Chapter 43

Conservation Value of Africa's Flooded Habitats to Non-human Primates

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Introduction

Non-human primates occur in, and use, a variety of permanently and seasonally flooded habitats in sub-Saharan Africa. Such habitats include swamp, mangrove, marsh, littoral, riparian and gallery forests, as well as bais (open swampy clearings) and seasonally flooded grasslands (Bennett et al.; Chapter 2, this volume). To date, the study and conservation of most African primate species have focused on populations in terra firma (never-flooded) habitats, while flooded habitats have been under-emphasized in the primate ecology and conservation literature and under-represented in Africa's protected area network (Gautier-Hion & Brugiere 2005). In Central Africa (from the Nigeria-Cameroon border eastward to the Albertine Rift), only 6.6% of the region's vast swamp forests lie within protected areas, compared to 17.0% of terra firma forests; mangroves are better represented, but occur within just 13.5% of protected areas in the region (Table 43.1).

In this chapter, we discuss how African primates use flooded habitats, describe species for which these habitats are critical for conservation, and name the major threats to these environments. Several chapters in this volume contain related data. We do not summarize all of their findings here, but point to relevant chapters. Our intent is to expand on what has been discussed elsewhere in this volume, to further illustrate the role of flooded habitats in the conservation of many of Africa's primate communities. Herein, we follow the primate taxonomy presented in Butynski et al. (2013), with these exceptions: (1) for red colobus other than Procolobus verus, we use the genus Piliocolobus and not Procolobus per the forthcoming IUCN Red List; (2) we elevate the Niger Delta red colobus to species level as Piliocolobus epieni following Oates (2011), and (3) we follow the latest assessment for lemurs as presented by the IUCN (2017). For threatened taxa only, we note their current conservation status as assessed by the IUCN Red List.

An Awakening: Apes in the Congo Basin

Although the preference of several African primate species for flooded habitats has been known for decades, it was only relatively recently that the conservation significance of inundated forests for primate communities was brought to the fore. In particular, several studies prompted global attention to the central Congo Basin, home to the greatest expanses of flooded forest in Africa. Many of these studies focused on the Lake Télé–Lake Tumba

Landscape, Africa's largest wetland and the world's largest swamp forest at 126 000 km² (Twagirashyaka & Inogwabini 2009). Partly in the Democratic Republic of the Congo (DRC) and partly in the Republic of Congo (Congo), this region also contains patches of *terra firma* forest and (often seasonally flooded) savanna.

Three ape taxa have long been known to use the swamp forests of Lake Télé-Lake Tumba: the Critically Endangered western lowland gorilla (Gorilla gorilla), Endangered central chimpanzee (Pan troglodytes troglodytes) and Endangered bonobo (Pan paniscus) south of the Congo River. However, the importance of these forests for primates was not recognized until surveys, beginning in the late 1980s, showed that the area supports high densities of apes, especially western lowland gorillas (Blake 1993; Blake et al. 1995; Fay et al. 1989; Fay & Agnagna 1992). The area is now considered to be a stronghold for gorillas; the swamp forest they inhabit is impenetrable and possesses poor-quality timber, making it unfavourable to humans and thus more impervious to anthropogenic change (Poulsen & Clark 2004). Subsequent surveys estimated more than 18 000 gorillas in the swamp forests of the Lake Télé-Likouala Landscape in Congo (Ivenguet et al. 2012; Maisels et al. 2012; Malanda et al. 2010; Rainey et al. 2010; Stokes et al. 2010). Across the Congo River in the Lake Tumba Landscape, bonobos and chimpanzees are both strongly associated with swamp and flooded forests (Inogwabini et al. 2012).

Studies elsewhere in the Congo Basin further support the significance of flooded habitats for primate conservation in this region. Western lowland gorillas in southern Cameroon prefer swamp habitats (but avoid riparian forest) when constructing nests (Willie et al. 2013). In the Central African Republic, Brugiere et al. (2005) found high densities of primates and higher primate species richness in flooded forest compared with terra firma forest. A follow-on assessment of 12 primate communities in Central Africa showed that riparian forests support 1.5-times more primate species than terra firma forests (Gautier-Hion & Brugiere 2005). Outside the Congo Basin, other flooded habitats are important for primates, including freshwater and mangrove swamp forests of Nigeria, particularly in the Niger Delta (Chapter 40), as well as several other coastal deltas, including Ogooué in Gabon, Tana in Kenya, and Rufiji in Tanzania (Chapter 30).

Flooded Habitats' Built-in Defence

Africa's flooded forests may hold particular conservation value because they are generally less affected by anthropogenic

Table 43.1 Protected areas within inland swamp or mangrove forests in Central Africa (from the Nigeria–Cameroon border eastward to the Albertine Rift). Total forest area: mangroves: 9013 km²; inland swamp forests: 191 463 km².

Forest type	Country	Protected area	Area of PA within flooded habitat type (km²)	% of total forest type
Mangrove	Cameroon	Campo-Ma'an National Park	13	0.14
	Cameroon	Rio Campo Natural Reserve	8	0.09
	Democratic Republic of Congo	Mangroves Natural Reserve	138	1.53
	Equatorial Guinea	Estuario del Muni Natural Reserve	146	1.62
	Gabon	Akanda National Park	58	0.64
	Gabon	Loango National Park	90	1.00
	Gabon	Moukalaba-Doudou National Park	225	2.50
	Gabon	Pongara National Park	534	5.92
	Gabon	Wonga-Wongue Presidential Reserve	3.4	0.04
Subtotal mangrove				13.48
Inland swamp forest	Cameroon	Boumba Bek National Park	22	0.01
	Cameroon	Kom National Park	117	0.06
	Cameroon	Lobeke National Park	9.7	0.01
	Cameroon	Santchou Faunal Reserve	36	0.02
	Central African Republic	Bangassou Forest Reserve	240	0.13
	Central African Republic	Botambi Classified Forest	43	0.02
	Central African Republic	Dzanga-Ndoki National Park	85	0.04
	Central African Republic	Dzanga-Ndoki Special Reserve	113	0.06
	Central African Republic	Mbaere-Bodingue Faunal Reserve	12	0.01
	Democratic Republic of Congo	Lake Tumba-Ledima Reserve	3045	1.59
	Democratic Republic of Congo	Lomako Natural Reserve	2	0.00
	Democratic Republic of Congo	Salonga National Park	1684	0.88
	Democratic Republic of Congo	Yangambi Biosphere Reserve	601	0.31
	Gabon	Minkebe National Park	204	0.11
	Gabon	Mwagna National Park	79	0.04
	Gabon	Wonga-Wongue Presidential Reserve	0.5	0.00
	Republic of Congo	Lake Télé Community Reserve	3226	1.68
	Republic of Congo	Nouabale Ndoki National Park	5.5	0.00
	Republic of Congo	Ntokou-Pikounda National Park	3126	1.63
	Republic of Congo	Odzala National Park	0.8	0.00
Subtotal inland swamp forest				6.69

Note: We acknowledge other sites of importance for which there are no habitat/vegetation data, including two coastal sites in Gabon: Mayumba NP and the Akaka swamps of Loango NP, and one site in the Republic of Congo: Conkouati-Douli NP.

threats. These habitats are often marginal lands for agriculture given the challenges of converting inundated habitat to farmland (Gautier-Hion & Brugiere 2005; Nowak 2012). Hunting pressure may also be lower. Local people living in or near flooded habitats may rely on fishing for their livelihoods and

therefore fish as a protein source, reducing hunting pressure on terrestrial wild species (Baker 2003; Werre 2001a). In addition, inundated environments are generally less accessible to hunters. Travelling on foot is hindered by thick, muddy terrain and by the stilt roots or aerial roots of trees typical of these forests, such as species of *Uapaca* (Phyllanthaceae) and *Pandanus* (Pandanaceae) in swamp forests, and *Rhizophora* (Rhizophoraceae) in coastal mangroves. *Pandanus* and *Raphia* spp. (Arecaceae) and rattans (lianescent palms), also common in swamp forest, are generously laced with spines along their leaves and/or stems. In Lake Télé in Congo, Rainey *et al.* (2010) describe *Raphia* swamp forest as providing natural protection against hunting for gorillas. Although colobus monkeys are commonly hunted across Central Africa, populations of Oustalet's red colobus (*Piliocolobus oustaleti* in the forthcoming IUCN Red List) and guereza colobus (*Colobus guereza*) resident in swamp forests of Lake Télé are so well protected by the impenetrability of this habitat that they behave naively towards humans (H. Rainey, pers. obs.).

For similar reasons, mangroves afford protection to some primate populations. Due to the relatively lower hunting pressure and degradation in mangroves versus neighbouring terra firma forests, researchers have suggested that primate populations seek refuge in mangroves, including two Endangered red colobus species: the Zanzibar red colobus (Piliocolobus kirkii) in Zanzibar and Temminck's red colobus (Piliocolobus temminckii) in Senegal (Galat-Luong & Galat 2005; Chapters 7 and 39). In southeastern Ivory Coast, mangroves are important for two Endangered species: roloway monkey (Cercopithecus roloway) and white-naped mangabey (Cercocebus lunulatus). Researchers suggest that these species have adapted to permanently flooded mangroves to not only avoid severe hunting pressure in adjacent flooded forest (deemed more accessible than mangroves), but also take advantage of the food resources found in mangroves (Bi et al. 2013).

The relative inaccessibility of flooded habitats likely contributes to the survival of a population of the Critically Endangered greater bamboo lemur (*Prolemur simus*) in the Torotorofotsy wetlands (Ramsar Site #1453), a large marshland in Madagascar (Dolch *et al.* 2008), as well to the survival of the Critically Endangered Niger Delta red colobus (*Piliocolobus epieni*), found only in marsh forest in the central Niger Delta (Werre 2000, 2001a), and the recently rediscovered Bouvier's red colobus (*Piliocolobus bouvieri*) in the swamps of northern Congo west of the Sangha River (Devreese 2015).

Elsewhere in southern Nigeria, high human population density and associated pressures on natural habitats have led to widespread forest loss and degradation. Most of the largest remaining primate habitats in the region are seasonally and permanently flooded forests, which confer a degree of protection on populations of some species, including the Endangered redcapped mangabey (Cercocebus torquatus) and two Endangered endemics, the Sclater's monkey (Cercopithecus sclateri) and white-throated monkey (Cercopithecus erythrogaster pococki) (Baker 2005; Baker & Olubode 2008; Oates 1989; Oates & Anadu 1988; Chapters 30 and 40). In the Niger Delta, many swamp and riparian forests persist as they are more difficult to access and farm, although some productive flooded habitats, such as forests along the Niger River floodplain, have nevertheless been converted to cropland because of human 'ingenuity' (Ikemeh 2014; Oates 1989).

Diversity of Flooded Habitat Use

Our knowledge of primates in flooded habitats has progressed quickly in recent decades (Table 43.2). Researchers have discovered that primates use flooded habitats for a variety of reasons and to varying extents. Some species vary geographically in their use of inundated habitats. For instance, guereza colobus is a terra firma specialist in East Africa, but is associated with water where it occurs in Central Africa (Gautier-Hion & Brugiere 2005). Similarly, Oustalet's red colobus, the most widespread of the P. rufomitratus subspecies, uses a variety of tropical forest types (Oates et al. 2008), but in the Ngotto Forest in Central African Republic, it inhabits only flooded forests on alluvial river banks (Gautier-Hion & Brugiere 2005). In flooded and swampy areas, this monkey spends more than one-quarter of its time at below 10 m above ground and regularly enters water to collect bulbs of aquatic plants (Galat-Luong & Galat 1979; A. Galat-Luong & G. Galat, pers. comm., 2014).

Other species rely heavily, if not exclusively, on flooded habitats. In Madagascar, the Critically Endangered Lac Alaotra bamboo lemur (Hapalemur alaotrensis) feeds almost exclusively on papyrus and reeds in marshland, making it the only primate uniquely adapted to marsh habitat (Chapter 34). Allen's swamp monkey (Allenopithecus nigroviridis) occurs only in swamp and riparian forests, where it is sympatric with De Brazza's monkey (Cercopithecus neglectus), Tshuapa (or Thollon's) red colobus (P. tholloni), guereza colobus monkeys, and either red-tailed (Cercopithecus ascanius) or moustached (C. cephus) monkeys depending on the location (Gautier 1985; Maisels et al. 2006b). De Brazza's monkey is always associated with riverine or swamp forest (Chapter 39; Gautier-Hion & Gautier 1978; Gautier-Hion 2013b). Like De Brazza's, the northern talapoin monkey (Miopithecus ogouensis) is considered a flooded forest specialist, preferring riparian habitats (Gautier-Hion 2013c; Maisels et al. 2006a); the southern talapoin monkey (Miopithecus talapoin) likely has similar preferences (Gautier-Hion 2013d). In addition, both red-capped mangabeys and golden-bellied mangabeys (Cercocebus chrysogaster) prefer wet habitats, including seasonally flooded and swamp forests (Ehardt 2013; Ehardt & Butynski 2013). The presence of some primates in parts of their ranges, as well as the extent to which they rely on flooded habitats, may have been overlooked by researchers due to the difficulties associated with surveying wildlife in these habitats (e.g. Maisels et al. 2006a, 2007b).

Gorillas were thought to avoid water until the 1970s, when investigators began to learn otherwise. Casimir (1975) found that Critically Endangered eastern lowland gorillas (*Gorilla beringei graueri*) wade through streams up to 60 cm deep in the eastern DRC. Western lowland gorillas in Equatorial Guinea frequently 'bathe' in streams, according to local reports (Groves & Sabater Pi 1985), and they regularly cross streams and nest in sites surrounded by water in Lopé National Park, Gabon (Williamson *et al.* 1988). In northern Congo, gorillas use swamp forests almost exclusively for at least part of the year and feed on the abundant herbaceous monocotyledons (Fay *et al.* 1989). The rich herb layer in *bais* also provides a highly digestible, sodium-rich food source for gorillas (Blake

Table 43.2 Studies of African primates in flooded habitats (non-exhaustive list).

Habitat type	Country	Common name	Genus	Species	Source(s)
Freshwater swamp, including <i>Raphia</i> swamp forests	Cameroon	Western lowland gorilla	Gorilla	gorilla gorilla	Willie et al. 2013
	Democratic Republic of Congo	Bonobo	Pan	paniscus	Inogwabini & Matungila 2009
	Nigeria	Red-capped mangabey	Cercocebus	torquatus	Baker 2005; Baker & Olubode 2008
	Nigeria	Sclater's monkey	Cercopithecus	sclateri	Baker 2005; Baker & Olubode 2008; Baker et al. 2011
	Republic of Congo	Allen's swamp monkey	Allenopithecus	nigroviridis	Maisels et al. 2006
	Republic of Congo	Chimpanzee	Pan	troglodytes	Poulsen & Clark 2004; Rainey et al. 2010; Stokes et al. 2010
	Republic of Congo	Western lowland gorilla	Gorilla	gorilla gorilla	Blake 1993, Blake <i>et al.</i> 1995; lyenguet <i>et al.</i> 2008 & 2012; Kalan <i>et al.</i> 2010; Malanda <i>et al.</i> 2010; Poulsen & Clark, 2004; Rainey <i>et al.</i> 2010; Stokes <i>et al.</i> 2010
Mangrove	Gabon	Western gorilla	Gorilla	gorilla	Chapter 12
	Guinea	Chimpanzee	Pan	troglodytes	Hockings, pers. comm., 2013
	Madagascar	Pygmy mouse lemur	Microcebus	myoxinus	Ganzhorn pers. comm., 2013
	Senegal	Green monkey	Cercopithecus	sabaeus	Galat & Galat-Luong 1976
	Senegal	Senegal red colobus	Piliocolobus	temmickii	Galat-Luong & Galat 2005
	Zanzibar	Zanzibar red colobus	Piliocolobus	kirkii	Nowak & Lee 2010
Littoral	Madagascar	Collared brown lemur	Eulemur	collaris	Ganzhorn et al. 2007
	Madagascar	Mouse lemur	Microcebus	spp.	Ganzhorn et al. 2007
	Madagascar	Southern woolly lemur	Avahi	meridionalis	Ganzhorn et al. 2007
Riverine	DRC & Gabon	Western gorilla	Gorilla	gorilla	Chapter 24
	Kenya	Tana River mangabey	Cercocebus	galeritus	Wieczkowski & Butynski 2013
	Kenya	Tana River red colobus	Piliocolobus	rufomitratus	Butynski & Mwangi 1994; Mbora & Meikle 2004
	Tanzania	Red-tail monkey	Cercopithecus	ascanius	Chapter 33
Marsh swamp	Nigeria	Niger Delta red colobus	Piliocolobus	epieni	lkemeh 2015; Werre 2000, 2001a
Seasonally flooded inland delta	Botswana	Chacma baboon	Papio	ursinus	Cheney <i>et al.</i> 2004; Hamilton <i>et al.</i> 1976; Johnson 2003
Intertidal zone	South Africa	Chacma baboon	Papio	ursinus	Chapter 20

1994; Olejniczak 1994; Vanleeuwe et al. 1998). Similarly, chimpanzees and guereza colobus monkeys feed on algae in bais in Congo (Devos et al. 2002).

Flooded habitats clearly provide some primate populations with unique opportunities for refuge and feeding. Such habitats may have a higher relative abundance of invertebrates; high protein foods, such as shellfish (in mangrove areas); and a high density of monocotyledonous foods. In Salonga National Park, DRC, sympatric Tshuapa red colobus and Angola colobus (*Colobus angolensis angolensis*) are common in flooded forests where they eat a diet full of seeds (Maisels *et al.* 1994). A population of red-capped mangabeys in Gabon occurs in mangrove forest significantly more often than in *terra firma* forest (Cooke 2012); in mangroves, the species feeds on crabs (Cooke

2015). In the Tsinjoriake region of southwestern Madagascar, Endangered ring-tailed lemurs (*Lemur catta*) retreat to flooded habitats during the dry season because of cooler temperatures (J. Youssouf, pers. comm., 2014; Chapter 7).

Using flooded habitats can be risky for primates. Chacma baboons (*Papio ursinus*) can occur in high densities in the Okavango Delta, an inland delta in Botswana (Johnson 2003); the baboons use *terra firma* islands, edged with woodland, but also feed on the floodplain (Hamilton *et al.* 1976). More than any other food item, aquatic plant underground storage organs are the primary fallback foods for one population (Wrangham *et al.* 2009). There are costs associated with exploiting the floodplain, however: baboon mortality is highest during the 3-month peak flood period (June–October) when baboons

navigate the flooded plains and move among islands (Cheney et al. 2004; R. Seyfarth, pers. comm., 2014). Crocodiles make water crossings dangerous, and the only documented lion attacks on baboons occurred when baboons emerged onto dry islands after crossing water.

These examples illustrate the value – but also risk – of flooded habitats for several African primates; however, for many of these species, additional habitats are required for survival. The Zanzibar red colobus population on Uzi Island, in the Zanzibar archipelago, uses mangroves to a significant degree, yet the species must have access to upland coral rag forest (Nowak & Lee 2011). Exclusive use of mangroves would likely impede this population's health given the high level of tannins and salt in mangrove-derived foods (Nowak 2008). Additionally, consumption of mangrove leaves by this population has resulted in rates of water foraging higher than those known for any other red colobus species or population; an energy-intensive activity, water foraging by the Uzi Island red colobus population occurs daily and throughout the day.

Flooded Habitats: Threats and Conservation

Given that flooded habitats are relatively inaccessible and difficult to convert to agricultural land, they provide a degree of natural protection for many primates in Africa. They also harbour key resources for some populations. Although rivers and flooded zones can act as barriers to dispersal and gene flow (e.g. Chapman *et al.* 1999; Eriksson *et al.* 2004; Quéméré *et al.* 2010; Chapter 38), riparian forests, due to their linear nature, may function as dispersal corridors for certain populations and species (e.g. lemurs, Ganzhorn *et al.* 2006; chimpanzees, McLennan 2008; several guenons, Chapter 39). Protection of riparian forests and adjacent *terra firma* forests may be the best way to safeguard much of Africa's primate diversity (Gautier-Hion & Brugiere 2005). Inundated habitats, consequently, deserve special conservation attention (see Foreword).

Increasing human populations across sub-Saharan Africa are placing greater pressure on already stressed flooded habitats. Threats to these environments are manifold, and many sites lack effective protection. Africa's ten largest river deltas, some of which support at least several threatened primate taxa, are largely unprotected and unrecognized formally as biodiversity sanctuaries (Chapter 30). Only half (10 of 20) of the protected areas within inundated and flooded forests in Central Africa are national parks (IUCN Category II), although one is a Presidential Reserve (which carries a high level of protection). The rest are Faunal Reserves, Forest Reserves, or other less strictly and formally protected areas (Table 43.1).

The very important Lake Télé-Lake Tumba Landscape in the Congo Basin is under threat as a result of commercial hunting, road building, and impacts associated with human refugees. Two protected areas within the landscape cover less than 10% of the region, although several new protected areas have been proposed (Twagirashyaka & Inogwabini 2009). Some African habitats under protection are not secure and require

careful monitoring. For example, the Okavango Delta, which comprises one protected area (Moremi Game Reserve) and became a UNESCO World Heritage Site in 2014, faces several risks, including diversion of water upstream for a hydropower plant (Boyes 2014), as well as fencing, overgrazing, overfishing, and climate change (Darkoh & Mbaiwa 2014). Dam construction would force the Delta's primate populations to adapt to anthropic flooding (Chapter 36). Similarly, severe vegetation changes due to dam construction, irrigation projects, and water diversion have negatively affected populations of the Endangered Tana River red colobus (*P. rufomitratus*) (Oates *et al.* 2008; Chapter 30).

Other areas are remarkably underprotected. The Niger Delta region is important for many of Nigeria's primates, including the country's only endemic species (C. sclateri and P. epieni), but the Delta has no effectively protected areas (Chapters 30 and 40). The region has long experienced degradation due to a number of threats, notably impacts associated with oil-related development and a growing human population. Although flooded forests may limit logging activities where timber cannot be readily cut and transported, loggers in some inundated forests in the Niger Delta float valuable trees in 'timber gutters' (narrow canals dug in the forest) and then assemble these into timber rafts; the rafts are often pulled by boats to coastal trading centres (Baker 2005; Ikemeh 2015; Werre 2000). One economically valuable species, Abura (Fleroya ledermannii = Hallea ledermannii or Mitragyna ledermannii, Rubiaceae), a preferred food of P. epieni, has been heavily exploited in the Niger Delta, notably within the range of P. epieni (Werre 2000). Intensive logging may have contributed to severe population declines of this highly threatened primate (Ikemeh 2015).

Globally, mangroves face threats from shrimp and timber industries and are declining at a rate of 1% each year (Polidoro et al. 2010). Although mangroves have been receiving greater attention for the ecosystem services and economic benefits they provide (Polidoro et al. 2010; UNEP-WCMC 2006), they generally do not receive the same level of official recognition as terra firma forests and may simply be designated as 'Mangrove Forest Reserves' (e.g. in Tanzania; K. Nowak, pers. obs.). This is in contrast to terrestrial protected areas, which have distinct names, identities, biodiversity inventories and internet websites, and can often be immediately recognized by name and reputation (e.g. 'the Serengeti', 'the Virungas'). Such ubiquity can greatly aid conservation efforts (Chapters 7 and 12). Only five of the nine protected areas within the Central African mangrove region are national parks (IUCN Category II); one is a Presidential Reserve; and the other four are Natural Reserves (Table 43.1).

Both research and conservation actions are urgently needed in flooded zones across sub-Saharan Africa. New research is likely to uncover additional evidence of the use of, and reliance on, flooded habitats by primates. Ultimately, effective protection of these habitats will be essential to conserving Africa's primates as pressure on *terra firma* forests escalates. For example, conservation of gorillas and other primates in the Congo Basin requires the integration of riverine, swamp and coastal forests

outside of current protected areas into surveys, monitoring, and protection plans (Maisels 2006b, 2007a; Rainey *et al.* 2010). In early 2015, negotiations were underway to expand the boundaries of the Lake Télé Community Reserve; such an extension would benefit large numbers of great apes (Rainey *et al.* 2010). This vast swamp also benefited from particular attention in the most recent IUCN great ape action plan for the region (IUCN 2014). Finally, key sites that lack any protection, such as the

Niger Delta, should be prioritized by the conservation community to ensure that the degradation of these areas does not result in unrecoverable loss of Africa's primate diversity.

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