

Primate Communities: Their Structure and Role in Tropical Ecosystems¹

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The structure of primate communities living in a number of undisturbed areas is described and compared. Species richness is highest in tropical rain forests of Africa and South America, where up to 14 different species can share the same habitat. The number of sympatric primates in woodlands and savannas is always much lower. Some striking differences in community structure may be observed between communities living in apparently similar habitats. Three major factors may be held responsible for such discrepancies: history and paleoecology, present spatial heterogeneity of the vegetation, and competition with other taxonomic groups. The role of primates in the functioning of forest ecosystems is discussed. Though their trophic impact may be important, the role they play in seed dispersal appears to be more significant; they contribute greatly to homeostasis, as well as to regeneration, of the rain forests. A number of ecological traits are particularly developed among primates and may have contributed to the rapid evolutionary success of the order. Their predominantly vegetarian diet allows them to build up higher population densities than sympatric carnivorous mammals; their arborealism permits them to make use of all edible plant material available in a tridimensional environment; the opportunistic tendencies of some cebids, cercopithecids, and pongids enable them to take advantage of a variety of habitats and situations; and finally, an extended socialization period and a long life-span, allowing them to develop social traditions, give to many of them a further possibility to adapt quickly to novel situations.

KEY WORDS: primate communities; spatial heterogeneity; competition; rain-forest homeostasis.

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INTRODUCTION

The attention of primatologists has mostly been focused, during the past two decades, on the demographic and social characteristics of single species populations. Much less attention has, in fact, been given to the inter-specific relationships between sympatric primate populations or to the competitive interactions between primate communities and the other vertebrate and invertebrate species sharing the same kinds of resources.

The purpose of this paper is to review the literature on these problems and to provide at least some preliminary answers to the following questions: (1) What is the place of nonhuman primates in tropical ecosystems and their relationship with sympatric vertebrates? (2) Do primates play any specific role in the functioning of these systems? (3) Are there any ecological attributes which make primates unique in comparison with other tropical mammals of similar size and give them a definite advantage over other mammalian orders?

THE COMMUNITY CONCEPT

Primates are not distributed at random in physically suitable environments. They tend to form communities, that is, taxonomic assemblages of interacting populations living in a given area and usually having rather similar life habits (Odum, 1959; MacNaughton and Wolf, 1973; Ricklefs, 1975). Each of these communities is made up of a number of species which can themselves be grouped in a number of gross ecological categories or "clusters of functionally similar species" (Roots, 1967). A preliminary allocation of primate species into such "guilds" has already been undertaken by the pioneer field primatologists. Nowadays the most commonly used ecological categories are those proposed by Clutton-Brock and Harvey (1977) on the basis of (a) the time of activity of the species (nocturnal versus diurnal), (b) their primarily arboreal or terrestrial habits, and (c) their primarily frugivorous, folivorous, or "insectivorous" diet. In this way seven primate guilds can be distinguished (Table I), within which every participating species maintains its own more or less clearly defined "ecological niche" (*sensu* Hutchison, 1978).

Within such taxonomically based communities, the co-occurring species not only interact with one another, however. In many cases they also compete, permanently or seasonally, with other vertebrate and even invertebrate groups which can either "share the cake" with the primates, or conversely prevent them from advantageously exploiting most of the available resources. This is probably why, as shown in Table I, some "potential guilds" are not presently represented among modern primates;

Table I. Primate Guilds

	Codes
Extant	
Diurnal, arboreal, frugivorous (gums included)	DAF
Diurnal, arboreal, folivorous	DAL
Diurnal, terrestrial, frugivorous	DTF
Diurnal, terrestrial, folivorous (grass included)	DTL
Nocturnal, arboreal, "insectivorous"	NAI
Nocturnal, arboreal, frugivorous (gums included)	NAF
Nocturnal, arboreal, folivorous	NAL
Missing	
Diurnal, arboreal, "insectivorous"	DAI
Diurnal, terrestrial, "insectivorous"	DTI
Nocturnal, terrestrial, "insectivorous"	NTI
Nocturnal, terrestrial, frugivorous	NTF
Nocturnal, terrestrial, folivorous	NTL

other animal groups, better adapted morphologically, physiologically, or behaviorally, can prevent primates from competing successfully with them.

A study of present-day primate communities cannot, therefore, be limited to a mere study of the ways in which sympatric species partition among themselves the resources of their environment. We have also to take into account the role of other species in the entire biotic community, of which the primates are only a small, though particularly fascinating, component. This has very seldom been attempted, for obvious technical reasons, but should be one of the major tasks of tropical ecology in the years to come.

One of the unexpected characteristics of the primate communities, as defined above, is their often striking differences in structure and function, not only between continents but also between otherwise very similar tropical landscapes. Why is this so? This is the first question to be answered, by comparing some undisturbed primate communities.

THE PLACE OF PRIMATES IN TROPICAL ECOSYSTEMS

Species Richness

The number of primate species present in 20 areas located in the three major categories of tropical landscapes, in both the Old and the New Worlds, is shown in Table II. Most of these study sites can be considered as presently undisturbed by recent human activities, especially poaching and logging, and have been protected for more than a decade.

Table II. Primate Species Richness

		Number of Species	Sources ^a
Rain forest (RF)			
Africa			
M'Passa, Gabon	Lowland forest	14	1
Tai, Ivory Coast	Lowland forest	11	2
Kibale, Uganda	Mountain forest	10	3
Liboy River, Gabon	Swamp forest	13	4
Madagascar			
Perinet	Lowland forest	6	5
Asia			
Kutai, Kalimantan	Lowland forest	8	6
Kuala Lompat, W. Malaysia	Lowland forest	7	7
Neotropics			
Cocha Cashu, Peru	Lowland forest	13	8
Rio Aripuana, Brazil	Lowland forest	11	9
Raleighvallen-Votzberg, Suriname	Lowland forest	8	10
Suframa, Brazil	Lowland forest	7	9
Barro Colorado, Panama	Lowland forest	5	11
Woodland (Wd)			
Africa			
Gombe, Tanzania	Woodland with gallery forest	7	12
Madagascar			
Berenty	<i>Didierea</i> bush with gallery forest	5	13
Asia			
Polonnaruwa, Sri Lanka	Archeological site	4	14
Savanna (S)			
Africa			
Bole valley, Ethiopia	Tree savanna	5	15
Amboseli, Kenya	Tree savanna	3	16
N'Dioum, Senegal	Gallery forest in Sahelian Zone	2	17
Fété Olé, Senegal	Sahelian savanna	1	18
Neotropics			
Masaguaral, Venezuela	<i>Llanos</i> with gallery forest	2	19

^aSources: (1) same sources as in Table III; (2) same sources as in Table V; (3) Struhsaker (1975, 1978), Struhsaker and Leland (1979), Rudran (1978), Oates (1977); (4) same sources as in Table IV; (5) Pollock (1975), J. J. Petter and R. Albignac (personal communication); (6) Rodman (1978); (7) Chivers (1980), Chivers and Davies (1979), Curtin and Chivers (1978), Mackinnon and Mackinnon (1980), Raemekers and Chivers (1980); (8) Freese *et al.* (1982), Janson (1975); (9) Ayres (1981); (10) Mittermeier (1977), Mittermeier and Van Roosmalen (1981), Van Roosmalen (1980, personal communication), Van Roosmalen *et al.* (1981), Buchanan *et al.* (1981); (11) Eisenberg and Thorington (1973), Smith (1977); (12) Teleki *et al.* (1976), Ransom (1981), Clutton-Brock (1975); (13) Richard (1978), Richard and Sussman (1975), Budnitz and Dainis (1975), Charles-Dominique and Hladik (1971), Sussman (1977), Hladik *et al.* (1980); (14) Hladik and Hladik (1972), Eisenberg *et al.* (1972), Dittus (1975); (15) Dunbar and Dunbar (1974); (16) DeVore and Hall (1965), Struhsaker (1967); (17) Galat and Galat-Luong, personal communication; (18) Poulet in Bourlière (1978); (19) Eisenberg *et al.* (1979).

It immediately becomes apparent that primate species are more numerous in forest habitats than in savanna environments, as is the case for most animal groups (Bourlière, 1983a). Their maximum number, 13 or 14, is always found in rain forests, in Africa, Asia, and the Neotropics. The relatively high species richness of primates in woodlands and savannas, on the other hand, is due to the customary mixture of open grasslands and gallery forests, which enable a number of true forest species to enter savannas along rivers, sometimes for hundreds of miles. Very few primate species live permanently in extensive treeless areas, *Erythrocebus patas* being an exception, though it usually prefers tree savannas to grasslands.

It must also be noted at this stage that species richness of forest primates is of the same order of magnitude as that of sympatric ungulates. For example, 10 species of prosimians, monkeys, and apes and 16 species of ungulates live in the Tai National Park, Ivory Coast, whereas 14 primate and 15 ungulate species have been recorded on the M-Passa plateau, near Makokou, Northeast Gabon. At Kuala Lompat, West Malaysia, the two taxonomic groups are represented by 7 species each, and at Barro Colorado by 5 species each.

This is no longer the case in savanna environments, where ungulates generally outnumber primates, in both number of species and of individuals. For instance, the number of ungulate species ranges from 11 to 20 in eight African savanna sites and from 6 to 10 in six Asian areas (Bourlière, 1983b). It is only in the neotropics that ungulates are not, for well-known historical reasons, more numerous in species than primates. In the *llanos* of Masaguaral, Venezuela, for example, the two groups are represented by two species each.

When comparing the variety of species in different habitats, most community ecologists prefer to use indices of diversity rather than the simple number of species present in the community. Besides species richness, these indices also take into account the relative abundance of each species. Unfortunately, population censuses are notoriously difficult, if not impossible, to carry out in forest environments; it therefore seems premature to use diversity indices for the comparison of primate forest communities, particularly since Shannon's and Margalef's indices can give contradictory results (Mittermeier, 1977).

Community Structure

The best way to demonstrate the differences in number of species and guild composition of primate communities living in apparently similar environments is to compare the structure of a number of well-studied com-

munities. This is done in Tables III to V, which tabulate the species actually present, or which have existed in the recent past at three African rain-forest study sites, one in the Ivory Coast and two in Northeast Gabon. In each case, information is given on estimated densities (ind/km²), guilds (see Table I), preferred habitats (RF, mature rain forest; SG, second growth; SF, riparian forest), forest layer(s) most frequently used (C, canopy; M, middle forest layer; L, lower forest layer; G, ground level), and average body weights (kg). Not all species live permanently in the small areas studied; in addition to permanent residents, some species with very large home ranges are listed as transients (T). For further details, the reader is referred to the original publications mentioned in the footnotes to each table.

The major difference in community structure among these three West African sites lies in the absence of *Colobus* monkeys at M'Passa, as opposed to the Liboy River study site (located less than 40 km to the northeast, as the crow flies, and the Tai forest, where three sympatric species of *Colobus* are common.

Differences in community structure are also found in the three neotropical forest sites shown in Table VI. Nocturnal primates are conspicuously absent in the Raleighvallen-Voltzberg Nature Reserve in Suriname, whereas *Aotus trivirgatus* is found both in Pamama (Barro Colorado) and in Eastern Peru (Cocha Cashu). The two undisturbed

Table III. Rain Forest, M'Passa (Ipasa) Plateau, Gabon (Latitude, 0.34 N; Longitude, 12.52 E; Altitude, 500 m; Study Area, 3 km²)^a

Species	Density (ind/km ²)	Guild ^b	Habitat ^c	Layer ^d	Body wt (kg)
<i>Cercopithecus</i>					
<i>C. cephus</i>	12-39	DAF	RF	L/M	3.5
<i>C. pogonias</i>	22.5	DAF	RF	C/M	3.8
<i>C. nictitans</i>	22.5	DAF	RF	C/M	5.4
<i>C. neglectus</i>	30-50	DAF	SF/RF	L/G	5.5
<i>Miopithecus talapoin</i>	92	DAF	SF	L	1.2
<i>Cercocebus albigena</i>	Extinct	DAF	RF	L/G	7.7
<i>Mandrillus sphinx</i>	Transient	DTF	RF	G/M	18.0
<i>Pan troglodytes</i>	Scarce	DAF	RF	M/G	45.0
<i>Gorilla gorilla</i>	Extinct	DTL	RF	G	115.0
<i>Perodicticus potto</i>	8	NAF	RF	C	1.1
<i>Euoticus elegantulus</i>	15	NAF	RF	C	0.3
<i>Galago alleni</i>	15	NAF	RF	L	0.26
<i>Galago demidovii</i>	50	NAI	RF/SG	C	0.06
<i>Arctocebus calabarensis</i>	2	NAI	SG	L(Tf) ^e	0.21

^aSources: Charles-Dominique (1971, 1977, personal communication); Gautier-Hion (1980); Gautier-Hion and Gautier (1974); Gautier-Hion *et al.* (1980, personal communication).

^bAbbreviations as in Table I.

^cRF, mature rain forest; SG, second growth; SF, riparian forest.

^dC, canopy; M, middle forest layer; L, lower forest layer; G, ground level.

^eTf, tree falls.

Table IV. Swamp Forest, Liboy (Liboui) River, Gabon (Latitude, 0.45 N; Longitude, 13.2 E; Altitude, 550 m; Study Area, 2 km²)^a

Species	Density (ind/km ²)	Guild ^b	Habitat ^b	Layer ^b	Body wt (kg)
<i>Cercopithecus</i>					
<i>C. neglectus</i>	28.0	DAF	SF	L/G	5.5
<i>C. nictitans</i>	22.5	DAF	RF	C/M	5.4
<i>C. pogonias</i>	22.5	DAF	RF	C/M	3.8
<i>C. cephus</i>	16.5–27.7	DAF	RF	L/M	3.5
<i>Miopithecus talapoin</i>	26–92	DAF	SF	L	1.2
<i>Cercocebus</i>					
<i>C. galeritus</i>	7.7–12.5	DAF	SF	L/G	7.8
<i>C. albigena</i>	8.5	DAF	RF	L/G	7.7
<i>Colobus guereza</i>	Transient	DAL/F	RF	M/C	9
<i>Pan troglodytes</i>	Transient	DAF	RF	M/G	45
<i>Gorilla gorilla</i>	Transient	DTL	RF	G	115
<i>Perodicticus potto</i>	Likely	NAF	RF	C	1.1
<i>Galago alleni</i>	Likely	NAF	RF	L	0.26
<i>Euoticus elegantulus</i>	Likely	NAF	RF	C	0.3

^aSources: Quris (1975, 1976, personal communication); Charles-Dominique (personal communication).

^bAbbreviations as in Table III.

dipterocarp forests of Southeast Asia are much more similar to each other, floristically and structurally, than the three tropical American ones and this might account for their very similar primate communities (Chivers, 1980; Freese *et al.*, 1982; Mittermeier and Van Roosmalen, 1981). As for the lemurs of the Madagascar rain-forest site (Perinet), they quite likely per-

Table V. Rain Forest, Tai National Park, Ivory Coast (Latitude, 5.52 N; Longitude, 7.27 W; Altitude, 123 m; Study Area, CH Zone, 3 km²)^a

Species	Density (ind/km ²)	Guild ^b	Habitat ^b	Layer ^b	Body wt (kg)
<i>Cercopithecus</i>					
<i>C. diana</i>	17.5	DAF	RF	C	4.3
<i>C. petaurista</i>	29.3+	DAF/I	RF	L	1.8
<i>C. campbelli</i>	15.0	DAF	RF	L/M	4.1
<i>C. nictitans</i>		DAF	RF	C/M	
<i>Cercocebus atys</i>	10.0	DAF	RF	G/L	5.8
<i>Colobus</i>					
<i>C. badius</i>	66.0	DAL	RF	C(e) ^c	6.9
<i>C. polykomos</i>	23.5	DAL/F	RF	M	7.1
<i>C. verus</i>	21.0	DAL	RF/SF	L	3.9
<i>Pan troglodytes</i>	1.3	DAF	RF	M/G	45.0
<i>Perodicticus potto</i>	No figures	NAF	RF	C	1.1
<i>Galago demidovii</i>	No figures	NAI	RF/SG	C	0.06

^aSources: Galat and Galat-Luong (1982, personal communication); C. Boesch (personal communication).

^bAbbreviations as in Table III.

^ce, emergent trees.

Table VI. Allocation of Species to Major Primate Guilds in 17 Study Sites^a

	Guild							Total
	DAF	DAL	DTF	DTL	NAI	NAF	NAL	
Africa								
Rain forest (RF)								
M'Passa, Gabon	7		1	1	2	3		14
Tai, Ivory Coast	5	3			1	1		10
Kibale, Uganda	5	2			1	2		10
Swamp forest (SF)								
Liboy River, Gabon	8	1		1		3		13
Woodland (Wd)								
Gombe, Tanzania	5	1				1		7
Savanna landscape with gallery forest (S)								
Bole valley, Ethiopia	1	1	1	1	1			5
Amboseli, Kenya	1			1		1		3
N'Dioum, Senegal	1			1				2
Fété-Olé, Senegal				1				1
Madagascar								
Rain forest (RF)								
Perinet	2	2			1	1		6
<i>Didierea</i> bush								
Berenty	2				1	1	1	5
Asia								
Rain forest (RF)								
Kutai, Kalimantan	6	1			1			8
Kuala Lompat, W. Malaysia	5	1			1			7
Woodland (Wd)								
Polonnaruwa, Sri Lanka	1	2			1			4
Neotropics								
Rain forest (RF)								
Cocha Cashu, Manu N.P., Peru	11	1				1		13
Raleighvallen-Votzberg, N.R., Suriname	7	1						8
Barro Colorado, Panama	3	1				1		5

^aSources as in Table II.

form the same functional roles within the forest community as the monkeys and galagines of the African continent (Martin, 1977; Charles-Dominique, 1977; Tattersall, 1982).

In woodlands (Wd) and savannas (S), species richness is everywhere much lower than in most rain-forest sites (Table II), but a variety of guilds is still represented. The poorest sites, in numbers of both species and guilds, are those areas which are most remote from the forested regions, such as the Sahel of Northern Senegal (N'Dioum and Fété Olé; Galat and Galat-Luong, personal communication), or those located in the middle of large open grasslands such as the Venezuelan *llanos* (Masaguaral; Eisenberg *et al.*, 1979).

Mangroves are a very particular habitat which is nevertheless exploited by *Nasalis larvatus* in Kutai and elsewhere in Borneo and by *Cercocebus aethiops sabaeus* in the Sine-Saloum delta of Senegal (Galat and Galat-Luong, 1976).

Some general trends in community structure nevertheless emerge from Table VI. The most striking is the scarcity of nocturnal arboreal primates in the neotropics as compared with the numerous prosimian species of Africa, Madagascar, and tropical Asia. Furthermore, *Aotus trivirgatus* is far from ubiquitous throughout the lowland rain-forest zone of South America, being conspicuously absent from Suriname and French Guiana, for instance. Nocturnal arboreal frugivores do not exist in Asia and nocturnal arboreal folivores are restricted to Madagascar (*Lepilemur mustelinus*).

Among diurnal primates, the arboreal and frugivorous species are the most numerous everywhere, except in the extremely seasonal savannas, where trees are scarce and fruit production is both small and limited in duration. Diurnal terrestrial frugivores are restricted to the Old World. In Africa, the two forest baboons (*Mandrillus sphinx* and *M. leucophaeus*) are mostly frugivorous (Jouventin, 1975), whereas their savanna relatives tend to become more graminivorous (feeding on fresh grass, roots, and rhizomes as much as on fruits and seeds) and even omnivorous (supplementing their basically vegetarian diet with invertebrates and small vertebrates). The patas (*Erythrocebus patas*) has a similar diet and some Asiatic macaques probably behaved in the same way in the more open areas of their ranges before the advent of modern humans.

How can we explain the differences in community structure so often encountered between similar environments, often located only a few tens of kilometers apart? Three major categories of factors are probably responsible for the unexpected absence of particular taxonomic and ecological categories in some tropical habitats.

History has to be taken into consideration first. It is obvious that the present-day geographical distribution of primates depends primarily on the past history of the order. There is no mystery, for instance, about the absence of prosimians in the neotropics. What is not so obvious is the extreme scarcity (and sometimes the total absence) of nocturnal primates in neotropical rain forests. History also enters the picture through the differences of geographical history between different tropical forest areas, particularly through their different degrees of fragmentation during the wet and dry climate phases of the Pleistocene. However, such an explanation cannot tell us why there are no colobus monkeys in the M'Passa area, whereas *Colobus guereza* is found 40 km upstream to the northeast, and *C. satanas* 30 km downstream to the southwest, despite the fact that the whole Makokou area is part of the Gabon-South Cameroon forest refuge, one of

the two most important refuges in Africa during the driest climatic phases of the Pleistocene (Hamilton, 1976).

The second, and probably most important, factor underlying diversity in community structure is spatial heterogeneity. As human observers familiar with the often monotonous and frequently impoverished ecosystems of our native northern latitudes, we tend to consider that tropical environments are more uniform than they actually are. This is the customary attitude of most visitors of the tropics, who often complain of the monotony of the "Green Hell" or of the endless "game plains." The naturalist cannot share such a simplistic attitude, and as soon as he/she starts to study in depth the vegetation as well as the fauna, he/she very quickly realizes that tropical environments are very seldom homogeneous; spatial heterogeneity is the rule rather than the exception, even over small surface areas undisturbed by human activities.

The forest landscape, for instance, is actually a mosaic of various stages of regeneration of the mature forest, following small but frequent natural accidents, such as tree falls or landslips. On the M'Passa plateau, for instance, the high number of uprooted and broken trees and of tree stumps is striking. Florence (1980) has carefully mapped all gaps due to recent tree falls on the primatologists' study area of the plateau and found that the younger ones (less than 5 years old) covered 8% of the 35 ha surveyed. Both the floristic and the physical structures of the vegetation in a young gap are, of course, very different from those of older gaps and mature forest itself, thus creating a patchwork of habitats whose flora and fauna are often very dissimilar. The situation in M'Passa is not at all exceptional; both Whitmore (1975) in Southeast Asia and Oldeman (1974) in French Guiana indicate higher percentages of tree falls than those recorded at M'Passa. For primates, there are two consequences of this mosaic structure of a mature rain forest: not only do the food resources (leaves, fruit, insect prey) vary from one forest patch to the next, but the stratification of the vegetation, the density of the undergrowth, and the size, nature, and orientation of the supports of locomotion vary simultaneously. Although very little attention has been given, so far, to such factors of habitat selection among primates, we do know that some species can be restricted to certain microhabitats within a given forest. At M'Passa, for instance, Charles-Dominique (1977) has shown that the needle-clawed bushbaby *Euoticus elegantulus* is closely associated with *Entada gigas*, a liana whose sap constitutes an important part of its diet. In the same area, the Angwantibo *Arctocebus calabarensis* is confined to the undergrowth of old tree falls, where the forest is particularly rich in lianas. Again at M'Passa, Gautier-Hion *et al.* (1981) have shown that *Cercopithecus cephus*, when living in monospecific troops, consistently rest during the day in the densest forest

patches, whereas they select those with the more open undergrowth for night resting. Of the two sympatric species of *Cercocebus* living in the Liboy River study site, only *C. galeritus* is permanently restricted to periodically flooded forest, *C. albigena* being a temporary visitor (Quris, 1975, 1976).

Spatial heterogeneity is less obvious in savanna than in forest environments, but it readily becomes apparent once a detailed analysis of the grass cover is made. For primates, however, the most important environmental parameters in these open landscapes are the structure and extent of the tree and shrub layers, the availability of raised resting places for the night (whether they be tree groves, cliffs, "kopjes," or termite mounds), and the presence of sources of permanent water. Every savanna species has, for instance, its own preferred sleeping sites. This led Hans Kummer (1971) to write that in east Africa "trees but no cliffs meant anubis (baboons), cliffs but no trees meant hamadryas."

The pervasive influence of the spatial heterogeneity of most tropical environments should not be overlooked by ecologists and conservationists who wish to monitor population changes of primates. Following Eisenberg's and Lockhart's (1972) suggestion, great care should be taken to distinguish crude densities from ecological densities. A crude density refers to the number of individuals censused within the total area surveyed; it does not correct for microhabitat differences. An ecological density relates to the number of individuals living in a surface area including only the suitable habitat for the species in question.

The third possible major cause of differences in community structure is competition, both between sympatric species of primates and between primates and other animal taxa. Numerous attempts have been made during the past two decades to quantify at least certain parameters of the multi-dimensional niche of primates. This has led to a number of detailed studies of time, space, and food partitioning between sympatric primate species. I do not intend to review here all the relevant literature on this subject but limit my comments to a few points.

On the whole, it remains true to say that sympatric species belonging to the same guild are generally not active at the same time, do not make use of the same vegetation layers, and do not eat the same amount of the same food (unless food is temporarily superabundant). However, prolonged field studies extended over a whole-year cycle, and even a number of consecutive years, have recently shown that resource partitioning between sympatric primates is not always as simple as used to be thought not so long ago.

First, seasonal changes in the diet are the rule, even in species sharing one small area in a "predictable" habitat. This is well illustrated by the three *Cercopithecus* species studied by Gautier-Hion (1980) at M'Passa (*C. nictitans*, *C. cephus*, and *C. pogonias*) which, furthermore, may frequently

live in mixed troops. Fruits, leaves, and animal prey form the bulk of the diet of the three species, with subtle differences among the three: *C. nictitans* eats fewer fruits and insects and more leaves, *C. pogonias* eats more fruits and insects and fewer leaves, and the diet of *C. cephus* is intermediate between the two. However, fewer fruits are eaten by the first two species during the major dry season and the beginning of the minor dry season, fewer leaves during the minor dry season and the two rainy seasons, and less animal matter during the two dry seasons and the beginning of the major rainy season. Seasonal variations are less marked for *C. cephus*. On the whole, diet overlap of these three sympatric monkeys is great during most of the year, but decreases when fruits, young leaves, and animal prey become less abundant. Other examples of seasonal variations in diet have been documented for species as different as Verreaux's sifaka (Richard, 1978), the rhesus monkey (Lindburg, 1977), leaf-monkeys (Hladik, 1977), the guereza (Oates, 1977), the tantalus monkey (Kavanagh, 1978) and the mountain gorilla (Fossey and Harcourt, 1977).

Intraspecific, nonseasonal, variations in the dietary parameters of a primate's niche are, furthermore, the rule in some opportunistic species which can live in a broad spectrum of environments. It is easy to understand, for instance, the differences in diet of the populations of green monkeys (*Cercopithecus aethiops sabaeus*) inhabiting the sahelian riverine forest of the Lower Senegal River and the mangrove of the Sine-Saloum delta (Galat and Galat-Luong, 1978). In the *Acacia nilotica* gallery forest, animal prey is rarely eaten and represents only 11% of the ingestion scores, compared to 40.9% in the mangrove, where the abundant fiddler crabs are a favorite prey. But there are also obvious dietary differences between populations of species living in apparently similar environments. For instance, fruits and seeds account for 73.2% of the diet of *Cercocebus albigena* in the Liboy River area, compared to only 58.8% in the Kibale forest. For *Colobus guereza* the difference is even more impressive: 48.5% vs 14.1%. Although part of these differences might be explained by the different techniques of diet analysis used by Quris (1975), Gautier-Hion (1978), and Struhsaker (1978), some additional explanation is plausible. Gautier-Hion (1983) feels that the higher consumption of fruits and seeds by the two species in Gabon might be due to the higher species richness of trees (hence a higher fruit diversity) at M'Passa [95 species of trees $DBH \geq 5$ cm on 0.4 ha (A. Hladik, 1978)] than at Kibale [32.8 to 35.7 tree species per ha (Struhsaker, 1975)].

The more sophisticated studies of diet and feeding behavior carried out during the past decade have also revealed some unexpected factors influencing the selection of food. Gautier-Hion (1980) has shown, for example, that in a given season the diet of males and females of the same

species of *Cercopithecus* can differ in the same habitat. Indeed, some of these sex differences in diet can be as important as those occurring between adults of other sympatric species of *Cercopithecus*.

Competition between co-occurring species within a given guild may, however, be sometimes reduced—if still occurring at all. Old World forest monkeys, for instance, can form semistable associations with a superspecific social organization. Such polyspecific troops are particularly frequent in African rain forests, where they have been studied for years by a number of primatologists; see Gautier and Gautier-Hion (1969, 1983), Gartlan and Struhsaker (1972), Galat Luong and Galat (1978), Struhsaker (1981), and Gautier-Hion *et al.* (1983). The associated troops may stay together for part or most of the day, but they are not temporary assemblages; they can last for months and, quite likely, years. Gautier-Hion *et al.* (1983) convincingly demonstrated that such mutual relationships result in a change in habitat use for the participating species, leading to an increased foraging efficiency resulting from a better selection of fruiting trees. When associated, the three *Cercopithecus* species (*C. nictitans*, *C. pogonias*, and *C. cephus*) tend to be less closely confined to their customary forest layer and to exploit vegetation types they seldom visit while foraging alone; their diet is therefore more diversified. Furthermore, a polyspecific troop's daily range is always larger than that of single troops of the contributing species; however, the area visited appears to be less intensively exploited—a fact which, if general, might be considered as a definite benefit for the habitat itself.

In addition to interspecific competition between primate species, competition with other sympatric animal taxa exploiting the same resource categories may at times occur. Fruits and young leaves are two kinds of food which are exploited in a rain forest by a large number of “vegetarian” animals, both vertebrates and invertebrates. The sloths (*Choloepus* and *Bradypus*) of the neotropics and the African tree-hyraxes (*Dendrohyrax*) certainly compete with sympatric primate leaf-eaters, especially since some of them can reach very high biomasses [2130 kg/km² for sloths at Barro Colorado, for instance, according to Montgomery and Sunquist (1975)]. Competition with sloths has in fact been advocated to explain the relatively low biomass of howler monkeys at Barro Colorado (438 kg/km²), as opposed to the huge biomass of howlers found at Hacienda Barqueta (4170 kg/km²), where there are no sloths (Baldwin and Baldwin, 1976). However, such a simple explanation cannot be considered valid, as the biomass of howlers is also very low at Raleighvallen-Votzberg (119 kg/km²) and at Cocha Cashu (178 kg/km²), two study sites where sloths are lacking or very scarce. Insects, particularly caterpillars, can also become very serious competitors. Whitmore (1975) records the case of an unidentified tussockmoth

(Hymantridae) defoliating the crowns of *Shorea albida* in Sarawak, to such an extent that the trees subsequently died. The scale was spectacular, the largest area affected being 31 km long! For fruits, major competitors of monkeys are frugivorous bats and birds. The latter, however, are much scarcer in Africa than in Asia and the neotropics. There is also a certain partitioning of fruits, depending on their size, and possibly color and odor (Janson, 1983). On the whole, primates feed on larger fruits than bats and birds, figs being an obvious exception. As for animal prey, the major competitors of small tamarins and marmosets in neotropical forests might conceivably be didelphid marsupials. The latter are, however, mainly active at night, which means that they probably do not catch the same kind of prey as diurnal monkeys. Scansorial reptiles might possibly be more important competitors, but the matter has never been properly investigated.

In savannas, the few well-adapted and generally opportunistic primate species do not face any real competitors among the ungulates. The vegetarian part of their diet is far more varied than that of most hoofed mammals and their omnivorous tendencies are shared only by the wild pigs (Suidae).

THE ROLE OF PRIMATES IN TROPICAL ECOSYSTEMS

The functions of primates in tropical ecosystems are hard to evaluate. Their present-day populations have recently been so much affected by human activities that they cannot be considered as representative of those existing even a century ago. Monkeys have been hunted for food by most forest hunter-gatherers down the ages, both in the paleotropics and in the neotropics, and the impact of such traditional hunting was already selective; large and medium-sized species were more often killed than the smaller (often nocturnal) species. The spread of firearms has further accentuated this trend. Comparing primate densities in 14 Peruvian and Bolivian sites, Freese *et al.* (1981) have shown that hunting significantly reduces the average densities of monkeys the size of *Saimiri* and larger, below the densities found in protected areas. On the contrary, the small callitrichids show no evidence of having depressed densities in unprotected areas. Forest exploitation by modern humans has an even stronger effect on primate communities. The selective exploitation of larger trees and the poisoning of unmarketable species such as many *Ficus* spp. endanger many primate species, but some of them are particularly affected. For example, the selective felling of tall emergent trees in the Tai forest seems to be more harmful for the Diana monkey, *Cercopithecus diana*, than for most other sympatric species of *Cercopithecus* and *Colobus* (Galat, personal communication).

Nowadays an evaluation of the role played by primate communities in tropical ecosystems can therefore be attempted only in the few remaining areas of large size enjoying complete protection for a few decades at least. Smaller reserves, being no more than "forest islands" isolated in the middle of large "developed" areas, cannot be considered as representative samples of the conditions prevailing in the same zones a century ago; they are mere refuges whose plant and animal communities are often quite "unbalanced," due to the mass immigration of a few "generalist" species and the disappearance of many "specialist" species whose populations are, in any case, often very small.

It is, therefore, dangerous to generalize on the basis of the limited data presently available. What is certain, however, is that the trophic impact of some "undisturbed" primate communities is far from negligible. Contrary to what has often been stated, primates sometimes do constitute an important group of mammalian primary consumers. Struhsaker (1975) was the first to call attention to this point: in compartment 30 of the Kibale forest he recorded primate biomasses reaching 2217 to 3578 kg/km². This was equivalent to about 55 to 89% of the ungulate biomass of the Serengeti ecosystem. More figures on primate community biomasses are given in Table VII for tropical forests. Figures averaging 1000 kg/km² are (or were recently) more common in the rain forests of Africa, Asia, and the neotropics than commonly realized. We do not have similar data for primate communities living in savannas, but the few figures available for single species populations listed in Table VIII show that biomasses over 1000 kg/km² are also not exceptional in such areas, when little disturbed by human activities.

Primates are notable consumers of plant and, to a much lesser extent, of animal material. At the ecosystem level they also exert a very important feedback control on the vegetation itself; they are essential for maintenance of homeostasis of the forest ecosystem. They share this role with relatively few other animal groups, mostly some insects, birds, and bats. The respective influence of these three taxonomic categories varies according to locality and circumstances, but it is always critical for forest regeneration and survival.

The role of primates in pollination is certainly discreet. A number of lemurs and bushbabies have been recorded feeding on nectar without destroying the flowers (Sussman, 1978). They all belong to nocturnal species and appear to visit flowers normally pollinated by bats. Most of the relevant observations have been made in Madagascar and it is quite possible that the nocturnal prosimians here occupy, at least to some extent, the plant-visiting bat niche, nectarivorous bats being rare or absent. Some

Table VII. Biomass Estimates (kg/km²) for 18 Primate Communities, Rain-Forest Sites, Except Where Otherwise Mentioned (Same Sources as for Table II, Except Where Specified)

Africa		Asia		Neotropics ^a	
Kibale forest, Uganda (10 sp)	2217	Polonnaruwa, Sri Lanka (Wd) (4 sp)	2840	Hacienda Barqueta, Panama (3 sp)	4712-5022
Tai forest, Ivory Coast (10 sp)	1025	Kuala Lompat, W. Malaysia (7 sp)	736-1295	Rupununi River, Guyana (4 sp)	1306
Liboy River, Gabon (13 sp) (SF)	> 595-761	Mean of 5 lowland sites in		El Triunfo, Bolivia (4 sp)	704-1129
M'Passa, Gabon (14 sp)	> 524-749	W. Malaysia (6 sp) ^b	750	Cocha Cashu, Peru (11 sp)	367-798
		Ketambe, Sumatra (6 sp)	727	Essequibo River, Guyana (6 sp)	620
		Kutai, Kalimantan (9 sp)	312	Barro Colorado Island, Panama (5 sp)	418-542
				Ralleighvallen-Voltzberg N.R., Suriname (8 sp)	287
				Samiria, Peru (7 sp)	272
				La Macarena, Colombia (4 sp)	129-233

^aSource: Freese *et al.* (1982).

^bSource: Marsh and Wilson (1981).

Table VIII. Densities and Biomasses of Primarily Terrestrial Primates in Some Woodland and Savanna Habitats

Site	Density (ind/km ²)	Biomass (kg/km ²)	Mean body wt (kg)	Sources ^a
Gombe, Tanzania				
<i>Papio anubis</i>	104–156	1040–1560	10	1
Ishasha, Uganda				
<i>Papio anubis</i>	> 73	> 730	10	2
Amboseli, Kenya				
<i>Papio cynocephalus</i>	> 65	> 650	10	3
Nairobi N.P., Kenya				
<i>Papio anubis</i>	26	260	10	3
Bole valley, Ethiopia				
<i>Papio anubis</i> ^b	26	206	7.9 ^c	4
<i>Theropithecus gelada</i> ^d	82	1361	5.6 ^c	4

^aSources: (1) Ransom (1981); (2) Rowell (1966); (3) DeVore and Hall (1965); (4) Dunbar and Dunbar (1974).

^bGrasses account for 39.3% of the diet.

^cAverage weights taking into account the age structure of the population; all juveniles and infants were counted as equal to half the weight of an adult female.

^dGrasses account for 97.6% of the diet.

diurnal neotropical monkeys may also be important as pollinators (Janson *et al.*, 1981; Tores de Assumpção, 1981; Janson, 1983; Happel, 1984).

Primates play a much more important role in ensuring the dissemination of seeds of forest trees and lianas (zoochory). Even though the importance and fate of this "seed flux" has not yet been properly quantified, it is certainly of major importance as shown by the Hladiks (1967, 1969) in Gabon and Barro-Colorado. Most mature forest trees are indeed unable to produce healthy seedlings, if their seeds are not carried by frugivorous mammals and birds some distance from the parent tree and preferably dropped in some forest gap, such as a young treefall, where they can germinate. Here, a partitioning of roles between vertebrate frugivores is apparent, depending (a) on their body size, which influences the size of the fruit consumed, and (b) on their locomotor abilities. Volant animals, such as birds or bats, can disperse seeds much farther away from the parent tree than arboreal mammals or some sedentary forest ungulates, such as African duikers. Forest monkeys, however, have a definite advantage, from the plant's point of view, over other scansorial mammals, such as frugivorous squirrels. They have larger home ranges and their social groupings are more numerous than those of sympatric mammals of similar size. Furthermore, they consume the fleshy part of the fruit, rather than the harder stones. *Chiropotes* spp. are an exception (Ayres, 1981). The flux of viable seeds is, therefore, maximized. As for the few terrestrial frugivores, such as the drill or the mandrill, it has been shown that the home range of their large troops is very extensive (Jouventin, 1975). They can, therefore, become long-range

seed dispersers. Whereas small seeds are preferentially dispersed by bats and birds, and very large ones by elephants (Alexandre, 1978), monkeys in most cases specialize in medium-sized ones, together with Old World fruit bats and larger frugivorous birds, such as toucans and hornbills.

It is fair to say that, in the long run, most rain-forest plants depend as much for their own reproduction and propagation on some of their animal consumers as these animals depend on them for their daily survival. The overwhelming importance of the “web of adaptations,” as David Snow (1976) once put it, is still too often minimized in the tropical world.

THE “UNIQUENESS” OF PRIMATES

It is often said that primates are unique among mammals. The reasons for this privileged status, however, are not often clearly stated. In most cases, one cannot even escape the feeling that the major reason for an author to make a statement of this kind is that he is intimately convinced that it has to be so, because we ourselves belong to the order Primates.

Can an ecologist share such an anthropocentric point of view? Do the present-day nonhuman primates share a number of features with regard to their relationships with their environment, which could set them apart from all the other mammals of similar size? If this is not the case, could not some adaptive characteristics, existing also in some other mammalian group(s) (albeit at a rudimentary stage) be particularly developed among them and, combined together, give the primates a decisive advantage in their use of available environmental resources?

The answer to the first question is obviously negative. None of the adaptive strategies adopted by primates is unique to them. However, it is quite true that a number of ecological traits are particularly developed among them and that, taken together, these traits have contributed to the rapid evolutionary success of the order. These characteristics can be listed, and even ranked, as follows.

(1) *Their Predominantly Vegetarian Diet.* This allows the primates to make use of the most abundant energy source in their environment and, thus, to build up higher population densities than sympatric “carnivorous” mammals of comparable size. This is a consequence of the well-known low efficiency of energy transfer between trophic levels within an ecosystem. As shown in Table IX, this allows primates to reach population densities up to nine times higher than those of secondary mammalian consumers such as bears, canids, or felids. This is a definite demographic advantage.

(2) *Their Propensity for Arboreal Life.* Compared to most other primary consumers of similar body size, arboreal primates are at a decisive advantage, because they can make use of all edible plant materials—fruits as well as fresh leaves, gums, sap, and even bark—of their tridimensional

Table IX. Densities (n/km²) of Primates and Carnivores of Comparable Sizes

Gorilla (93-160 kg)					Brown bear (145-380 kg)
Virunga N.P.:					Yellowstone N.P.:
Kahuzi:	0.75 (Harcourt <i>et al.</i> , 1981)			0.011 (Craighead, 1976)	Mount MacKinley N.P.:
Bwindi:	0.35 (Harcourt <i>et al.</i> , 1981)			0.026-0.041 (Dean, 1976)	Yukon:
Tshiaberimu:	0.50 (Harcourt <i>et al.</i> , 1981)			0.04 (Pearson, 1972)	Glacier N.P.:
Alen:	0.55 (Harcourt <i>et al.</i> , 1981)			0.04 (Martinka, 1974)	
Abuminzok:	0.65 (Harcourt <i>et al.</i> , 1981)				Lion (120-170 kg)
Belinga, Gabon:	0.45 (Harcourt <i>et al.</i> , 1981)				Kruger N.P.:
	0.44 (Tutin and Fernandez, 1983)				Serengeti N.P.:
Orangutan (37-69 kg)				0.109-0.126 (Schaller, 1972)	Nairobi N.P.:
Sumatra, Ranun:				0.217 (Schaller, 1972)	Ngorongoro N.P.:
Sumatra, Ketambe:	± 1.0 (Mackinnon, 1974)			0.270 (Schaller, 1972)	
Sabah, Segama:	5.0 (Rijksen, 1978)				Spotted hyena (48-57 kg)
Kalimantan, Kutai:	± 1.5 (Mackinnon, 1974)			0.12 (Kruuk, 1972)	Serengeti N.P.:
	3.0 (Rodman, 1973)			1.7 (Kruuk, 1972)	Ngorongoro N.P.:
Chimpanzee (41-49 kg)					Wolf (45-54 kg)
Rio Muni:					Isle Royale, Mich.:
Mahali Mountains, Tanzania:	0.31-1.53 (Jones and Sabater Pi, 1971)			0.02-0.04 (Jordan <i>et al.</i> , 1967)	Minnesota:
Gombe N.P.:	1.0 (Nishida, 1968)			0.02 (Stenlund, 1955)	Wisconsin:
Tai N.P., Ivory Coast:	1.26 (Teleki <i>et al.</i> , 1976)			0.008-0.010 (Thompson, 1952)	Alaska:
	1.30 (Boesch, personal communication)			0.008 (Burkholder, 1959)	Michigan:
				0.005 (Stebler, 1944)	Minnesota:
				0.004 (Van Bellenberghe <i>et al.</i> , 1975)	

environment. They are not strictly confined to the grass and shrub layers, as ungulates are.

(3) *Their Opportunistic Tendencies.* True “specialists” are rare among primates. Most of them have varied food habits, supplementing their basically vegetarian diet with a variety of animal prey, particularly when their body size is small. This enables their populations to adapt more effectively to a wide range of environmental conditions. This is particularly obvious in three families (Cebidae, Cercopithecidae, and Pongidae), where a small number of clever opportunists, eclectic in their tastes and displaying a strong tendency to omnivory, are able to take advantage of a variety of habitats and situations. Such is the case for *Cercopithecus aethiops* among African guenons, *Presbytis entellus* among langurs, *Macaca mulatta* among macaques, *Papio anubis* and *P. ursinus* among baboons, and even the chimpanzee among apes. In the New World, only *Cebus apella* can be included in this ecological category.

(4) *The Extended Socialization Period of Monkeys and Apes.* This, coupled with their high potential longevity [22 years for *Saguinus imperator* (Anonymous, 1981), 47 years for *Cebus capucinus*, and 50 years for *Pan troglodytes* (Maple and Cone, 1981), for example], gives them further possibilities to develop “social traditions,” which further facilitate their adaptation to local situations.

When one realizes the opportunities given to primates in tropical forest environments by the above-mentioned attributes, then the flexibility of their community structures, the subtle interspecific partitioning of resources, and the high population densities they are able to build up all become easier to understand. Conversely, one is also led to wonder why some of their ancestors ever ventured to enter more open environments, such as savannas.

The answer might be that they did so during the dry climatic episodes of the past, when the forested areas were greatly reduced in size and when some of their local populations living in gallery forests became isolated in “forest islands,” such as those we still find in the forest-savanna mosaic of Africa. During these dry episodes, the climate became increasingly seasonal, and fruit and fresh leaf production fell drastically during the prolonged dry seasons. It was probably at such times that some of the more opportunistic species began to leave the dwindling forest islands to enter open savannas. There they found new food sources—fresh grass sprouting after natural bush fires, soft roots and rhizomes, and small animal prey—all more abundant along the water courses lined with sparse trees. There they settled and became progressively adapted to this new environment.

Obviously, all this looks like pure speculation. However, this hypothesis is actually supported by recent paleoecological findings in the

Omo River Valley, Ethiopia. There, fossil fruits (hard stones) belonging to the genus *Antrocaryon* (Anacardiaceae) were found in 3 million-year-old deposits of the Shungura and Usno formations. These fossils are very close to the modern species *Antrocaryon micraster*, a rain-forest tree, and strongly suggest that *Australopithecus robustus*, a savanna australopithecine whose remains were found in the Sangura formation, formerly lived not far from gallery forests (Bonnefille and Letouzey, 1976).

A better understanding of the conditions under which the rapid evolution of our own ancestors took place obviously needs a better integration of the efforts of paleoecologists and ecologists. We cannot expect to correctly interpret paleontologists' findings, if we do not understand better the relationships of present-day monkeys and apes with the ecosystems to which they belong. This should be a major objective of the field studies for the next decade. The questions we have raised in this paper cannot be answered by laboratory experiments alone, although a better knowledge of primate metabolism, nutrition, and detoxification mechanisms is mandatory for interpreting the results of field observations. We must go back to the field because the last remnants of undisturbed rain forests are being destroyed at an alarming rate. In 10 years' time, it might be too late, and we would be left for ever alone with our wild speculations.

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