Primate Communities

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INTRODUCTION

Africa is an immense continent covering approximately 30 million km^2 and encompassing 49 countries. For decades Africa has been considered a continent of great mystery, partly stemming from the fact that when Europeans first traveled to Africa, they found large expanses of seemingly impenetrable forests. Further, the first explorers often pressed inland by following rivers and thus often encountered only long stretches of riverine forest. In reality, the majority of the rainforest in Africa is situated in a belt that extends less than 10° north and south of the equator, and it is frequently broken by savanna or dry forest (e.g., the 300 km wide Dahomey Gap in West Africa). Thus, unlike the initial impressions of continuous homogenous forest, Africa actually contains a myriad of habitats from multistrata tropical forest, to dry deciduous forest, woodland, savanna, and desert. Along with the variety of habitats found within the continent, Africa harbors a great diversity of primate communities: at least 64 species of primates are found in Africa (15 prosimians, 46 monkeys, and 3 apes, Oates, 1996*a*; Fig. 1.1).

The objective of this chapter is to provide a template with which to begin to understand the diversity of primate communities in Africa's tropical forests. To do this, we first review the nature of the forested habitats in which primates occur, describing general habitat characteristics and, when possible, providing detailed contrasts of rainfall and forest structure. Subsequently, since the majority of primate research taking a community level approach is derived from only a handful of sites, we describe each of these field locations and the key studies conducted at each site. This descriptive information is then used to evaluate how data from Africa can provide insights into determinants of primate community structure. Finally, we describe the major threats faced by primate communities in Africa. It is clear that African tropical forests and the primate communities they support are seriously threatened by accelerating rates of forest conversion and degradation and by subsistence and commercial hunting. The impact of these threats is so great that some primate communities have been lost altogether, while others have been irrevocably changed before they can even be described.

ENVIRONMENTS OF AFRICAN PRIMATES

Tropical Africa covers a larger area than either tropical Asia or America, but the climate is generally drier. Only a few regions in Africa receive more than 2500 mm of rain a year, and many areas experience a pronounced dry season. Many central and eastern African forests lie close to the equator and therefore have two rainy seasons and two dry seasons each year. Any particular region receives rain when the rainbelt passes over the area as it moves to its southern maximum in January and once again when it moves to its northern-most extent in July (Fig. 1.2). In some regions in West Africa, winds blow parallel to the coast and not towards it from the ocean, producing a single peak in rainfall (Fig. 1.3).

Partially as a result of the continent's drier climate, the forests of Africa are fragmented by what was likely dry forest or woodland prior to human activities, but is now savanna and cultivated land (Fig. 1.2). In addition, major rivers further divide sections of forest, often isolating primate populations on either side. For example, before the central block of forest in Africa reaches Cameroon, it is cut by the Congo River, which can be over 15 km across

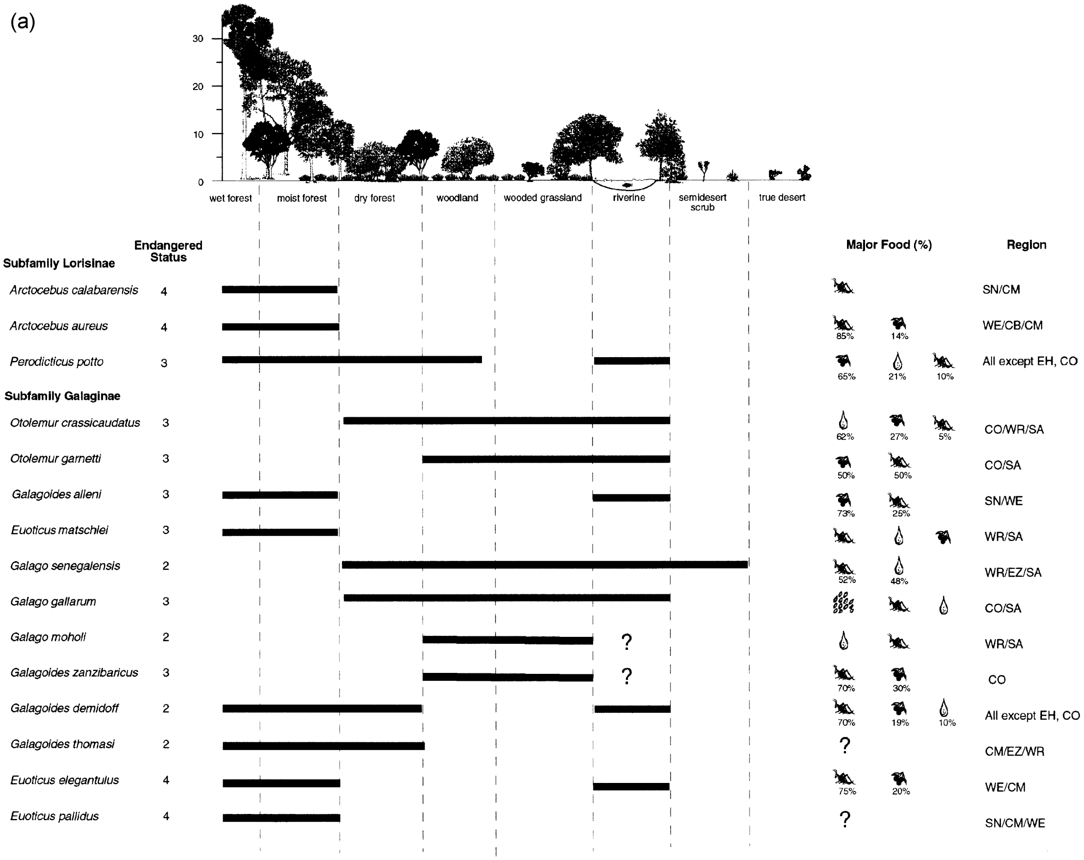
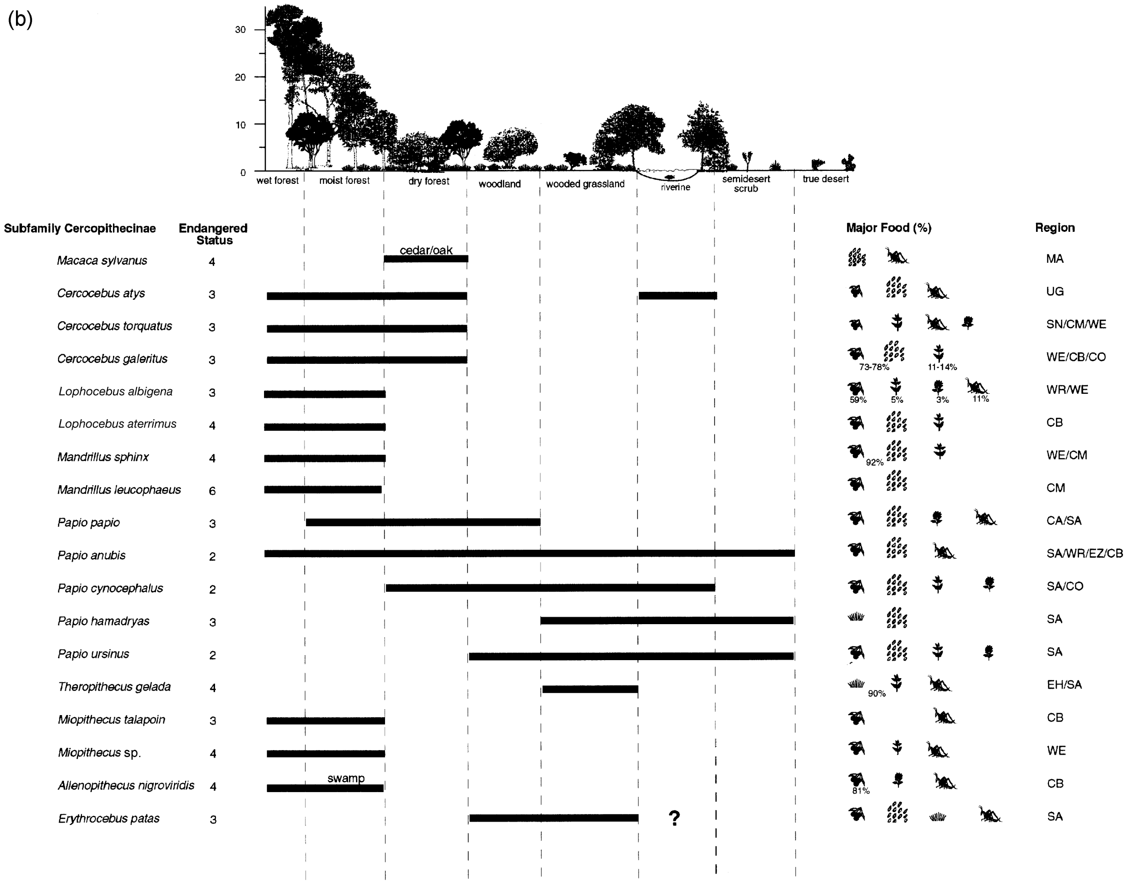


Fig. 1.1. A description of the primates found on the African continent, their endangered status, habitat preference, diet, and the region in which they are endemic.

(Beadle, 1981). The forest continues westward following the coast. However, from the western frontier of Nigeria to just west of the Volta River in Ghana, the forest belt is broken by the Dahomey Gap, a 300 km wide stretch of what is now savanna and farmland, but was probably once dry forest. After the Dahomey Gap, forest continues westward until it eventually gives way to dry forest and grassland in Sierra Leone and Guinea-Bissau at about 10° north of the equator. There is evidence that even more arid conditions affected much of Africa in the past and further divided and isolated blocks of forest (Booth, 1958; Struhsaker, 1981; Chapman, 1983; Colyn *et al.*, 1991). For example, layers of Kalahari sand underlie some parts of the central basin, indicating that much of this forest area was severely reduced in the Pleistocene (Moreau, 1966).

The richest primate communities in Africa are found in forest habitats. Relative to drier savanna and desert habitats, these areas usually are rich in plant species, harbor luxuriant plant growth, and are structurally complex. However, corresponding to Africa's generally dry climate, there are very few areas that are classified as true wet-evergreen forests. Rather, the majority of Africa's forests are considered moist forests, which do not receive as much rainfall as wet-evergreen forests, and as little as 50–100 mm of rain may fall in some months. Interestingly, original descriptions considered genuine rainforest to occur only in areas that receive more than 2000 mm of rain a year (Richards, 1996). However, a number of areas in Africa that receive as little as 1250 mm of rain a year have tall closed-canopy forest. This has led a number of researchers to re-consider



the minimum rainfall level for true rainforest (Lawson, 1986). One reason some African areas can maintain closed canopy forests while receiving little rain has to do with patterns of cloud cover. For example, during the four month dry season in Gabon and Congo, a quasi-permanent and non-precipitating stratiform cloud cover extends at least 800 km inland from the ocean. This cloud cover dramatically reduces temperature and evaporation. Maley (in press) speculates that without this atmospheric humidity, the severity of the dry season would result in the replacement of forest by savanna.

The tall closed-canopy forests of Africa are by no means homogenous, and the richness of plant species found in different forested areas can vary greatly. Hall (1977) and Hall & Swaine (1976, 1981) documented patterns of plant diversity in Nigeria and Ghana and found that in areas where annual precipitation is at least 1750 mm, one can find up to 200 plant species in a 25 m by 25 m plot. As areas become drier, the species richness declines, so that in areas that receive between 1500 and 1750 mm of rain a year, there are often less than 170 species in a 25 m by 25 m plot, and areas receiving between 1250 and 1500 mm of rain per year harbor between 40–100 plant species in the same sized plots.

Even within a single forested area receiving similar levels of rainfall, areas are by no means homogenous and the primate communities that occupy different areas can vary dramatically. For example, in the Ituri Forest in the Democratic Republic of the Congo, there are at least five distinct habitat types found in this area: mbau forest,

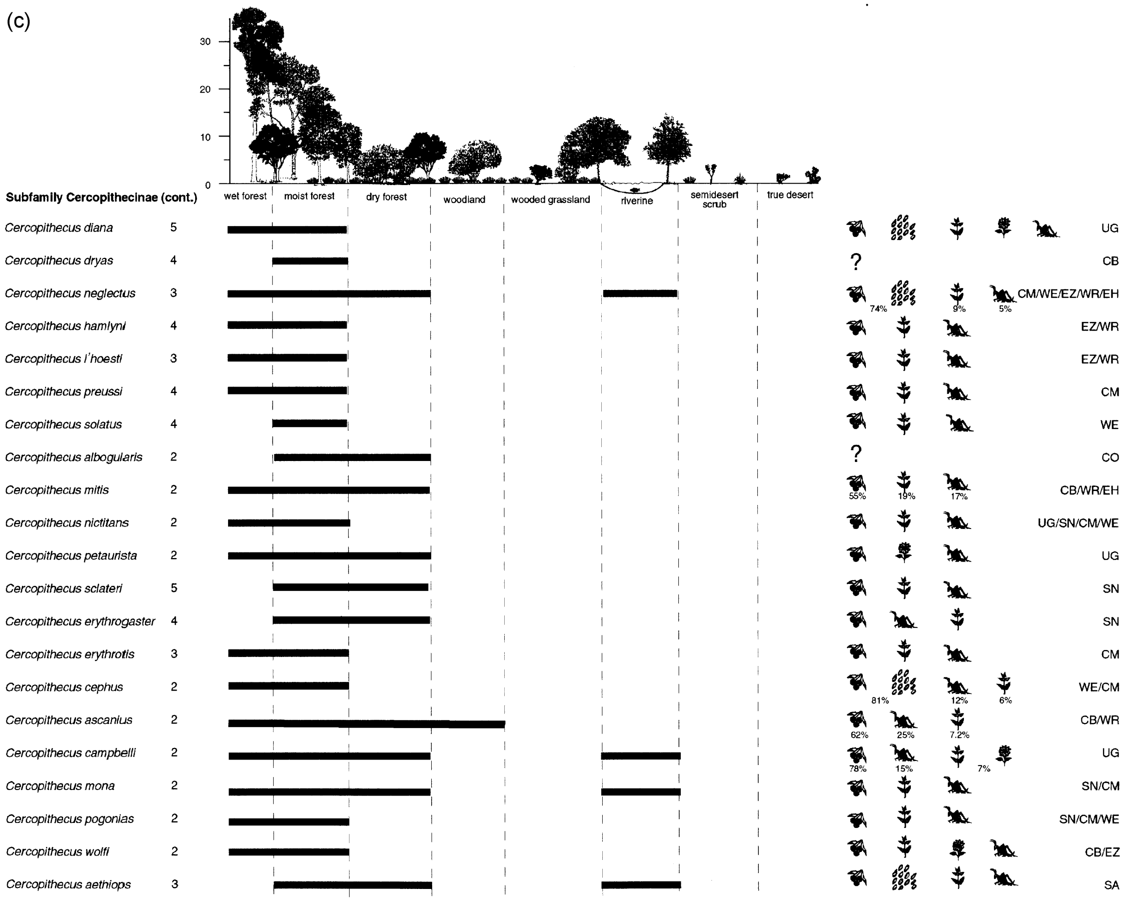
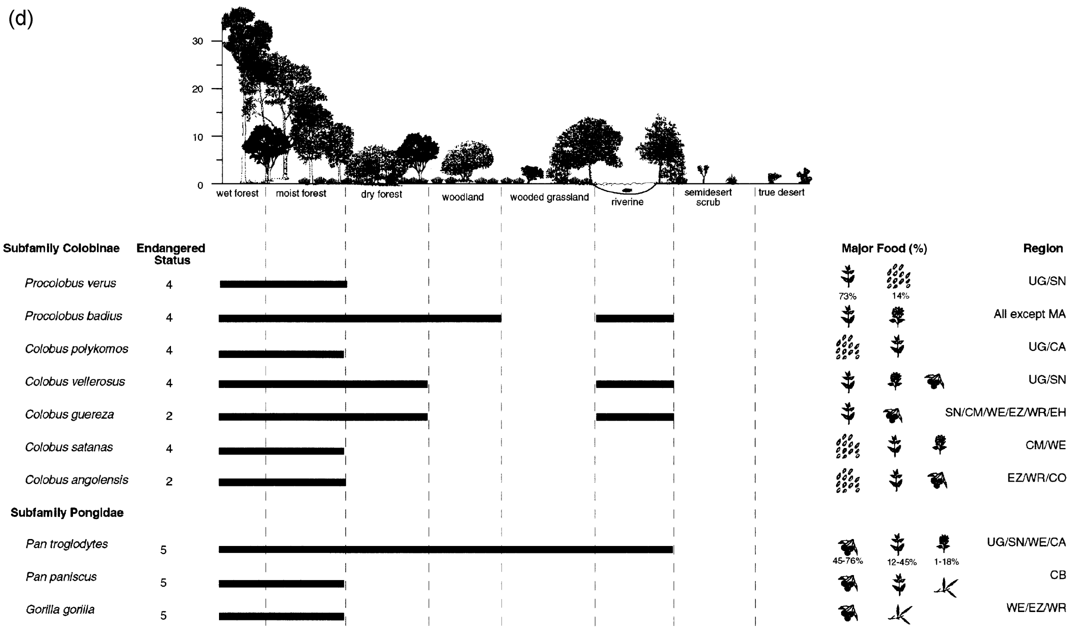


Fig. 1.1. (*cont.*)

which is dominated by *Gilbertiodendron dewevrei* (this one tree species comprises over 70–90% of the canopy level trees in these stands; Hart *et al.*, 1989; Hart, 1995), mixed forest, riparian forests, flooded forests, and secondary forests, which occur in areas of abandoned agricultural clearings and blow-downs. Because of the dominance of *Gilbertiodendron dewevrei,* the mbau forest exhibits a low diversity of trees (an average of 18 tree species greater than 10 cm DBH (diameter at breast height) in 0.5 ha plots; Hart, 1985). In contrast, the mixed forest has higher levels of tree diversity (an average of 65 tree species greater than 10 cm DBH in 0.5 ha plots). The richness and density of anthropoid primates varies between these habitat types, but can be fairly high (13 anthropoid species, 112 primates/km^2 or 710 kg/km^2). However, in monodominant stands of *Gilbertiodendron* all species are encountered at a low rate, and in the largest monodominant stand no primates were seen in nine samples of a 2.15 km transect. In spite of this generality such monodominant stands may be important to some species; observations of the owl-faced monkey (*Cercopithecus hamlyni*) suggest that, while they are still rare and hard to see in stands of *Gilbertiodendron*, they are more common here than elsewhere (Oates, pers. obs.).

Freshwater swamp forests are extremely extensive in Africa. Conservative accounts estimate that there are over 60 000 km^2 of permanent swamps and 400 000 km^2 of seasonally inundated swamps (Thompson & Hamilton, 1983). In the central basin of the Congo River alone, over 80 000 km^2 of forested land is permanently or seasonally inundated. Many of the plant species common in such



Conservation priorities follow Oates 1996 – higher numbers are more endangered. Distinct Regional Communities following Oates 1996 (see Figure 1) – MA = Maghreb, CA Casanance, UG = Upper Guinea, SN = Southern Nigeria, CM = Cameroon, WE = Western Equatorial, CB = Congo Basin, EZ = Eastern Zaire, WR = Western Rift, EH = Ethiopian Highlands, CO = Coastal East Africa. SA is used to depict species that are common in savanna regions. Dietary values are from Rowe 1996 Fruit Gum Insect Seeds Flowers Leaves Grass Terrestrial herbs. Distribution based on Kingdon 1984, Rowe 1996 (personal communication), and distribution maps – Typically this should be viewed as an estimate. 'Riverine' is meant as forested habitats along rivers in a savanna area.

swamps (e.g., *Ficus congensis, Raphia farinifera, Phoenix reclinata, Uapaca* sp.) are eaten by a variety of primate species. Considering the extent of inundated swamp forest, it is not surprising that there is a primate species whose name reflects its dependence on swamp habitat: Allen's Swamp Monkey (*Allenopithecus nigroviridis*) is described as being restricted to regularly inundated forests (Verheyen, 1963). Similarly, species such as *Cercocebus galeritus, C. torquatus, Miopithecus sp.*, and to some extent *Colobus guereza* can be dependent on inundated forests in certain areas.

Since the majority of the primate research taking a community-level approach is derived from studies conducted in forested habitats, we will only briefly mention other habitats. Savannas, which range from humid woodlands to dry grasslands, cover approximately 60% of Africa. Here, annual rainfall is often less that 1000 mm, and while trees and shrubs are often present, there is always extensive grass cover (Deshmukh, 1986). Compared to forested habitats, the primate communities in savanna areas are relatively depauperate. These communities are typically composed of only a few hardy species such as patas monkeys (*Erythrocebus patas*), vervet monkeys (*Cercopithecus aethiops*), baboons (*Papio* spp.), some bushbabies (e.g., *Galago gallarum, Galago moholi, Galago senegalensis, Otolemur crassidaudatus*), and possibly chimpanzees (*Pan troglodytes*). However, in such savanna regions, riverine forests play particularly important roles (Fig. 1.1). At Tana River, Kenya, an area receiving less than 500 mm of rain annually, one finds a riverine habitat that supports six primate species (*Procolobus badius, Cercocebus galeritus, Papio cynocephalus, Cercopithecus albogularis, Otolemur crassicaudatus, Galago senegalensis*; Marsh, 1979). The area surrounding Tana River is thorn scrubland, but there are a number of tall forest trees found near the river (e.g., *Ficus sycomorus, Diospyros mespiliformis*).

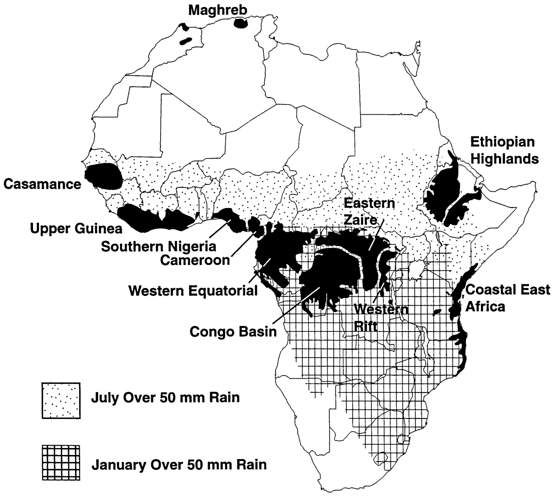


Fig. 1.2. Distinct regional communities of African primates (adapted from Oates, 1996*a*). The gridded area indicates the region where over 50 mm of rain falls in January, while the dotted area indicates the region over which 50 mm of rain falls in July.

A FOCUS ON FOREST STUDY SITES

By far the most diverse primate communities found in Africa are encountered in forest habitats. However, there is only a handful of study sites for which detailed data are available on the richness and abundance of the members of these communities, and even fewer that describe the behavior of the members and the ecological context in which they interact (Table 1.1).

In this section, we review the ecology and history of disturbance of these sites (reviewed from west to east) and outline the investigations that have taken place at each location. At these nine sites, there are on average nine anthropoid primate species (range 7 to 11; Table 1.2), and between three to six prosimians. Primate biomass is typically impressive, averaging 982 kg/km^2 and reaching values as high as 2710 kg/km^2. From these figures, it is clear that primates constitute a major component of the frugivore/folivore community in tropical forests (see Bourlière, 1985; Terborgh, 1986; Waser, 1987; Davies, 1994 for comparative data).

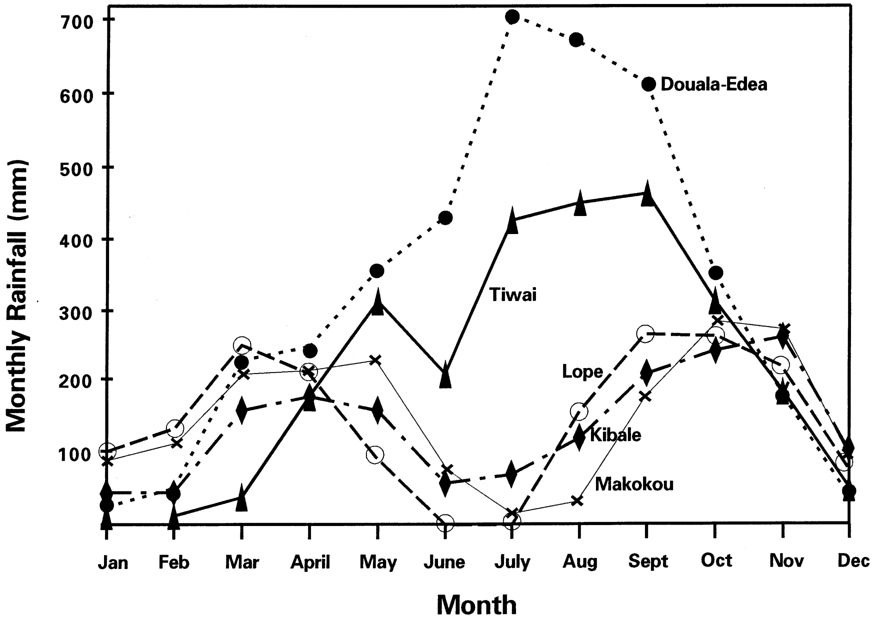


Fig. 1.3. Monthly rainfall at five African rainforest sites where detailed studies of primate communities have been conducted.

Table 1.1. *Descriptive characteristics of the major field sites where forest primates have been studied in Africa*

Site	Country	Vegetation classification	Rainfall	Elevation (m)	Coordinates	Source
Tiwai	Sierra Leone	Lowland moist forest	2708	85–112	7°31′N 11°20′W	Oates *et al.*, 1990 Oates, 1994; Fimbel, 1994*a*,*b*
Taï	Côte d'Ivoire	Lowland moist forest	1800	90	6°10′N 4°20′W	Boesch & Boesch 1983 Merz, 1986
Douala-Edéa	Cameroon	Lowland wet forest	4000	Sea level	3°29′N 9°50′E	McKey *et al.*, 1981
Lopé	Gabon	Lowland moist forest	1506	100–700	0°10′S 11°35′E	White, 1994*a*,*b* Tutin *et al.*, 1994
Forêt des Abeilles	Gabon	Lowland moist forest	1755	200–600	0°20′S 11°45′E	Gautier-Hion *et al.*, 1997
Makokou	Gabon	Lowland moist forest	1755	430	0°34′N 12°52′E	Gautier-Hion *et al.*, 1981 Gautier-Hion *et al.*, 1985
Botsima	DR Congo	Seasonally flooded forest	1774	350–700	1°15′S 20°00′E	Gautier-Hion & Maisels, 1994
Ituri	DR Congo	Lowland moist forest	1802	750	1°25′N 28°35′E	Hart, 1995
Kibale	Uganda	Mid-altitude moist forest	1662	1500	0°13′N 30°19′E	Struhsaker, 1975 Chapman *et al.*, 1997
Budongo	Uganda	Medium altitude moist forest	1495	1050	1°35′N 31°18′E	Eggeling, 1947 Plumptre *et al.*, 1994

Studies conducted at each of these major sites have had slightly different objectives, making it difficult to compare quantitative data from all sites. At all sites, however, estimates of annual rainfall have been made, which vary from 1495 to 4000 mm (Fig. 1.3). Rainfall strongly influences forest structure and productivity and, in doing so, could influence primate community structure.

Between them, the nine communities contain 40 of the 51 species of moist forest primates that we recognize in this chapter (see Fig. 1.1). More than half of the species not included are endemic to southern Nigeria and western Cameroon, a region in which primates are heavily hunted for their meat and where habituating animals for behavioral observation is difficult; as a consequence, reliable biomass and dietary data are not available from primate communities in this area (see chapter 17).

Tiwai Island, Sierra Leone

Tiwai is a 12 km^2 island located in southern Sierra Leone, 30 km from the Liberian border and approximately 60 km from the coastline at the mouth of the Moa River. The island harbors nine anthropoids and two prosimians (Table 1.2). Like many forests in Africa, the vegetation on the island has a history of human-induced disturbance. At the time that the majority of the primate research was conducted, there were only a few active farms on the island. However, approximately 30% of the island was regenerating forest growing on formerly agricultural lands that had been abandoned less than 20 years earlier (Fimbel, 1994*a*, *b*). Palm swamps and riverine forest fringe the island, and the remaining 60% of the island is old secondary high forest (Oates *et al.*, 1990). In this high forest, there are gaps resulting from felling of trees by local people for timber and canoes. Hunting in the area is believed to be relatively light, both because of the difficulty of crossing the river and because of antipathy towards Liberians who were the chief hunters of monkeys in southern Sierra Leone (Oates, 1994).

Primate studies were initiated on the island in 1982, and studies were conducted at various intervals until 1991, when regional unrest ended research. Studies were conducted

Table 1.2. *Descriptions of the primate community found at the major field sites where forest primates have been studied in Africa*

	Rainfall	Density	Biomass	Frugivore biomass	Folivore biomass	Group size	Diet		
Tiwai Island, Sierra Leone[a]									
	2708		1379	785.5	599.5		Leaves	Fruit	Flowers
Perodicticus potto						1			
Galagoides demidoff						1			
Cercocebus atys			196			35			
Cercopithecus campbelli			88			14			
Cercopithecus petaurista			120			14			
Cercopithecus diana			165			24	12.6	42.8	16.1 (27.7 Insect)
Cercopithecus aethiops			rare						
Colobus polykomos			382			9	58 (30Young)	35 (32seed)	3
Procolobus badius			380			35	52 (32Young)	32 (25seed)	16
Procolobus verus			23			6	70 (59Young)	19 (14seed)	11
Pan troglodytes			25						
Taï, Côte d'Ivoire[b]									
	1800	~183.6	802	244	558		Leaves	Fruit	Insects
Perodicticus potto									
Galagoides demidoff									
Cercocebus atys		10	58				1.3	93.5	1.3
Cercopithecus petaurista		29.3	52.7				5.5	77.2	7.3
Cercopithecus nictitans									
Cercopithecus diana		17.5	75.3				7.7	76.3	4.7
Cercopithecus campbelli		15	61.5				0	78.3	15.2
Procolobus badius		66	455.4			83.5	10.4	0	
Colobus polykomos		23.5	166.9				53.1	32.5	0
Colobus verus		21	81.9				94.1	0	0
Pan troglodytes		1.3	58.5						
Douala-Edéa, Cameroon[c]									
	4000	–	409	198	217				
Lophocebus albigena			88						
Cercopithecus mona			14						
Cercopithecus pogonias			15						
Cercopithecus nictitans			67						
Cercopithecus erythrotis			55						
Colobus satanas			198				43.1 (leaves)	53.2 (fruit and seeds)	
Pan troglodytes			25						
Gorilla gorilla			rare/ extinct(?)						
Forêt des Abeilles, Gabon[d]							Leaves + flowers	Ripe fruit	Unripe fruit + seeds
	1755								
Arctocebus aureus									

Table 1.2. (*cont.*)

	Rainfall	Density	Biomass	Frugivore biomass	Folivore biomass	Group size	Diet			
Perodicticus potto										
Euoticus elegantulus										
Galagoides alleni										
Galagoides thomasi										
Galagoides demidoff										
Mandrillus sphinx										
Lophocebus albigena		8.4					57	26	57	
Cercopithecus nictitans		31.8					14.5	35.5	50	
Cercopithecus pogonias		5.3					6.5	25.5	56	
Cercopithecus cephus		5.8					–	–	–	
Cercopithecus solatus		27.9					–	–	–	
Colobus satanas		20.5					49.5	9	40.5	
Pan troglodytes										
Gorilla gorilla										
Lopé Reserve, Gabon[e]							Fruit	Seeds	Leaves	Insects
	1506		318.6	227.9	90.7					
Cercopithecus nictitans		19.2	62.8			13.5				
Cercopithecus pogonias		4.6	10.1			12.6				
Cercopithecus cephus		5.1	10.2			9.6				
Lophocebus albigena		8.1	33.7			18.9	30	36	4	28
Colobus satanas		10.8	90.7			12.1	4	60	26	–
Gorilla gorilla		0.6	45.3			5.3				
Pan troglodytes		0.6	22.5			–				
Mandrillus sphinx		3.8	43.9			150				
Makokou, Gabon[f]										
	1755						Leaves	Ripe fruit	Unripe fruit	Insect
Arctocebus aureus						1	0 gum	14	0	85
Perodicticus potto						1	21 gum	65	0	10
Euoticus elegantulus						1	75 gum	5	0	20
Galagoides alleni						1	0 gum	73	0	25
Galagoides demidoff						1	10 gum	19	0	70
Galagoides thomasi						1				
Lophocebus albigena							6	81	5	6
Cercocebus galeritus		10.1				10	14	73	0.5	3
Mandrillus sphinx		~5								
Cercopithecus neglectus		33	110			4.5	9	74	3	5
Cercopithecus nictitans		30	100			20	28	61	1	8
Cercopithecus pogonias		22.5	60			15	2	84	0	14
Cercopithecus cephus		25	80			10	8	79	0	10
Miopithecus sp.		65	60			85	2	43	1.5	36
Colobus guereza							52	49		
Pan troglodytes										
Gorilla gorilla										

Table 1.2. (*cont.*)

	Rainfall	Density	Biomass	Frugivore biomass	Folivore biomass	Group size	Diet			
Botsima, Salonga National Park[g]	1774						Leaves + flowers	Ripe fruit	Unripe fruit + seeds	
Perodicticus potto										
Galagoides alleni										
Galagoides demidovii										
Lophocebus aterrimus							34	36	30	
Cercopithecus wolfi							43	39	18	
Cercopithecus ascanius							32	44	24	
Allenopithecus nigroviridis										
Colobus angolensis							33	17	50	
Procolobus badius							62	7	31	
Pan paniscus										
Ituri Forest, Democratic Republic of the Congo[h]	1802	~112.4	709.6	401.9	307.7		Leaves	Seed	Fruit	Flower
Lophocebus albigena		6.9	53.1			10				
Cercocebus galeritus		~2.0	15.4							
Papio anubis		?	?							
Cercopithecus ascanius		18.9	68.0			7				
Cercopithecus mitis		24.2	145.2			10				
Cercopithecus wolfi		23.1	87.8			14				
Cercopithecus neglectus		~.4	2.1							
Cercopithecus lhoesti		~.4	2.5							
Cercopithecus hamlyni		~.1	0.8							
Procolobus badius		26.7	218.9			28				
Colobus guereza		~1.2	12.6				57.9	22.0	24.6	2.9
Colobus angolensis		7.7	76.2			11	51.1	22.1	27.5	7.2
Pan troglodytes		~.8	27.7							
Kibale National Park, Uganda[i]	1662	~656.8	2710	633.5	2077		Leaves	Ripe fruit	Unripe fruit	Insect
Perodicticus potto		17.7	1.9			1				
Galagoides thomasi +*Euoticus matschiei*		79.5	12.6			1				
Lophocebus albigena		9.2	60			15	5.4	58.8	3.4	26
Papio anubis		–	–			–				
Cercopithecus ascanius		140	328			35	16.1	43.7	15.3	21.8
Cercopithecus mitis		41.8	133			25	20.9	45.1	12.5	19.8
Cercopithecus l'hoesti		8	13			–				
Cercopithecus aethiops		rare	rare			–				
Procolobus badius		300	1760			50	74.8	5.6	15.9	2.6

Table 1.2. (*cont.*)

	Rainfall	Density	Biomass	Frugivore biomass	Folivore biomass	Group size	Diet			
Colobus guereza		58.1	317			9	76.3	13.2	2.1	0
Pan troglodytes		2.5	85			7.1	8	80	0	0 (12% THV)
Budongo Forest Reserve, Uganda[j]										
	1495	67.4	545	261.5	283.5		Leaves	Ripe fruit	Unripe fruit	Insect
Perodicticus potto										
Galagoides demidoff										
Papio anubis		14	231							
Cercopithecus mitis		15.6	93.6				39	39	6	10
Cercopithecus ascanius		8.3	29.5							
Cercopithecus aethiops		rare								
Colobus guereza		27	284							
Pan troglodytes		2.5	89.2							

Note: Annual rainfall in mm, biomass in kg/km^2, density in individuals/km^2. Prosimians are only listed if they are described for the community, thus many lists are incomplete. Forêt des Abeilles and Lopé are neighboring sites, but since rainfall and diet differ they are presented separately.

[a] Oates *et al.* (1990) (mid-point in range used), Diet – Oates (1994), Oates & Whitesides (1990).

[b] Galat & Galat-Luong (1985) with *Pan* added from Bourlière (1985), Terborgh & van Schaik (1987).

[c] Oates *et al.* (1990).

[d] Gautier *et al.* (1997), Brugiere & Gautier unpublished data, Gautier-Hion & Gautier (in prep.).

[e] Primate density White (1994*a*, mean of 5 neighboring sites), diet data for *L. albigena* from Ham (1994), diet data for *Colobus satanas* from Harrison (1986).

[f] Makokou – from Waser (1987) – midpoint of pop density: diet – Charles-Dominique (1977). Gautier-Hion (1978, 1980, 1983), Gautier-Hion *et al.* (1980).

[g] Maisel *et al.* (1994), Maisel & Gautier-Hion (1994) – data only concerned plant diet.

[h] Thomas 1991, Group size was taken as the midpoint of estimated social group sizes which was a range corresponding to minimum and maximum values for “good” counts. Rainfall Hart (1985), *Colobus* diets from Bocian (1997)

[i] Struhsaker (1975, 1978, 1981), Struhsaker & Leland (1979), Weisenseal *et al.* (1993), Chapman and Wrangham (1993), Chapman unpublished data, Wrangham *et al.* (1996), Chapman *et al.* (1995)

[j] Plumptre *et al.* (1994), Plumptre & Reynolds (1994) (density – unlogged forest only), Harvey *et al.* (1987) (weights assuming 50/50 sex ratio and 1/2 group immature weighing 1/2 adult), Eggeling (1947) (rainfall), *C. mitis* diet (unlogged); Fairgrieve, 1995)

on *Procolobus verus* between 1983 and 1986 (Oates, 1988; Oates *et al.*, 1990), on *Colobus polykomos* (Dasilva, 1992; 1994) and *Procolobus badius* between 1984 and 1986 (Oates, 1994), on Diana monkeys (*Cercopithecus diana;* Whitesides, 1989; Oates & Whitesides, 1990; Hill, 1994), and on the success of the different primate species in the various modified habitats on the island (Fimbel, 1994*a*,*b*). Primate richness is comparable to Kibale, but biomass is approximately one half that of Kibale. Much of this difference in biomass is simply a reflection of the fact that red colobus (*Procolobus badius*) is extremely abundant in Kibale, but not at Tiwai (Table 1.2).

Taï National Park, Côte d'Ivoire

Taï National Park (3500 km^2) in Côte d'Ivoire received its first protected status in 1926 when it was declared a forest and wildlife refuge, and it received its park status in 1972

(IUCN, 1987). The perceived importance of this forest has been steadily increasing. It became a Biosphere Reserve in 1978, a World Heritage Site in 1982, and was included in the IUCN's list of eleven most threatened areas in 1984 (Galat & Galat-Luong, 1985; Merz, 1986). As with other parts of the Upper Guinea region of West Africa, the plant community found in Taï shows a high level of endemism; 54% of the 1300 plant species identified are endemic to the region (Martin, 1991). Possibly related to the richness of the plant communities, the area harbors a rich and abundant primate community. In Taï there are 11 species of primates (including two prosimians), and primate biomass has been estimated to exceed 800 kg/km^2 (Galat & Galat-Luong, 1985).

Certain areas in Taï have come under heavy pressure from new settlers. In 1972, the human population density surrounding Taï was estimated to be 1.3 individuals per km^2 (Martin, 1991). Since that time, timber exploitation has opened up large areas neighboring the park for agriculture, and farmers from the Sahel region have immigrated to the area. In eight years, the human population density increased sixfold. This led to increasing encroachment and slash-burn activities in the park. At times, rice was cultivated in swampy areas, and several hundred gold washers were active in the park (Martin, 1991). Further, timber companies have overstepped their concessions and cut extensively in northern areas of the park.

The majority of the primate research, which has focused on chimpanzees, has been conducted in the western part of the park, approximately 20 km from the nearest village and the Liberian border (Boesch & Boesch, 1983, 1989; Galat & Galat-Loung, 1985; Boesch, 1994; Zuberbuhler *et al.*, 1997). This region of the park is effectively protected against logging, and hunting pressure on primates is low (Boesch & Boesch, 1983).

Douala-Edéa Forest Reserve, Cameroon

The Douala-Edéa Forest Reserve (1300 km^2) is located in Cameroon at the mouth of the Sanaga River (McKey, 1978). The sandy soils of the reserve are impoverished and acidic with a pH as low as 2.7. Soils of this acidity are toxic to the roots of many plants, cause phosphorus to become unavailable, limit nitrogen fixation, and inhibit decay and nutrient cycling (Gartlan *et al.*, 1978; Newbery *et al.*, 1986). As a result, tree species diversity in the forest is relatively low; there was a mean of only 39 tree species ($\geq$ 30 cm GBH) in each of 104 80 × 80 m plots (Newbery *et al.*, 1986). The primate community of the reserve is not very rich or abundant. Originally, the low primate densities were ascribed to the abundance of plants that, as a result of poor soils, have high levels of chemical defenses (McKey *et al.*, 1978). However, Tiwai was recently documented to have sandy soils with markedly lower levels of all mineral nutrients than Douala-Edéa and a similarly low pH, yet it supports one of the highest estimates of primate biomass (Oates *et al.*, 1990). By contrasting results of studies from Douala-Edéa, Tiwai, and Kibale, Oates *et al.* (1990) argued that nutrient-poor soils and high tannin levels in tree foliage do not necessarily correlate with a low primate biomass. They did, however, find a positive relationship between the ratio of protein to fiber in the foliage and colobine biomass.

There has been only a handful of primate studies conducted in this region (Gartlan *et al.*, 1978; McKey *et al.*, 1981, McKey & Waterman, 1982). When studies were first initiated in the reserve in 1973, there had been little interference with the vegetation of the reserve, probably due to the poor soils and the scarcity of commercially valuable timber trees (Oates, 1994). Hunting in the area was probably light (Oates, 1994).

Lopé Forest Reserve, Gabon and Forêt des Abeilles – Makandé, Gabon

The Lopé Reserve of Central Gabon covers a 5000 km^2 area that is primarily mature semi-evergreen forest, but 300 km^2 along its northern and eastern border is a savanna and forest-savanna mosaic (Harrison & Hladik, 1986; White *et al.*, 1993; White, 1994*a*,*b*). Some areas of the reserve were logged in the 1960s (White, 1994*b*); however, with the recent construction of a railroad, it has become much more economically feasible to extract timber from the area, and thus logging has intensified (White, 1994*b*). Hunting is forbidden within the reserve, but with the increased presence of workers at forestry camps, it is a concern.

Research began at the Station d'Etudes des Gorillas et Chimpanzés (SEGC) in 1983 and is on-going. The main focus of the project has been studies of the ecology of gorillas and chimpanzees (Rogers *et al.*, 1990; Tutin *et al.*, 1994), but research interests have expanded to include forest elephants (*Loxodonta africana*; White *et al.*, 1993;

White, 1995) and forest ecology (Tutin & Fernandez, 1993; White, 1994*a*,*b*; White *et al.*, 1995). The majority of the primate studies have been conducted in the 50 km^2 SEGC study area, an area that was selectively logged for *Aucoumea klaineana* between 1960 and 1970 at an average density of 1.5 trees per hectare. Primates in this area are not overly abundant, at least in comparison to sites like Kibale and Tiwai, but this site presently offers unique opportunities for primate studies. Lopé is presently one of the few well-established sites where one can study sympatric gorillas and chimpanzees, as well as mandrills (*Mandrillus sphinx*), a species that the scientific community knows little about (Rogers *et al.*, 1996).

Makandé is a site that neighbors the Lopé Reserve and is located in the Forêt des Abeilles (approximately 10 000 km^2) in Central Gabon. It is mainly covered by primary dense forest dominated by Caesalpiniaceae (38% of the trees > 10 cm DBH). As with the neighboring Lopé Reserve, the area is home to a rich primate community with a total of 15 species including the endemic guenon, *Cercopithecus solatus*. Studies on primate populations began in 1993 and continued until 1996 (Gautier-Hion *et al.*, 1997). Unfortunately, the area has no protected status and is in the process of being logged.

M'passa Reserve – Makokou study site, Gabon

This study site was first located at Makokou, where a station was founded in 1962 under the name of the Mission Biologique au Gabon (Charles-Dominique, 1977). In 1968 a research station was built by the Centre National de la Recherche Scientifique (C. N. R. S.) (IUCN, 1987). Subsequently, a reserve was created in the forest of M'passa, 10 km from Makokou. Studies were undertaken in the reserve as well as in areas up to 100 km around Makokou. In the area, mature forest is interspersed with areas of riparian and swamp forest (C. M. Hladik, 1973; Quris, 1976; A. Hladik, 1978). Where the banks are not steep, the river often floods extensive areas, resulting in characteristic flooded forest communities that include *Uapaca* sp. and various palms. Some of the riparian areas contain sections of secondary forest where there were formerly villages and agricultural activity.

In the M'passa reserve and the area near Makokou, there are six species of nocturnal primates and 11 species of monkeys and apes. Except for the gorilla, all have been the subject of study (Gautier-Hion, 1978). Many of the projects conducted here were made in a comparative manner to provide information on the entire community (Gautier-Hion & Gautier, 1979; Emmons *et al.*, 1983; Gautier-Hion *et al.*, 1985). As a result, studies at this site remain some of the most comprehensive community-wide studies available.

As with Kibale, there is a great deal of small scale variation in the abundance and even presence of species between particular localities, making it difficult to rigidly define the primate community. For example, the mandrill (*Mandrillus sphinx*) only occurs on the right bank of the Ivindo River, and *Cercocebus galeritus* is only found on the left bank of the river. Furthermore, several species of this community are typically only observed in riverine forests: *Cercopithecus neglectus, Cercocebus galeritus, Colobus guereza,* and *Miopithecus talapoin*. These species consequently have a patchy distribution.

At the time when many of the primate studies were conducted, clearing for agriculture was conducted only on a very small scale and was restricted to areas near roads (Charles-Dominique, 1977). Hunting in the area was only intense near villages.

Salonga National Park, Democratic Republic of the Congo

The Salonga National Park, created in 1970, is located within the Congo Basin and covers 36 000 km^2 in two different blocks separated by a corridor about 45 km long. Research on the primate community in the area was conducted at Botsima, a site located within a meander of the Lomela River. Information on primate diets was obtained during 12 months in an inundated rainforest area largely dominated by Caesalpiniaceae (Gautier-Hion & Maisels, 1994). Studies in the area were initiated in 1989 but ended in 1991 following political troubles.

Ituri Forest, Democratic Republic of the Congo

The east of the Congo Basin is home to one of the world's richest primate communities: at least 17 species living sympatrically. There are four major protected areas in the region covering 38 300 km^2 (Parc National de Kahuzi-Biega, Parc National de la Maiko, Parc National des Virungas, Réserve de Faune à Okapis (Ituri Forest); Hart

& Hall, 1996). However, the only community-level primate research has been conducted in the Réserve de Faune à Okapis (13 000 km^2), part of the Ituri Forest. Studies in this region were initiated in 1981 and have been conducted more or less continuously since then. However, information on the primates in the area is limited to a study by Thomas (1991), in which he estimated total anthropoid primate density in several areas using line transect censuses, and a study by Bocian (1997) on niche separation of two sympatric species of black-and-white colobus.

Human populations in the reserve were estimated in 1993 at approximately 10 000–11 000, including about 5 000 Mbuti and Efe hunter-gatherers and approximately 5 000–6 000 shifting cultivators (J. Hart, unpublished data). There are currently no regulations controlling hunting in the reserve. However, human activities including hunting are typically concentrated within 10 km of the roads, with decreasing activity out to 35 km, and only sporadic human presence beyond 35 km (Hart & Hall, 1996). Evidence of larger scale market hunting has been found in remote areas of the forest, though. One of the greatest threats to the forest in this region is immigration. In a survey of villages in the area, 86% exhibited some level of immigration among the Bantu population (Stephenson & Newby, 1997). Of course, with the current political instability in the region, the long-term fate of all reserves in the area remains to be determined (Hart *et al.,* 1996; Hart & Hart, 1997).

Kibale National Park, Uganda

The Kibale National Park, located in western Uganda (0° 13′–0° 41′ N and 30° 19′–30° 32′ E) near the base of the Ruwenzori Mountains, is a moist, evergreen forest, transitional between lowland rainforest and montane forest (Wing & Buss, 1970; Struhsaker, 1975; Skorupa, 1988; Butynski, 1990; Chapman *et al.,* 1997). Kibale obtained its first legal status when it was gazetted a crown forest reserve in 1932. The reserve was established to provide sustained production of hardwood timber and for production of softwoods from plantations established in the grasslands (Osmaston, 1959; Kingston, 1967). During the 1960s, different areas within the reserve received different management treatments; some areas were left undisturbed, some were lightly logged, while others were more heavily harvested and "refined" (poisoning of unwanted species and cutting of vines). The diverse management of the area has provided opportunities to examine the effects of logging on primate communities (Skorupa, 1988; Struhsaker, 1997; Chapman & Chapman, 1997). In November 1993, Kibale was declared a National Park, providing long-term protection for the forest and the primate communities. The Batoro, the predominate people living around the park, do not eat monkeys (Struhsaker, 1975), and as a result there has been virtually no hunting of primates in the area.

Long-term studies began in the area in 1970, and research has been continuously conducted in Kibale since that date. The majority of the primate research conducted to date has been based at two research sites: Kanyawara and Ngogo. Recently three additional sites have been established in the park (Sebatoli, Dura River, and Mainaro). The placement of these five sites takes advantage of the north-south gradient in forest structure (*Parinari* forest in the north, *Cynometra* forest in the south) to examine how primate communities respond to small-scale variation in ecological conditions. Because of this extensive history of continuous primate research, a wealth of data on primate and plant communities is available over a 28 year period.

Kibale has one of the richest and most abundant primate communities in the world; it is home to 12 species of non-human primates (including three prosimians), and the primate biomass of the area is estimated to reach 2710 kg/km^2 (Table 1.2). However, all of these species rarely, if ever, inhabit the same area. For example, while vervet monkeys (*Cercopithecus aethiops*) and baboons (*Papio anubis*) are in the national park and adjacent areas, vervet monkeys have only been seen at the main study site at Kanyawara twice in 28 years (Struhsaker, pers. comm.), and baboons use this area typically only when a large fruiting crop is available. Furthermore, blue monkeys (*Cercopithecus mitis*) are one of the most abundant monkeys in the north of the park, but their densities decline as one travels south so that approximately a third of the way down the park on a north/south axis, blue monkeys are rare (Butynski, 1990), and approximately half-way down the park they drop out altogether (Chapman & Chapman, unpublished data). Such small scale variation in primate community structure is intriguing (see below).

Budongo Forest Reserve, Uganda

The Budongo Forest Reserve (793 km^2, 428 km^2 of which is forest) has a long history of exploitation. The reserve was gazetted in 1932, but commercial extraction of timber began as early as 1915, and rubber tapping began in 1905 (Paterson, 1991; Reynolds, 1993; Plumptre *et al.,* 1994). The first major sawmill was established in 1925 (Eggeling, 1947; Fairgrieve, 1995), and harvesting has occurred in approximately 77% of the reserve (Howard, 1991; Plumptre, 1996). The majority of this harvest has involved the extraction of mahogany (*Khaya* and *Entandrophragma*), but other species have been extracted as well. In addition to harvesting mahogany, the management of the reserve has also involved extensive mahogany replanting and a variety of silvicultural treatments. For example, poisoning of unwanted trees was carried out extensively in the 1950s and 60s, and by mid-1966 a total of approximately 4800 ha had been treated (Paterson, 1991). Part of the management involved setting aside a Nature Reserve, where timber harvest was prohibited. Despite the reserve's protected status, illegal timber extraction by pit-sawyers is widespread (Reynolds, 1993; Fairgrieve, 1995). Unlike other areas of Uganda, illegal hunting of primates is another problem in Budongo. It has been estimated that 40% of communities neighboring the reserve hunt, and some of the cultural groups in the area regularly eat primate meat (Johnson, 1996). Pressures such as these have been increasing as a result of both the growth of the local Banyoro population and immigration. Thus, areas adjacent to the park that were grasslands in the 1960s are now agricultural settlements (Reynolds, 1993).

A few primate studies were conducted in the reserve in the 1960s and 1970s (Reynolds & Reynolds, 1965; Sugiyama, 1968; 1969; Aldrich-Blake, 1970; Suzuki, 1979). However, there was a research hiatus until 1991, at which time the Budongo Forest Project was initiated. The main objective of this project was to investigate the responses of wildlife (including primates) to logging and the role of fruit eating primates in forest regeneration (Plumptre *et al.,* 1994).

PATTERNS AND CAUSES OF VARIATION IN PRIMATE COMMUNITY STRUCTURE AND BIOMASS

These sites display considerable variation both in the numbers and kinds of primates present, and in the total and relative abundances of these species. Here, we consider some possible explanations for these variations, both in terms of proximate ecological factors and long-term evolutionary processes.

The species structure of communities

Table 1.3 shows the species structure of the nine forest primate communities that we have described with the species grouped in six eco-taxonomic categories, or guilds: pottos, galagos, terrestrial cercopithecines, arboreal cercopithecines, colobines, and apes. Members of these categories vary in body size, activity pattern, locomotor behavior, and/or diet. The terrestrial cercopithecines are monkeys that often travel on the ground, but usually obtain at least part of their diet in the forest canopy.

The communities cluster into geographical sets, within which many species are shared, and between which there are considerable differences. These sets correspond to some of the large regional communities recognized in the IUCN/SSC Status Survey and Conservation Action Plan for African Primates (Oates, 1996*a*), and the "Primate Zones" of regional endemism described by Grubb (1990) (Fig. 1.2). Tiwai and Taï are part of the Upper Guinea region, or west African zone; Douala-Edéa, Lopé, and Makokou are part of a western equatorial region, or west-central zone; Salonga is in the Congo Basin region, or south-central zone; Ituri is in the eastern region of the Democratic Republic of the Congo, or east-central zone; and Kibale and Budongo are within the western Rift regional community.

Comparing species across communities, it can be seen that only two species are ubiquitous, occurring in every moist-forest community: the potto (*Perodicticus potto*) and the dwarf galago (*Galagoides demidoff*). The common chimpanzee (*Pan troglodytes*) is very widespread, occurring in all communities except Salonga, where it is replaced by the pygmy chimpanzee (*Pan paniscus*). A few species such as *Lophocebus albigena* and *Procolobus badius* occur widely, but patchily. Most species, however, are localized and occur in only two or three of the communities we have described. In some cases, these localized forms have no close relatives outside the limited geographical area in which they occur (e.g., *Euoticus matschiei, Cercopithecus diana, Cercopithecus hamlyni,* and *Procolobus verus*), but others are members of species groups or superspecies which have one form in all or most of the communities (such as *Colobus polykomos* and other black-and-white

Table 1.3. *The species structure of the nine forest primate communities that we have described, with the species grouped in six eco-taxonomic categories*

	Site								
Species	Tiwai	Taï	D-Edéa	Abeilles/ Lopé	Makokou	Salonga	Ituri	Kibale	Budongo
Pottos									
Arctocebus aureus			+?	+	+				
Perodicticus potto	+	+	+?	+	+	+?	+	+	+
Galagos									
Galagoides alleni			+?	+	+				
Euoticus matschiei							+?	+	
Galagoides demidoff	+	+	+?	+	+	+?	+	+	+
Galagoides thomasi				+	+		+?	+	
Euoticus elegantulus			+?	+	+				
Terrestrial cercopithecines									
Cercocebus atys	+	+							
Cercocebus galeritus					+		+		
Mandrillus sphinx				+	+				
Papio anubis							+	(+)	+
Cercopithecus hamlyni							+		
Cercopithecus lhoesti							+	+	
Cercopithecus solatus				+					
Cercopithecus aethiops	(+)							(+)	(+)
Arboreal cercopithecines									
Lophocebus albigena			+	+	+		+	+	
Lophocebus aterrimus						+			
Cercopithecus diana	+	+							
Cercopithecus neglectus					+		+		
Cercopithecus mitis						+?	+	+	+
Cercopithecus nictitans		(+)	+	+	+				
Cercopithecus petaurista	+	+							
Cercopithecus erythrotis			+						
Cercopithecus cephus				+	+				
Cercopithecus ascanius						+	+	+	+
Cercopithecus campbelli	+	+							
Cercopithecus mona			+						
Cercopithecus pogonias			+	+	+				
Cercopithecus wolfi						+	+		
Miopithecus sp.			+		+				
Colobines									
Procolobus verus	+	+							
Procolobus badius	+	+				+	+	+	
Colobus polykomos	+	+							
Colobus guereza					+		+	+	+
Colobus satanas			+	+					
Colobus angolensis						+	+		

Table 1.3 (*cont.*)

Species	Site Tiwai	Tai	D-Edéa	Abeilles/ Lopé	Makokou	Salonga	Ituri	Kibale	Budongo
Apes									
Pan troglodytes	+	+	+	+	+		+	+	+
Pan paniscus						(+)			
Gorilla gorilla			(+)	+	+				

Note: +, rare and/or localized; +?, presence suspected but not confirmed.

Table 1.4. *Composition of African forest primate communities according to eco-taxonomic groups, based on data in Table 1.3*

Site	Annual rainfall (mm)	Primate biomass (kg/km^2)	Number of species per group Pottos	Galagos	Terrestr. cercop.	Arboreal cercop.	Colobines	Apes	Total species number
Tiwai	2708	1379	1	1	1(–2)	3	3	1	11
Taï	1800	802	1	1	1	3(–4)	3	1	11
Douala-Edéa	4000	409	2?	3?	0	6	1	1(–2)	13–14
Lopé	1505	319	2	4	2	4	1	2	15
Makokou	1755	—	2	4	2	6	1	2	17
Salonga	1774	—	1?	1?	0	4	2	(1)	8–9
Ituri	1802	710	1	1(–3)	4	5	3	1	17
Kibale	1662	2710	1	3(?)	1(–3)	3	2	1	11–13
Budongo	1495	545	1	1	1(–2)	2	1	1	8

Note: Terrestr. cercop., terrestrial cercopithecines

colobus, and *Cercopithecus cephus* and closely related small guenons).

The eco-taxonomic composition of the different communities is summarized in Table 1.4. Except for Douala-Edéa and Salonga, which lack a terrestrial cercopithecine, each community contains one or more species in each eco-taxonomic category. However, the communities show considerable variation in their total number of species (from only eight in Budongo, to 17 in Makokou and the Ituri) and in the distribution of these species across eco-taxonomic categories. For example, communities in western-central Africa (Cameroon and Gabon) are relatively much richer than other sites in nocturnal prosimians (pottos and galagos), communities in Central Africa (Cameroon to the Democratic Republic of the Congo) are relatively rich in arboreal cercopithecines, and west Africa (Sierra Leone and Côte d'Ivoire) is relatively rich in colobines.

What has produced these patterns of variation in forest primate community structure, and in particular what have been the relative contributions of proximate ecological factors and more distant evolutionary events?

Habitat and community structure

Proximate ecology may play a significant role in producing the high species-richness at Makokou and Ituri. Oates *et al.* (1990) argued that habitat heterogeneity tends to increase both the species richness and biomass of primate communities, and both Makokou and Ituri display high habitat heterogeneity. The M'passa forest, where Makokou is located, is a mosaic of dry-land, riparian, and swamp forest,

Table 1.5. *The species of primates found in mainland forest and riverine forest at three sites in central Africa. These lists illustrate the increased diversity that is associated with the increased habitat heterogeneity of having riverine forest in the region*

	Mainland forests			Riverine forests		
Species	Makokou Gabon	Ngotto CAR	Odzala Congo	Makokou Gabon	Ngotto CAR	Odzala Congo
Subfamily Colobinae						
Procolobus badius	—	—	—	—	x	x
Colobus guereza	—	—	—	x	x	x
Subfamily Cercopithecinae						
Lophocebus albigena	x	x	x	x	x	x
Cercocebus galeritus	—	—	—	x	x	x
Cercopithecus cephus	x	x	x	x	x	x
Cercopithecus pogonias	x	x	x	x	x	x
Cercopithecus neglectus	—	—	—	x	x	x
Cercopithecus nictitans	x	x	x	x	x	x
Miopithecus talapoin	—	—	—	x	x	—
Subfamily Pongidae						
Gorilla gorilla	x	x	x	x	x	x
Pan troglodytes	x	x	x	x	x	x
Total	6	6	6	10	10	10

Table 1.6. *A description of the communities of primates found in mainland, swamp forest, and riparian forests at Odzala, Congo*

	Mainland		Swamp forest		Riparian forest	
Species	*n*	%	*n*	%	*n*	%
Colobus guereza	2	0.7	16	10.4	19	10.6
Cercocebus galeritus	0		1	0.6	10	5.6
Cercopithecus cephus	48	15.7	56	36.4	43	23.9
Cercopithecus neglectus	0		1	0.6	42	23.3
Cercopithecus nictitans	133	43.6	50	32.5	35	19.4
Cercopithecus pogonias	53	17.4	15	9.7	8	4.4
Miopithecus sp.	0		0		14	7.8
Number of species	7		9		10	
Diversity index	3.37		3.74		5.74	
Equitability	0.34		0.46		0.68	

Source: Gautier-Hion, 1996.
n, number of troops.

while the Ituri is a mosaic of mixed and monodominant *Gilbertiodendron* forest on dry land, veined with a network of rivers and streams which are often bordered by swamps. *Cercopithecus neglectus*, *Cercocebus galeritus*, and *Colobus guereza* are particularly associated with riverine forest in both the Makokou and Ituri communities; *Miopithecus* is restricted to these forests at Makokou; and in the Ituri, *Cercopithecus hamlyni* is most commonly encountered in *Gilbertiodendron* forest. Because of the habitat preferences of these primates, habitat heterogeneity contributes to high primate species-richness at these sites. A similar pattern is found in several other central African forests (Tables 1.5 and 1.6, Gautier-Hion, 1996).

Some of the patchiness in the distribution of the red colobus (*Procolobus badius*) may also be a reflection of habitat variation. Red colobus appear to select for diets that are diverse and contain relatively high proportions of young leaves, flowers, and buds (Struhsaker, 1975; Oates, 1994), and it may be that some habitats cannot provide such diets. However, it is far from certain that sites such as Makokou are incapable of supporting red colobus, and the great differences in pelage and other features among red colobus populations in different parts of the African forest zone (leading them to be classified in different subspecies, or even different species) suggest that the patchy distribution of these populations has a strong historical component. Indeed, many of the differences in the species composition among African forest primate communities can be best understood as resulting from long-term historical processes of evolution, dispersal, and extinction.

History and community structure

The moist and wet forests of tropical Africa have no doubt been greatly affected (like rainforests in other parts of the tropics) by the climatic vicissitudes of the last few million years. During the arid phases of the glacial cycle which began in the Pliocene, these forests would have greatly contracted, becoming restricted to distinct "refuges". During interglacial warming, the area of moist forest would have expanded. Between the peaks and troughs of the cycle, climate has changed erratically (deMenocal, 1995), so that forest vegetation rarely would have been stable for long periods. Such a pattern of environmental change would have led to a variety of evolutionary forces operating on primates living in African forests. As forests alternately contracted and expanded, and changed in their climate and species-composition, primate populations must have sometimes been fragmented into long-term isolates, have sometimes expanded, and sometimes gone extinct. During isolation, evolutionary processes such as genetic drift and adaptation to changing local conditions would often have caused populations to differentiate to the extent that taxonomists would regard them as distinct subspecies or species (Haffer, 1969; Hamilton, 1988). Further evolutionary change would have occurred during population dispersal at times of forest expansion (Grubb, 1978), and if populations of similar animals then met, hybridization may have occurred, or further adaptive change may have resulted as a consequence of competition. Different species no doubt responded differently to these events and opportunities, depending on their attributes. For example, at times of forest contraction, species able to maintain viable populations in small areas may have been most likely to persist in small refuges, while at times of forest expansion, differing dispersal abilities and ecological tolerances probably influenced the likelihood with which various species spread out and crossed ecogeographic boundaries. Such ecogeographic boundaries might be obvious barriers, such as large river or mountain ranges, or more subtle features such as forest types not providing appropriate food items at certain times of year.

Such historical events and adaptive features of these kinds would have played major roles in producing the patterns of variation seen in present-day primate communities. For example, the angwantibos (*Arctocebus aureus* and *A. calabarensis*), the western needle-clawed galagos (*Euoticus elegantulus* and *E. pallidus*), Allen's galago (*Galagoides alleni*), and mandrills (*Mandrillus leucophaeus* and *M. sphinx*) are all restricted to west-central forests. It may be hypothesized that the ancestors of these primates were isolated in this area during one or more glacial maxima, and that if any close relatives were living elsewhere they became extinct. During interglacial forest expansion, dispersal of these primates out of the west-central forests was inhibited, perhaps by rivers. For example, in the west, *A. calabarensis*, *E. pallidus,* and *G. alleni* have all been found living close to the east bank of the Niger River in southern Nigeria, but none of them occurs west of the Niger (Oates & Jewell, 1967). As we noted above, *M. sphinx* occurs only on one side of the Ivindo River in Gabon. That rivers have some important function in limiting the distribution of these taxa is shown also by the fact that the lower Sanaga River in Cameroon separates the members of the species pairs *A. aureus/calabarensis*, *E. elegantulus/pallidus*, and *M. leucophaeus/sphinx*. Indeed, a majority of primate taxa are represented by different forms on either side of the Sanaga, and similar differences are found on the left and right banks of the Congo River, accounting for some of the species differences between the Ituri and Salonga communities that we have described.

Major rivers also separate many primate taxa in other parts of the world, including Amazonia (Hershkovitz, 1977; Kinzey, 1982; Peres *et al.*, 1996), but there has been debate about the contribution of rivers to patterns of diversification. The present consensus view seems to be that other factors, such as forest fragmentation into refugia, are mainly responsible for producing initial population differentiation, with rivers acting later to limit dispersal, and thus to reinforce differentiation. Wide rivers with strong currents are more likely to limit dispersal (especially if they are fringed by special vegetation types such as flooded forest) than are narrow headwater channels or slow meandering rivers that frequently change their course.

We have described one historical process that could account for some part of the complex pattern of similarities and differences in species-structure among the different African forest communities we have described. The prosimians and mandrills of the west-central forest area may have differentiated there in a past period of forest retraction, and been subsequently limited in their spread by rivers or river-associated ecosystems. A similar but slightly different process may account for the distribution of species such as *Procolobus verus* (restricted to the forests of Upper Guinea, including Nigeria) and *Cercopithecus hamlyni* (in eastern Democratic Republic of the Congo). These two taxa appear to have originated, or been isolated, in a restricted area (perhaps with related forms going extinct elsewhere) and have subsequently not spread very widely, but their distributions are not obviously limited by rivers. Perhaps their dispersal has been limited by some other habitat feature. Each appears to be a habitat specialist, with *P. verus* being most common near water at low altitude, and *C. hamlyni* being most frequent in or near *Gilbertiodendron* forest in the Ituri.

Similarly, the various distinct populations of *Procolobus badius* across the African forest zone may have originally differentiated during episodes of forest fragmentation, and then been limited in their subsequent dispersal into some areas by habitat features. The absence of any red colobus monkeys between western Cameroon and the eastern part of the Congo Republic is not easily explained by any particular river barrier, but exactly what features have limited dispersal into this area remain unclear. There may be general habitat features of the west-central African forests (such as the seasonal pattern of food production and/or the chemistry of tree foliage) that make it a relatively unfavorable habitat for colobus monkeys, with the result that colobines have both few species and a low biomass in these forests.

The species groups which have different members in many of the forest communities (such as the *cephus* and *mona* groups of guenons, and the black-and-white colobus) are probably the result of yet other historical processes, where forest fragmentation has produced local differentiation, but with this differentiation accompanied either by the absence of widespread extinctions, or by good dispersal ability. Each of these attributes could be associated with broad ecological tolerance (particularly the ability to survive in a range of forest types), and could therefore explain why these groups are so widely distributed. Yet even in these cases, rivers have sometimes been found to form boundaries between taxa, such as the Cross River separating *Cercopithecus sclateri* and *C. erythrotis* in the *cephus* group, and the Sanaga separating *C. pogonias pogonias* and *C. p. grayi* in the *mona* group. This could be because rivers, even when they do not completely limit dispersal, may slow the spread of a population, allowing two different, but related, taxa to spread out from centers of differentiation to opposite river banks. In this case, occasional migration across a river might have little effect on the maintenance of population differences; the migrants might have low survivorship or breeding success in competition with members of a closely related taxon, or their genes might be swamped should they interbreed with members of the other taxon.

Whatever the validity of the particular evolutionary scenarios described here, long-term historical processes of some kind have surely contributed strongly to the present pattern of variation in the species structure of African forest primate communities. These processes have interacted with contemporary patterns of habitat diversity and forest size. Struhsaker (1981) has presented an argument for floristic diversity, proximity to a glacial refuge, and forest