	-	-	-	49
Jun 73......	36.36*	14.55	21.82	3.64	3.64	3.64	10.91	5.45	-	-	-	55
Jul 73......	31.37*	27.45	19.61	3.92	5.88	1.96	5.88	1.96	-	-	1.96	51
Aug 73......	35.71*	11.90	23.81	-	9.52	2.38	16.67	-	-	-	-	42
Sep 73......	30.65	12.90	32.26*	1.61	6.45	1.61	11.29	1.61	1.61	-	-	62
Oct 73......	32.43*	32.43*	18.92	2.70	5.41	2.70	2.70	-	2.70	-	-	37
Nov 73......	39.58*	12.50	25.00	2.08	2.08	10.42	6.25	-	-	-	-	48
Dec 73......	76.19*	2.38	2.38	2.38	7.14	2.38	7.14	-	-	-	-	42
Jan 74......	52.38*	-	-	-	33.33	4.76	4.76	4.76	-	-	-	21
Feb 74......	74.07*	7.41	3.70	-	3.70	-	11.11	-	-	-	-	27
Mar 74......	25.64	17.95	30.77*	5.13	7.69	2.56	10.26	-	-	-	-	39
Apr 74......	57.14*	21.43	7.14	-	-	-	14.29	-	-	-	-	14
May 74......	60.00*	6.67	20.00	-	-	-	6.67	6.67	-	-	-	15
Total.....												593

*Indicates microhabitat with the highest frequency of invertebrate ingestion score amount of visual scanning and/or manual examination of microhabitats, and followed by mastication of the invertebrate prey. Since a considerable proportion of the time budget of blue monkeys was apportioned to visual scanning and manual examination of microhabitats, I scored these as separate activity categories. A score for one of these investigative activities indicates that the activity was sustained for a period of five seconds, but that the search for invertebrates was unsuccessful during this period. However, if the search resulted in the capture and ingestion of an invertebrate food item, then I scored it as a separate category of activity, termed ingestion. Thus, the monthly frequency of ingestion scores divided by the sum of the frequencies of investigations and ingestions yields a relative measure of success in seeking out invertebrate prey during that month. Group I showed considerable intermonthly variation in their success in capture of invertebrate food items (Table 30). Usually they captured invertebrates in less than half the investigations in different microhabitats.

A relative measure of invertebrate capture success can also be obtained by comparing the rate of investigations and ingestions to the rate of ingestions of invertebrate food items. The rates of investigations and ingestions were generally higher during peak rainfall periods (April 1973 to May 1973 and September 1973 to November 1973) and one month after the peaks than during other periods, but the rates of capture (and ingestion) during many of these months were less than average. This suggests that Group I searched more intensively for invertebrates during peak rainfall periods (and immediately after them) than during other times, either because invertebrate populations reached low levels or because they remained less active and hence less conspicuous during these months. It is also possible that during the rains more of the insects were present as winged adults and, therefore, more mobile and relatively unavailable to blue monkeys.

The percentage success of capture of invertebrates from different microhabitats is given in Table 31. The greatest success in the capture of invertebrates occurred in unidentified microhabitats. Among the identified microhabitats, Group I was most successful in prey capture on bare trunks and branches, presumably because invertebrates were most easily detectable on these surfaces.

FRUITS AS A SOURCE OF INVERTEBRATE FOOD.—In addition to searching actively and ingesting invertebrates, blue monkeys also took them along with the fruits of certain species. Of special interest were the fruits of several species of *Ficus*, which were eaten by both groups. The fruits of these plants usually contained heavy infestations of the developmental stages of the wasps that aid in pollination, as well as chalcid and braconid wasps, which were parasitic on the pollinators (Table 32).

TABLE 30.—Group I, monthly percent of frequency of success in the capture of probable invertebrate food items during the first sample periods from February 1973 to May 1974, inclusive

Sample period	Frequency of successful and unsuccessful investigations for invertebrates	Frequency of successful investigation (i.e., capture) of invertebrates	Percent of success in capture of invertebrates	Total hours of group contact	Rate of all investigations for invertebrates (per hour)	Rate of capture of invertebrates (per hour)
Feb 73 (I)......	21	10	47.6	46.25	0.45	0.22
Mar 73 (I)......	76	43	56.6	54.00	1.41	0.80
Apr 73 (I)......	91	38	41.8	52.75	1.73	0.72
May 73 (I)......	99	49	49.5	44.25	2.24	1.13
Jun 73 (I)......	110	55	50.0	57.00	1.93	0.96
Jul 73 (I)......	74	46	62.2	60.00	1.23	0.77
Aug 73 (I)......	94	42	44.7	56.00	1.68	0.75
Sep 73 (I)......	159	60	37.7	51.25	3.10	1.17
Oct 73 (I)......	126	35	27.3	54.75	2.30	0.64
Nov 73 (I)......	126	41	32.5	54.75	2.30	0.75
Dec 73 (I)......	127	38	29.9	60.50	2.10	0.63
Jan 74 (I)......	42	16	38.1	56.00	0.75	0.29
Feb 74 (I)......	44	20	45.5	56.50	0.78	0.35
Mar 74 (I)......	56	27	48.2	20.75	2.70	1.30
Apr 74 (I)......	33	11	33.3	25.50	1.29	0.43
May 74 (I)......	18	9	50.0	18.00	1.00	0.50
Mean..........	-	-	43.4	-	1.69	0.71

TABLE 31.—Group I, percent of success of capture of probable invertebrates in different micro habitats (I-XI) during first sample periods from February 1973 to May 1974, inclusive (for key to categories of microhabitats, see Appendix Table D)

Capture	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Frequency of investigation and capture of invertebrates..	528.0	167.0	311.0	55.0	66.0	51.0	72.0	28.0	10.0	3.0	3.0
Frequency of capture..........	223.0	72.0	112.0	10.0	30.0	19.0	46.0	23.0	5.0	0	0
Percent of success in capture..	42.2	43.1	36.0	18.2	45.5	37.3	63.9	82.1	50.0	0	0

TABLE 32.—Percent of insect infestation of certain fruits eaten by Groups I and II

Species	Number of fruits examined	Number of fruits with insect infestation	Percent of fruits with insect infestation
F. exasperata.....	35	30	85.71
F. brachylepis....	30	28	93.33
F. dawei..........	39	35	89.74
F. natalensis.....	40	33	82.50
F. stipulifera....	16	16	100.00
M. bagshawei......	134	15	11.19
P. turbinata......	32	30	93.75

Some *Ficus* spp. also carried infestations of other insects; the fruits of *F. brachylepis* sometimes contained the large larvae of the weevil, *Omophorus stomachosus* (P. Waser, pers. comm.); a small black unidentified species of ant was frequently found on the surfaces of the fruits of *F. stipulifera*. Other fruits that were found to be infected with insects were those of *P. turbinata* and *M. bagshawei*. During certain months, the fruits of these two species and those of *F. exasperata* and *F. dawei* were very important in the diet of Group I (Appendix Table C). Similarly, during certain months the diet of Group II contained large amounts of the fruits of *F. exasperata* and *F. brachylepis* (see section on intergroup dietary differences).

WATER REQUIREMENTS OF THE BLUE MONKEYS.—Water requirements of the blue monkeys were probably largely satisfied by the succulent fruits that they ate. By comparing wet and dry weights of fruits, I estimated that the fruits of *F. exasperata, F. brachylepis, F. natalensis, C. durandii,* and *T. nobilis* contained over 70% water, while those of *M. bagshawei* and *U. congensis* contained about 55% and 67%, respectively. Occasionally, after a shower of rain blue monkeys also drank water from holes in trees. This they did either by applying their mouths directly to the surface of the water or dipping one hand into it and lapping up the moisture from the fur.

VERTEBRATE FOOD EATEN BY BLUE MONKEYS.—I once observed a subadult male of Group II eating an African wood owl (*Ciccaba woodfordii bohndorffi*). The bird vocalizations heard at the beginning of this observation and freshness of the small quantity of meat that remained after the meal indicated that the bird was captured alive rather than taken as carrion. The subadult male did not share any of the meat with other members of his group, most of whom watched him from within five m. During the time he fed on the bird, he once chased a juvenile who approached him. This behavior is in contrast to the meat-sharing behavior reported in the chimpanzees (Van Lawick-Goodall, 1971; Teleki, 1973), and, unlike chimps, the subadult male blue monkey did not eat leaves along with the meat. The wings of the bird that were recovered after the meal spanned 33 cm. This indicated that the bird was an adult, and adults of this species weigh about 450 gms (Mackworth-Praed and Grant, 1952). This observation was recorded after nearly 2070 hours of contact with blue monkeys and, hence, predation on adult birds must be considered a rare occurrence.

INTRASPECIFIC FOOD NICHE SEPARATION.—In this analysis, I compared the relative frequency of feeding and the composition of diet of four age/sex classes. In order to do this, it was important that (1) the exact age/sex composition from which the feeding observations were derived be known and (2) each age/sex class was equally likely to be scored for feeding. Feeding data collected from Group II during the December 1973 to September 1974 period (when each group member was individually identifiable) best satisfied these two criteria. All members of this group were completely habituated to my presence, but one of the four adult females (female RLT) remained peripheral to the group and was less likely to be scored for feeding than the others. Therefore, feeding data recorded from this female were discarded; adjustments were also made for the disappearance of another adult female in January 1974.

During the period of observations mentioned above, excluding infants, Group II comprised of a mean of one adult male, 2.175 females (excluding RLT), two subadults, and four juveniles (Table 33). Feeding observations recorded from these age/sex classes showed that their relative frequencies of feeding differed significantly from expected (χ^2 = 47.94, df=3, p <0.005). The adult females and subadults fed more frequently than expected, while the adult male and the juveniles fed less frequently than expected. Pairwise comparisons of feeding frequency suggested that (1) the adult male apportioned less time to feeding activity than the other three age/sex classes, (2) juveniles spent less time feeding than adult females and subadults, and (3) adult females and subadults spent similar amounts of time attending to their dietary needs (Table 34).

The proportion of different food items constituting the diet of each of these four classes also differed significantly (χ^2=36.94, df=12, p <0.01). The composition of the diet of the adult male was different from that of the other three classes; the variations in the diet of these three classes were not statistically significant (Table 34). Evidently the adult male concentrated more on fruits and far less on invertebrates than the others. Invertebrates were most important in the diet of immature individuals (i.e., subadults and juveniles).

INTERGROUP DIETARY DIFFERENCES.—Dietary comparisons between Groups I and II were restricted to the period when monthly observations were made on both groups (i.e., between February 1973 and January 1974). Also these comparisons were made only between those sample periods of observations of both groups with the shortest time interval between them, regardless of whether these periods occurred within the same month or in adjacent months. This reduced the possibility of intergroup differences in diet being affected by the time interval between sample periods. When a period of observations of a group was comparable to two sample periods of the other group, I compared both pair combinations.

TABLE 33.—Group II, proportion of different food items eaten by four classes of individuals during sample periods from December 1973 to September 1974, inclusive

Age/sex class	Mean number of individuals	Number of feeding observations	Percent of different food items in diet: Foliar items	Floral items	Fruits	Other plant items	Inverte-brates
Adult male......	1.0	97	22.7	10.3	59.9	2.1	5.2
Adult female....	2.175	369	23.0	11.4	43.6	3.8	18.2
Subadult........	2.0	347	25.4	11.5	33.7	4.9	24.5
Juvenile........	4.0	499	23.1	11.2	36.3	4.2	25.3

TABLE 34.—Group II, χ^2 statistic for comparisons between different pair combinations of age/sex classes

Pair combination	Adult male/ adult female	Adult male/ subadult	Adult male/ juvenile	Adult female/ subadult	Adult female/ juvenile	Sub-adult/ juvenile
			Feeding Frequency			
χ^2....................	24.620	26.350	5.160	0.07	20.140	22.470
df......................	1.0	1.0	1.0	1.0	1.0	1.0
Level of significance...	0.005	0.005	0.025	0.05	0.005	0.005
			Composition of Diet			
χ^2....................	13.43	28.81	27.16	8.82	7.81	1.12
df......................	4.0	4.0	4.0	4.0	4.0	4.0
Level of significance...	0.01	0.01	0.01	0.05	0.05	0.05

TABLE 35.—Time interval between comparable sample periods of observations on Groups I and II

Month/year	Number of sample periods of observation		Comparable sample periods		Interval between sample periods (days)
	Group I	Group II	Group I	Group II	
Feb 73.....	1	1	Feb 73 (I)	Feb 73 (I)	2
Mar 73.....	2	1	Mar 73 (II)	Mar 73 (I)	4
Apr 73.....	2	1	Apr 73 (I)	Mar 73 (I)	4
May 73.....	2	1	May 73 (I)	Apr 73 (I)	5
Jun 73.....	2	1	Jun 73 (I)	May 73 (I)	3
Jul 73.....	2	0	Jul 73 (I)	Jun 73 (I)	4
Aug 73.....	2	1	Sep 73 (I)	Aug 73 (I)	2
Sep 73.....	1	1	Sep 73 (I)	Sep 73 (I)	10
Oct 73.....	1	1	Nov 73 (I)	Oct 73 (I)	3
Nov 73.....	2	1	Nov 73 (II)	Nov 73 (I)	7
Dec 73.....	1	1	Dec 73 (I)	Dec 73 (I)	7
Jan 74.....	1	1	Jan 74 (I)	Jan 74 (I)	4
Feb-May 74....	4	3	-	-	-
Jun-Sep 74....	-	4	-	-	-
Total....	23	18	-	-	-
Mean.....	-	-	-	-	4.58

Eleven periods of observations of each group between February 1973 and January 1974 inclusive provided 12 pair combinations of sample periods for comparison (Table 35). The mean time interval between comparable sample periods was 4.58 days (range 2-10 days). During these sample periods, I observed Group I for 584 hours and recorded a total of 2329 plant and invertebrate feeding scores at the rate of 4.0 feeding scores per hour of group contact. Of these feeding scores, 1977 were recorded from the use of 60 food plants and 102 specific food items (Appendix Table G). Group II was observed for 558 hours, and 2268 feeding scores were collected at the rate of 4.1 feeding scores per hour of contact. Feeding on plant food accounted for 1856 scores from this group and were recorded from the use of 47 plant species and 86 specific food items (Appendix Table G). In view of the small differences in duration of group contact and similar rates of feeding data collection, it appears that Group II utilized a less diverse plant diet than Group I. The less diverse nature of the diet of Group II was also indicated by the fact that this group exploited its top 13 food plants to the same extent that Group I used its top 21 food plants.

Both groups exploited a total of 74 food plants, but only 33 (44.6%) of these were shared by them; 27 were used exclusively by Group I and 14 were used only by Group II. In general, mutually exploited food plants were used at different frequencies, these differences being most appreciable in the use of *F. exasperata* and *T. nobilis*, which were top-ranking food plants of Groups I and II. Intergroup differences in the frequency of use of *U. congensis*, *M. platycalyx*, and *M. bagshawei* were also relatively large. Due to intergroup variability in the frequency of use of food plants, only 13 mutually exploited species occur among the top 20 food plants of each group. The top 20 food plants account for as much as 89.65% and 95.80% of the vegetable diet of Groups I and II respectively, and therefore, must be considered as an important component of their diet. Included among the top 20 ranks were *P. turbinata*, which was exclusively used by Group I, and *F. stipulifera*, which was used only by Group II. There were also several species, such as *M. bagshawei* and *L. johnsonii*, that occur only among the top 20 food plants of one group and occupy lower ranks in the diet of the other group.

In order to assess intergroup differences in food preferences, I computed selection ratios. These ratios were computed only on the basis of the densities of food plants, because it was reasonable to assume that canopy size was more or less constant for a particular plant species. Estimates of food plant densities within the home ranges of Groups I and II were obtained from Struhsaker (1975) and Waser (pers. comm.), respectively, and from personal investigations.

Selection ratios indicate that intergroup differences in the frequency of use of some species (*C. durandii* and *D. abyssinica*) were probably due to differences in their densities within the two home ranges (Table 36). In terms of selection ratios, however, certain species were more preferred by Group I than by Group II (e.g., *C. africana*, *P. angolensis*, *F. exasperata*, and *M. bagshawei*), while some others were more preferred by Group II than Group I (e.g., *F. brachylepis* and *C. gorungosanum*). Since the frequency of use of food plants may also have been affected by the size of their canopies, selection ratios given in Table 36 do not reflect intragroup preference of food plants.

Comparisons of the proportions of food items constituting the vegetable diet of the two groups show that Group I used 25.1% of foliar foods, while Group II used about 17.0% of these food items (Appendix Tables F, G). Group I also used relatively higher proportions of blossoms and lower proportions of fruits in its vegetable diet than Group II. Intergroup dietary differences can also be shown by considering the use of plant as well as invertebrate food items exploited by both groups during comparable sample periods (Figure 10). During the February 1973 sample periods recorded from Groups I and II, their diets varied appreciably in the frequency of use of fruits (by 18.3%), blossoms (by 27.0%), and invertebrates (by 10.7%). Similarly in the May 1973–April 1973 pair combination intergroup variability in diet was largely due to a 13.7% difference in the use of foliar items and a 12.1% difference in the use of blossoms. In the July 1973–June 1973 pair combination, the two groups showed large differences in the frequency of use of fruits (28.5%) and blossoms (25.4%). Considerable intergroup variability in the use of food items can also be found in the September 1973–August 1973, September 1973–September 1973, December 1973–December 1973, and January 1974–January 1974 pair combinations of sample periods.

Intergroup variability in diet was also apparent in the relative importance and the frequency of use of specific food items used by the two groups. Among the top 20 ranks of specific food items exploited by each group, only 11 were mutually exploited, and the top-ranking specific food item of each group occupied a much lower rank in the diet of the other group (Table 37). Usually, both groups used a food plant for the same food items, but the frequencies of use of these food items by the two groups were quite variable. Thus, in the diet of Group I, *M. myristica* was included within the top

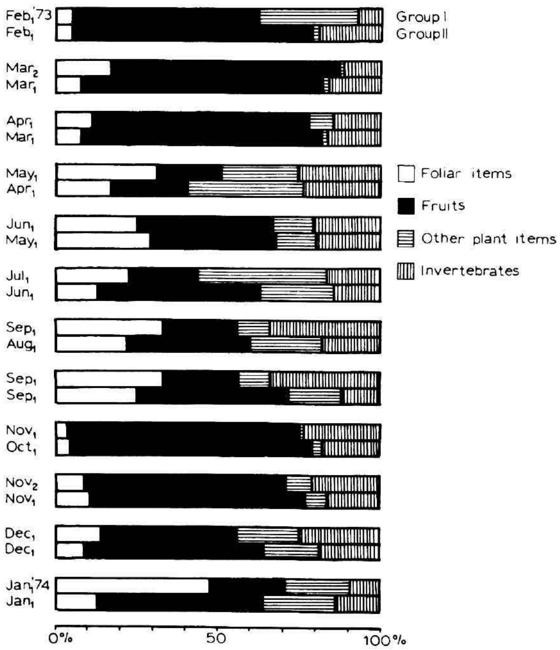


FIGURE 10.—Cumulative percentage frequency of use of different food items by Groups I and II during comparable sample periods.

TABLE 36.—Selection ratios of important food plants exploited by Groups I and II

Species	Percent of frequency of use		Density/hectare		Selection ratio	
	Group I	Group II	Group I home range	Group II home range	Group I	Group II
T. nobilis	13.06	4.47	20.0	12.3	0.62	0.36
C. africana	11.39	11.48	2.1	7.4	5.42	1.55
D. abyssinica	10.02	7.70	65.7	35.7	0.15	0.22
U. congensis	6.98	11.53	25.2	14.8	0.28	0.78
C. durandii	6.52	7.17	34.3	31.4	0.19	0.23
P. angolensis	5.11	1.94	1.4	1.9	3.65	1.05
F. exasperata	4.76	19.61	0.2	1.6	23.80	12.30
M. bagshawei	4.61	0.48	2.1	0.6	2.20	0.77
M. platycalyx	3.90	7.49	58.0	45.5	0.07	0.16
F. latifolia	2.88	4.04	14.7	9.9	0.20	0.41
F. brachylepis	0.05	6.63	0.1	0.4	0.40	16.60
C. gorungosanum	1.06	1.78	2.1	0.6	0.60	2.97

TABLE 37.—Groups I and II, percent of frequency of use of top 20 specific food items

Group I		Group II	
Rank order and specific food item	Percent of frequency of use	Rank order and specific food item	Percent of frequency of use
1. *Teclea nobilis*, fruits	11.53	1. *Ficus exasperata*, fruits	15.09
2. *Celtis africana*, fruits	10.52	2. *Uvariopsis congensis*, fruits	11.53
3. *Uvariopsis congensis*, fruits	6.83	3. *Celtis africana*, fruits	9.16
4. *Celtis durandii*, fruits	6.52	4. *Celtis durandii*, fruits	7.00
5. *Ficus exasperata*, fruits	4.66	5. *Ficus brachylepis*, fruits	6.63
6. *Diospyros abyssinica*, fruits	4.55	6. *Teclea nobilis*, fruits	4.36
7. *Mimusops bagshawei*, fruits	3.85	7. *Funtumia latifolia*, seeds	4.04
8. *Premna angolensis*, blossoms	3.80	8. *Ficus exasperata*, leaf buds	3.50
9. *Markhamia platycalyx*, petioles	3.14	9. *Markhamia platycalyx*, nectar	3.18
10. *Funtumia latifolia*, seeds	2.88	10. *Markhamia platycalyx*, petioles	2.96
11. *Diospyros abyssinica*, blossoms	2.78	11. *Diospyros abyssinica*, blossoms	2.69
12. *Diospyros abyssinica*, young leaves	2.68	12. *Diospyros abyssinica*, young leaves	2.37
13. *Dombeya mukole*, young leaves	2.07	13. *Monodora myristica*, fruits	2.21
14. *Parinari excelsa*, fruits	2.02	14. *Linociera johnsonii*, fruits	2.10
15. *Vangueria apiculata*, mature leaves	1.82	15. *Diospyros abyssinica*, fruits	1.78
16. *Pancovia turbinata*, fruits	1.72	16. *Chrysophyllum gorungosanum*, blossoms	1.40
17. *Monodora myristica*, leaf buds	1.62	17. *Premna angolensis*, blossoms	1.24
18. *Teclea nobilis*, mature leaves	1.37	18. *Ficus exasperata*, young leaves	0.97
Neoboutonia macrocalyx, mature leaves		19. *Monodora myristica*, blossoms	0.86
Chaetachme aristata, fruits		*Olea welwitschii*, mature leaves	
Total	77.10	Total	83.93

20 ranks because of the use of its leaf buds, and in the diet of Group II it was included among these ranks due to the use of its fruits and blossoms. Group II used the nectar of *M. platycalyx* more frequently than its petioles, but Group I used the petioles more frequently than the nectar of this species. The frequencies of use of food items from *D. abyssinica* were also reversed in the diet of the two groups.

Most of the high-ranging specific food items exploited by both groups showed restricted periods of use (and importance), but their patterns of use were somewhat variable. For example, *M. bagshawei* fruits were important (i.e., included within the top five ranks) in the diet of Group I during four sample periods, but were never important in the diet of Group II (Figure 11). The fruits of *U. congensis* were important in the diet of Group II during the mid and late 1973 sample periods, but their importance in the diet of Group I was restricted to the midyear sample periods. The use of *P. angolensis* blossoms showed a pattern where a specific food item was exploited during similar sample periods, but assumed importance in the diet of the two groups during different sample periods. The fruit of *F. brachylepis*, which was the fifth ranking specific food item in the diet of Group II, was important to this group in two sample periods, but was not used at all by Group I during the comparable sample periods between February 1973 and January 1974.

Perhaps the most striking intergroup variation in the pattern of use of specific food items was found in the use of the fruits of *F. exasperata* (Figure 12). There were periods when Group I used little or none of these fruits, but Group II used them more or less continually from February 1973 to January 1974 and always at a higher frequency than Group I. In addition to the fruits of *F. exasperata*, Group II also used its leaf buds and young leaves, both of which were available to, but not exploited by, Group I. When the use of these fruits decreased, Group II took appreciable amounts of leaf buds from *F. exasperata*. Therefore, this species remained important in the diet of Group II through all sample periods except June 1973, but its importance in the diet of Group I was restricted to three sample periods.

Usually Group II exploited fewer specific food items than Group I (Table 38). The Shannon-Wiener indices of diet diversity showed that in 9 of the 12 pair combinations of sample periods, Group II utilized a less diverse diet than Group I. During comparable sample periods the number of mutually exploited specific plant food items was generally low when compared to the total number

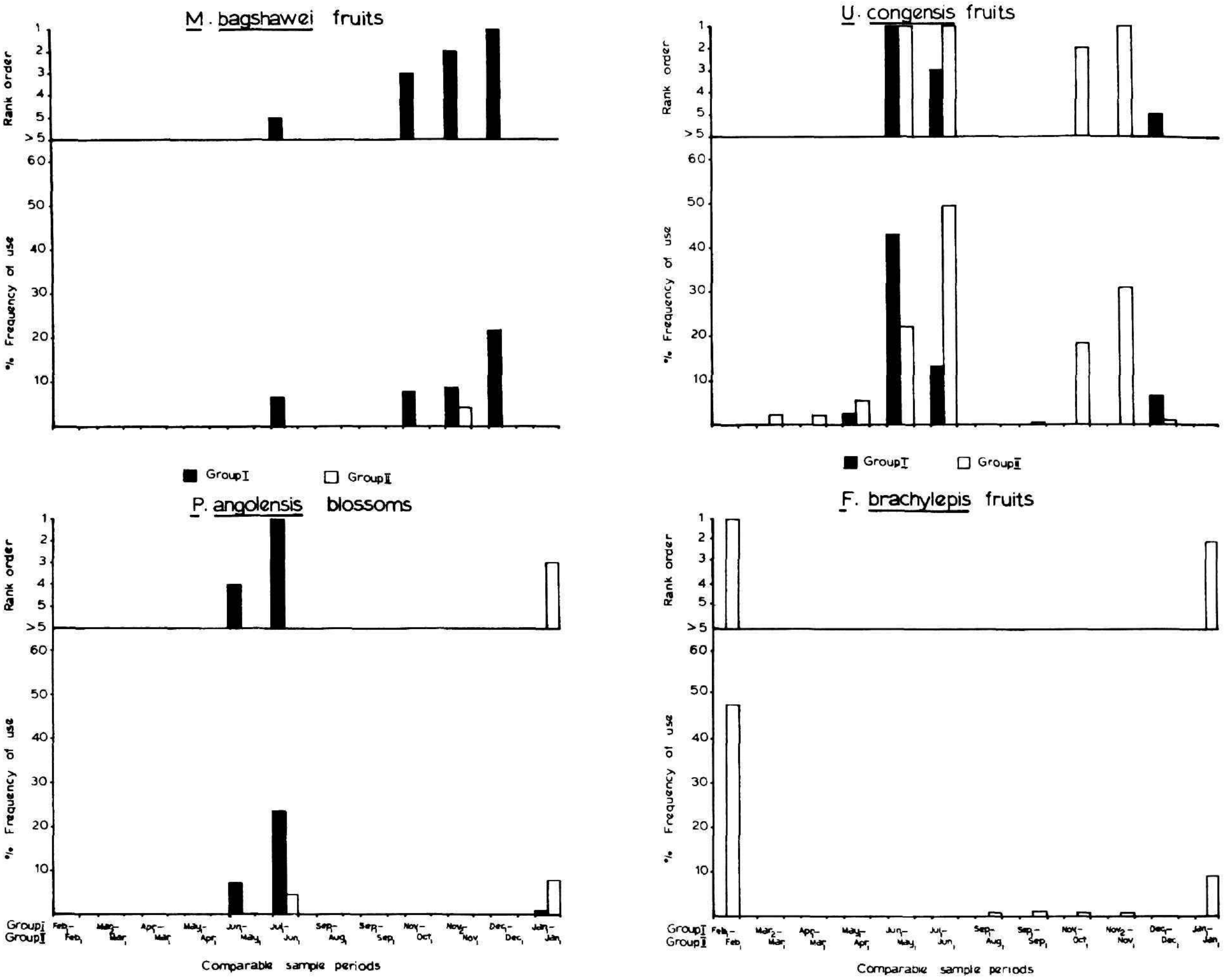


FIGURE 11.—Percentage frequency of use of selected specific food items and their rank order of importance in the diets of Groups I and II during comparable sample periods.

of specific plant foods used by each group. Intergroup diet overlaps due to mutual use of specific plant foods range from 22.6% to 65.2% (mean = 40.1%), which, in view of all the variables of sampling methods, vegetation, and phenology of tree species, may be considered to be usually low or moderate.

DISCUSSION

BLUE MONKEY FEEDING PATTERNS AND ADAPTIVE SIGNIFICANCE OF DIET.—Although blue monkeys exploited a relatively diverse diet, they appeared to be fairly selective feeders. Their use of food resources seemed to be affected by their selectivity as well as the relative abundance and availability of food items.

Fruits were the most important component of the diet of blue monkeys but foliar foods were also periodically important. The folivorous aspect of the diet was perhaps adaptive in the context of the life-style of this species and the periodic fluctuations in the abundance of various food resources (see "Introduction"; also Ellefson, 1964). During

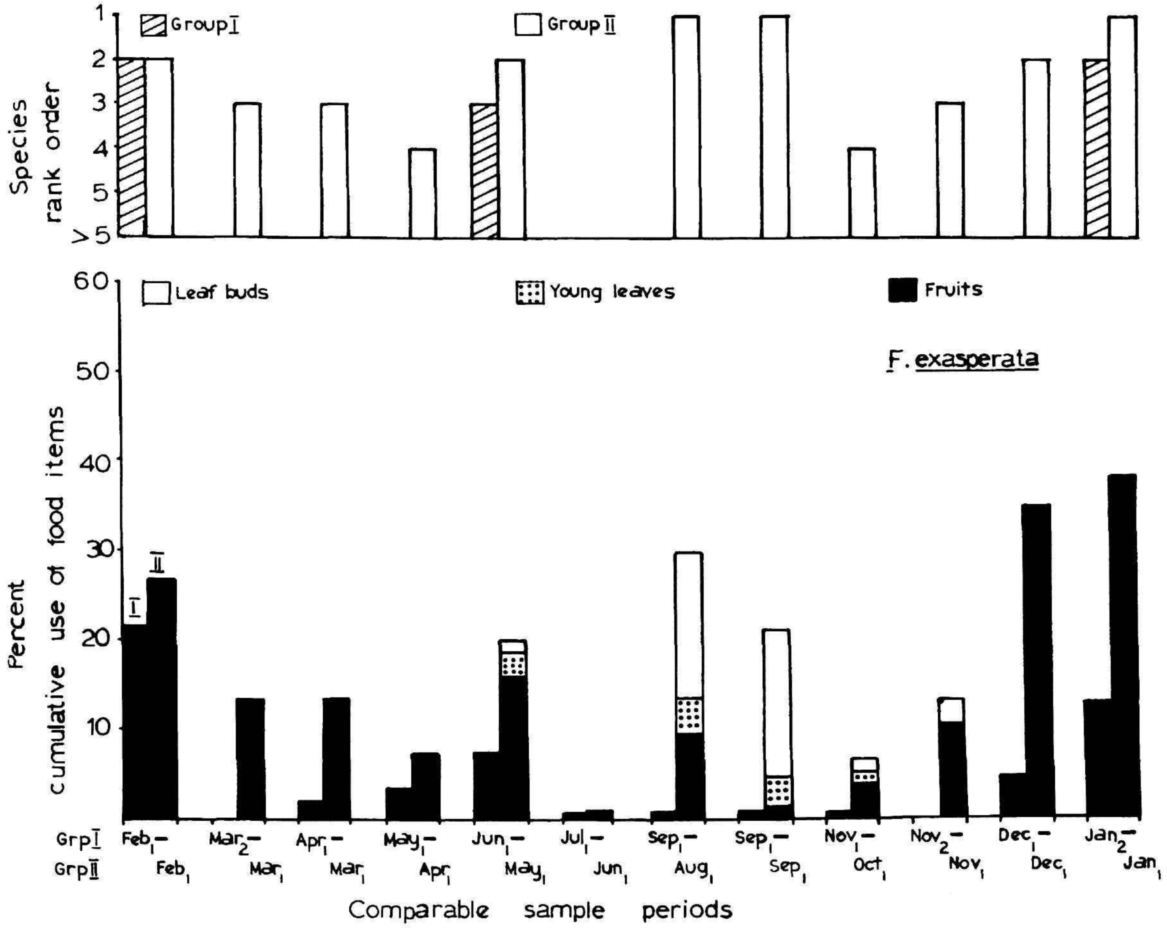


FIGURE 12.—Percentage frequency of use of food items exploited from *F. exasperata* and the rank order of importance of this species in the diet of Groups I and II.

TABLE 38.—Indices of diet diversity and percent of overlaps in diet of Groups I and II

Comparable sample period		Number of specific food items used		Indices of diet diversity		Number of specific items shared	Percent of overlap in diet
Group I	Group II	Group I	Group II	Group I	Group II		
Feb 73 (I)	Feb 73 (I)	20	8	2.2996	1.3455	3	38.2
Mar 73 (II)	Mar 73 (I)	14	12	2.0434	1.7319	4	41.8
Apr 73 (I)	Mar 73 (I)	22	12	1.7451	1.7319	4	56.4
May 73 (I)	Apr 73 (I)	38	27	3.1294	2.5340	11	34.7
Jun 73 (I)	May 73 (I)	22	25	2.1272	2.6369	10	53.5
Jul 73 (I)	Jun 73 (I)	25	20	2.4139	1.9214	11	39.0
Sep 73 (I)	Aug 73 (I)	24	15	2.5412	2.1733	7	35.4
Sep 73 (I)	Sep 73 (I)	24	16	2.5412	2.2159	8	38.7
Nov 73 (I)	Oct 73 (I)	15	15	1.3427	1.6993	6	65.2
Nov 73 (II)	Nov 73 (I)	20	20	1.7344	2.0934	6	22.6
Dec 73 (I)	Dec 73 (I)	23	19	2.4613	2.0501	9	26.4
Jan 74 (I)	Jan 74 (I)	30	25	2.9105	2.3894	13	29.3
	Mean.........						40.1
	Range........						22.6-65.2

periods of fruit shortage, blue monkeys were left with two possible options. One was to range over extensive areas in search of fruits like the mangabeys do in the Kibale Forest, and the other was to switch to more readily available foods, such as foliar foods. In view of the relatively small size of blue monkeys, energetic considerations may make movements over extensive areas unfeasible (McNab, 1963). Thus when fruits were in short supply, the only possible alternative appeared to be to switch to foliar foods that were more readily available than fruits. Since the diet of adult males contained a large proportion of fruits, the one-male social structure may also be viewed as an adaptation to periods of fruit shortage. The use of foliar foods also probably satisfied certain nutrient requirements of blue monkeys. Some young leaves contain a very high percentage of crude protein (Struhsaker, 1975), and mature leaves have fairly high concentrations of calcium (Biddulph, 1959).

Morton (1973) has noted that among frugivorous birds there may be intense selection favoring abilities to find other types of food even if periods of fruit scarcity were relatively improbable. Primates like the blue monkey, which depend a great deal on fruits, also probably experience the same selection pressure. This affords an explanation for the wide variety of food items used by blue monkeys. The wide variety of foods used by blue monkeys was the result of a diverse diet during periods of fruit shortage as well as exploitation of small quantities of different items when fruits were being used extensively. Freeland and Janzen (1974) hypothesize that herbivores must continuously sample a variety of foods available to them in order to maintain enzymatic pathways for detoxifying secondary compounds. This allows them to ingest large quantities of relatively toxic foods if necessary (i.e., when preferred foods were in short supply) without suffering any ill effects. It is possible that blue monkeys used several foods, especially foliar foods (that usually contain toxic substances), in order to keep periodically important metabolic pathways open. The use of a wide variety of foods may also have been necessary (1) to maximize nutrient intake and (2) to increase total food consumption (Smith, 1959).

INTRASPECIFIC FOOD NICHE SEPARATION.—Food niche separation between the age/sex classes occurred along at least two dimensions, and the greatest similarity in diet was between subadults and females. The adult male seemed to adopt a "time minimizing" strategy (Schoener, 1971) and maintained himself on a fairly bulky diet, primarily of fruits. Fruits normally contain relatively large amounts of simple sugars, which are readily utilizable sources of energy (Jenkins, 1969). On the other hand, immature individuals concentrated more on food resources rich in proteins (i.e., invertebrates), which were probably important during the growth phase of individuals. The fact that adult females also used invertebrates more frequently than the adult male may be related to their reproductive cycle and nutrient requirements of infant care. Compared to adult females and subadults, the juveniles fed less frequently, which may be because they were smaller and therefore required lesser quantities of food than adult females and subadults. Also a portion of the time budget of juveniles was allotted to group socialization processes, such as play, in which the older age classes rarely indulged. In the field, I sometimes observed play between juveniles, while older individuals were involved in a bout of feeding.

FOOD NICHE SEPARATION BETWEEN SYMPATRIC CERCOPITHECINES.—The feeding motor patterns employed in the acquisition of invertebrates suggested that blue monkeys most frequently used slow-moving or immobile forms, such as insect larvae and pupae. In contrast redtails used rapid motor patterns more often than blue monkeys to capture their invertebrate source of food, indicating that they concentrated more on fast-moving forms, such as winged (adult) insects (Struhsaker, pers. comm.). Apparently, these two species reduced overlap along this niche dimension by focusing their activity at different points on the spectrum of invertebrates available to them. The redtails, which were socially subordinate to blue monkeys, exploited a wider range of invertebrates, showing that there was an inverse relationship between dominance rank and niche breadth (Morse, 1974) along this resource dimension. The plant diets of these two species were quite similar.

The mangabeys, which were larger than blue monkeys, were able to use their heavy jaw musculature to bite through wood, bark, and lianas with channeled piths to obtain invertebrates (Waser, 1975) that neither the blue monkeys nor the redtails were able to exploit. Also the mangabeys specialized in selecting and eating hard latex-filled (*F. brachylepis*) fruits, which contained the relatively large larvae of a weevil, *Omophorus stomachosus* Bah. This type of feeding behavior was not seen in the blue monkeys. The greater strength of the mangabeys also allowed them to strip and eat bark that blue monkeys did not use as food. The extensive home ranges of mangabeys seemed to enable them to rely on abundant sources of fruits and to maintain a highly frugivorous diet throughout the year. Thus their diet consisted only of 5.4% of foliar food, which strongly contrasted with the folivorous component of the diet of blue monkeys.

Very little is known of the food habits of *C. lhoesti*, but its dental structure indicates that it may be the most folivorous of the four cercopithecines found within the study area (Kay and Hylander, in press). Moreover, being a largely terrestrial species, it probably exploited food plants different from those used by the other three more arboreal cercopithecines.

Cercopithecines have been variously classified as opportunistic omnivores (Struhsaker, 1967, 1969), arboreal frugivores, frugivore-omnivores (Eisenberg et al., 1972), and frugivore-insectivores (Gartlan and Brain, 1968; Jones and Sabater Pi, 1968; Bourliere, Hunkeler, and Bertrand, 1970; Dittus, 1974). The broad ecological categories used to describe their diet sometimes obscure the varying degrees of importance of different dietary components, which in the case of the cercopithecines of the Kibale Forest probably led to a substantial separation of their feeding niches. Gautier and Gautier-Hion (1975) also found similar dietary differences between *Cercopithecus pogonias*, *C. cephus*, and *C. nictitans*, which were sympatric in Gabon, west Africa. Although these species were mainly frugivorous, *C. pogonias* was the most insectivorous, while *C. nictitans*, which belongs to the same superspecies as *C. mitis*, was the most folivorous in food habits.

Although the food niche of blue monkeys seemed distinct enough to allow for their coexistence with other species, they apparently met with intense competition for certain food items. For example, their use of unripe fruits of certain species (e.g., *C. durandii*, *C. africana*, and *C. betacea*), which probably contained starch rather than sugars and considerable amounts of acid (Winton and Winton, 1935), was probably due to interspecific competition for these resources. Also the fact that many of the interspecific conflicts of blue monkeys occurred in a feeding context suggests that blue monkeys competed for certain food resources with other species.

INTERGROUP DIETARY DIFFERENCES.—Intergroup variability in diet was expressed by the relatively low percentage of mutually exploited food plants and by differences in the total number of food plants used by each group. Since the difference between the total durations of contact with the two groups was small (being less than 5% of the duration of contact with either group), this alone could not have caused the appreciable difference in the total number of food plants used by the two groups during comparable sample periods. Differences in group size and visibility within the two home ranges could affect the rate of collection of feeding observations and, therefore, the rate of discovery of the food plants of each group. The fact that the rates of collection of feeding observations from both groups were similar suggests that these factors were also probably not important in causing food plant diversity differences found between the two groups.

Selective felling operations for commercially valuable timber within the home range of Group II involved the removal of certain large food plant species (e.g., *P. excelsa*, *O. welwitschii*, *A. altissima*, *M. bagshawei*, etc.). Felling of large trees invariably resulted in the destruction of the lower story vegetation that included some of the important food plants of blue monkeys. This destruction to habitat provides an explanation for the less diverse nature of the diet of Group II and the lowered frequency of use of the above species as well as some of the smaller species by Group II. Comparison of densities from the two home ranges, however, also showed that some important food plants (*F. exasperata*, *F. brachylepis*, *C. africana*) were found at higher densities within the felled area and some (*C. durandii*, *P. angolensis*) were found at more or less equal densities in both areas (Table 36). Thus selective felling does not entirely explain the density differences between the two home ranges and suggests that, at least in some respects, the study area was more heterogeneous prior to selective felling.

Differences resulting from vegetational heterogeneity at least in part explain why Groups I and II had exclusive access to certain species. For example, *F. dawei* and *P. microcarpa* occurred only within the home range of Group I, while *F. congensis* and *D. battiscombei* were located only within the home range of Group II. *Ficus dawei* occupied top rank as a food plant and constituted nearly 35% of the feeding scores of Group I during the second sample period of May 1973, and it exemplified the profound intergroup dietary differences that can be caused by the use of food plants available to only one group.

In considering present density differences within the two home ranges, it can be reasonably assumed that the densities of tree species that did not produce commercially valuable timber and were also large (e.g., *F. exasperata, F. brachylepis, F. dawei, P. microcarpa,* etc.) would have been relatively unaffected by selective felling. Hence any intergroup dietary variability caused by the exploitation of these species must be a reflection of density differences due to vegetational heterogeneity rather than due to selective felling. This is particularly true of large species that are presently found at higher densities within the selectively felled area (*F. exasperata* and *F. brachylepis*).

Ficus exasperata provided some of the greatest intergroup dietary variations through its markedly different patterns of use by both groups. Phenological study of this species showed that asynchronous activity of individuals provided both groups with one to three potential food items throughout all months of observations (Rudran, unpubl.). During any particular month, however, the relative abundance of these items was much greater within the home range of Group II. Group I used only the fruits of this species, while Group II used all three food items. *Ficus exasperata,* which was used fairly continuously and at relatively high frequencies by Group II, provided at least some of the intergroup dietary differences during every month. The manner in which Group II used this food plant was also probably responsible for its less diverse diet. *Ficus brachylepis* was another species that was an important food plant to Group II that was hardly ever used by Group I.

Local variations in the phenological activity of a food plant also gave rise to dietary differences between the two groups. In November 1973, when Group II used *Uvariopsis congensis* at high frequency (Figure 11), much of its feeding activity was centered around a grove of this species, whose phenological activity was presumably out of phase with the majority of its individuals found within both home ranges. The variable patterns of use of *Premna angolensis* by the two groups were also probably due to differences in relative abundances of these blossoms caused by local variations in the activity of this species. The flowering activity of *Markhamia platycalyx,* which was far more conspicuous within the home range of Group II, provided an important food source (nectar) to this group during August 1973, whereas nectar was never important in the diet of Group I. This may have been due to local variations in the phenology of this species, but Struhsaker (in press) also provides evidence to suggest that the heavier predation of these blossoms (particularly by the red colobus) within the home range of Group I made them less readily available to this group than to Group II. The red colobus, being best adapted to old mature forest, occurred at higher densities within the home range of Group I than Group II (Struhsaker and Oates, 1975). The extensive predation of *M. platycalyx* blossoms within the home range of Group I and its effect on fruit crop size (Struhsaker, in press) was probably responsible for the fact that only Group II used the fruits of this species.

INTERPOPULATIONAL COMPARISONS OF BLUE MONKEY DIET.—In Kahuzi-Biega National Park, Zaire, Schlichte (1975) found that a large proportion of blue monkey diet was restricted to a small proportion of the total food plant list. This is consistent with my findings in the Kibale Forest. Schlichte recorded a total of 36 food plants used by his groups, while I noted more than twice that number in my study groups. This may have been due to differences in the durations of the two studies and/or to the floristically depauperate nature of the Zaire study area. Schlichte found group-specific food preference for *Kotyschya* blossoms, which were available to both his study groups but were used only by one. Similar observations were also made by me in the Kibale Forest. Due to methodological differences, direct comparisons of the proportions of different food items constituting the diet of the two populations cannot be made. In both populations, however, fruits formed a major part of the diet, while foliar food was used more frequently than invertebrate food. The major component of the diet of blue monkeys of Budongo Forest was also fruits (Aldrich-Blake, 1970a).

The blue monkeys of the Kibale Forest did not use 30 food plants exploited by the Zaire population, and 20 food plants of a total of 30 eaten by the Budongo Forest population. Interpopulational differences found in the diet of blue monkeys, as in several other primate species (see Chalmers, 1968; Gartlan and Brain, 1968; Oates, 1974; Dunbar and Dunbar, 1974; Clutton-Brock, 1975; Struhsaker, 1975; Waser, 1975), were probably mainly due to differences in floristic composition between widely separated areas.

The Ranging Patterns of Blue Monkeys

Methods

While observing a blue monkey group, I mapped the locations of individuals soon after recording their activity during 10-minute scan periods of systematic sampling (see "Introduction"). From March 1973 to June 1973, these plots consisted only of locations of the greatest concentration of individuals during the scan periods centered at the hour and at the half hour. From July 1973 onward I plotted locations (1) during all four scan periods recorded during the hour, and (2) of every individual whose activity was noted. In the analysis I segregated these location plots into quadrats, and for most of the data analysis used a 50 m × 50 m (¼ hectare) grid system. Measurements of home range size were also obtained by using two smaller grid systems, each comprising $\frac{1}{16}$ to $\frac{1}{64}$ hectare quadrats, respectively. In the following sections, reference to the quarter hectare quadrats used by Group I has been made with respect to its location—first along numbered rows and then along numbered columns.

Throughout each day I also recorded the paths of movement of the group. When the group was widely dispersed, I mainly relied on recognizable animals to plot the movements of the group, and when it was compact, I noted the path of movement of the greatest number of individuals. Since these paths of group progression do not take into account vertical movements, they must be considered as minimal distances moved by the group. From September 1973 onward, daily movements were subdivided into hourly movements.

During each hour of group contact, I collected climatic data on a subjective basis by using a scale from 1–4 to denote sunny, hazy, cloudy and rainy weather conditions respectively. When the weather changed drastically within the hour, the weather condition with the longest duration was assigned to that particular hour.

In order to calculate range overlaps, I used Holmes and Pitelka's (1968) method, which I had used earlier in the computation of diet overlap. Using this method, I computed two measures of range overlap between sample periods and in both cases considered the ¼ hectare quadrat as the unit of overlap. In one case, I measured overlaps considering only the number of overlapping quadrats and in the other took into account the frequencies of use of these quadrats also. The first measure is related to spatial overlap between sample periods while the second is related to temporal overlap in areas of overlap. Range overlaps between different days of a sample period were also computed, but only as a measure of spatial overlap. Quadrat utilization diversity was computed using the Shannon-Wiener diversity equation (Pielou, 1966).

Results

Home Range Size.—From March 1973 until May 1974 inclusive (i.e., through 22 sample periods), Group I entered a total of 290 ¼ hectare quadrats, which amounted to a home range size of 72.5 hectares. Grassland abutted the northwestern and western periphery of their home range, and a small stream that ran along the southeastern and eastern edge separated their home range from that of Group III (Figure 13). The stream was not a barrier to movements and could have been crossed at several points via arboreal pathways. Aldrich-Blake (1970a) also noted that a road overhung by arboreal pathways served as a boundary between the home ranges of some of his study groups of blue monkeys. This suggests that when easily recognizable physical features of the habitat were available, blue monkeys used them to demarcate range boundaries.

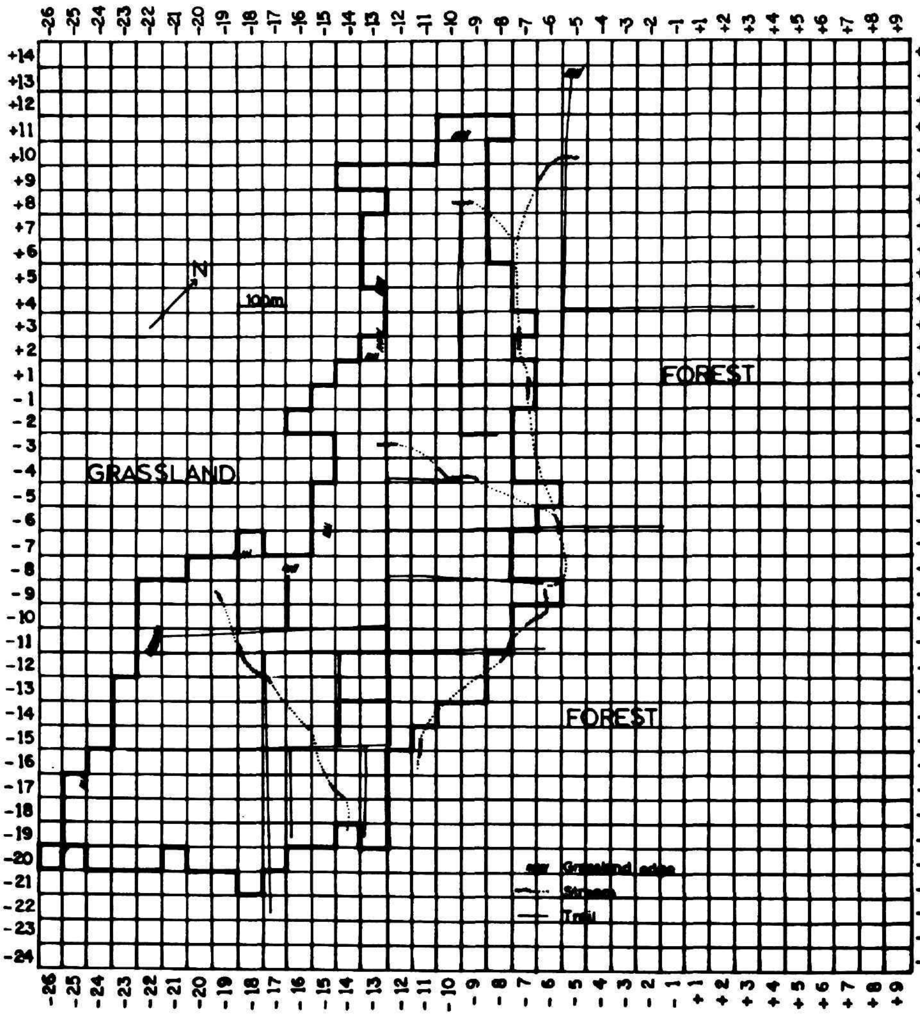


FIGURE 13.—The home range of Group I. The 290 quarter-hectare quadrats used by Group I are enclosed within the dark outline.

The cumulative area used by Group I increased during the first 1008 hours of group contact but remained stable over the last 64 hours of observations (Figure 14). This suggests that during my observations of Group I, I had discovered their entire home range. The range estimate of 72.5 hectares, however, may be considered an overestimation because group members were not mapped in every part of each ¼ hectare quadrat they entered.

In order to exclude small lacunae from the ¼ hectare quadrats used by Group I, I used two grid systems of smaller dimensions. A grid composed of 1/16 hectare quadrats yielded a home range size of 60.8 hectares, and a grid of 1/64 hectare quadrats yielded an estimate of 48.5 hectares. The home range estimate decreased by 33% of the original value when quadrat size was reduced by 1/16.

AREAS USED DURING DIFFERENT SAMPLE PERIODS.—In Figure 15 I have segregated the estimates of the areas used by Group I during different sample periods in accordance with the slightly different methods used in plotting locations before and after

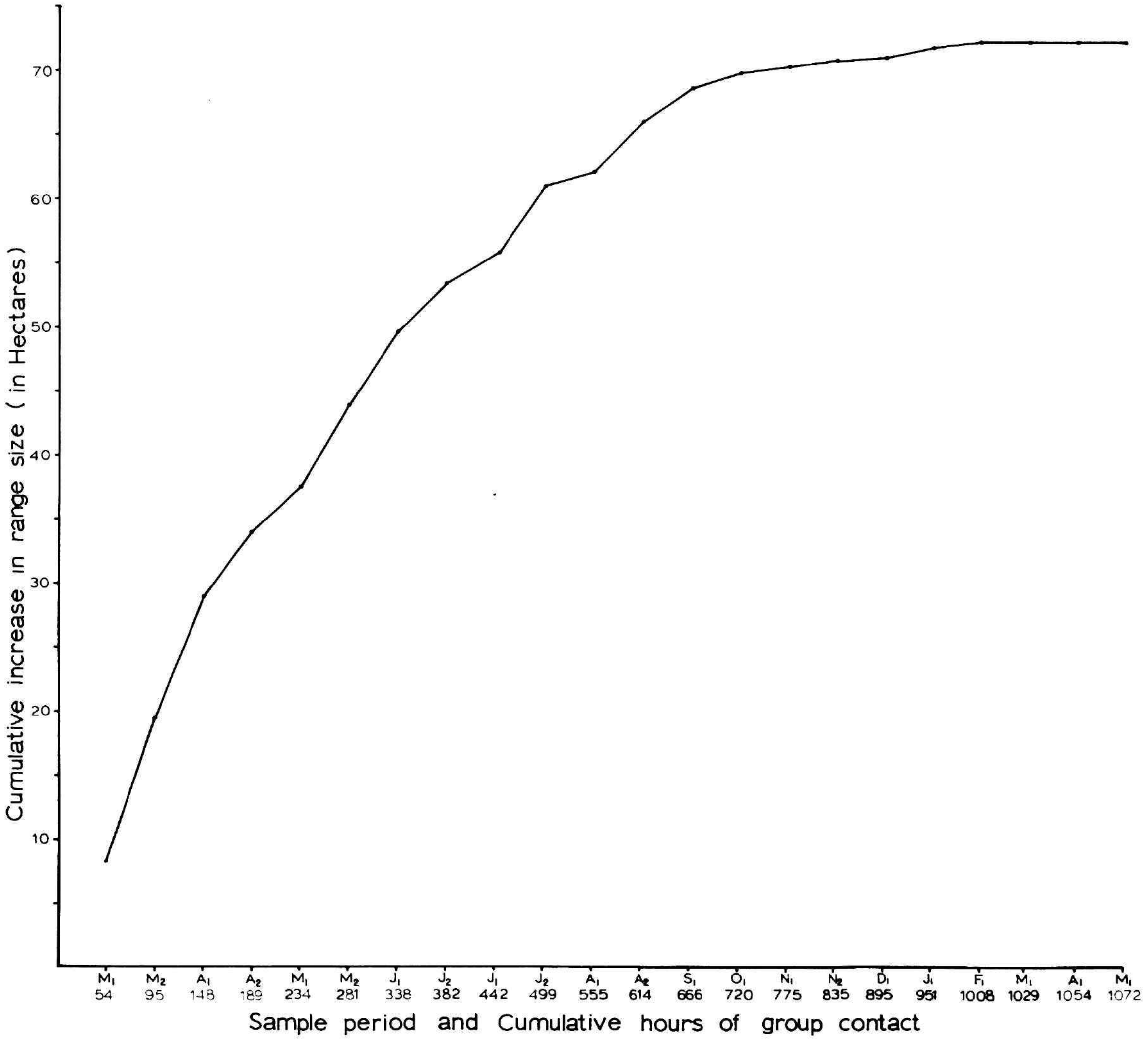


FIGURE 14.—Cumulative increase in the area used by Group I during group contact through all sample periods from May 1973 to May 1974, inclusive.

June 1973. The fewer locations plotted by the method used from March 1973 to June 1973 were probably largely responsible for the smaller areas used during this period. Nevertheless, even between July 1973 and February 1974, Group I used only a small proportion of the entire range during any one sample period. The first sample period of November 1973 was the only time that Group I visited more than half its home range during a five consecutive day period.

Within the segregated data, it can also be seen that the total area used during different sample periods showed considerable variation. Since these variations may have been due to differences in the durations of group contact, the areas used were standardized to the least durations of group contact during sample periods. The least durations of contact during March 1973 and June 1973 and July 1973 to February 1974 sample periods were 41 hours and 51 hours, respectively. Since the

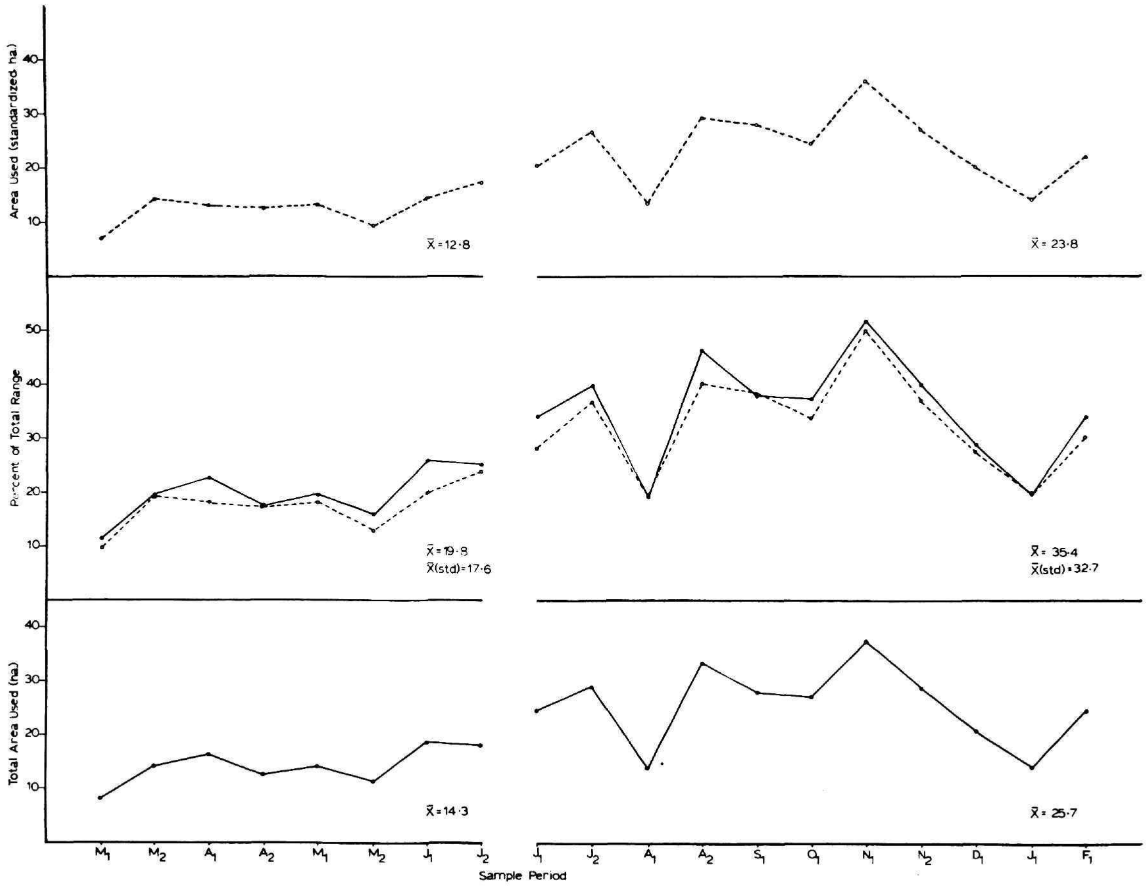


FIGURE 15.—The total and standardized measures of the areas used during different sample periods and the percentage of the home range used during each sample period.

methods used during these two time periods were somewhat different, I felt it was unnecessary to standardize the areas used during all sample periods to one fixed time period. The standardized measures of areas used between March 1973 and June 1973 showed little variation; however, the areas used between July 1973 and February 1974 varied significantly from the mean area used during this period (χ^2 = 18.8, df = 10, $p<0.05$). The variability in the areas used during different sample periods is depicted by movements during two sample periods in Figure 16.

RANGE OVERLAP BETWEEN SAMPLE PERIODS.—As mentioned before, I computed range overlaps between sample periods as a measure of area overlap as well as a measure of time overlap in areas of overlap. Overlap measures were computed only between sample periods during which similar methods of data collection were used. Neither the areas used during different sample periods (Tables 39 and 40) nor the proportions of time spent in areas of overlap (Tables 41 and 42) were high, and three pair combinations of sample periods—March (I) 1973 and May (II) 1973, March (I) 1973 and June (II) 1973, September (I) 1973 and January (I) 1974—showed the extreme case of zero overlap (see Figure 17). This suggests that usually Group I not only used relatively small areas, but also somewhat different parts of their range during different sample periods.

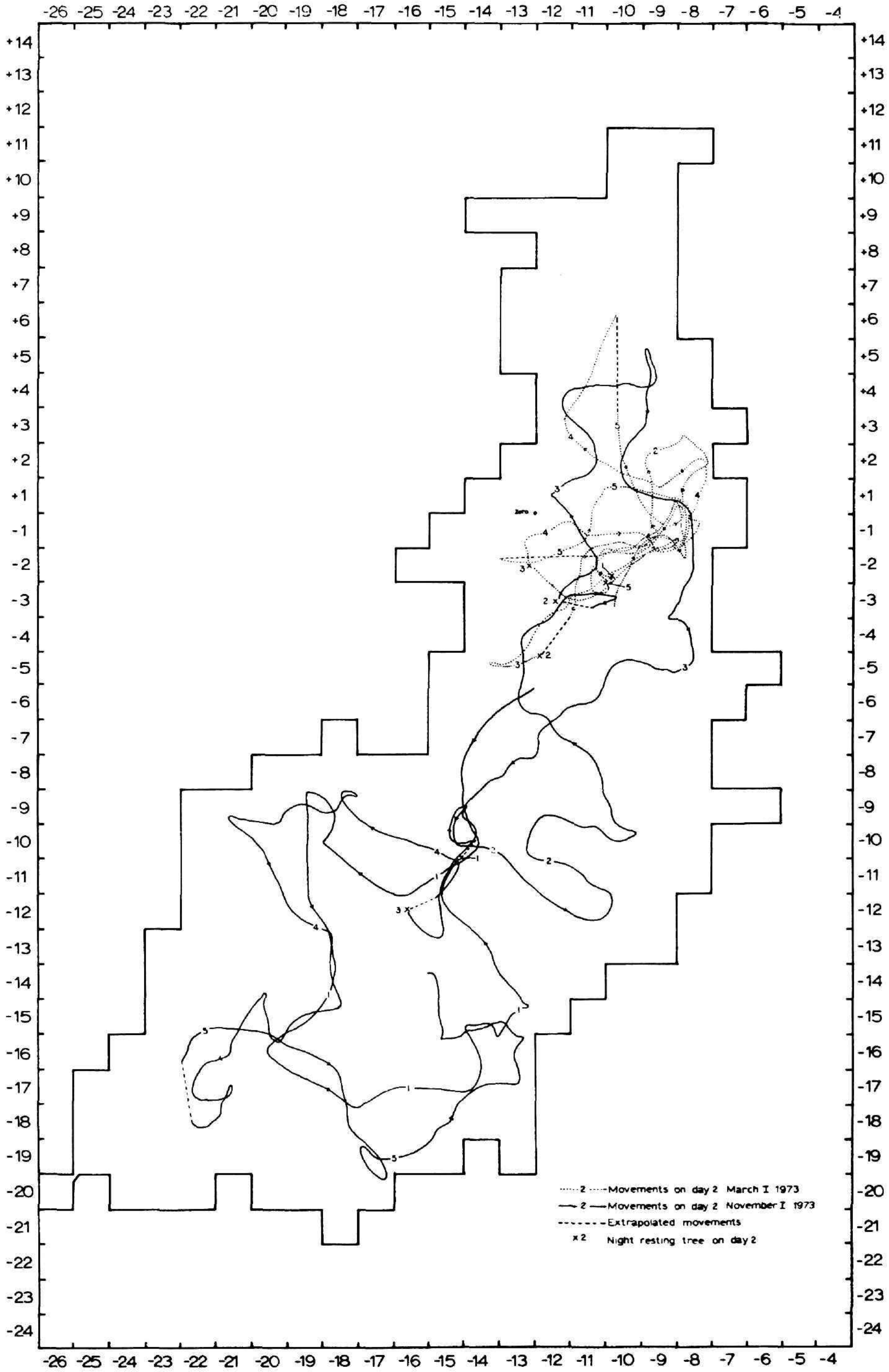


FIGURE 16.—Group movements on different days of the first sample periods of March 1973 and November 1973 depicting variability in the areas used during different sample periods.

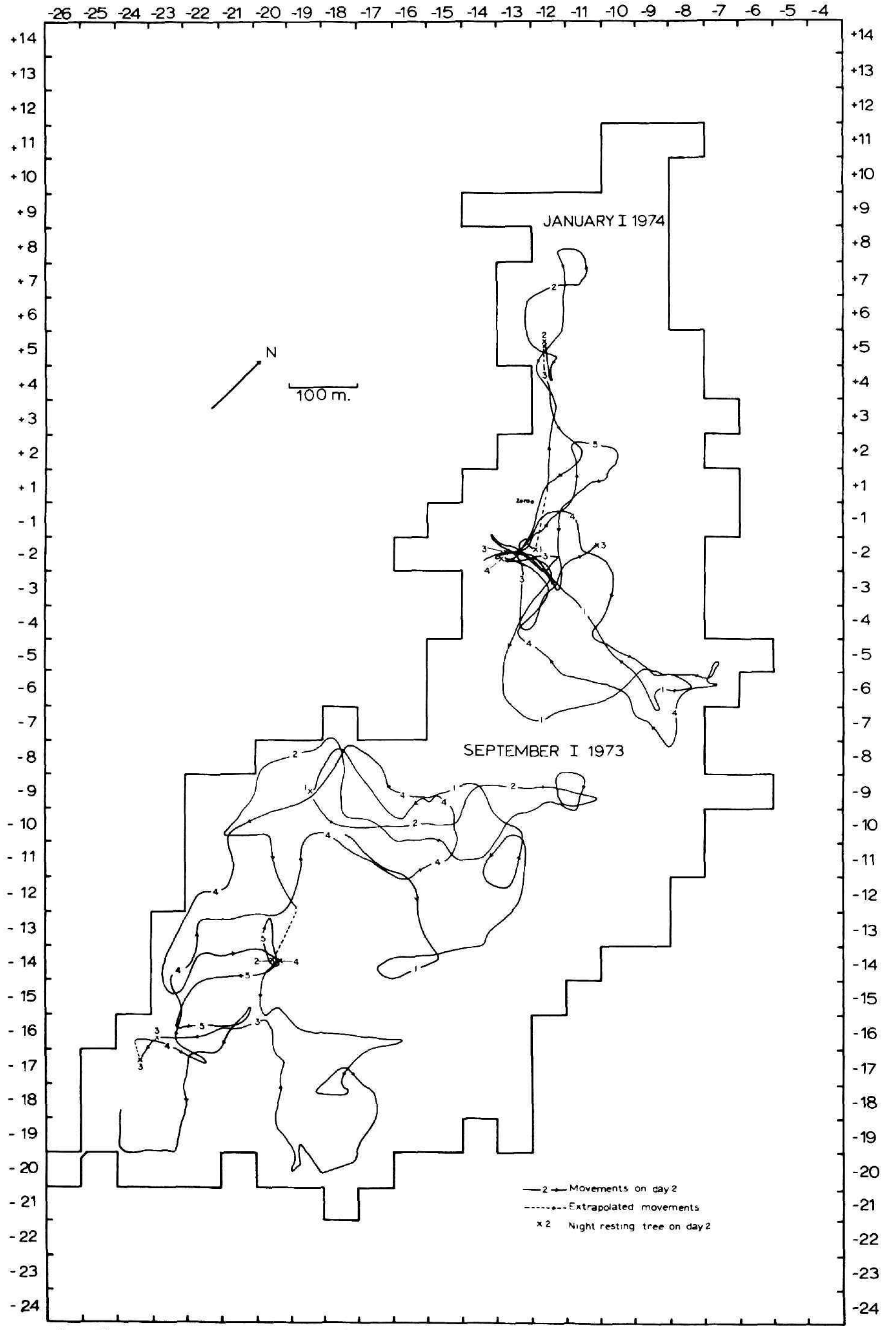


FIGURE 17.—Group movements during the first sample periods of September 1973 and January 1974 showing nonoverlap in the areas used.

TABLE 39.—Group I, percent of overlap in home range use based on the area of quadrats used in common during sample periods from March 1973 to June 1973, inclusive (all pair combinations of sample periods: N = 28, X = 21.1%, range = 0%–43.9%; successive combinations of sample periods: N = 7, X = 24.5%, range = 3.4%–43.9%)

Sample period	Mar (II)	Apr (I)	Apr (II)	May (I)	May (II)	Jun (I)	Jun (II)
Mar 73 (I)....	21.0	21.3	13.7	37.8	0	4.0	0
Mar 73 (II)...	-	35.0	38.5	27.5	15.8	22.6	27.4
Apr 73 (I)....	-	-	27.4	31.9	1.5	37.2	21.9
Apr 73 (II)...	-	-	-	20.6	19.6	26.6	16.4
May 73 (I)....	-	-	-	-	3.4	16.0	2.7
May 73 (II)...	-	-	-	-	-	20.0	37.0
Jun 73 (I)....	-	-	-	-	-	-	43.9

The low values of time overlap indicate that during different sample periods the proportion of time Group I spent in overlapping quadrats was greatly variable. From this it can be inferred that during each sample period Group I used different quadrats at proportionately high frequencies. This can also be shown by comparing the overlap between sample periods due to area of use (Tables 39 and 40) with those weighted with the frequency of use of overlapping quadrats (Tables 41 and 42), where the latter measures of overlap were consistently lower than the former.

DAILY RANGE.—Since duration of group contact affected the records of areas used, I limited the computations of daily ranges to 67 days with 11 or more hours of group contact. The mean and the range of areas used on these days are presented in Figure 18. Frequently the areas used on different days of a sample period as well as mean daily ranges of different sample periods varied considerably. Comparison of Figures 15 and 18 shows that usually day ranges also constituted a small proportion of the total area used during a sample period. On any particular day of a sample period, Group I infrequently used over half the total area used during that sample period, which suggests that daily ranges of Group I must have frequently included areas that were previously not used during the same sample period. This can be illustrated by considering the cumulative increase in the number of quadrats used through days of each sample period. In 16 of 19 sample periods there were continuous increases in the area used through five days of group contact (Figure 19). Only in three sample periods (March (I) 1973, August (I) 1973, and January (I) 1974) did the increase in cumulative area of use reach a plateau prior to the end of five days of observations.

A restricted analysis for 19 days (between March and June 1973) with 11 or more hours of observations per day showed that the daily distances moved were positively correlated with the sizes of the areas used on these days (P = 0.004 two-tailed Kendall's correlation test; Sokal and Rohlf, 1969). Thus, revisits to quadrats or back-and-forth movements within a limited number of quadrats must have been infrequent.

In order to find out if the area used by Group I would stabilize over a 10-day period, I combined the ranging data from two sample periods conducted during the same month in six months of the study. I excluded the data from the sample periods in March 1973 from this analysis since there was a relatively long (seven days) interval between sample periods. During the months of April to August 1973 and November 1973 intervals between sample pe-

TABLE 40.—Group I, percent of overlap in home range use based on the area of quadrats used in common during sample periods from July 1973 to February 1974, inclusive (all pair combinations of sample periods: N = 55, X = 36.6%, range = 0%–66.8%; successive combinations of sample periods: N = 10, X = 42.8%, range = 19.8%–66.8%)

Sample period	Jul (II)	Aug (I)	Aug (II)	Sep (I)	Oct (I)	Nov (I)	Nov (II)	Dec (I)	Jan 74 (I)	Feb (I)
Jul 73 (I)....	48.2	42.4	45.8	34.7	36.4	39.5	54.2	47.5	29.3	44.4
Jul 73 (II)...	-	19.8	47.3	43.0	38.7	42.9	41.3	33.5	16.3	35.3
Aug 73 (I)....	-	-	24.0	0.9	4.6	20.8	43.9	47.6	56.0	33.3
Aug 73 (II)...	-	-	-	39.8	43.5	55.6	49.5	40.5	21.8	45.0
Sep 73 (I)....	-	-	-	-	66.8	47.6	18.9	19.6	0	24.9
Oct 73 (I)....	-	-	-	-	-	46.9	26.7	23.7	9.1	35.5
Nov 73 (I)....	-	-	-	-	-	-	50.3	38.2	19.4	41.5
Nov 73 (II)...	-	-	-	-	-	-	-	47.3	37.8	49.9
Dec 73 (I)....	-	-	-	-	-	-	-	-	45.2	54.5
Jan 74 (I)....	-	-	-	-	-	-	-	-	-	39.4

TABLE 41.—Group I, percent of overlap in home range use based on the frequency of use of quadrats during sample periods from March 1973 to June 1973, inclusive (all pair combinations of sample periods: N = 28, X = 13.6%, range = 0%–32.1%; successive pair combinations of sample periods: N = 7, X = 16.9%, range = 4.2%–32.1%)

Sample period	Mar (II)	Apr (I)	Apr (II)	May (I)	May (II)	Jun (I)	Jun (II)
Mar 73 (I)....	12.2	15.6	9.3	24.3	9.0	1.6	0
Mar 73 (II)...	-	17.6	20.5	14.3	10.2	10.5	18.5
Apr 73 (I)....	-	-	21.9	16.8	2.1	21.3	18.5
Apr 73 (II)...	-	-	-	12.9	7.5	15.6	10.6
May 73 (I)....	-	-	-	-	4.2	12.5	4.8
May 73 (II)...	-	-	-	-	-	17.2	27.8
Jun 73 (I)....	-	-	-	-	-	-	32.1

riods were 2, 0, 0, 2, 3, and 2 days, respectively. The combined data for the above months show that the cumulative area of use increased even over 10-day periods of observations (Figure 20), although during some months the rate of increase declined somewhat toward the latter stages of observations.

RANGE OVERLAP BETWEEN DAYS OF THE SAME SAMPLE PERIOD.—The use of somewhat different areas on days of a sample period can also be shown by computing area overlaps between days of the same sample period. With two exceptions I restricted this analysis to those sample periods with either four or five days of 11 or more hours of group contact. The exceptions included in this analysis were one day in July (II) 1973 and another in February (I) 1974 when group contact was maintained for 10.5 hours. Thus, the time bias was minimized in this analysis, which is summarized in Table 43. The relatively low mean and maximal overlaps indicate that repeated use of quadrats was infrequent. Generally the greatest overlaps occurred between successive days, and the mean overlaps between successive days were normally greater than the mean overlaps between all pair combinations of days. During successive days as well as during other pair combinations of days, however, Group I sometimes used mutually exclusive areas of their range.

Since daily ranges were relatively small and at least partially different, large proportions of the areas used during a sample period were used only on one day of a sample period. This is illustrated for the sample periods considered in the above analysis in Figure 21. On the average nearly two-thirds of the area used during a sample period was not revisited during the same sample period, and in most sample periods more than half the area used was visited only on one day. Group I, however, repeatedly used small areas for four and five days of a sample period. This shows that Group I used their home range rather unevenly.

Given the area used during a sample period, the ranging patterns during 5 of the 11 sample periods considered in Table 43—i.e., March (I) 1973, July (II) 1973, August (I and II) 1973, and December (I) 1973 sample periods—differed significantly from that expected from the mean ranging patterns (using χ^2 test, df=4, $p<0.025$ in all cases). The ranging patterns of the other six sample periods did not differ significantly from the mean ranging patterns (χ^2 test df=4, $p>0.05$). As mentioned earlier, however, the areas used during sample periods between July 1973 to February 1974 differed significantly from the mean area used during these sample periods.

TABLE 42.—Group I, percent of overlap in home range use based on the frequency of use of quadrats during sample periods from July 1973 to February 1974, inclusive (all pair combinations of sample periods: N = 55, X = 23.3%, range = 0%–42.4%; successive pair combinations of sample periods: N = 10, X = 29.1%, range = 21.3%–42.4%)

Sample period	Jul (II)	Aug (I)	Aug (II)	Sep (I)	Oct (I)	Nov (I)	Nov (II)	Dec (I)	Jan 74 (I)	Feb (I)
Jul 73 (I)....	26.5	38.3	30.8	17.8	17.5	20.4	37.7	33.7	20.9	29.6
Jul 73 (II)...	-	11.4	31.2	23.9	26.0	27.0	16.5	15.9	6.5	16.8
Aug 73 (I)....	-	-	21.3	0.3	1.6	13.2	39.9	34.3	28.4	23.1
Aug 73 (II)...	-	-	-	25.3	30.8	34.8	30.8	23.4	15.9	31.5
Sep 73 (I)....	-	-	-	-	42.4	29.4	8.8	15.1	0	12.3
Oct 73 (I)....	-	-	-	-	-	36.7	11.4	18.5	4.4	17.4
Nov 73 (I)....	-	-	-	-	-	-	24.5	28.2	10.8	26.5
Nov 73 (II)...	-	-	-	-	-	-	-	39.6	28.8	27.7
Dec 73 (I)....	-	-	-	-	-	-	-	-	27.5	34.4
Jan 74 (I)....	-	-	-	-	-	-	-	-	-	36.1

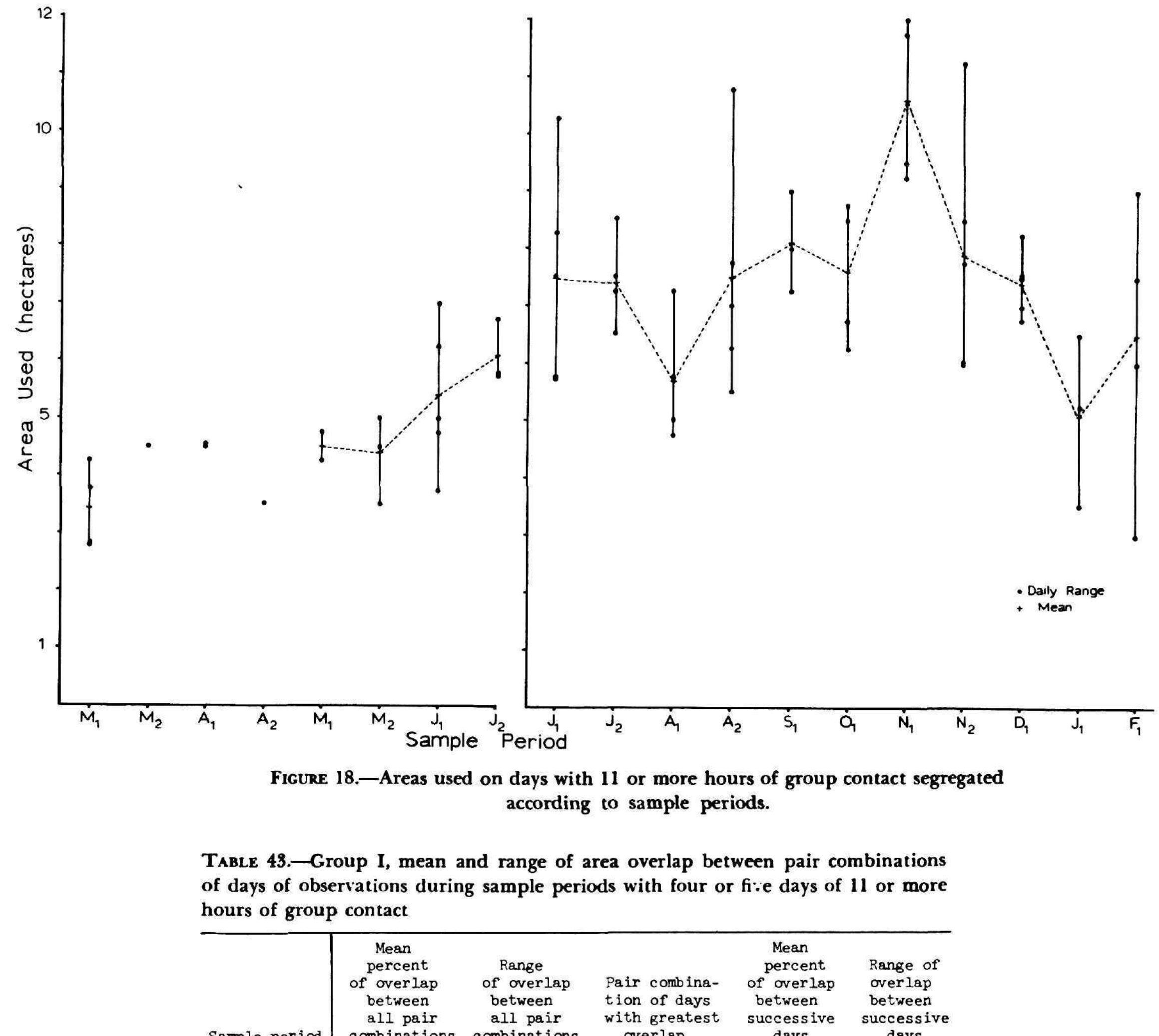


FIGURE 18.—Areas used on days with 11 or more hours of group contact segregated according to sample periods.

TABLE 43.—Group I, mean and range of area overlap between pair combinations of days of observations during sample periods with four or five days of 11 or more hours of group contact

Sample period	Mean percent of overlap between all pair combinations	Range of overlap between all pair combinations	Pair combination of days with greatest overlap	Mean percent of overlap between successive days	Range of overlap between successive days
Mar 73 (I)....	36.6	29.4-46.7	Day 1 & Day 2	36.5	29.4-46.7
Jun 73 (I)....	15.3	0-35.7	Day 1 & Day 2	19.6	0-35.7
Jul 73 (I)....	19.3	0-48.5	Day 2 & Day 3	24.8	0-48.5
Jul 73 (II)...	10.8	0-34.5	Day 1 & Day 2	21.9	5.9-34.5
Aug 73 (I)....	36.3	24.2-47.7	Day 1 & Day 4	38.0	31.1-45.0
Aug 73 (II)...	4.5	0-12.9	Day 2 & Day 4	6.95	4.6-12.0
Oct 73 (I)....	23.8	3.7-42.9	Day 3 & Day 4	21.2	3.7-42.9
Nov 73 (I)....	14.7	4.3-29.1	Day 1 & Day 4	11.3	4.3-17.0
Nov 73 (II)...	16.8	0-35.3	Day 2 & Day 3	19.32	0-35.3
Dec 73 (I)....	27.9	3.3-54.5	Day 1 & Day 5	25.4	9.1-39.0
Feb 74 (I)....	13.6	2.8-19.5	Day 1 & Day 4	12.7	6.7-19.3

DISTRIBUTION OF TIME IN SPACE.—The amount of time that Group I spent in different parts of their range can be considered in terms of frequency of location plots in the different quadrats as well as in terms of days, sample periods, and months each quadrat was used. Figures 22 and 23 clearly show that there was considerable variation in the distribution of these time-related elements among the 290 quadrats that comprised home range of Group I.

If the number of days of use and the number of

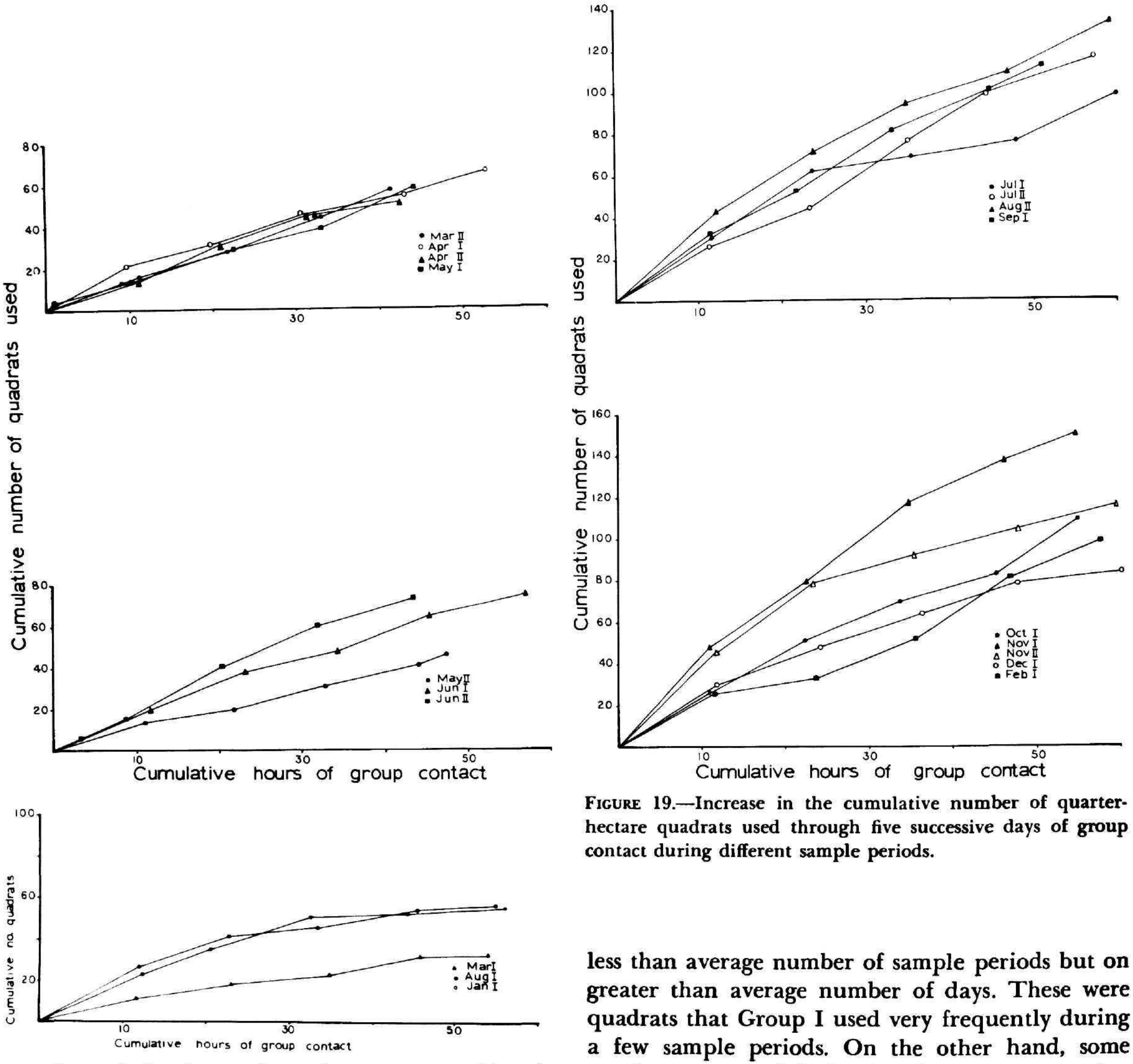


FIGURE 19.—Increase in the cumulative number of quarter-hectare quadrats used through five successive days of group contact during different sample periods.

sample periods of use of quadrats were considered together, then each quadrat would occupy one of four classes depending on whether or not it was used above or below the mean number of days or sample periods of use. The 290 quadrats that made up the home range of Group I belonged to all four classes, which again illustrates the differential use of quadrats (Figure 24). The greatest number of quadrats (141 = 48.6%) was used less than the mean number of days of use (8.2 days) and mean number of sample periods of use (6 sample periods). The smallest number of quadrats (3 = 1.0%) belonged to the class that consists of those that were used on less than average number of sample periods but on greater than average number of days. These were quadrats that Group I used very frequently during a few sample periods. On the other hand, some quadrats were used during less than average number of days, but on greater than average number of sample periods, showing that they were visited only for one and sometimes two days each sample period on more than the average number of sample periods. Figure 24 also shows that more than half the home range (168 quadrats = 57.9%) was used on less than the mean number of days of use and about half the total number of quadrats was used more than the mean number of sample periods.

Figure 25 considers the number of days of use of the quadrats together with their frequency of use. Here again there was an unequal distribution of

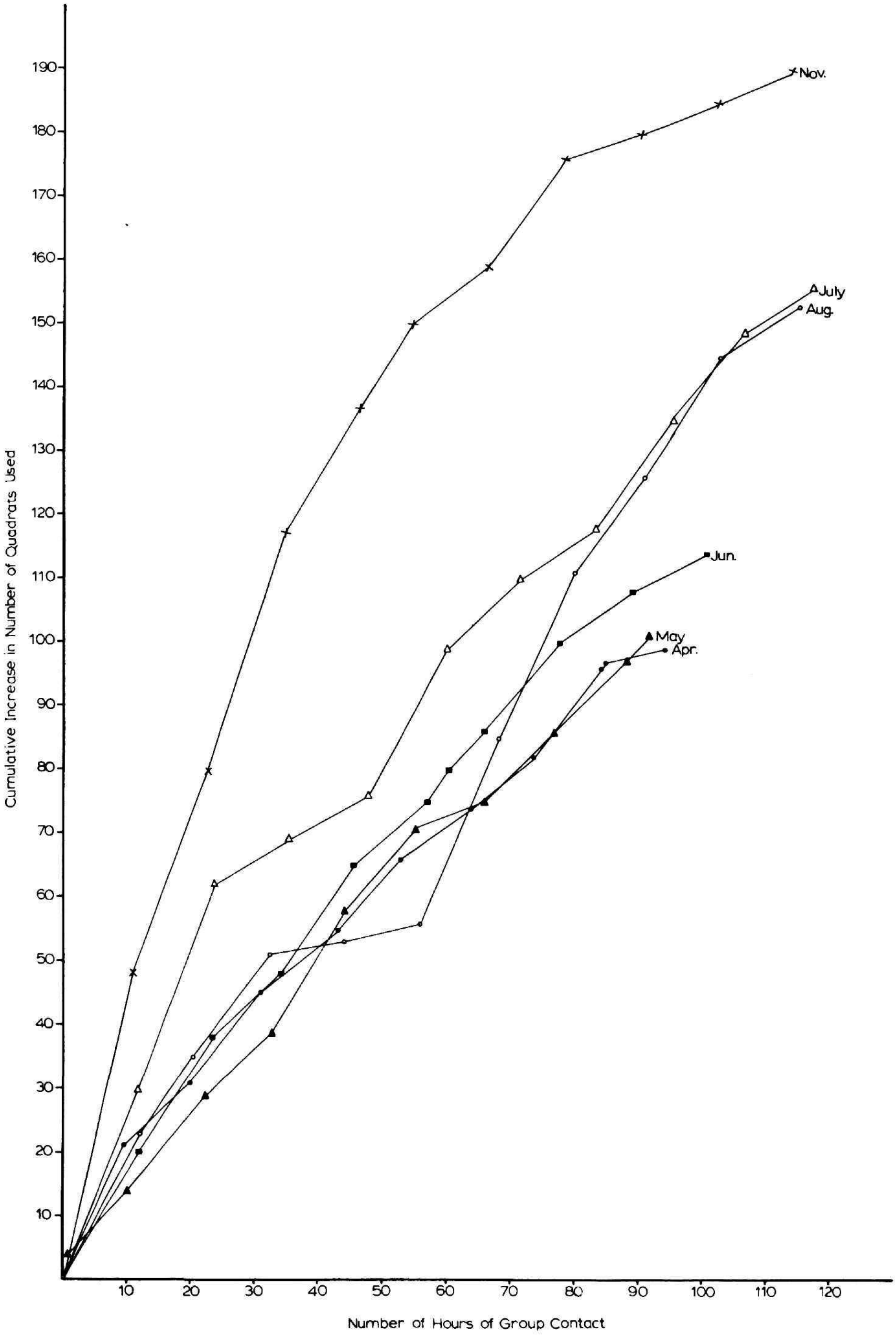


FIGURE 20.—Increase in the cumulative number of quarter-hectare quadrats used through 10-day periods of observations during different months.

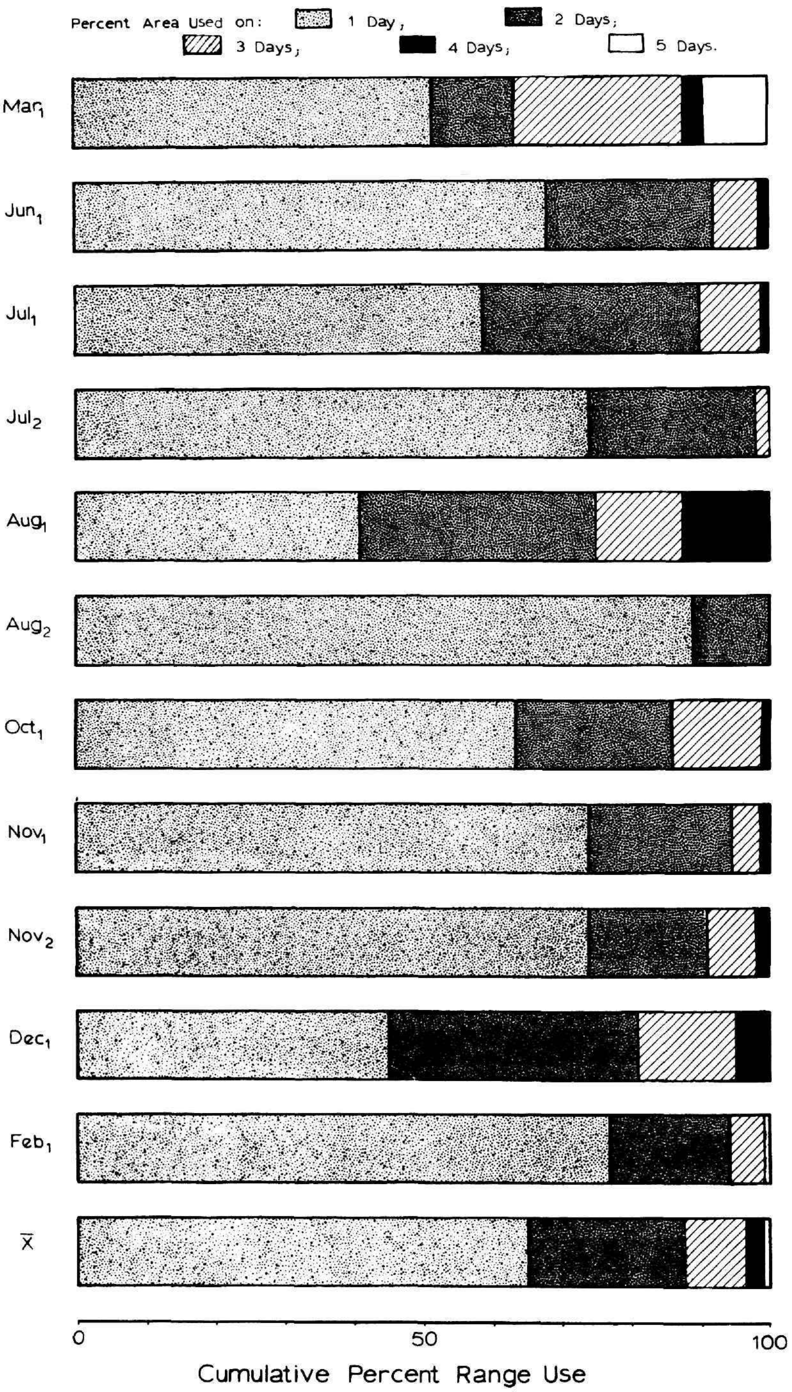


FIGURE 21.—Cumulative percentage of areas used for different numbers of days of a sample period illustrated for a selection of sample periods.

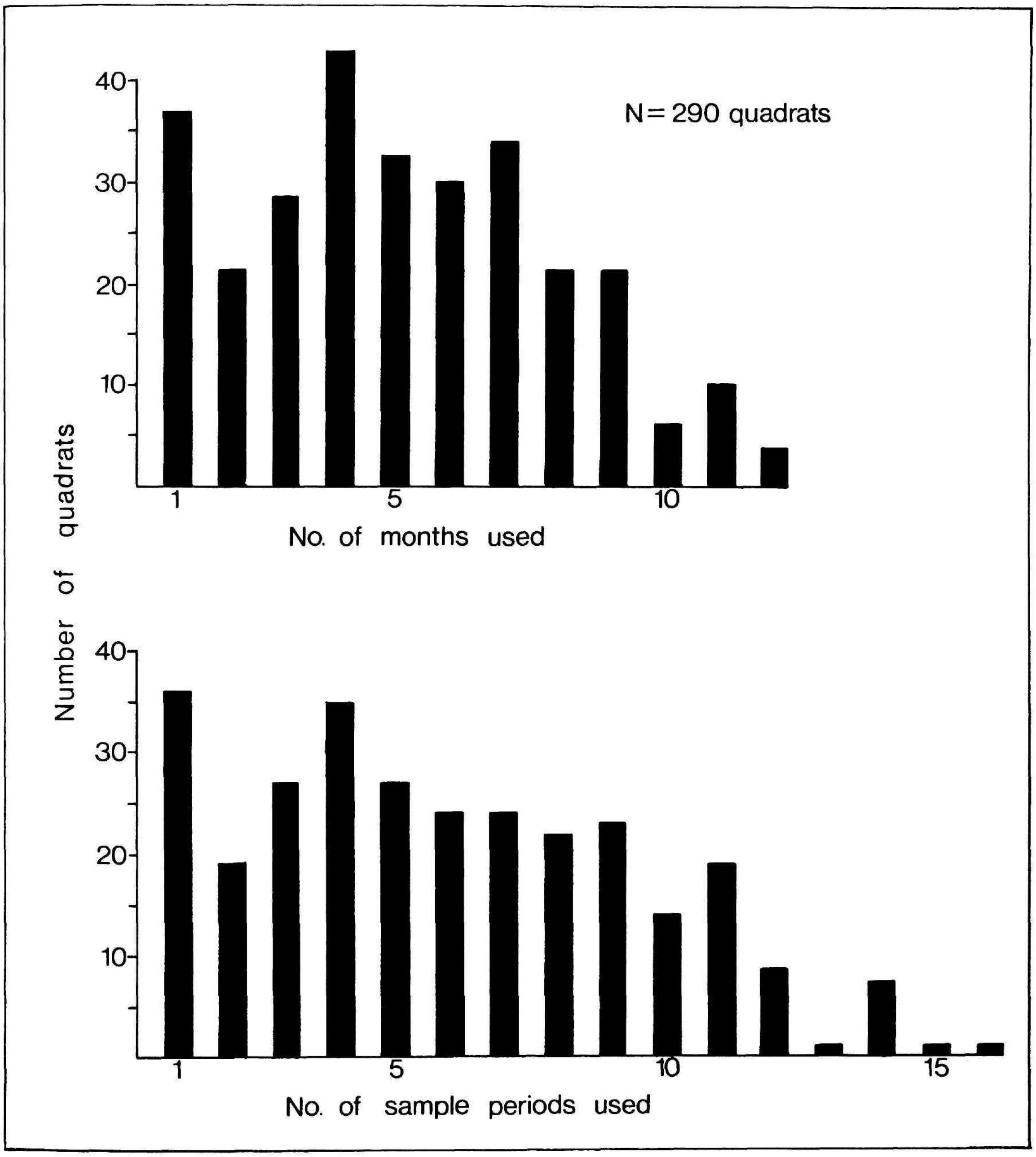


FIGURE 22.—Quadrats comprising the home range of Group I segregated according to number of months and sample periods of use.

quadrats among all four possible classes of quadrats. Group I used more than half their home range (150 quadrats = 51.7%) on less than average number of days and below average frequency. They used 17 quadrats (5.8%) below average number of days but at greater than mean frequency, indicating that these quadrats were intensively used at least on one occasion they were visited. Conversely, 28 quadrats (9.7%) were visited more often than the average number of days but used at less than average frequency. Comparison of Figures 24 and 25 show that the number of days of use, the number of sample periods of use, and the frequency of use of a quadrat were not always interdependent. In other words, the quadrat with the highest frequency of location plots was not the one with the greatest number of days of use. Similarly the quadrat used on the greatest number of days was not the same as the one that was used during the greatest number of sample periods.

Through all sample periods (i.e., from March 1973 to May 1974) a total of 15,094 location plots was recorded from the 290 quadrats used by Group I (Figure 26). The steady increase of the cumulative percent frequency of location plots in rank ordered quadrats comprising the entire home range (Figure 27) further illustrates the differential use of the habitat. Just over 50% of the total number of location plots belonged to quadrats occupying rank orders 1 to 59, which amount to only 20.34% of the total number of quadrats used (Table 44). Similarly, quadrats that occupied the top 50% of the rank orders included 84.12% of the total number of location plots that were recorded.

Also, during each sample period, Group I used different quadrats at variable frequencies. This is shown in Table 45, which gives the percent fre-

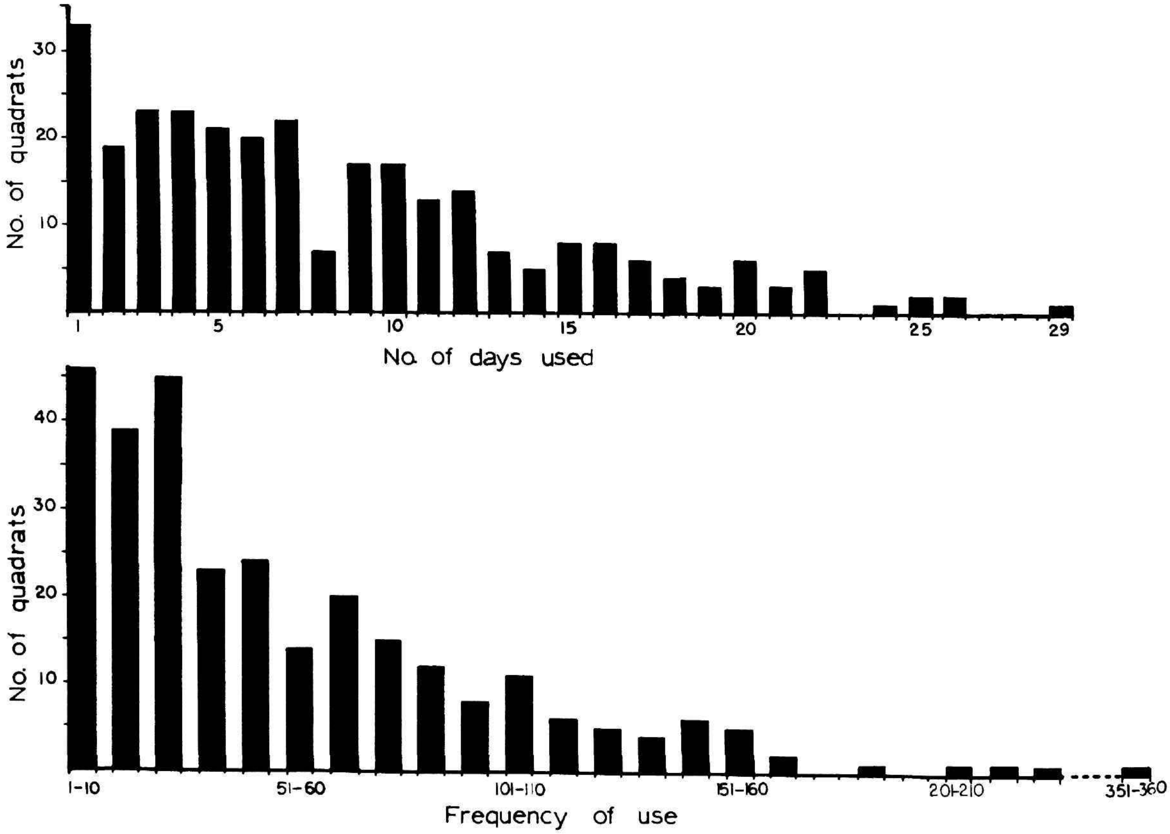


FIGURE 23.—Quadrats comprising the home range of Group I segregated according to number of days of use and frequency of location plots.

quency of use of quadrats occupying top five ranks. Quadrats occupying these ranks constituted a small fraction of the areas used, but included relatively large proportions of the locations plotted during each sample period. Moreover, different quadrats frequently occupied these high ranks during different sample periods.

DIFFERENTIAL USE OF QUADRATS AND FOOD ABUNDANCE.—Perhaps one of the more obvious reasons for the differential use of quadrats is the fluctuations in food availability within quadrats. Therefore, for a phenological study, I selected individuals of three important food plants of Group I that periodically produced extensive amounts of fruits. My sample consisted of five *P. turbinata* and all *F. exasperata* and *F. dawei* trees found within the home range of Group I. The two *Ficus* species, which were large and sometimes had their canopies extending over more than one quadrat, periodically produced such extensive amounts of fruits that they were good indicators of the temporal variation in food abundance in the quadrats they were located.

TABLE 44.—Group I, summary of the cumulative percent of frequency of use of 290 rank-ordered one-fourth hectare quadrats constituting the area used from March 1973 (I) to May 1974 (I), inclusive

Cumulative percent of frequency of use	Rank order of quadrats	Percent of quadrats
2.34	1 (-2-13)	0.3
10.12	1-7	2.4
24.66	1-22	7.6
50.19	1-59	20.34
75.02	1-114	39.31
84.12	1-145	50.0
89.83	1-165	56.9
100.0	1-290	100.0

Since I collected phenological data at the end of each month, just prior to the observation of Group I the following month, in the results presented below I have considered the phenological data from February 1973 to January 1974 in relation to the frequency of quadrat use between March 1973 and February 1974.

Table 46 shows that during the fruiting period of the five *P. turbinata*, all quadrats in which they

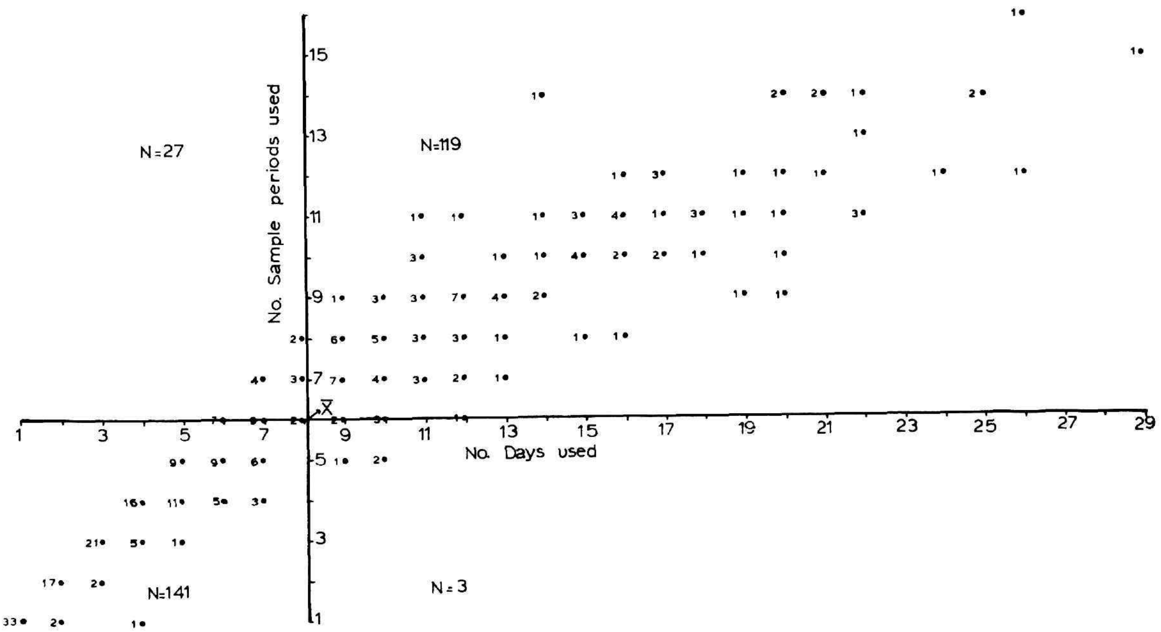


FIGURE 24.—Four-way classification of quadrats comprising the home range of Group I based on mean number of days and mean number of sample periods of use of a quadrat. The number beside each point represents the number of quadrats occupying identical intersects.

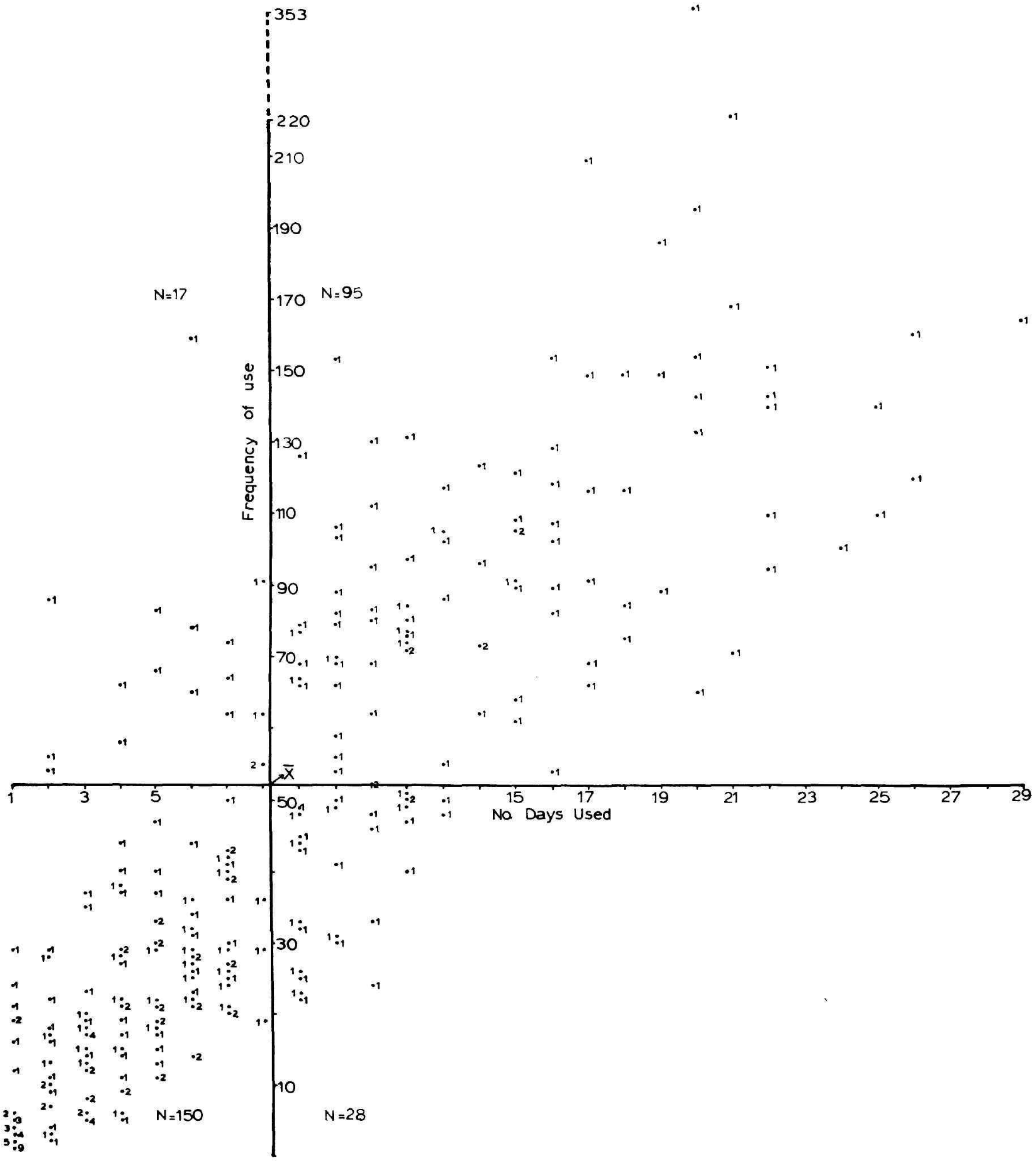


FIGURE 25.—Four-way classification of quadrats comprising the home range of Group 1 based on mean number of days and the mean frequency of use (i.e., location plots) of a quadrat. The number beside each point represents the number of quadrats occupying identical intersects.

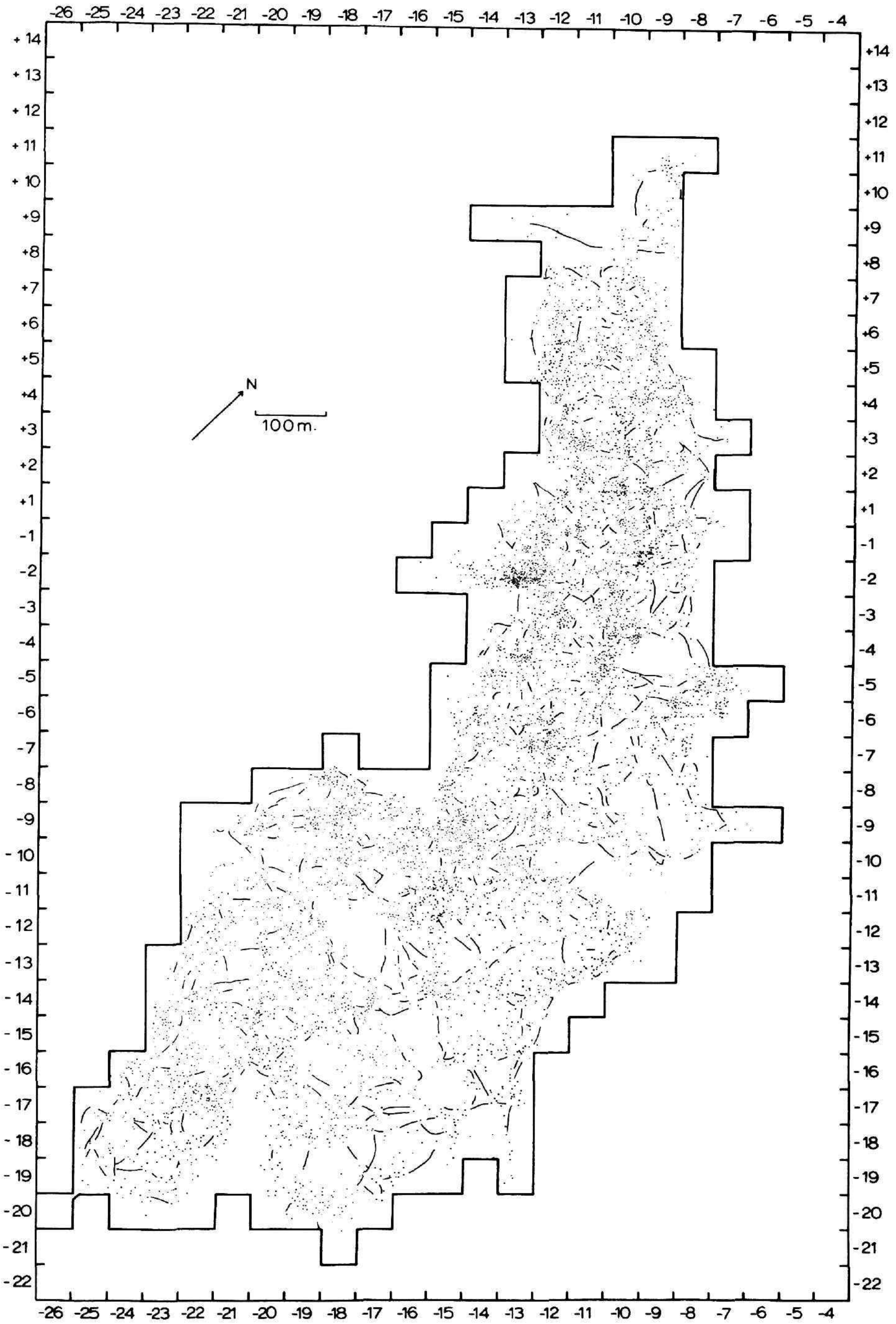


FIGURE 26.—Distribution of location plots and some paths of movements recorded within the home range of Group I between February 1973 and May 1974 (N = 15,094 location plots).

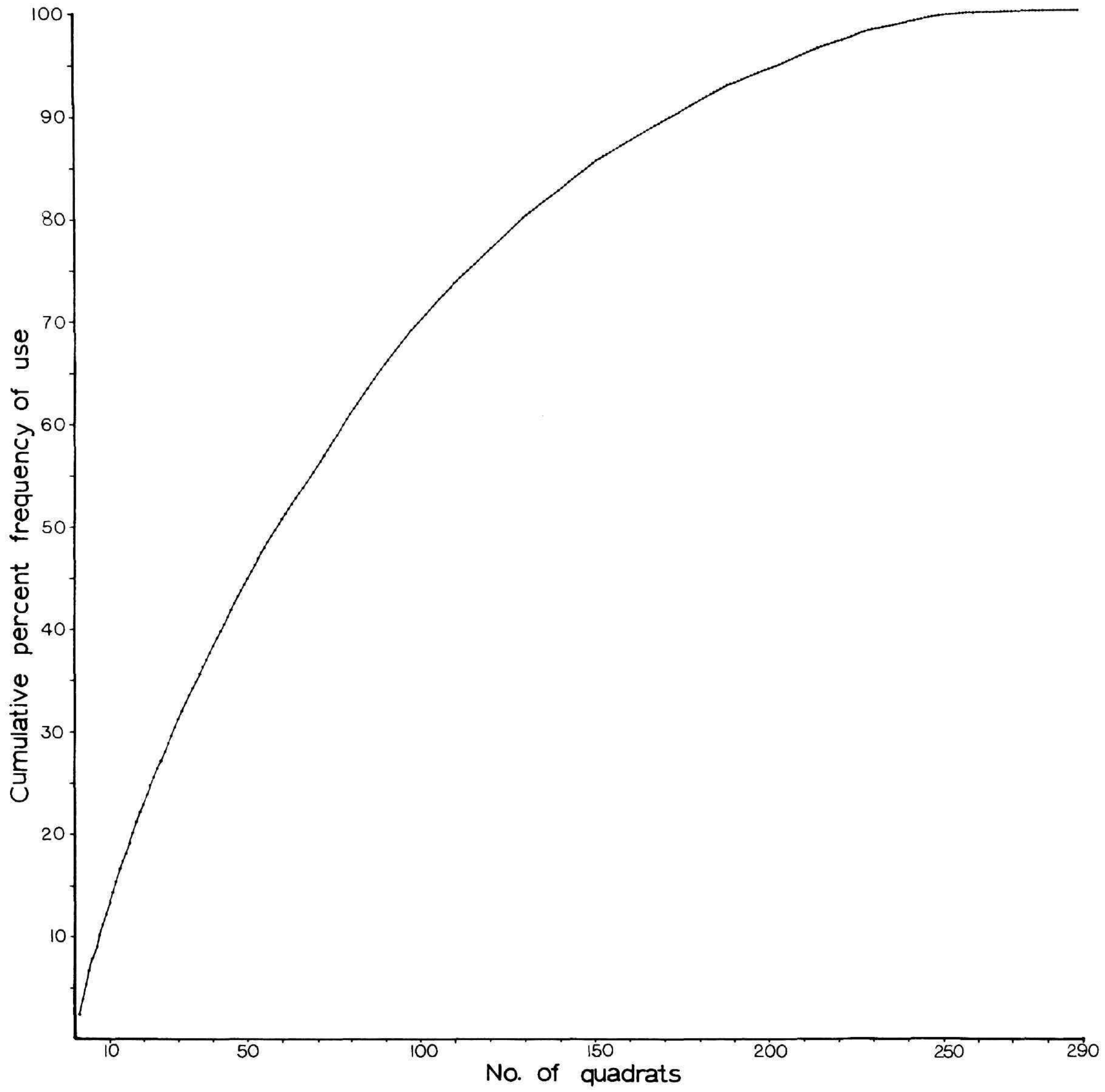


FIGURE 27.—Cumulative percent frequency of use (i.e., location plots) of 290 rank-ordered quadrats comprising the home range of Group I.

were located were used more frequently than would be expected if their frequency of use were equally distributed through all months. In fact these five trees formed part of a grove of this species in this area that was extensively used for its fruits in March (I) 1973 (see Figure 4). Nearly 49% of the locations plotted during this sample period were recorded from these five quadrats, which constituted only 15% of total area used during this 5-day period. Moreover, the locations plotted in these quadrats in March (I) 1973 made up about 41% of the locations recorded in them through all sample periods.

The quadrats in which *F. exasperata* Nos. 50, 51, 52, 53, 55, and 58 and *F. dawei* No. 2 were located

TABLE 45.—Group I, percent of frequency of use of top five rank-ordered quadrats during all full-day sample periods March 1973 to February 1974

Sample period	Total frequency of location plots	I		II		III		IV		V		Percent of frequency of use of top 5 ranks	Percent of area of top 5 ranks
		Quad-rat number	Percent of frequency of use	Quad-rat number	Percent of frequency of use	Quad-rat number	Percent of frequency of use	Quad-rat number	Percent of frequency of use	Quad-rat number	Percent of frequency of use		
Mar 73 (I).....	509	-1-9	17.9	-2-10	13.8	-1-10	10.8	+1-8	7.9	+2-8	6.1	56.5	15.1
Mar 73 (II)....	323	-16-18	16.1	-15-21	6.2	-9-15	4.6	+1-9 -17-15 -15-17	3.4	-	-	37.1	10.5
Apr 73 (I).....	291	-6-13	9.6	-4-13	4.8	-6-11 -14-12	4.5	-	-	-6-12	4.1	27.5	7.8
Apr 73 (II)....	279	-12-22	13.3	-18-16	6.1	-9-19	5.7	+1-10	5.4	-14-15 -1-9	4.7	39.9	11.7
May 73 (I).....	310	-9-7	6.1	+7-12	5.2	-4-12	4.5	-10-9 -10-18	3.9	-	-	23.6	8.8
May 73 (II)....	496	-16-17	17.7	-15-16	11.7	-19-15	10.5	-15-17	7.3	-15-19 -10-18	4.2	55.6	13.0
Jun 73 (I).....	473	-10-18	5.7	-12-10	5.1	-15-20	4.4	-16-19	3.4	-5-11	3.0	21.6	6.7
Jun 73 (II)....	463	-10-18	5.6	-14-20	4.8	-13-22	4.3	-15-13 -15-20 -15-21 -16-19 -16-23	3.0	-	-	29.7	11.0
Jul 73 (I).....	1077	-8-15	5.0	+5-10	4.7	+3-11	4.2	-9-15	4.0	+1-10	3.6	21.5	5.1
Jul 73 (II)....	900	-14-17	4.0	+11-9	3.2	+9-9 -13-18	3.1	-	-	+8-10	3.0	16.4	4.3
Aug 73 (I).....	943	-4-10	11.7	+5-11	5.6	+4-9	5.2	+1-9	4.8	+2-9	4.5	31.8	8.9
Aug 73 (II)....	1003	-9-19	3.6	-15-23	3.3	+3-10	3.1	-8-15	3.0	-2-14 -12-10	2.5	18.0	4.5
Sep 73 (I).....	906	-14-17	4.1	-8-18	3.5	-11-15	3.2	-10-13	3.1	-14-20	3.0	16.9	4.5
Oct 73 (I).....	854	-14-20	6.7	-14-22	4.8	-9-13	3.5	-18-19	3.3	-9-16	2.9	21.2	4.6
Nov 73 (I).....	1004	-17-14	3.9	-15-20	2.9	-15-13 -9-18	2.7	-	-	-10-15	2.4	14.6	3.3
Nov 73 (II)....	1013	-1-12	6.5	-9-15	6.3	-9-15	3.4	+6-10	3.2	-1-13	3.0	22.4	4.3
Dec 73 (I).....	1077	-9-15	5.2	-6-11 -7-13	4.2	-	-	-1-9 -4-11	4.0	-	-	21.6	6.0
Jan 74 (I).....	911	-2-13	22.1	-6-9	7.1	-6-7	6.0	-2-12	5.7	+5-12	5.1	46.0	8.8
Feb 74 (I).....	1023	-6-9	8.0	+6-12	6.8	-5-7	6.7	-7-12	5.2	-5-8	4.8	31.5	5.1

were also used more frequently than expected during their fruiting period. This suggests that temporal variations in the frequency of use of quadrats were related to the variations in food abundance in them. Details of two examples may be given to further illustrate this point. During the sample period of January 1974, *F. exasperata* No. 51 bore ripe fruits and provided an abundant food resource to Group I. Nearly 28% of all locations plotted during this sample period were recorded from the quadrats in which *F. exasperata* No. 51 was situated, although this area comprised only 3.5% of the total area used in January 1974. Also nearly 49% of the locations plotted throughout study in this area were recorded in January 1974.

Ficus dawei No. 2, which had ripe fruits from late April 1973 through May 1973, provides a similar example. Its fruits were not eaten by Group I during the first sample period of May 1973 (when Group I used an area farther to the north of these quadrats), but these fruits became the top-ranking food resource during the second sample period. Nearly 38% of all locations plotted in May (II) 1973 were recorded from the quadrats in which this tree was situated, which composed only 8.7% of the area used during this period. Moreover, 70.8% of all locations plotted in these quadrats were recorded in May (I) 1973.

Quadrats in which *F. exasperata* Nos. 54, 56, 57, 59, 60, and 61 and *F. dawei* No. 1 were located were used less frequently than expected when food was abundant. A possible explanation for this may be the fact that the fruiting activity of these individuals was more or less synchronized with that of the individuals in the previous category. For example, the fruiting periods of *F. exasperata* Nos. 56, 57, 59, 60, and 61 and *F. dawei* No. 1 coincided or overlapped with those of *F. exasperata* Nos. 50–53, and the fruiting period of *F. exasperata* No. 54 coincided with that of *F. exasperata* No. 55. When there are several foci of abundant food resources, one or more of these appeared to be overlooked or missed. *Ficus exasperata* Nos. 54, 59, and 60 and *F. dawei* No. 1 were situated in relatively infrequently used quad-

TABLE 46.—Group I, fruiting periods of individual trees (between February 1973 and January 1974) and the frequency of use of their locations

Species	Tree number	Location	Fruiting period	Total frequency of use	Observed frequency of use during fruiting period	Expected frequency of use during fruiting period
P. turbinata...	1	-3-11	Feb	51	7	4.3
	2	-2-10	Feb, Jan	131	76	21.8
	3	-1-10	Feb, Jan	142	55	23.7
	4	-2-9	Feb	52	14	4.3
	5	-1-9	Feb, Jan	230	95	38.3
F. exasperata..	50	-3-12	Feb, Oct-Jan	118	97	49.1
	51	-2-13 -2-14	Sep-Jan	390	286	162.5
	52	-4-13	Sep-Jan	152	75	63.3
	53	-11-13 -10-17	Jul-Nov	44	35	18.3
	55	-10-18	Feb-Jun, Dec-Jan	202	157	117.8
	58*	-17-21	Apr-May	51	18	10.2
	54	-11-14	Feb-May, Jan	26	0	10.83
	56*	-10-20	Oct-Jan	26	5	11.6
	57	-12-19 -17-24	Feb, Aug-Jan	72	37	42.0
	59*	-18-24	Nov-Jan	56	0	18.7
	60	-13-13	Feb-Mar, Jan	26	0	6.5
	61*	-13-10	Dec-Jan	30	6	6.7
F. dawei......	1	-15-16 -15-16, -15-17	Jul-Aug	58	0	9.7
	2	-16-16, -16-17	Apr-May	264	199	44.0

*The phenology of these trees was monitored only for 9 months between February 1973 and January 1974; hence, the frequency of use of the quadrats they occupied was adjusted accordingly.

rats, which were not used throughout the sample periods these individuals were in fruit (Table 46).

GROUP SPREAD.—In order to obtain a measure of group spread, Struhsaker and I made simultaneous plots of individuals belonging to Group I while maximizing interobserver distance via the use of walkie-talkies. This was done on four days, and the maximum group spread in terms of linear distances was about 120 m with a median value of 50 m. Sometimes when working alone I was able to make reasonably accurate estimates of maximum group spread when the adult male moved away from the group and emitted loud calls (termed "Pyows" by Marler, 1973). In Group I these estimates of group dispersal did not exceed 125 m. Considering the poor visibility conditions within the forest canopy, these group spreads appear to be large enough to prevent continuous visual contact between group members. Aldrich-Blake (1970a) found that blue monkey groups in the Budongo Forest dispersed over greater distances than in the Kibale Forest.

GROUP MOVEMENTS.—Group movements were coordinated and normally began with the directed movements of a few individuals who were then followed by other members of the group. Initiators of group movements did not appear to belong to any particular age or sex class. Occasionally when the adult male moved away from the main body of the group and emitted loud calls, others then moved in the direction of the call. Sometimes, however, the adult male rejoined the group after emitting "Pyows" and moved with the others in quite a different direction.

In order to obtain unbiased estimates of total daily distances moved, I confined the analysis of group movements to 65 days of observations when movements were monitored for 11 or more hours. On these days Group I moved an average of 1298 m per day (range 445–1961 m, std deviation = ±345). The modal value of daily movements was between 1000 and 1100 m, but on over 50% of the days this group moved greater than 1200 m (Figure 28).

Comparison of mean daily movements of different sample periods shows considerable variation, with peaks occurring in June (I) 1973 and October (I) 1973 (Figure 29); however, the variations in the

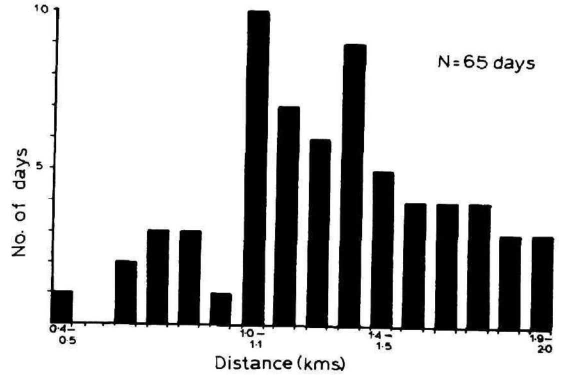


FIGURE 28.—Group movements segregated according to daily distances moved by the group on 65 days with 11 or more hours of group contact.

daily distances traveled within each sample period were also large, making interpretation of the variations of mean distances moved difficult. It is likely that, during certain sample periods, daily movements were related to the pattern of distribution of food resources. For example in March (I) 1973, Group I moved very little when they repeatedly used a grove of *P. turbinata* whose fruits served as their primary food resource. During many other sample periods also, they fed in areas where food was concentrated, but distribution of these areas was probably different to that in March (I) 1973.

As mentioned earlier, total daily distances were subdivided into hourly movements during the sample periods from September 1973 to February 1974. In the analysis of hourly movements, I have treated rainy and nonrainy hourly periods separately, since rainfall was found to inhibit movements (see below). Occasionally, movements for the half hour between 0630 hours and 0700 hours were also recorded. When data of group movements during nonrainy hourly periods from September 1973 to February 1974 were lumped, mean hourly movements showed a clear bimodal pattern where peaks occurred between 0700 and 0800 hours and between 1700 and 1800 hours, and the period of least movements occurred between 1300 and 1400 hours (Figure 30). The upper limits of the range of hourly movements also showed a similar pattern, but the range itself was great, suggesting that some variable(s) other than rainfall also affected hourly movements.

The pattern of hourly movements during each sample period differed from the above pattern, but belonged to two distinct classes. During the sample periods from September 1973 to November 1973, peaks of movements occurred during midday as well as during early morning and late afternoon hours (Figure 31). Also throughout the day hourly movements were usually greater than the mean distances of travel computed for the September 1973 to February 1974 period. Hourly movements during the sample periods from December 1973 to February 1974 better represent the bimodal pattern, but they were usually less than for previously considered sample periods and the mean hourly movements for all sample periods considered together.

EFFECT OF CLIMATIC FACTORS ON GROUP MOVEMENTS.—Between September 1973 and February 1974, heavy rain affected 18 hourly periods of group contact. These periods were distributed throughout the day and because of the small sample size the distances moved during these periods were pooled regardless of the time of day of records. The mean rate of movement was 63 m per hour (range 8–183 m, std. deviation ±39), which is less than the least mean rate of movement during nonrainy periods (Figure 30). In general at the beginning of a period of heavy rain, individuals sat hunched up without regard to exposed and unexposed areas of a tree. If heavy rain continued for more than 30–45 minutes, they usually left their sitting places and moved relatively slowly while indulging in some activity such as feeding. Slight drizzles did not appear to affect adversely the movements of the group.

Although rainfall appeared to inhibit movements, Group I moved greater total distances during the September 1973 to November 1973 sample periods that were more affected by rain than the December

TABLE 47.—Group I, percent of number of hours of sunshine and cloud cover on days with 11 or more hours of observations and mean of total daily distances moved during sample periods from September 1973 to February 1974, inclusive

Sample period	Sunny	Hazy	Cloudy	Rain	N (hr)	Mean total movements (m)
Sep 73 (I)....	22.7	31.8	31.8	13.6	22	1497
Oct 73 (I)....	24.4	26.7	40.0	8.9	45	1665
Nov 73 (I)....	16.3	32.7	42.9	8.2	49	1625
Nov 73 (II)...	15.5	25.9	51.7	6.9	58	1374
Dec 73 (I)....	64.9	15.8	17.5	1.8	57	1148
Jan 74 (I)....	54.6	9.1	36.4	-	33	1069
Feb 74 (I)....	34.9	30.2	32.6	2.3	43	1245

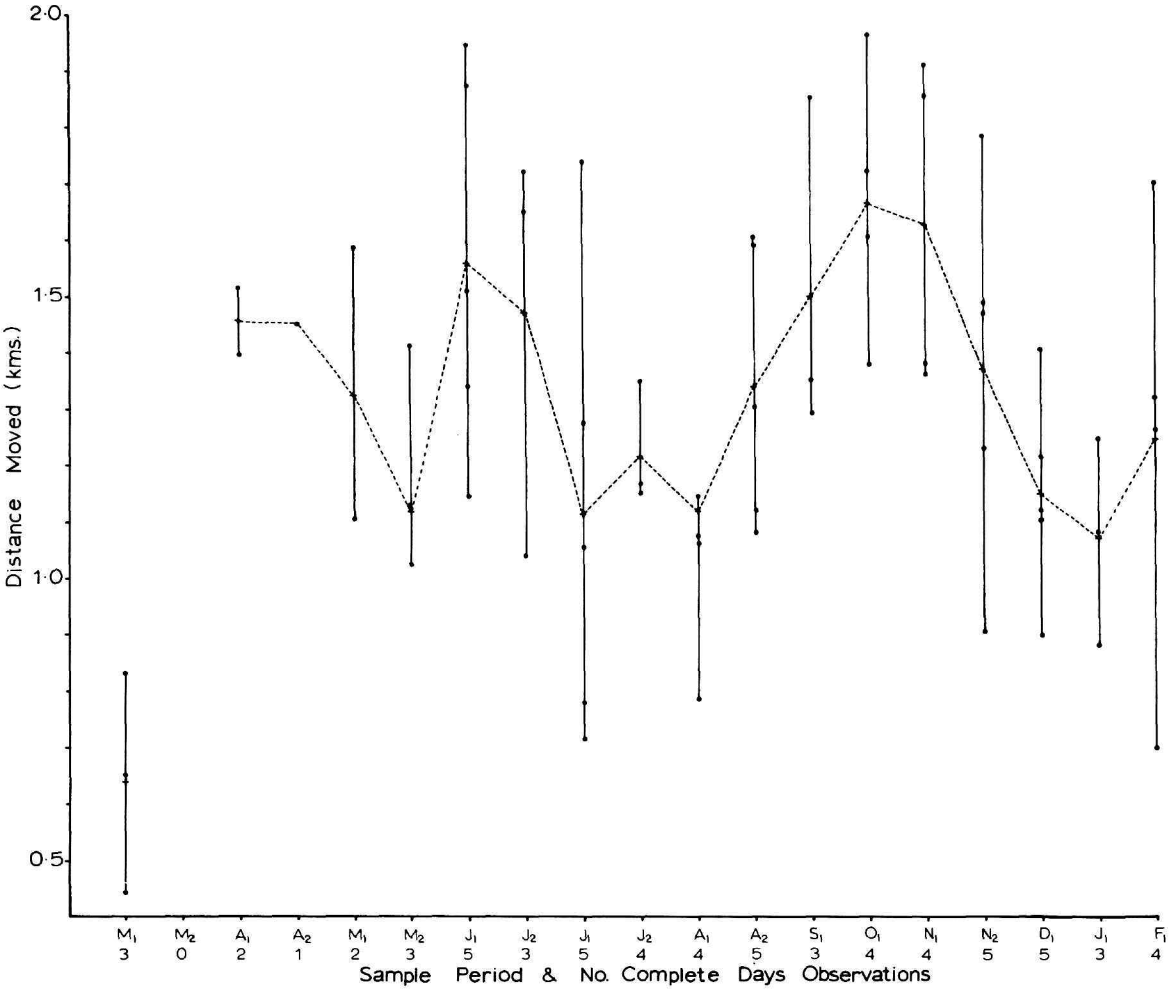


FIGURE 29.—Group movements on days with 11 or more hours of group contact (indicated by the points on the vertical lines) segregated according to sample periods. Variations in the mean daily distance moved is shown by the dashed line.

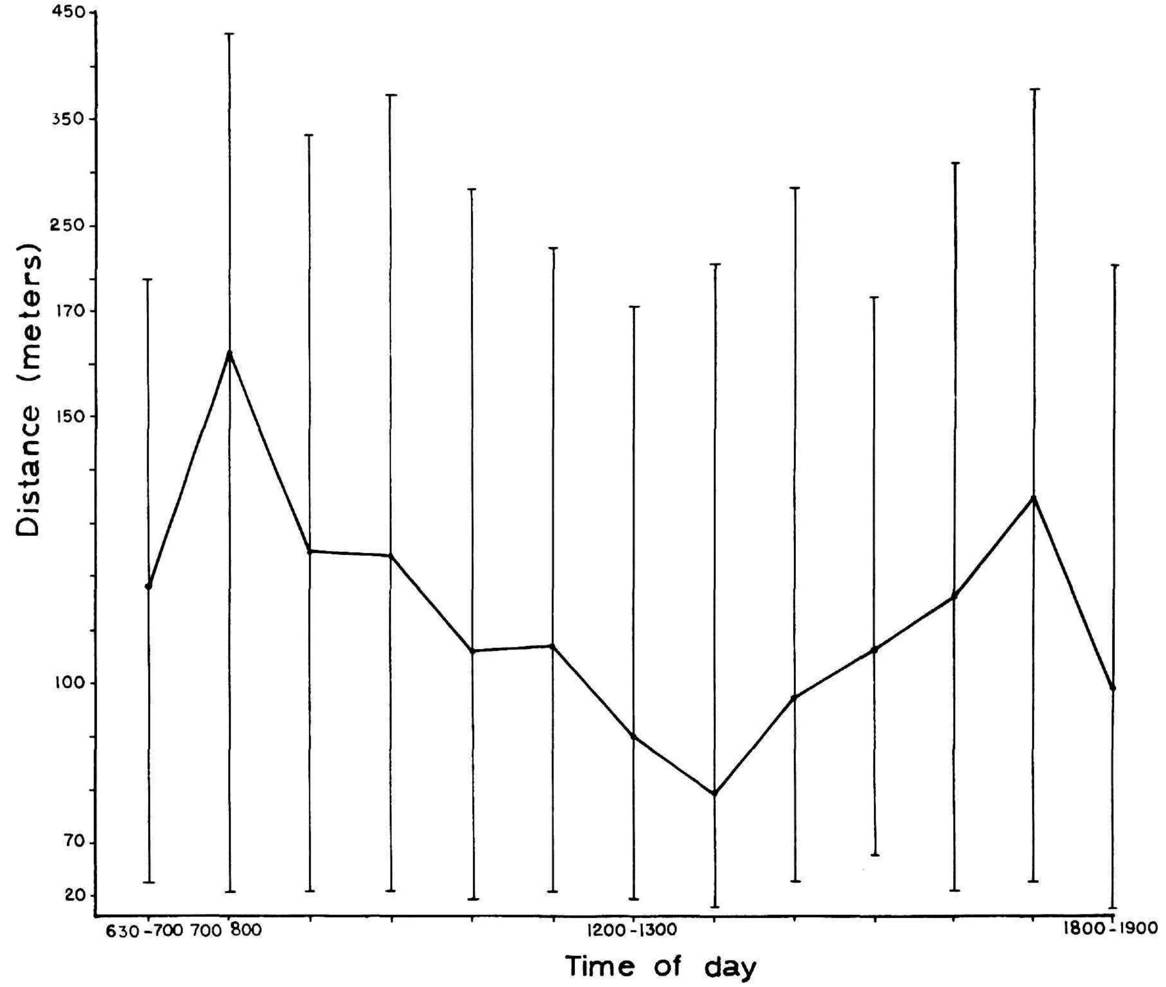
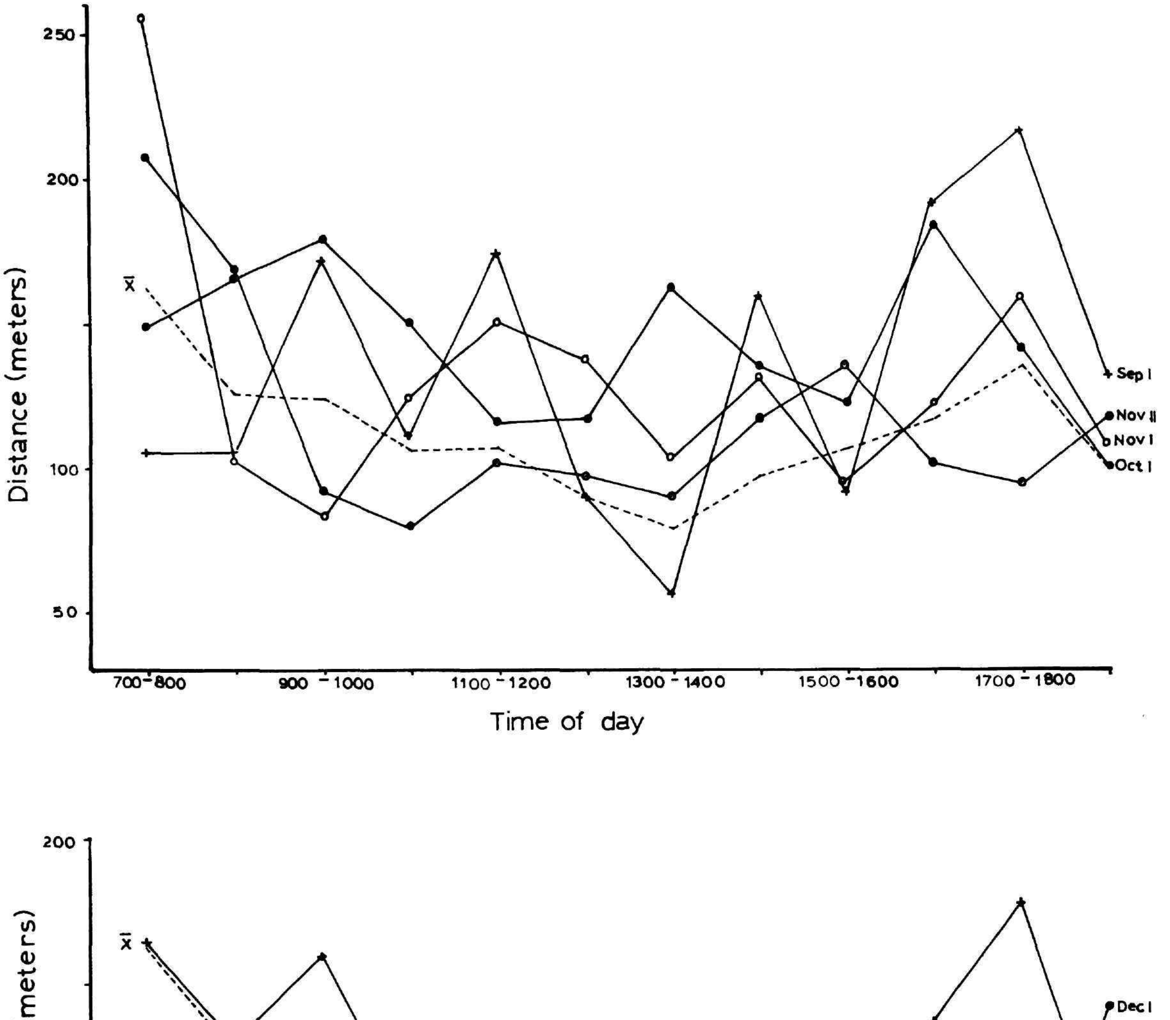


FIGURE 30.—Mean and range of group movements during nonrainy hourly periods between September 1973 and February 1974.

1973 to February 1974 sample periods (Table 47). This may be explained as the effect of cloudy weather (which is usually associated with rainfall) in enhancing group movements.

Considering only the data from days with less than one hour of heavy rain, it was found that the mean daily distances moved during nonrainy hours (obtained from daily movements during nonrainy hours standardized to a 12-hour period) were positively correlated with the corresponding mean cloud cover indices during the September 1973–February 1974 period (Spearman Rank Correlation Coefficient, $r_s=0.786$, $df=5$, $P<0.05$). When days with two or more hours of rain were included in the analysis, however, the mean distances moved during nonrainy hours were not significantly correlated with the respective mean cloud cover indices ($r_s=0.714$, $p>0.05$). This suggests that long durations of rainfall inhibited movements during subsequent hours under different weather conditions. This may have been due partly to the relatively long bouts of grooming activity that usually followed heavy rainfall and the wetness of the substrate that may have retarded progression.

Hourly movements from September to November 1973 and December 1973 to February 1974 indicate



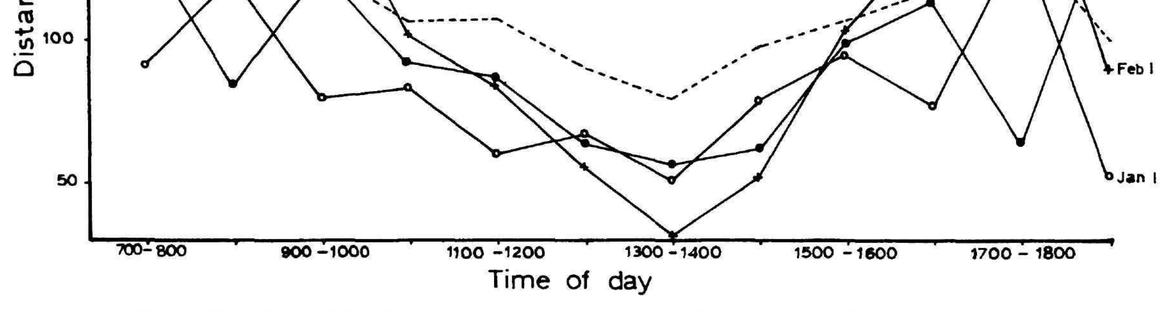


FIGURE 31.—Mean of hourly group movements during sample periods from September 1973 to November 1973 and from December 1973 to February 1974 compared with mean of hourly group movements between September 1973 and February 1974.

that one peak of movements always occurred before 1000 hours and after 1600 hours, and the greatest variations between the two periods occurred during the interim hours (Figure 31). Indices of hourly weather conditions showed that movements during early morning and late evening hours were more or less independent of weather conditions, but they were affected by weather conditions during the intervening period. Climatic factors were, however, not the only variables that affected group movements. Movements during the same hour with similar weather conditions on different days varied appreciably, and conversely, Group I sometimes moved the same or equivalent distances during the same hourly periods under different weather conditions. It must also be pointed out that although movements, particularly during midday, were shown to be influenced by cloud cover, it is possible that they were actually affected by some related factor, such as temperature.

Areas and Trees Used for Night Resting.—Late in the evening I recorded the areas used for night resting and usually reconfirmed the presence of monkeys in these areas early next morning. Night resting areas used by Group I were located on a total of 83 evenings, on days just prior to and during sample periods from February 1973 to February 1974 inclusive (Table 48). On these days Group I used a total of 50 quadrats for night resting. Since the group moved until it was almost completely dark, normally I was able to locate only one of possibly several quadrats that they used for resting each night. Occasionally, however, I was able to locate two or three adjacent quadrats used for night resting. On these occasions, I assigned each quadrat a score of one for a night's use and therefore the total of evenings on which Group I used the 50 quadrats for night resting (i.e., 104 evenings) exceeded the total of evenings that I located their night resting areas.

Table 48.—Group I, location of quadrats used for night resting during and just prior to sample periods from February 1973 to February 1974

Sample period	Two days prior to sample period	One day prior to sample period	Day 1	Day 2	Day 3	Day 4	Day 5
Feb 73 (I)....	-	-	-6-13	-	-2-13 -3-12	-	-5-12
Mar 73 (I)....	-	-2-10	-2-10	-5-12	-2-13	-	-3-10
Mar 73 (II)...	-	-10-13	-	-	-	-2-10	-4-12
Apr 73 (I)....	-	-	-5-11 -6-11	-9-19	-6-13	-3-10	-6-12 -6-13
Apr 73 (II)...	-	-4-12	-5-11	-	-	-	-
May 73 (I)....	-	-	-8-13	-4-12	+7-12	-5-12	-6-13
May 73 (II)...	-	-	-	-	-	-15-21	-
Jun 73 (I)....	-	-	-14-20 -13-20	-14-22	-	-4-12	-13-22 -14-21
Jun 73 (II)...	-	-	-	-14-22 -15-22 -15-21 -14-22	-10-19	-	-
Jul 73 (I)....	-	-13-19	-5-11 -4-11 -4-10	-4-12	+5-10	-2-10	-
Jul 73 (II)...	-	-2-10 -3-9	+9-13	-4-12	-9-18	-	-
Aug 73 (I)....	-	-	-5-10	-5-13	+6-11	-4-10	-5-11
Aug 73 (II)...	-5-13	+4-9	-11-15	-11-18	-9-19	-4-12	+7-12
Sep 73 (I)....	-	-	-9-19	-14-20	-16-23 -17-24	-14-21 -14-20	-
Oct 73 (I)....	-	-	-15-15 -16-15	-9-19	-14-20 -15-20	-14-20	-
Nov 73 (I)....	-	-6-13	-10-15	-3-12	-12-16	-	-
Nov 73 (II)...	-	-15-20	-5-11	-2-12 -3-12	-2-13 -2-12 -1-12	-2-13 -2-12	-
Dec 73 (I)....	-	-4-10	-	-2-12	+7-11	-4-12 -4-11	-2-13
Jan 74 (I)....	-	-2-13	-2-12	+5-12	-2-11 -2-13	-2-13	-
Feb 74 (I)....	-	+5-10 +6-10	-5-8	-4-12	-4-12	-12-10	-

The distribution and the frequency of use of the quadrats used for night resting showed that there was probably some selectivity in the area used for night resting (Figure 32). For example, Group I most frequently slept in an area consisting of several quadrats located at approximately the center of their range and rarely slept in the eastern part of their range. Nine of 11 quadrats rank ordered according to the number of nights of use (i.e., quadrats used on 3 or more nights in Figure 32) occurred at the center of their range while the other two were located farther to the south. Group I spent a total of 56 nights (i.e., 54%) in these 11 quadrats that were distributed such that they formed a part of three large discrete clusters of adjacent quadrats used for night resting (Figure 32). These clusters consisted of 33 quadrats, and the group spent a total of 84 nights (i.e., 81%) in them.

The blue monkeys of Budongo did not appear to sleep in particular areas of their home range, but rather spent the night in the area in which they had been feeding during the evening (Aldrich-Blake, 1970a). Similarly mangabeys (Chalmers, 1968; Waser, pers. comm.) and the vervet monkeys of Lolui Island (Gartlan, 1966) also did not have regular sleeping areas. On the other hand, the vervets of Masai-Amboseli Game Reserve (Struhsaker, 1967) and the olive baboon of the same area (Altmann and Altmann, 1970), the black and white colobus of the Kibale Forest (Oates, 1974), and the primates of Semliki Forest (Lumsden, 1951) used certain parts of the range more frequently than others for night resting.

Certain aspects of movement patterns of Group I can be elucidated by considering the pattern of use of the areas used for night resting. Group I spent all or several successive nights of many sample periods in the large cluster of quadrats located at the center of the home range indicating that they began and ended their diurnal movements in more or less the same area (Table 48). Sometimes use of quadrats in the central area alternated with the use of quadrats in the two clusters to the south. Movements to the north of the range were more frequent than would be expected from the number of nights Group I used this area for night resting, but these movements usually began and ended at the central cluster of quadrats. During two sample periods (September (I) 1973 and October (I) 1973) areas used for night resting alternated between the two clusters of quadrats in the south of the range. This suggests that the locations of preferred night resting areas had some effect on the patterns of movements of Group I.

On four pairs of successive nights, Group I used the same quadrat for night resting, and on five pairs of successive nights their movements began and ended in adjacent quadrats (Table 48). On these occasions, they described a loop using different quadrats on their outward and return journey to night resting areas. Circuitous rather than direct movements from one night resting area to another may also be shown by considering the straight line distances between quadrats used for night resting (i.e., "travel distance," Mason, 1968) on successive nights and the actual distances traveled during the intervening daytime periods (i.e., "path length"). Figure 33 relates both of these measures for 50 pairs of successive nights. The path length was usually much greater ($\bar{X}=1290$ m, range 699–1900 m) than the travel distance ($\bar{X}=291$ m, range=0–675 m), which shows the movement patterns were not entirely dependent on the locations of night resting areas.

The use of a quadrat for night resting does not necessarily mean that Group I used all trees in that quadrat for this purpose. Group I seemed to prefer large trees (frequently over 30 m tall) to small ones for night resting. About two-thirds of 29 individual trees that they used for night resting were large trees belonging to one unidentified and seven identified species (Table 49). The large tree species were also used on more nights and monkey-nights than the smaller tree species. A monkey-night is defined as a single night's use of a tree by an individual monkey (Struhsaker, 1967). Thus, if three individuals used a sleeping tree on a single night, the tree would be scored for three monkey-nights of use. *Parinari excelsa* was the most commonly used night resting tree. The 29 trees that Group I used for night resting were located in 19 quadrats, two of which contained a maximum of three individuals. On the few evenings that I was able to locate two or more night resting trees, the distances between sleeping subgroups using these trees ranged from 10–90. Because of the difficulty in locating sleeping trees, the maximum number of night resting trees per quadrat and dispersion between sleep-

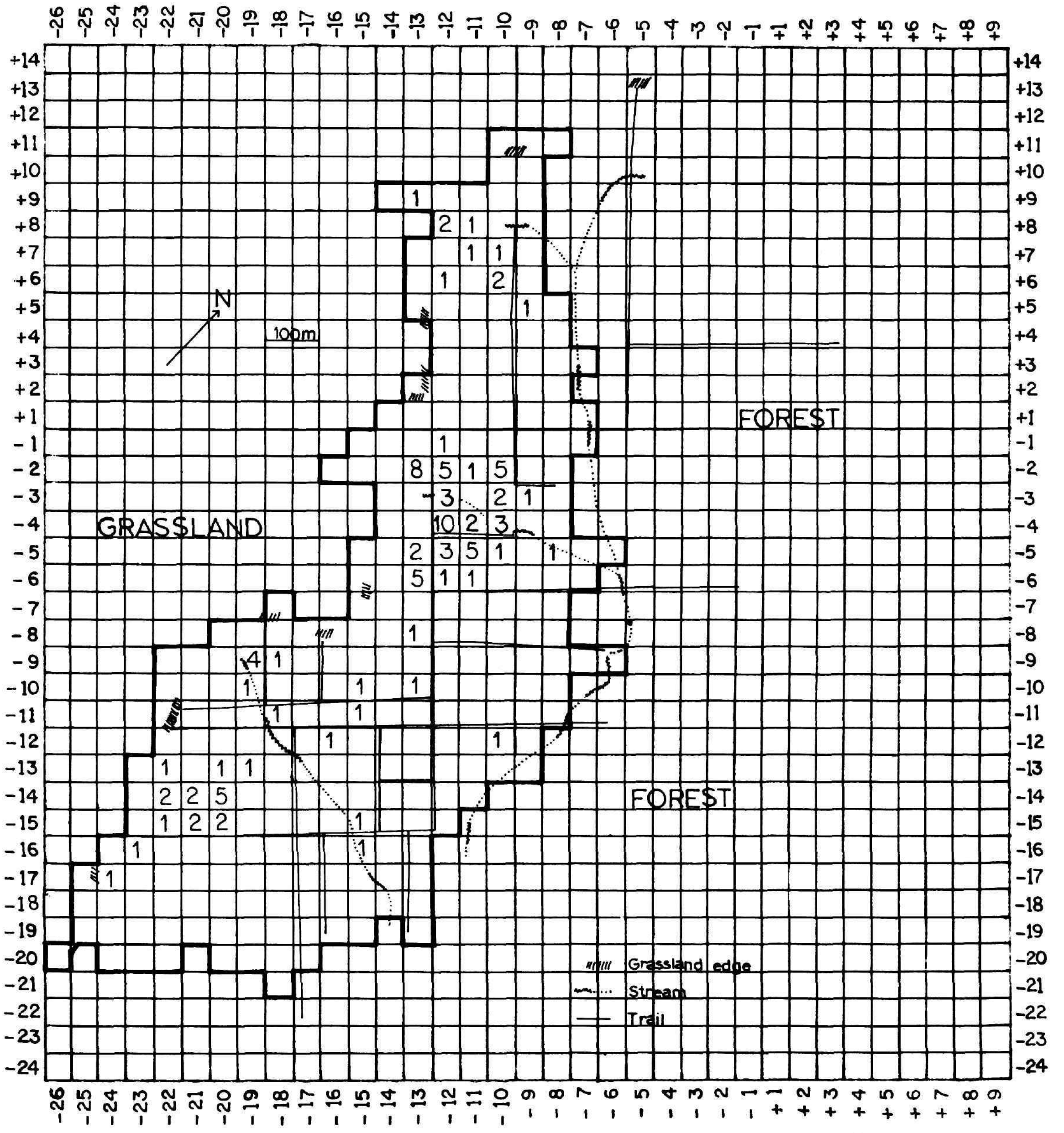


FIGURE 32.—Distribution of 50 quadrats used by Group I for night resting. The number of nights spent in a quadrat is indicated by a number within that quadrat.

ing subgroups may be underestimations of the actual values.

Group I spent only 6% of the nights when night resting trees were located in trees laden with ripe fruit. By selecting a tree that did not bear ripe fruits, they probably avoided being disturbed by nocturnal visitors to fruiting trees (e.g., bats, viverrids, etc.). Usually their last feeding bout for the evening

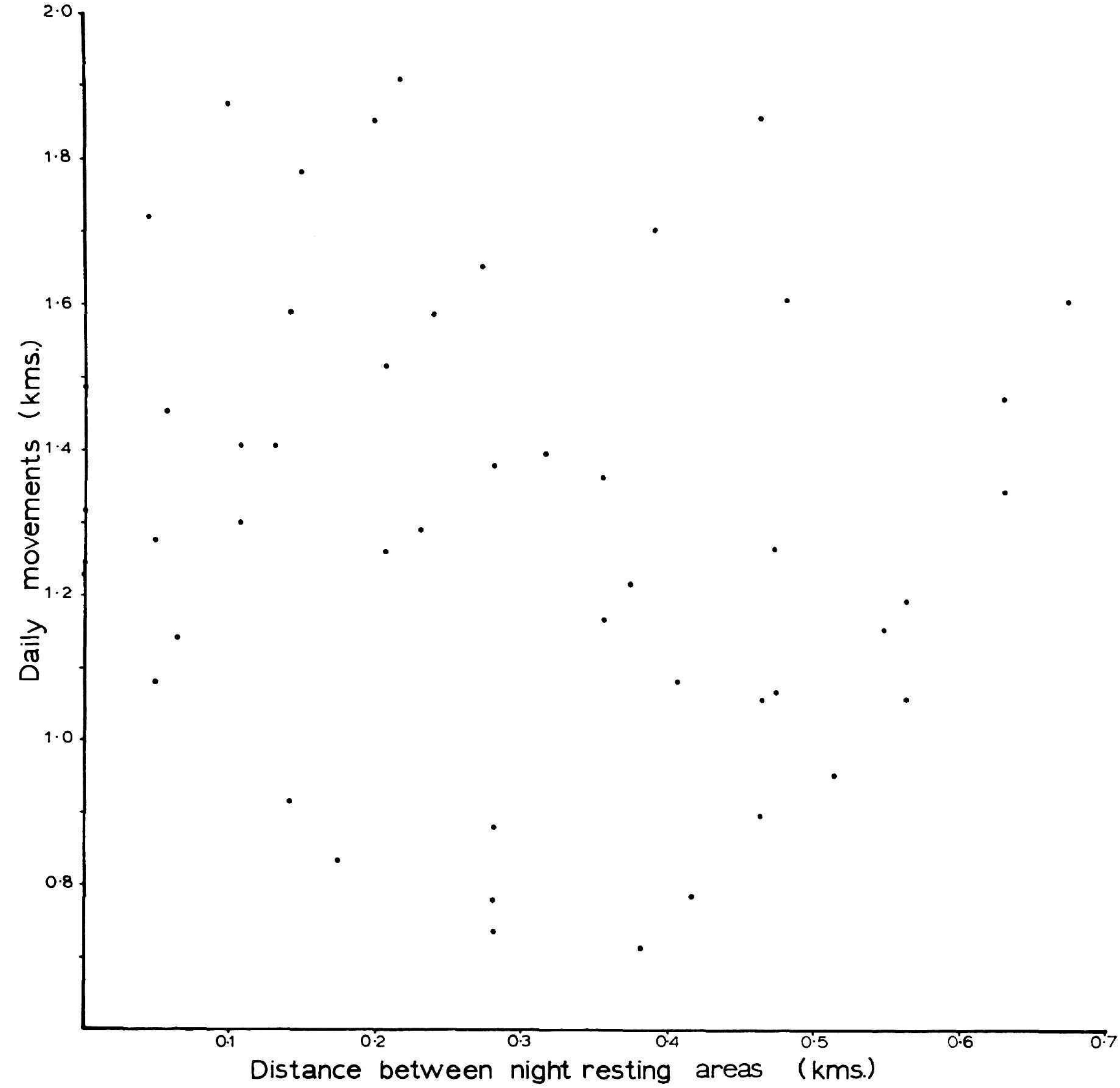


Figure 33.—Comparison of distance between night resting areas on 50 pairs of successive nights and distance moved during intervening daytime periods.

was at a fruit-laden tree, from which they moved out to nearby night resting areas and returned early next morning for their first bout of feeding.

Quadrat Utilization Diversity.—I computed measures of quadrat utilization diversity on the basis of the proportionate frequency of use of quadrats entered during a sample period. Measures of H′ (in Shannon-Wiener equation, Pielou, 1966) segregated according to differences in methodology between March 1973 to June 1973 and July 1973 to February 1974 showed considerable variations (Figure 34). In an attempt to explain these variations, Spearman rank correlation tests were done comparing quadrat utilization diversity with various

TABLE 49.—Group I, tree species used for night resting

Species	Number of individual trees used	Number of nights used	Number of monkey nights of use
*P. excelsa**......	5	10	25
*M. bagshawei**....	4	8	22
*B. wilsoniana**...	2	7	22
*O. welwitschii**..	3	6	19
*A. altissima**....	2	3	12
D. abyssinica....	4	4	10
S. scheffleri....	3	3	9
*N. buchanani**....	1	1	4
C. durandii......	1	1	2
*T. splendida**....	1	1	2
C. africana......	1	1	1
Unidentified (2 species).....	2	2	5
Total..........	29	47	133

*Large tree species.

aspects of diet and weather. The results of these tests are given in Table 50.

Quadrat utilization diversity was not significantly correlated with several measures of diet diversity, proportion of fruits and foliar food in diet, density of food plants, or their dispersion (Table 50). It was significantly correlated, however, with the percentage concentration of plant feeding or food related activities (i.e., plant feeding considered together with search and ingestion of invertebrates and chewing of food) in a few quadrats used at relatively high frequencies. The concentration of plant feeding (or food related) activities in a quadrat is a percentage measure of the plant feeding scores recorded in that quadrat during a sample period divided by the plant feeding scores recorded from all quadrats used during the same period. The percentage frequencies of plant feeding and food-related activities in the most frequently used quadrat, and in the top three and top five quadrats of each sample period are given in Table 51.

Quadrat utilization diversity during March 1973 to June 1973 was negatively correlated with the percentage concentration of plant feeding in the three most frequently used quadrats ($r_s = -0.881$ $p<0.01$), and with the concentration of food-related activities in the top-ranking quadrat ($r_s = -0.881$, $p<0.01$) as well as in the top three quadrats ($r_s = -0.857$, $p<0.01$). Similarly ranging diversity during the July 1973–February 1974 period was negatively correlated to the concentration of plant feeding in the top five quadrats ($r_s = -0.609$, $p<0.05$) and with the concentration of food-related activities in the top three quadrats ($r_s = -0.627$, $p<0.05$). The requirements of larger numbers of quadrats in the July 1973 to February 1974 period for significant correlation with ranging diversity may be the result of methodological differences, whereby greater number of locations were plotted during this period than during March 1973 to June 1973. From this analysis, however, it may be inferred that during sample periods when food was concentrated in a small area, Group I ranged less diversely than during periods when food was widely dispersed.

Significant negative correlations between quadrat utilization diversity and percentage hours of rainfall and insolation during sample periods suggest that climatic factors also affected the ranging patterns of blue monkeys.

INTERGROUP HOME RANGE OVERLAP.—At the southern end the home range of Group I overlapped with that of Group V. Group V was first seen (at 1000 hours on 25 December 1973) in quadrats −10–19 and −10–20, which were located well within the home range of Group I (see Figure 13). During three hours of observations that day they used an area of 2¼ hectares (9 quadrats), and the following day for two hours prior to leaving the home range of Group I (at 1100 hours) they used another 2¼ hectares. The areas used by Group V on these two days were separated by a straight line distance of about 200 m, some parts of which must also have been traversed by this group between observation periods. Therefore, the total time spent (25 hours) and area used (4½ hectares) by Group V within the range of Group I should be considered minimal estimates of overlap. Group V left the home range of Group I via quadrat −20–19, which showed that their incursion had taken them about 475 m into the home range of Group I. On one day (the evening of 7 May 1973) I suspected that Group V used an area about 250 m within the home range of Group I where a fruit-laden *Ficus dawei* was located. Group V was not in the vicinity of this tree when Group I used this area a few hours earlier and when Group I returned to it early the following morning. Therefore, if Group V had used this area, their stay must have been relatively short on this occasion.

At the northern end of the home range, Group I used a ¼ hectare quadrat (+8–9), which was also

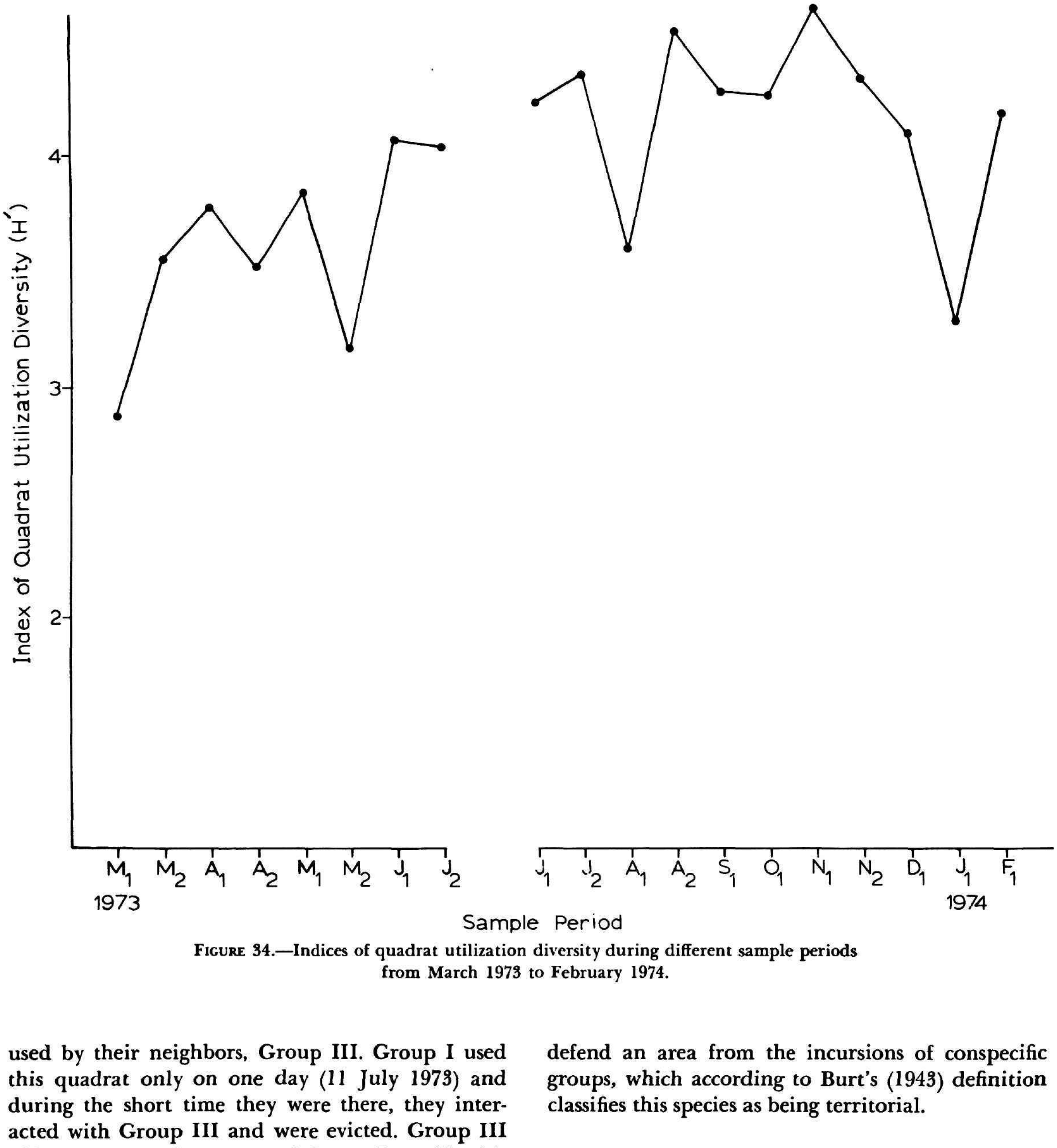


FIGURE 34.—Indices of quadrat utilization diversity during different sample periods from March 1973 to February 1974.

used by their neighbors, Group III. Group I used this quadrat only on one day (11 July 1973) and during the short time they were there, they interacted with Group III and were evicted. Group III did not pursue the retreat of Group I outside this quadrat, which suggests that spatially as well as temporally range overlaps between these two groups were small. These interactions as well as those between Group II and Group III in areas of overlap were always aggressive, with chases and threats being extremely common. Thus each group appeared to defend an area from the incursions of conspecific groups, which according to Burt's (1943) definition classifies this species as being territorial.

DISCUSSION

HOME RANGE SIZE.—The size estimates of the home range of Group I decreased appreciably as the size of the grid system used was reduced. Although the smaller grids yielded more precise measures of the physical presence of Group I in

TABLE 50.—Group I, results of Spearman rank correlation tests comparing ranging diversity with various aspects of diet and weather (for the two time intervals, left column = r_s values, right column = p values)

Correlation with —	Mar 73 - Jun 73		Jul 73 - Feb 74	
1. Food plant diversity.........................	0.310	0.05	-0.216	0.05
2. Specific food item diversity.................	0.310	0.05	-0.291	0.05
3. Food item diversity..........................	0.381	0.05	-0.264	0.05
4. Percent of fruits in diet....................	-0.238	0.05	0.318	0.05
5. Percent of foliar items in diet..............	0.214	0.05	-0.246	0.05
6. Density of top-ranking food plant............	0.630	0.05	0.142	0.05
7. Mean density of top 3 food plants............	0.240	0.05	0.409	0.05
8. Mean density of top 5 food plants............	-0.140	0.05	0.346	0.05
9. Mean density of top 10 food plants...........	0.050	0.05	0.500	0.05
10. Dispersion index of top food plant...........	0.399	0.05	0.518	0.05
11. Mean dispersion indices of top 3 food plants..	0.452	0.05	0.366	0.05
12. Mean dispersion indices of top 5 food plants..	0.380	0.05	0.039	0.05
13. Percent of concentration of plant feeding in top ranking quadrats.....................	-0.476	0.05	-0.246	0.05
14. Percent of concentration of plant feeding in top 3 quadrats...........................	-0.881	0.01*	-0.291	0.05
15. Percent of concentration of plant feeding in top 5 quadrats...........................	-0.691	0.05	-0.609	0.05*
16. Percent of concentration of food related activities in top ranking quadrat............	-0.881	0.01*	-0.538	0.05
17. Percent of concentration of food related activities in top 3 quadrats.................	-0.857	0.01*	-0.627	0.05*
18. Percent of concentration of food related activities in top 5 quadrats.................	-0.714	0.05	-0.570	0.05
19. Percent of hours of rainy weather............	-0.821	0.05*	0.286	0.05
20. Percent of hours of sunshine.................	0.439	0.05	-0.618	0.05*

*Significant correlations with ranging diversity.

TABLE 51.—Group I, percent of frequency (i.e., concentration) of plant feeding and food-related activities in the top-ranking, top three, and top five quadrats (ranked according to frequency of use) of each sample period

Sample period	Percent of plant-feeding activities in quadrat			Percent of food-related activities in quadrat		
	Rank 1	Ranks 1-3	Ranks 1-5	Rank 1	Ranks 1-3	Ranks 1-5
Mar 73 (I).....	15.8	34.9	40.7	11.6	26.3	32.3
Mar 73 (II)....	4.1	9.7	13.8	2.9	7.7	10.6
Apr 73 (I).....	5.6	10.7	12.6	3.2	6.1	7.5
Apr 73 (II)....	7.0	12.0	13.5	5.3	10.6	13.3
May 73 (I).....	1.4	2.1	5.5	2.6	4.4	7.6
May 73 (II)....	1.5	15.4	30.2	3.3	11.4	17.1
Jun 73 (I).....	3.7	8.8	12.4	2.7	6.8	9.9
Jun 73 (II)....	3.6	6.2	14.9	2.4	4.2	10.8
Jul 73 (I).....	6.0	11.3	18.1	4.1	9.0	15.2
Jul 73 (II)....	6.6	11.5	18.0	4.5	11.5	18.3
Aug 73 (I).....	16.1	24.2	37.9	12.3	22.1	31.0
Aug 73 (II)....	3.8	9.6	15.0	2.9	7.8	15.3
Sep 73 (I).....	4.6	15.6	22.0	3.9	8.6	15.0
Oct 73 (I).....	15.7	20.0	20.7	8.9	16.5	21.7
Nov 73 (I).....	2.0	9.8	10.5	0.9	5.5	9.7
Nov 73 (II)....	17.1	26.1	35.2	8.0	14.0	21.1
Dec 73 (I).....	1.9	2.9	10.5	1.6	6.3	14.3
Jan 74 (I).....	12.5	25.9	36.5	11.9	24.8	34.7
Feb 74 (I).....	3.7	10.6	29.0	4.5	15.6	30.0

different parts of their range, the lacunae included within the larger quadrats were not used by other groups. Therefore, there was some justification for using the larger quadrats; this analysis, however, points out the importance of considering methods of home range estimation before valid home range size comparisons can be made between different studies. Among primate studies particularly, several methods have been used in the estimation of home range size (see Aldrich-Blake, 1970a; Waser, 1974; Struhsaker, 1975; Clutton-Brock, 1975b).

FACTORS AFFECTING RANGING PATTERNS.—The factors that affect the ranging patterns of blue monkeys are best understood by considering several aspects of ranging patterns, such as areas used during different time periods, differential use of quadrats, group movements, group spread, ranging diversity, and the pattern of use of night resting trees. This is so because, for example, the relative abundance of food may not affect movements as much as it would the differential use of quadrats.

Considering the area used, Group I normally exploited only a relatively small proportion of its home range during each sample period. Figure 15 shows that the areas used during the sample periods from March 1973 to June 1973 were usually smaller than during the sample periods from July 1973 to February 1974. This may have been partly due to the difference in methodology used during these two time periods. Group movements that were noted using the same method throughout the study, however, also showed that blue monkeys used only a small part of their home range during any one sample period (see Figures 16 and 17), suggesting that this type of ranging pattern was not a mere artifact of the methodology employed in this study. Also it was quite unlike the ranging behavior of the mangabeys of Eastern Uganda, which used almost their entire range within a single day (Chalmers, 1968). Since blue monkeys are comparatively small in size, energetic considerations may have precluded the possibility of exploiting the entire range during a 5-day period. The question then is why do they occupy relatively large home ranges?

The direct relation betwen temporal variations in the frequency of use of quadrats and food abundance in them (Table 46), and the inverse relation between indices of quadrat utilization diversity and concentration of feeding activity in a small part of the area used during a sample period (Table 50) suggest that (1) the relative abundance of food was an important factor that led to the preferential use of quadrats and (2) when food was concentrated in a small area, Group I ranged less diversely than when food was more widely distributed. In other words, the ranging patterns of Group I were related to the location and exploitation of concentrated sources of food. Since fruits were the major food resources of blue monkeys, their abundance probably had the greatest effect on the ranging patterns of this species.

Also, it was pointed out earlier (see "Introduction") that many of the important food plants of Group I exhibited a clumped distribution. Due to the interplay of this pattern of plant distribution and the phenological behavior of food plants, blue monkey foods can be highly variable in their temporal as well as spatial abundance. Thus, since blue monkeys relied on concentrated food resources, frequent temporal shifts in the area used, and the occupancy of a relatively large home range are necessitated.

A large proportion of the area used during a sample period was visited only on one day of that sample period (Figure 21). These transitory movements probably enable blue monkeys to monitor changes in the conditions of resource availability in different parts of their range and to locate areas of food abundance. The efficacy of locating areas of food abundance was probably increased by blue monkeys associating particularly with the redtails during movement. Moreover, transitory movements tend to maximize their use of the available resources of invertebrates. In the previous section, it was shown that blue monkeys depended largely on slow-moving or immobile forms of invertebrates. These invertebrate types are likely to remain depleted from an area for relatively long periods because, unlike winged adults, they cannot move in quickly from nearby areas. Thus blue monkeys have to continually exploit "new" areas of their range for this particular type of invertebrate resource.

Another aspect of the ranging patterns of blue monkeys that tends to maximize the use of invertebrate food is the relatively large spread of the group. This reduces intragroup conflict over choice but sparsely distributed food and thereby promotes the efficient use of the home range. The large spread within the group also probably enhanced the location of abundant food resources.

The ranging patterns of Group I were also affected by climatic factors. Similar observations were made on the black and white colobus, the red colobus, and the mangabey of the Kibale Forest (Oates, 1974; Struhsaker, 1975; Waser, 1975). The fact that the ranging patterns of all four species were affected by climatic factors suggests that the ecological implications of this may have a common physiological basis. Extensive cloud cover probably produces optimal conditions of ambient temperature under which the net energy gained by the exploitation of food resources may be greater than under conditions of intense insolation or rainfall. Thus it is beneficial for a group to range more diversely during periods of cloudy weather than during other times.

Two other factors had limited effects on the ranging patterns of Group I. One was the presence of arboreal pathways across streams and swamps. The lack of a continuous canopy in some areas produced "bottle-necks" that had to be used frequently for movement from one part of the home range to another (Rudran, unpubl.). Thus, these predetermined crossing points probably affected the direction of movement and quadrat use at least for a short period before they were negotiated. The second was the location of preferentially used sleeping areas. Since path length was always greater than travel distance (Figure 33), the locations of sleeping areas probably did not affect movements throughout the day. Unless they partially affected group movements (probably during late evenings), however, certain areas would not have been preferentially used for night resting purposes.

Comparison with Other Studies.—The home range size of Group I far exceeded the range sizes reported for the blue monkeys of the Budongo Forest (mean 8.0 ha, range 5.1–11.7 ha, Aldrich-Blake, 1970a). These differences are all the more appreciable considering the fact that I used a more conservative method of range estimation. Had I used the method that Aldrich-Blake used (encircling of the most peripheral locations), the home range of Group I would have been larger and included a relatively large section of grassland that Group I never used. The Sykes monkey (*C. m. kolbi*), which is a related subspecies found in Kenya, occupied home ranges varying in size from 13.2 to 16.0 ha (DeVos and Omar 1971).

Interpopulational differences in home range size have been reported for other primate species, such as the gray langur (Jay, 1965; Ripley, 1967; Yoshiba, 1968), the purple-faced langur (Rudran, 1970), the black and white colobus (Marler, 1969; Oates, 1974), the red colobus (Clutton-Brock, 1975b; Struhsaker, 1975), the mangabey (Chalmers, 1968; Waser and Floody, 1974), and many others. Variations in home range size and optimal area defended have been found to be related to group size (Dittus, 1974). Also Sugiyama (1967) points out that differences in vegetation and influences of adjacent troops may also be important in regulating range sizes. Gross habitat differences were not apparent between the Kibale and the Budongo study areas (pers. observation); neither were group sizes significantly different in these two forests. In the Kibale Forest, however, the population density of blue monkeys was about 35 individuals/km^2 while in the Budongo Forest it was about 185/km^2 (Aldrich-Blake, 1970b). It is possible that the greater density of blue monkeys in the Budongo Forest may have resulted in the compression of the home ranges there. The Indian gray langur that has also been studied in several areas was found to occupy small home ranges in places where they occurred at high densities (Yoshiba, 1968).

Unfortunately Aldrich-Blake's data does not allow further comparisons to be made between the ranging patterns of the two populations; however, Aldrich-Blake also suggests that food was an important factor that influenced the ranging patterns of blue monkeys. Although one may intuitively feel that the ranging patterns of primates were related to some aspect of the foods they eat, Struhsaker (1974) has shown that this was not the case in the red colobus of the Kibale Forest.

Summary and Conclusions

The blue monkeys of the Kibale Forest normally lived in cohesive "one-male" social groups. Emigration of young males from their parental groups partially served to maintain the integrity of this social structure. Although these groups were relatively widely dispersed during their daily activities, group cohesion was facilitated by the loud "Pyow" calls of the adult male.

These monkeys exploited a diverse diet but they were fairly selective feeders. Fruits were the most frequently used food item although blue monkeys periodically exploited invertebrates and foliar foods at high frequencies. Blue monkeys concentrated their invertebrate feeding on slow-moving and immobile forms, thereby reducing niche overlap with the redtails and the mangabeys along this resource dimension.

The patterns of use of food resources depended on the phenological activity of food plants, relative abundance of food, as well as the food preference of blue monkeys.

Intragroup, intergroup, and interspecific conflicts most frequently occurred in a feeding context. Intragroup conflicts for food were probably minimized by different age/sex classes concentrating on different aspects of the dietary spectrum of the species. The diet of the adult male consisted of a higher proportion of fruits and a lower proportion of invertebrates than the diet of other age/sex classes. Intergroup conflicts for food were largely averted through the territorial nature of this species, while interspecific conflicts appeared to be reduced by avoidance of polyspecific associations during the times when plant foods were being exploited.

The formation of polyspecific associations with the folivorous red colobus seemed to enhance the acquisition of invertebrates by blue monkeys. Also blue monkeys may have been able to efficiently locate areas of food abundance by associating with other species (particularly with redtails) during movement. In addition, predator avoidance was probably an important function of the associations between blue monkeys and other primate species.

Blue monkeys of the Kibale Forest occupied relatively large home ranges, but during 5-day periods of observations they used only a small proportion of their home range. Daily ranges also constituted only a small fraction of the area used during a 5-day period, and on different days of a 5-day period, blue monkeys used somewhat different areas of their home range. Thus they frequently revisited only a small proportion of the area used during a 5-day period, while using the remainder of the area for transitory movements.

These ranging patterns of blue monkeys were dependent on the location and exploitation of concentrated food resources. Blue monkeys ranged less diversely when food was concentrated than when food was more widely distributed. Climatic factors and location of night-resting areas also had limited effects on the ranging patterns of these monkeys.

Blue monkeys of the Kibale Forest occupied relatively large home ranges presumably because they depended on the exploitation of concentrated food resources in a habitat where food availability showed a great deal of temporal and spatial fluctuations. Their transitory movements through parts of their home range probably enabled them to monitor changes in food availability and to locate areas of food abundance. Transitory movements could have also maximized the use of slow-moving and immobile invertebrates by blue monkeys. In addition, the exploitation of these invertebrate forms may have been enhanced by the relatively large spread within groups, which probably reduced intragroup conflicts for these sparsely distributed food resources. Thus, this study tends to support the hypothesis that space utilization patterns arising from the peculiarities of diet and food dispersion affected the social organization of primates.

Appendix

TABLE A.—Group I, percent of frequency of use of specific food items exploited during first 5-day periods of observations from February 1973 to January 1974, inclusive (N = 2039 observations; * = food plants not used by Group II; other species were used by both groups)

Species	Leaf buds	Young leaves	Mature leaves	Dry leaves	Petioles	Stems	Flower buds	Blossoms	Fruits	Seeds	Nectar	Galls	Unidentified plant items	Total frequency	Total percent of frequency
Diospyros abyssinica	-	4.59	-	0.15	-	-	-	2.65	3.29	-	-	-	0.05	222	10.74
Celtis africana	0.34	0.24	-	-	-	-	0.10	0.15	8.22	-	-	-	-	187	9.04
Pancovia turbinata*	-	0.24	-	-	-	-	-	-	8.17	-	-	-	-	174	8.41
Teclea nobilis	-	-	1.55	-	-	-	-	0.15	6.53	-	-	-	-	170	8.22
Uvariopsis congensis	-	0.15	-	-	-	-	-	-	6.53	-	-	-	-	138	6.67
Premna angolensis	0.92	0.05	0.05	-	-	-	-	-	5.32	-	-	-	-	131	6.33
Celtis durandii	-	-	-	-	-	-	-	-	5.07	-	-	-	0.10	107	5.17
Ficus exasperata	0.05	0.05	-	-	-	-	-	-	4.49	-	-	-	-	95	4.59
Mimusops bagshawei	-	-	-	-	-	-	0.19	0.53	3.05	-	-	-	-	78	3.77
Markhamia platycalyx	0.05	-	-	-	2.42	-	0.10	0.05	-	-	0.53	-	-	65	3.14
Bosquiea phoberos	-	-	-	-	-	-	0.05	1.40	0.73	-	-	0.58	0.19	61	2.95
Funtumia latifolia	-	-	-	-	-	-	-	-	-	2.76	-	-	-	57	2.76
Parinari excelsa	-	0.10	-	-	-	-	-	-	2.13	-	-	-	-	46	2.22
Vangueria apiculata	-	-	1.89	-	-	-	0.05	-	0.19	-	-	-	-	44	2.13
Monodora myristica	1.60	0.44	0.05	-	-	-	-	0.05	-	-	-	-	-	44	2.13
Illigera pentaphylla	-	0.19	1.74	-	-	-	-	-	-	-	-	-	-	41	1.98
Dombeya mukole	-	1.55	0.39	-	-	-	-	-	-	-	-	-	-	40	1.93
Chaetachme aristata	-	0.05	-	-	-	0.15	-	-	1.40	-	-	0.10	-	35	1.69
Neoboutonia macrocalyx	-	-	1.60	-	-	-	-	-	0.05	-	-	-	-	34	1.64
Clausena anistata	-	1.21	-	-	0.05	-	-	-	-	-	-	-	-	26	1.26
Linociera johnsonii	0.50	0.73	-	-	-	-	-	-	0.34	-	-	-	-	23	1.11
Aningeria altissima*	-	0.19	-	-	-	-	-	0.92	-	-	-	-	-	23	1.11
Olea welwitschii	-	-	0.53	-	-	-	0.39	0.10	-	-	-	-	-	21	1.02
Chrysophyllum gorungosanum	-	-	-	-	-	-	-	0.97	0.05	-	-	-	-	21	1.02
Balanites wilsoniana	-	-	0.39	-	-	-	-	0.44	-	-	-	-	-	17	0.82
Pseudospondias microcarpa*	-	-	-	-	-	-	-	-	0.77	-	-	-	-	16	0.77
Milletia dura	-	0.53	-	-	-	-	0.10	0.10	-	-	-	-	-	15	0.73
Blighia unijugata	-	0.68	-	-	-	-	-	-	-	-	-	-	-	14	0.68
Symphonia globulifera	-	-	-	-	-	-	-	-	0.05	-	0.34	-	-	8	0.39
Newtonia buchanani	0.19	-	-	-	-	-	-	-	-	0.15	-	-	-	7	0.34
Coffea eugenoides*	-	-	-	-	-	-	0.34	-	-	-	-	-	-	7	0.34
Loeseueriella apiculata*	-	-	-	-	-	-	-	0.34	-	-	-	-	-	7	0.34
Trichilia splendida*	-	0.34	-	-	-	-	-	-	-	-	-	-	-	7	0.34
Dichapetalum ugandense*	-	-	0.05	-	-	-	-	0.24	-	-	-	-	-	6	0.29
Trema orientalis	-	-	-	-	-	-	-	-	0.29	-	-	-	-	6	0.29
Urera cameroonensis	-	0.15	-	-	-	0.10	-	-	-	-	-	-	-	5	0.24
Albizia gummifera*	-	0.10	-	-	-	-	0.15	-	-	-	-	-	-	5	0.24
Strombosia scheffleri	-	0.05	0.10	-	-	-	-	-	0.10	-	-	-	-	5	0.24
Spathodea campanulata*	-	0.19	-	-	-	-	-	-	-	-	-	-	-	4	0.19
Ficus natalensis	-	-	-	-	-	-	-	-	0.19	-	-	-	-	4	0.19
Ficus kisantuensis	-	-	-	-	-	-	-	-	0.15	-	-	-	-	3	0.15
Cyphomandria betaceae	-	-	-	-	-	-	-	-	0.15	-	-	-	-	3	0.15
Fagaropsis angolensis	-	-	-	-	-	-	-	-	0.10	-	-	-	-	2	0.10
Cardiospermum grandiflorum	-	0.05	0.05	-	-	-	-	-	-	-	-	-	-	2	0.10
Polystachya sp.*	-	-	0.05	-	-	-	-	0.05	-	-	-	-	-	2	0.10
Belonophora glomerata*	-	-	-	-	-	-	-	-	0.10	-	-	-	-	2	0.10
Erythrina sp.*	-	-	-	-	-	-	-	0.10	-	-	-	-	-	2	0.10
Vangueria acutiloba*	-	-	-	-	-	-	-	-	0.10	-	-	-	-	2	0.10
Ficus brachylepis	-	0.05	-	-	-	-	-	-	-	-	-	-	-	1	0.05
Randia urcelliformis	-	-	0.05	-	-	-	-	-	-	-	-	-	-	1	0.05
Diaphananthe sp.	-	-	-	-	-	-	-	0.05	-	-	-	-	-	1	0.05
Harungana madagascariensis*	-	-	-	-	-	-	-	-	0.05	-	-	-	-	1	0.05
Landolphia sp.*	-	-	-	-	-	-	-	0.05	-	-	-	-	-	1	0.05
Platycerium elephantotis*	-	-	0.05	-	-	-	-	-	-	-	-	-	-	1	0.05
Saba florida*	-	-	-	-	-	0.05	-	-	-	-	-	-	-	1	0.05
Unidentified species (4)	-	-	0.34	-	-	-	0.10	-	0.29	-	-	-	0.58	27	0.31
Number of specific food items	7	23	15	1	2	3	9	18	27	2	2	2		2068	
Percent of frequency of use	3.20	11.92	8.93	0.15	2.47	0.30	1.57	8.34	57.89	2.91	0.87	0.68	0.92		

TABLE B.—List of food plants exploited by the blue monkeys

- ACANTHACEAE
  - *Brillantasia nitens* Lindau
- ANACARDIACEAE
  - *Pseudospondias microcarpa* (A. Rich.) Engl.
- ANNONACEAE
  - *Monodora myristica* (Gaertn.) Dunal
  - *Uvariopsis congensis* Robyns and Chesquiere
- APOCYANACEAE
  - *Funtumia latifolia* (Stapf) Stapf ex Schltr.
  - *Pleiocarpa pycnantha* (K. Schum.) Stapf
  - *Tabernaemontana odoratissima* Stapf
  - *Tabernaemontana usamberensis* Stapf
- BASELLACEAE
  - *Basella alba* L.
- BIGNONIACEAE
  - *Markhamia platycalyx* (Bak.) Sprague
  - *Spathodea nilotica* Seem.
- CAESALPINIACEAE
  - *Loeseneriella apiculata* R. Wilkzell
- CAPPARIDACEAE
  - *Ritchiea albersii* Gilg
- CHAILLETIACEAE
  - *Dichapetalum ugandense* M. B. Moss
- EBENACEAE
  - *Diospyros abyssinica* (Hiern) F. White
- EUPHORBIACEAE
  - *Acalypha bipatita* Muell. Arg.
  - *Drypetes battiscombei* Hutch.
  - *Neoboutonia macrocalyx* Pax
- FLACOURTIACEAE
  - *Dovyalis macrocalyx* (Oliv.) Warb.
  - *Scolopia rhamniphylla* Gilg
- GUTTIFERAE
  - *Symphonia globulifera* L. f.
- HERNANDIACEAE
  - *Illigera pentaphylla* Welw.
- HYPERICACEAE
  - *Harungana madagascarensis* Lam.
- ICACINACEAE
  - *Apodytes dimidiata* E. Mey. ex Arn.
  - *Pyrenacantha* sp.
- LOGANIACEAE
  - *Strychnos mitis* S. Moore
- MELIACEAE
  - *Carapa grandiflora* Sprague
  - *Trichilia splendida* A. Chev.
- MIMOSACEAE
  - *Albizia gummifera* (Gmel.) C. A. Sm.
  - *Newtonia buchanani* (Baker) Gilb. and Bout.
- MORACEAE
  - *Bosqueia phoberos* Baill.
  - *Ficus brachylepis* Welw. ex Hiern
  - *Ficus congensis* Engl.
  - *Ficus dawei* Hutch.
  - *Ficus exasperata* Vahl
  - *Ficus kisantuensis* Warb.
  - *Ficus natalensis* (Miq.) Hochst.
  - *Ficus stipulifera* Hutch.
- OLACACEAE
  - *Strombosia scheffleri* Engl.
- OLEACEAE
  - *Linociera johnsonii* Baker
  - *Olea welwitschii* (Knobl.) Gilg and Schelleng
- ORCHIDACEAE
  - *Anagraecum distichum* Lindl.
  - *Diaphananthe* sp.
  - *Polystachya* sp.
- PAPILIONACEAE
  - *Erythrina* sp.
  - *Milletia dura* Dunn
- POLYPODIACEAE
  - *Loxogramme lanceolata* C. Presl.
  - *Platycerium elephantotis* Schweinf.
- RHIZOPHORACEAE
  - *Cassipourea ruwensorensis* (Engl.) Alston
- ROSACEAE
  - *Parinari excelsa* Sabine
- RUBIACEAE
  - *Belonophora glomerata* M. B. Moss
  - *Canthium* sp.
  - *Coffea eugenoides* S. Moore
  - *Euclinia longiflora* Salisb.
  - *Randia urcelliformis* Hiern.
  - *Tarenna pavettoides* (Harv.) Sim.
  - *Vangueria acutiloba* Robyns
  - *Vangueria apiculata* K. Schum.
- RUTACEAE
  - *Clausena anistata* (Willd.) Hook f. ex Benth.
  - *Fagara mildbraedii* Engl.
  - *Fagaropsis angolensis* (Engl.) Dale
  - *Teclea nobilis* Del.
- SAPINDACEAE
  - *Blighia unijugata* Bak.
  - *Cardiospermum grandiflorum* Sw.
  - *Lepisanthes senegalensis* (Poir.) Radlk.
  - *Pancovia* sp. nr *P. turbinata* Radlk.
  - *Paulinia pinnata* L.
- SAPOTACEAE
  - *Aningeria altissima* (A. Chev.) Aubr. and Pellegr.
  - *Chrysophyllum gorungosanum* Engl.
  - *Mimusops bagshawei* S. Moore
- SIMAROUBACEAE
  - *Balanites wilsoniana* Dawe and Sprague
- SOLANACEAE
  - *Cyphomandrea betacea* Sendtu.
- STERCULIACEAE
  - *Dombeya mukole* Sprague
- TILIACEAE
  - *Glyphaea lateriflora* (G. Don) Hutch and J. M. Dalz.
- ULMACEAE
  - *Celtis africana* Burm. f.
  - *Celtis durandii* Engl.
  - *Chaetachme aristata* Planch.
  - *Trema orientalis* (L.) Bl.
- URTICACEAE
  - *Urera cameroonensis* Wedd.
- VERBANACEAE
  - *Premna angolensis* Guerke
- VITACEAE
  - *Cissus oliveriana* Engl. j. Gilg

TABLE C.—Group I, rank order (I-V) and percent of frequency of use of top five food plants and specific food items during the first 5-day period of observations from February 1973 to May 1974, inclusive

Sample period	I		II		III		IV		V		
	Species	Percent	Species	Percent	Species	Percent	Species	Percent	Species	Percent	N
					FOOD PLANTS						
Feb 73 (I)..	*D. abyssinica*	22.1	*F. exasperata*	21.4	*B. phoberos*	14.0	*A. altissima* *P. excelsa*	10.7	-	-	149
Mar 73 (I)..	*P. turbinata*	85.6	*P. excelsa*	4.6	*D. mukole*	1.5	*C. africana* *O. welwitschii* *B. unijugata* *T. nobilis*	1.0	-	-	194
Apr 73 (I)..	*C. africana*	53.3	*D. abyssinica*	14.7	*P. excelsa* *M. platycalyx*	8.1	-	-	*M. bagshawei*	4.2	210
May 73 (I)..	*C. gorungosanum*	16.1	*P. angolensis*	12.9	*O. welwitschii*	8.0	*N. macrocalyx*	6.4	*M. bagshawei*	4.8	124
Jun 73 (I)..	*U. congensis*	43.5	*D. abyssinica*	14.3	*F. exasperata*	7.6	*P. angolensis*	7.1	*T. nobilis*	4.7	209
Jul 73 (I)..	*D. abyssinica*	29.1	*P. angolensis*	23.6	*U. congensis*	13.3	*M. bagshawei*	6.6	*N. macrocalyx*	5.9	254
Aug 73 (I)..	*D. abyssinica*	24.8	*P. angolensis*	18.3	*I. pentaphylla* *T. nobilis*	8.6	-	-	*P. microcarpa* *B. phoberos*	8.1	185
Sep 73 (I)..	*C. anistata*	21.3	*C. africana*	19.6	*C. durandii*	13.9	*B. phoberos* *M. platycalyx*	11.4	-	-	122
Oct 73 (I)..	*C. durandii*	28.1	*T. nobilis*	24.4	*D. mukole*	11.8	*M. dura*	8.8	*M. platycalyx* *C. africana*	7.4	135
Nov 73 (I)..	*T. nobilis*	57.8	*C. durandii*	24.3	*M. bagshawei*	7.8	*I. pentaphylla*	2.6	*F. angolensis* *D. mukole* *C. africana*	1.3	152
Dec 73 (I)..	*M. bagshawei*	21.7	*F. latifolia*	16.9	*M. myristica*	13.7	*C. africana*	10.4	*U. congensis*	6.4	124
Jan 74 (I)..	*V. apiculata*	13.3	*F. exasperata*	12.8	*F. latifolia*	11.4	*C. aristata*	8.5	*M. myristica*	7.6	210
Feb 74 (I)..	*A. altissima*	21.9	*P. turbinata*	14.1	*F. exasperata*	9.1	*V. apiculata*	8.7	*M. platycalyx*	5.8	241
Mar 74 (I)..	*M. platycalyx*	22.7	*D. abyssinica*	14.7	*C. africana*	11.3	*O. welwitschii*	9.0	*M. dura*	6.8	88
Apr 74 (I)..	*D. mukole*	17.7	*T. nobilis*	13.1	*P. angolensis*	11.1	*C. africana*	7.2	*M. platycalyx*	6.5	152
May 74 (I)..	*M. bagshawei*	34.0	*M. platycalyx*	20.0	*D. abyssinica* *C. africana*	13.0	-	-	*T. nobilis*	5.0	100
					SPECIFIC FOOD ITEMS						
Feb 73 (I)..	*D. abyssinica*, fruits	22.1	*F. exasperata*, fruits	21.4	*B. phoberos*, blossoms	12.0	*P. excelsa*, fruits	10.7	*A. altissima*, blossoms	8.0	149
Mar 73 (I)..	*P. turbinata*, fruits	85.5	*P. excelsa*, fruits	4.6	*D. mukole*, young leaves	1.5	*A. gummifera*, young leaves *B. unijugata*, young leaves *T. nobilis*, mature leaves *C. africana*, fruits	1.0	-	-	194
Apr 73 (I)..	*C. africana*, fruits	53.3	*D. abyssinica*, fruits	14.7	*P. excelsa*, fruits	8.1	*M. platycalyx*, petioles	7.6	*M. bagshawei*, blossoms	4.2	210
May 73 (I)..	*C. gorungosanum*, blossoms	16.1	*P. angolensis*, leaf buds	12.9	*N. macrocalyx*, mature leaves	6.4	*O. welwitschii*, flower buds	4.8	*T. nobilis*, mature leaves	4.0	124
Jun 73 (I)..	*U. congensis*, fruits	43.0	*D. abyssinica*, young leaves	13.4	*F. exasperata*, fruits	7.6	*P. angolensis*, blossoms	7.1	*T. nobilis*, mature leaves	4.7	209
Jul 73 (I)..	*P. angolensis*, blossoms	23.6	*D. abyssinica*, blossoms	20.4	*U. congensis*, fruits	13.3	*D. abyssinica*, young leaves	8.6	*M. bagshawei*, fruits	6.6	254
Aug 73 (I)..	*D. abyssinica*, young leaves	23.2	*P. angolensis*, blossoms	17.8	*I. pentaphylla*, mature leaves	8.6	*P. microcarpa*, fruits	8.1	*T. nobilis*, fruits	4.8	185
Sep 73 (I)..	*C. anistata*, young leaves	20.4	*C. africana*, fruits	17.2	*C. durandii*, fruits	13.9	*D. mukole*, young leaves	9.0	*M. platycalyx*, petioles	6.5	122
Oct 73 (I)..	*C. durandii*, fruits	28.1	*T. nobilis*, fruits	24.4	*D. mukole*, young leaves	11.1	*M. dura*, young leaves	6.6	*M. platycalyx*, nectar	4.4	135
Nov 73 (I)..	*T. nobilis*, fruits	57.8	*C. durandii*, fruits	24.3	*M. bagshawei*, fruits	7.8	*F. angolensis*, fruits *C. africana*, fruits *I. pentaphylla*, mature leaves	1.3	-	-	152
Dec 73 (I)..	*M. bagshawei*, fruits	21.7	*F. latifolia*, seeds	16.9	*M. myristica*, leaf buds	13.7	*C. africana*, fruits	10.4	*U. congensis*, fruits	6.4	124
Jan 74 (I)..	*V. apiculata*, mature leaves	13.3	*F. exasperata* fruits	12.8	*F. latifolia*, seeds	11.4	*C. aristata*, fruits	7.6	*M. myristica*, leaf buds	6.1	210
Feb 74 (I)..	*A. altissima*, blossoms	21.1	*P. turbinata*, fruits	14.1	*F. exasperata*, fruits	9.1	*V. apiculata*, mature leaves	8.7	*M. platycalyx*, petioles	5.8	241
Mar 74 (I)..	*M. platycalyx*, petioles	22.7	*D. abyssinica*, young leaves *C. africana*, fruits	10.2	-	-	*O. welwitschii*, mature leaves	9.0	*B. wilsoniana*, mature leaves *F. exasperata*, fruits	5.6	88
Apr 74 (I)..	*D. mukole*, young leaves	17.7	*P. angolensis*, leaf buds	10.5	*T. nobilis*, mature leaves	9.8	*M. platycalyx*, petioles	6.5	*M. bagshawei*, flower buds	5.9	152
May 74 (I)..	*M. bagshawei*, flower buds	22.0	*M. platycalyx*, petioles	20.0	*M. bagshawei*, blossoms	12.0	*D. abyssinica*, young leaves	11.0	*C. africana*, fruits	9.0	100

TABLE D.—Group I, percent of frequency of ingestion of probable invertebrates from specific microhabitats (I-XI) during first 5-day periods of observations from February 1973 to January 1974, inclusive (N = 498 observations, I = foliage, II = lichen-covered branch, III = moss-covered branch, IV = moss- and epiphyte-covered branch, V = dry leaf, VI = epiphyte-covered branch, VII = trunk or branch (bare), VIII = unidentified microhabitat, IX = bark or twig, X = lichen- and epiphyte-covered branch, XI = moss- and lichen-covered branch)

Species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Total percent of frequency
P. excelsa	4.61	2.41	7.43	0.80	0.40	1.20	0.60	0.20	-	-	-	17.67
S. scheffleri	6.02	0.40	2.61	0.20	0.20	0.60	0.60	0.80	-	-	-	11.45
D. abyssinica	5.62	2.21	0.80	-	0.60	0.20	1.00	0.20	-	-	-	10.64
M. platycalyx	0.80	1.00	0.40	0.20	1.61	0.20	0.80	-	-	-	-	5.02
C. durandii	1.81	0.80	0.60	-	0.40	0.40	0.40	-	-	-	-	4.42
B. wilsoniana	1.00	1.81	0.80	-	0.20	-	-	0.40	-	-	-	4.22
T. nobilis	1.81	0.20	0.40	-	0.20	-	0.60	-	-	-	-	3.21
P. turbinata	1.61	-	0.20	-	0.60	-	0.20	-	-	-	-	2.61
C. africana	0.80	0.60	0.80	-	-	-	0.20	0.20	-	-	-	2.58
N. buchanani	0.40	0.60	0.60	-	-	0.40	0.40	-	-	-	-	2.41
O. welwitschii	0.40	1.41	-	-	-	-	0.20	-	-	-	-	2.01
U. congensis	1.41	-	-	-	-	-	0.20	-	-	-	-	1.61
M. bagshawei	0.60	0.20	0.40	0.20	0.20	-	-	-	-	-	-	1.61
A. altissima	0.60	0.20	0.80	-	-	-	-	-	-	-	-	1.61
F. brachylepis	0.20	-	0.80	-	0.20	-	-	-	0.20	-	-	1.41
S. globulifera	0.80	-	0.20	-	-	-	0.20	0.20	-	-	-	1.41
P. angolensis	0.60	0.20	0.40	-	-	-	-	-	-	-	-	1.20
B. phoberos	0.80	-	0.20	-	-	-	-	-	-	-	-	1.00
F. latifolia	0.40	0.20	0.20	-	-	-	0.20	-	-	-	-	1.00
C. gorungosanum	0.40	0.20	-	-	-	-	0.20	-	-	-	-	0.80
D. mukole	-	-	0.20	-	0.20	-	0.20	-	-	-	-	0.60
M. dura	0.60	-	-	-	-	-	-	-	-	-	-	0.60
Chaetachme aristata	0.40	-	-	-	-	-	-	-	-	-	-	0.40
F. dawei	-	-	-	0.20	-	-	0.20	-	-	-	-	0.40
Fagaropsis angolensis	0.20	-	-	-	-	-	-	-	-	-	-	0.20
M. myristica	-	-	0.20	-	-	-	-	-	-	-	-	0.20
M. macrocalyx	0.20	-	-	-	-	-	-	-	-	-	-	0.20
T. splendida	0.20	-	-	-	-	-	-	-	-	-	-	0.20
V. apiculata	0.20	-	-	-	-	-	-	-	-	-	-	0.20
Unidentified species	6.22	1.20	3.41	0.40	1.41	1.00	1.61	2.21	1.00	0.20	0.20	18.88
Total percent of frequency	38.75	13.65	21.49	2.01	6.22	4.02	8.03	4.22	1.20	0.20	0.20	

TABLE E.—*Cercopithecus mitis*, Groups I and II, frequency of use of different motor patterns in the capture of probable invertebrate food from different microhabitats, I-XI (see Appendix Table D; data collected from Group II given within parentheses)

Motor Patterns	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Total
Rapid Movements												
Run first, grab with both hands into mouth	-	-	-	-	-	-	-(1)	-	-	-	-	0(1)
One-hand grab, placed with hand into mouth	2(9)	-(1)	3(2)	-	-(1)	1	2(7)	3	-	-	-	11(20)
Two-hand grab, placed with both hands into mouth	11(10)	-	1	-	1(4)	-	-(1)	-(1)	-	-	-	13(16)
Series of picks with mouth applied to substrate	-	-	-	-	-	1	-	-	-	-	-	1(0)
Repeated one-hand picks, placed with hand into mouth	-(1)	-(3)	-(1)	-(1)	-	-	9(6)	1(2)	-	-	-	10(14)
Quick grab*	8(3)	1	2(1)	1	-	-	1(5)	2(2)	-	-(1)	-	15(12)
Quick slap*	-	2	2(1)	-	-	-	1	-	-	-	-	5(1)
Total	21(23)	3(4)	8(5)	1(1)	1(5)	2	13(20)	6(5)	-	-(1)	-	55(64) 6.6%(9.9%)
Slow Movements												
One-hand reach for food item:												
Rub on branch, placed with hand into mouth	1	-	-	-	-	-	1	5(1)	-	-	-	7(1)
No rub, placed with hand into mouth:												
Not repeated	17(56)	11(31)	12(15)	2	1(3)	1(1)	5(24)	-(2)	-(2)	-(1)	1(2)	49(137)
Repeated in succession	-(5)	-	-(1)	-	-	-	-(2)	-	-	-	-	0(8)
One-hand reach for substrate:												
Mouth directly applied to substrate	7(33)	-	-	-	-(1)	-	1	-	-	-	-	8(34)
Food item picked, placed with hand into mouth	3	-	-	-	1	-	-	-(1)	-	-	-	4(1)
Two-hand reach for substrate:												
Mouth applied to substrate, licking food item	2(1)	-	-	-	-	-	1	-	-	-	-	3(1)
Picking with lips	22(48)	-	1	-	5(8)	-	1(1)	-	-(1)	-	-	29(58)
Uncurl or manually examine	-	-	-	-	-	-	-	-	-	-	-	-
Mouth applied to substrate	1(1)	-	-	-	2(15)	-	-	-	-	-	-	3(16)
Repeated licking	-	-	-	-	1	-	-	-	-	-	-	1(0)
Remove substrate, mouth applied to o substrate	5(3)	-	-	-	1	-	-	-	-	-	-	6(3)
Lick without reaching for or holding substrate	-	-	-	-	-	-	1	-	-	-	-	1(0)
Mouth applied to substrate without reaching for or holding	1	2(4)	2(3)	-	-	-	1(5)	-	-(2)	-	-	6(14)
Initial movement not seen:												
Rub on branch, placed with hand into mouth	-	-	-	-	-	-	-(2)	1	-	-	-	1(2)
Rub between hands, placed with hand(s) into mouth	-	-	-	-	-	-	-(1)	-(1)	-	-	-	0(2)
Hold, place with hand(s) into mouth	-	-	-	-	-	-	-	1	-	-	-	1(0)
Pluck foliage and mouth applied to substrate*	3(2)	-	-	-	-	-	-	-	-	-	-	3(2)
Licking substrate*	14(15)	7(4)	6(2)	-(1)	1(1)	-	4(3)	1(2)	1(1)	-	-	34(29)
Picking with mouth or hands*	255(128)	88(37)	143(33)	19(3)	35(17)	23(4)	41(35)	15(12)	8(2)		1(1)	628(272)
Total	331(297)	108(76)	164(54)	21(4)	47(45)	24(5)	56(74)	23(19)	9(8)	-(1)	1(3)	784(586) 93.4%(90.1%)
Total frequency of motor patterns	352(320)	111(80)	172(59)	22(5)	48(50)	26(5)	69(94)	29(24)	9(8)	-(2)	1(3)	839(650)

*Incomplete descriptions that were used between February and December 1973, inclusive, but were further subdivided later through fuller descriptions of feeding motor patterns. Note also that after December 1973 Group II was observed for longer periods than Group I.

TABLE F.—Group I, percent of use of specific plant food items during 11 observation periods most comparable to those of Group II between February 1973 and January 1974, inclusive

Species	Leaf buds	Young leaves	Mature leaves	Dry leaves	Petioles	Stems	Flower buds	Blossoms	Fruits	Seeds	Nectar	Galls	Total frequency	Total percent of frequency
Teclea nobilis	0.05	0.10	1.37	-	-	-	-	-	11.53	-	-	-	258	13.06
Celtis africana	0.35	0.25	-	-	-	-	0.05	0.15	10.52	-	-	-	225	11.39
Diospyros abyssinica	-	2.68	-	-	-	-	-	2.78	4.55	-	-	-	198	10.02
Uvariopsis congensis	-	0.15	-	-	-	-	-	-	6.83	-	-	-	138	6.98
Celtis durandii	-	-	-	-	-	-	-	-	6.52	-	-	-	129	6.52
Premna angolensis	1.27	0.05	-	-	-	-	-	3.80	-	-	-	-	101	5.11
Ficus exasperata	-	-	-	-	-	-	-	-	4.76	-	-	-	94	4.76
Mimusops bagshawei	-	-	-	-	-	-	0.20	0.56	3.85	-	-	-	91	4.61
Markhamia platycalyx	0.05	-	-	-	3.14	-	0.10	0.05	-	-	0.56	-	77	3.90
Funtumia latifolia	-	-	-	-	-	-	-	-	-	2.88	-	-	57	2.88
Dombeya mukole	-	2.07	0.40	-	-	-	0.10	-	-	-	-	-	51	2.58
Bosquiea phoberos	-	-	-	-	-	-	0.05	1.21	1.01	-	-	0.20	49	2.48
Monodora myristica	1.62	0.46	0.05	-	-	-	-	0.05	-	-	-	-	43	2.18
Parinari excelsa	-	0.10	-	-	-	-	-	-	2.02	-	-	-	42	2.13
Vangueria apiculata	-	-	1.82	-	-	-	-	-	0.30	-	-	-	42	2.13
Pancovia turbinata	-	0.25	-	-	-	-	-	-	1.72	-	-	-	39	1.97
Chaetachme aristata	-	-	-	-	-	0.25	-	-	1.37	-	-	0.10	34	1.72
Neoboutonia macrocalyx	-	-	1.37	-	-	-	-	-	-	-	-	-	27	1.37
Clausena anistata	-	1.27	-	-	0.05	-	-	-	-	-	-	-	26	1.32
Illigera pentaphylla	-	0.20	1.07	-	-	-	-	-	-	-	-	-	25	1.27
Milletia dura	-	0.91	0.10	-	-	-	0.15	0.10	-	-	-	-	25	1.27
Linociera johnsonii	0.05	0.76	-	-	-	-	-	-	0.30	-	-	-	22	1.11
Chrysophyllum gorungosanum	-	-	-	-	-	-	-	1.01	0.05	-	-	-	21	1.06
Olea welwitschii	-	-	0.46	-	-	-	0.40	0.10	-	-	-	-	19	0.96
Aningeria altissima	-	0.20	-	-	-	-	-	0.71	-	-	-	-	18	0.91
Balanites wilsoniana	-	-	0.40	-	-	-	-	0.46	-	-	-	-	17	0.86
Blighia unijugata	-	0.61	-	-	-	-	-	-	-	-	-	-	12	0.61
Symphonia globulifera	-	-	-	-	-	-	-	-	0.05	-	0.35	-	8	0.40
Newtonia buchanani	0.20	-	-	-	-	-	-	-	-	0.15	-	-	7	0.35
Coffea eugenoides	-	-	-	-	-	-	0.35	-	-	-	-	-	7	0.35
Loeseneriella apiculata	-	-	-	-	-	-	-	0.35	-	-	-	-	7	0.35
Trichilia splendida	-	0.35	-	-	-	-	-	-	-	-	-	-	7	0.35
Dichapetalum ugandense	-	-	0.05	-	-	-	-	0.25	-	-	-	-	6	0.30
Urera cameroonensis	-	0.15	-	-	-	0.10	-	-	-	-	-	-	5	0.25
Cyphomandria betaceae	-	-	-	-	-	-	-	-	0.20	-	-	-	4	0.20
Loxogramme lanceolata	-	0.20	-	-	-	-	-	-	-	-	-	-	4	0.20
Strombosia scheffleri	-	0.10	-	-	-	-	-	-	0.10	-	-	-	4	0.20
Ficus natalensis	-	-	-	-	-	-	-	-	0.20	-	-	-	4	0.20
Polystachya sp.	-	-	0.10	-	-	-	-	0.05	-	-	-	-	3	0.15
Ficus kisantuensis	-	-	-	-	-	-	-	-	0.15	-	-	-	3	0.15
Pseudospondias microcarpa	-	-	-	-	-	-	-	-	0.10	-	-	-	2	0.10
Fagaropsis angolensis	-	-	-	-	-	-	-	-	0.10	-	-	-	2	0.10
Albizia gummifera	-	-	-	-	-	-	-	0.10	-	-	-	-	2	0.10
Cardiospermum grandiflorum	-	0.05	0.05	-	-	-	-	-	-	-	-	-	2	0.10
Apodytes dimidiata	-	-	-	-	-	-	-	0.10	-	-	-	-	2	0.10
Belanophora glomerata	-	-	-	-	-	-	-	-	0.10	-	-	-	2	0.10
Erythrina sp.	-	-	-	-	-	-	-	0.10	-	-	-	-	2	0.10
Vangueria acutiloba	-	-	-	-	-	-	-	-	0.10	-	-	-	2	0.10
Spathodea campanulata	-	0.05	-	-	-	-	-	-	-	-	-	-	1	0.05
Ficus brachylepis	-	0.05	-	-	-	-	-	-	-	-	-	-	1	0.05
Randia urcelliformis	-	-	0.05	-	-	-	-	-	-	-	-	-	1	0.05
Diaphananthe sp.	-	-	-	-	-	-	-	0.05	-	-	-	-	1	0.05
Harungana madagascarensis	-	-	-	-	-	-	-	-	0.05	-	-	-	1	0.05
Landolphia sp.	-	-	-	-	-	-	-	0.05	-	-	-	-	1	0.05
Platycerium elephantotis	-	-	0.05	-	-	-	-	-	-	-	-	-	1	0.05
Saba florida	-	-	-	-	-	0.05	-	-	-	-	-	-	1	0.05
Unidentified species (4)	-	-	-	-	-	-	-	-	-	-	-	-	4	0.20
Total	3.59	11.01	7.34	-	3.19	0.40	1.40	12.03	56.48	3.03	0.91	0.30	1977	

TABLE G.—Group II, percent of use of specific plant food items during 11 observation periods between February 1973 and January 1974, inclusive

Species	Leaf buds	Young leaves	Mature leaves	Dry leaves	Petioles	Stems	Flower buds	Blossoms	Fruits	Seeds	Nectar	Galls	Total frequency	Total percent of frequency
Ficus exasperata	3.50	0.97	-	-	0.05	-	-	-	15.09	-	-	-	364	19.61
Uvariopsis congensis	-	-	-	-	-	-	-	-	11.53	-	-	-	214	11.53
Celtis africana	0.65	0.32	-	-	-	-	0.65	0.70	9.16	-	-	-	213	11.48
Diospyros abyssinica	-	2.37	0.05	-	-	-	0.81	2.69	1.78	-	-	-	143	7.70
Markhamia platycalyx	-	-	0.05	-	2.96	-	0.05	-	0.59	-	3.18	-	139	7.49
Celtis durandii	-	0.05	0.05	0.05	-	-	-	-	7.00	-	-	-	133	7.17
Ficus brachylepis	-	-	-	-	-	-	-	-	6.63	-	-	-	123	6.63
Teclea nobilis	-	-	0.11	-	-	-	-	-	4.36	-	-	-	83	4.47
Funtumia latifolia	-	-	-	-	-	-	-	-	-	4.04	-	-	75	4.04
Monodora myristica	0.32	0.43	-	-	-	-	-	0.86	2.21	-	-	-	71	3.83
Linociera johnsonii	-	0.27	-	-	-	-	-	-	2.10	-	-	-	44	2.37
Premna angolensis	0.65	-	0.05	-	-	-	-	1.24	-	-	-	-	36	1.94
Chrysophyllum gorungosanum	-	-	-	-	-	-	0.05	1.40	0.32	-	-	-	33	1.78
Cyphomandria betaceae	-	0.16	-	-	0.05	-	-	0.37	0.54	-	-	-	21	1.13
Olea welwitschii	-	-	0.86	-	-	-	-	0.11	-	-	-	-	18	0.97
Clausena anistata	-	0.75	-	-	-	-	0.22	-	-	-	-	-	18	0.97
Illigera pentaphylla	-	0.22	0.54	-	-	-	-	0.05	-	-	-	-	15	0.81
Ritchia albersii	-	0.05	-	-	-	-	-	-	0.65	-	-	-	13	0.70
Ficus stipulifera	-	-	-	-	-	-	-	-	0.59	-	-	-	11	0.59
Bosquiea phoberos	-	-	-	-	-	-	-	-	0.59	-	-	-	11	0.59
Neoboutonia macrocalyx	-	-	0.54	-	-	-	-	-	-	-	-	-	10	0.54
Mimusops bagshawei	-	-	-	-	-	-	-	-	-	-	-	-	9	0.48
Urera cameroonensis	-	-	0.05	-	-	-	-	0.38	-	-	-	-	8	0.43
Strombosia scheffleri	-	-	0.05	-	-	-	-	0.05	0.27	-	-	-	7	0.38
Fagaropsis angolensis	-	-	-	-	-	-	-	-	0.32	-	-	-	6	0.32
Ficus kisantuensis	-	-	-	-	-	-	-	-	0.27	-	-	-	5	0.27
Vangueria apiculata	-	-	0.11	-	-	-	-	-	0.05	-	-	-	3	0.16
Symphonia globulifera	-	-	-	-	-	-	-	-	-	-	0.16	-	3	0.16
Lepisanthes senegalensis	-	-	-	-	-	-	-	-	0.16	-	-	-	3	0.16
Dombeya mukole	-	0.05	0.05	-	-	-	-	-	-	-	-	-	2	0.11
Angraecum distichum	-	-	0.11	-	-	-	-	-	-	-	-	-	2	0.11
Chlorodendrum schweinfurthii	-	-	0.11	-	-	-	-	-	-	-	-	-	2	0.11
Drypetes battiscombei	-	-	0.11	-	-	-	-	-	-	-	-	-	2	0.11
Newtonia buchanani	-	0.11	-	-	-	-	-	-	-	-	-	-	2	0.11
Parinari excelsa	-	-	-	-	-	-	-	-	0.11	-	-	-	2	0.11
Chaetachme aristata	-	-	-	-	-	-	-	-	0.05	-	-	-	1	0.05
Trema orientalis	-	-	-	-	-	-	-	-	0.05	-	-	-	1	0.05
Basella alba	-	-	-	-	-	-	-	0.05	-	-	-	-	1	0.05
Brachystephanus africana	-	-	0.05	-	-	-	-	-	-	-	-	-	1	0.05
Diaphananthe sp.	-	-	-	-	-	-	-	-	0.05	-	-	-	1	0.05
Fagara angolensis	-	0.05	-	-	-	-	-	-	-	-	-	-	1	0.05
Ficus congensis	-	-	-	-	-	-	-	-	0.05	-	-	-	1	0.05
Glyphaea laterifolia	-	0.05	-	-	-	-	-	-	-	-	-	-	1	0.05
Tabernaemontana usamberensis	-	-	-	-	-	-	-	-	0.05	-	-	-	1	0.05
Unidentified species (3)	-	-	-	-	-	-	-	-	-	-	-	-	3	0.16
Total	5.12	5.85	2.89	0.05	3.06	-	1.78	8.05	64.42	4.04	3.34	-	1856	

Literature Cited

Aldrich-Blake, F. P. G.
1970a. The Ecology and Behaviour of the Blue Monkey *Cercopithecus mitis stuhlmanni*. Unpublished Ph.D. dissertation, University of Bristol.
1970b. Problems of Social Structure in Forest Monkeys. Pages 79–101 *in* Crook, editor, *Social Behaviour in Birds and Mammals*. London: Academic Press.

Altmann, S. A., and J. Altmann
1970. *Baboon Ecology: African Field Research*. Chicago: University of Chicago Press.

Biddulph, O.
1959. Translocation of Inorganic Solutes. Pages 553–602 *in* Steward, editor, *Plant Physiology*. New York: Academic Press.

Bourliere, F., C. Hunkeler, and M. Bertrand
1970. Ecology and Behaviour of Lowe's Guenon (*C. campbelli lowei*) in the Ivory Coast. Pages 297–350 *in* Napier and Napier, editors, *Old World Monkeys*. New York and London: Academic Press.

Burt, W. H.
1943. Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy*, 24:346–352.

Chalmers, N.
1968. Group Composition, Ecology, and Daily Activities of Free Living Mangabeys in Uganda. *Folia Primatologica*, 8:247–262.

Clutton-Brock, T. H.
1975a. Feeding Behaviour of Red Colobus and Black and White Colobus in East Africa. *Folia Primatologica*, 23:165–207.
1975b. Ranging Behavior of Red Colobus (*Colobus badius tephrosceles*) in Gombe National Park. *Animal Behaviour*, 23:706–722.

Crook, J. H.
1970. The Socio-ecology of Primates. Pages 103–168 *in* Crook, editor, *Social Behaviour in Birds and Mammals*. London and New York: Academic Press.

Crook, J. H., and J. S. Gartlan
1966. Evolution of Primate Societies. *Nature*, 210:1200–1203.

DeVore, I.
1963. A Comparison of the Ecology and Behavior of Monkeys and Apes. Pages 301–319 *in* Washburn, editor, *Classification and Human Evolution*. Chicago: Aldine.

DeVos, A., and A. Omar
1971. Territories and Movements of Sykes Monkeys (*Cercopithecus mitis kolbi* Neuman) in Kenya. *Folia Primatologica*, 16:196–205.

Dittus, W. P. J.
1974. The Ecology and Behavior of the Toque Monkey, *Macaca sinica*. Ph.D. dissertation, University of Maryland.

Dorst, J., and P. Dandelot
1970. *A Field Guide to the Larger Mammals of Africa*. London: Collins.

Dunbar, R. I. M., and E. P. Dunbar
1974. Ecology and Population Dynamics of *Colobus guereza* in Ethiopia. *Folia Primatologica*, 21:188–209.

Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran
1972. The Relation between Ecology and Social Structure in Primates. *Science*, 176:863–874.

Ellefson, J. C.
1968. Territorial Behavior in the Common White-handed Gibbon. Pages 180–199 *in* Jay, editor, *Primates: Studies in Adaptation and Variability*. New York and London: Holt, Rinehart and Winston.

Freeland, W. J., and D. H. Janzen
1974. Strategies in Herbivory by Mammals: The Role of Plant Secondary Compounds. *American Naturalist*, 108:269–289.

Gartlan, J. S., and C. K. Brain
1968. Ecology and Social Variability in *Cercopithecus aethiops* and *C. mitis*. Pages 253–292 *in* Jay, editor, *Primates: Studies in Adaptation and Variability*. New York and London: Holt, Rinehart and Winston.

Gartlan, J. S., and T. T. Struhsaker
1972. Polyspecific Associations and Niche Separation of Rain-forest Anthropoids in Cameroon, West Africa. *Journal of Zoology, London*, 168:221–266.

Gautier, J. P.
1969. Emissions sonores d'espacement et de ralliement par deux Cercopitheques arboricoles. *Biologica Gabonica*, 23:117–145.

Gautier-Hion, A., and J. P. Gautier
1975. Les associations polyspecifiques de cercopitheques du Plateau de M'passa (Gabon). *Folia Primatologica*, 23:134–177.

Goodall, J. van Lawick
1971. *In the Shadow of Man*. Boston: Houghton Mifflin Company.

Holmes, R. T., and F. A. Pitelka
1968. Food Overlap among Coexisting Sandpipers on Northern Alaskan Tundra. *Systematic Zoology*, 17:305–318.

Hrdy, B. S.
1975. Male-male Competition and Infanticide among the Langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica*, 22:19–58.

Jay, P. C.
1965. The Common Langur of North India. Pages 197–249 *in* DeVore, editor, *Primate Behavior: Field Studies*

of Monkeys and Apes. New York: Holt, Rinehart and Winston.

Jenkins, R.
1969. Ecology of Three Species of Saltators with Special Reference to Their Frugivorous Diet. Ph.D. dissertation, Harvard University.

Jones, C., and J. Sabater Pi
1968. Comparative Ecology of *Cercocebus albigena* (Gray) and *Cercocebus torquatus* (Kerr) in Rio Muni, West Africa. *Folia Primatologica*, 9:99–113.

Kingdon, J.
1971. *East African Mammals: An Atlas of Evolution in Africa*. Volume I. London and New York: Academic Press.

Kingston, B.
1967. *Working Plan for Kibale and Itwara Central Forest Reserves*. Entebbe, Uganda: Forest Department.

Krebs, J. R.
1974. Colonial Nesting and Social Feeding as Strategies for Exploiting Food Resources in the Great Blue Heron (*Ardea herodias*). *Behaviour*, 51:99–130.

Lawrence, G. M. M.
1951. *Taxonomy of Vascular Plants*. New York: Macmillan Company.

Lumsden, W. H. R.
1951. The Night-resting Habits of Monkeys in a Small Area on the Edge of the Semliki Forest, Uganda: A Study in Relation to the Epidemiology of Sylvan Yellow Fever. *Journal of Animal Ecology*, 20:11–30.

Mackworth Praed, C. W., and C. H. B. Grant
1952. *African Handbook of Birds: Birds of Eastern and Northeastern Africa*. London and New York: Longmans Green and Company.

Marler, P.
1969. *Colobus guereza:* Territoriality and Group Composition. *Science*, 163:93–95.
1973. A Comparison of Vocalizations of Red-tailed Monkeys and Blue Monkeys, *Cercopithecus ascanius* and *C. mitis*, in Uganda. *Zeitschrift für Tierpsychologie*, 33:223–247.

Mason, W. A.
1968. Use of Space by *Callicebus* Groups. Pages 200–216 *in* Jay, editor, *Primates: Studies in Adaptation and Variability*. New York: Holt, Rinehart and Winston.

McNab, B. K.
1963. Bioenergetics and the Determination of Home Range Size. *American Naturalist*, 97:133–140.

Metcalfe, C. R., and L. Chalk
1950. *Anatomy of the Dicotyledons, I and II*. London: Oxford University Press.

Mohnot, S. M.
1971. Some Aspects of Social Changes and Infant Killing in the Hanuman Langur, *Presbytis entellus* (Primates: Cercopithecidae) in Western India. *Mammalia*, 35:175–198.

Morse, D. H.
1970. Ecological Aspects of Some Mixed-species Foraging Flocks of Birds. *Ecological Monograph*, 40:119–168.
1974. Niche Breadth as a Function of Social Dominance. *American Naturalist*, 108:818–830.

Morton, E. S.
1973. On the Evolutionary Advantages and Disadvantages of Fruit Eating in Tropical Birds. *American Naturalist*, 107:8–22.

Moynihan, M.
1962. The Organization and Probable Evolution of Some Mixed Species Flocks of Neotropical Birds. *Smithsonian Miscellaneous Collections*, 143:1–140.

Neave, S. A.
1910. On the Birds of Northern Rhodesia and the Katanga District of Congoland, Part I. *Ibis*, 1910:78–155.

Oates, J. F.
1974. The Ecology and Behaviour of the Black-and-White Colobus Monkey (*Colobus guereza* Ruppell) in East Africa. Unpublished Ph.D. dissertation, University of London.

Pielou, E. C.
1966. Measurement of Diversity in Different Types of Biological Collections. *Journal of Theoretical Biology*, 13:131–144.

Rahm, U. H.
1970. Ecology, Zoogeography, and Systematics of Some African Forest Monkeys. Pages 589–626 *in* Napier and Napier, editors, *Old World Monkeys*. London and New York: Academic Press.

Ripley, S.
1967. Intertroop Encounters among Ceylon Gray Langurs (*Presbytis entellus*). Pages 237–252 *in* Altmann, editor, *Social Communication Among Primates*. Chicago: University of Chicago Press.

Rowell, T. E.
1969. Variability in the Social Organization of Primates. Pages 283–305 *in* Morris, editor, *Primate Ethology*. New York: Doubleday.

Rudran, R.
1970. Aspects of Ecology of Two Subspecies of Purple-faced Langurs (*Presbytis senex*). M. S. thesis, University of Ceylon.
1973. Adult Male Replacement in One-male Troops of Purple-faced Langurs (*Presbytis senex senex*) and Its Effect on Population Structure. *Folia Primatologica*, 19:166–192.

Schlichte, H. J.
1975. Nahrungsverhalten von didemmeerkatzen im Nationalpark Kahuzi-Biega, Kivuhochland, Zaire. *Zeitschrift für Säugetierkunde*, 40:193–214.

Schoener, T. W.
1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*, 2:369–404.

Smith, A. D.
1959. Adequacy of Some Important Browse Species in Overwintering Mule Deer. *Journal of Range Management*, 12:8–13.

Snedecor, G. W., and W. G. Cochran
1969. *Statistical Methods*. Ames: Iowa State University Press.

Sokal, R. R., and F. J. Rohlf

1969. *Biometry: The Principles and Practice of Statistics in Biological Research.* San Francisco: W. H. Freeman and Company.

Struhsaker, T. T.

1967. Ecology of Vervet Monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology*, 48:891–904.

1969. Correlates of Ecology and Social Organization among African Cercopithecines. *Folia Primatologica*, 11:80–118.

1970. Phylogenetic Implications of Some Vocalizations of *Cercopithecus* Monkeys. Pages 365–444 *in* Napier and Napier, editors, *Old World Monkeys.* New York: Academic Press.

1974. Correlates of Ranging Behavior in a Group of Red Colobus Monkeys (*Colobus badius tephrosceles*). *American Zoologist*, 14:177–184.

1975. *Behavior and Ecology of Red Colobus Monkeys.* Chicago: University of Chicago Press.

Struhsaker, T. T., and J. F. Oates

1975. A Comparison of the Behavior and Ecology of Red Colobus and Black-and-White Colobus Monkeys in Uganda: A Summary. Pages 103–124 *in* Tuttle, editor, *Socioecology and Psychology of Primates.* The Hague: Mouton.

Sugiyama, Y.

1965. On the Social Change of Hanuman Langurs (*Presbytis entellus*) in Their Natural Condition. *Primates*, 6:381–429.

1967. Social Organization of Hanuman Langurs. Pages 221–236 *in* Altmann, editor, *Social Communication Among Primates.* Chicago: University of Chicago Press.

1968. Social Organizaiton of Chimpanzees in the Budongo Forest, Uganda. *Primates*, 9:225–258.

Teleki, G.

1973. *The Predatory Behavior of Wild Chimpanzees.* Lewisburg: Bucknell University Press.

Ward, P., and A. Zahavi

1973. The Importance of Certain Assemblages of Birds as "Information-Centres" for Food-finding. *Ibis*, 115:517–534.

Waser, P. M.

1975. Monthly Variations in Feeding and Activity Patterns of the Mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife Journal*, 13:249–263.

Waser, P. M., and O. Floody

1974. Ranging Patterns of the Mangabey, *Cercocebus albigena*, in the Kibale Forest, Uganda. *Zeitschrift für Tierpsychologie*, 35:85–101.

Willis, E. O.

1972. The Behavior of Spotted Ant Birds. *Ornithological Monographs*, 10:1–162.

Winton, A. L., and K. B. Winton

1935. *The Structure and Composition of Foods.* Volume II. New York: John Wiley and Sons.

Yoshiba, K.

1968. Local and Intertroop Variability in Ecology and Social Behavior of Common Indian Langurs. Pages 217–242 *in* Jay, editor, *Primates: Studies in Adaptation and Variability.* New York: Holt, Rinehart and Winston.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with approval of the appropriate museum authority on Form SI–36. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of designated committees or museum directors.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of the manuscripts and art.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1¼″ margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9b." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9b." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.