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Research Article

Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: implications for the conservation of forest fragments

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Abstract

As a result of forest modification, primates are increasingly having to rely on fragments; so too are the human populations that have historically relied on continuous forest for critical resources. The role of primates in seed dispersal is increasingly understood to have significant unique effects on plant demography and forest regeneration. Our aim in this paper is to explore the potential for monkey seed dispersers to maintain the utility of forest fragments for humans through seed dispersal in the Taï region, western Côte-d'Ivoire. We established a list of fruit species whose seeds are dispersed by seven of eight monkey species occurring in the Taï National Park by using primary data and published accounts of their fruit diet, and determined the abundance of human-used and monkey-dispersed tree species in forest fragments in the broader Taï region. The monkeys of the Taï National Park consumed 75 tree species. Of this total set of 75 species, 52 (69%) were dispersed almost exclusively by monkeys and were found in neighboring forest fragments. Of the 52 fruiting forest tree species that are dispersed by Taï monkeys, 25 (48%) have some utility to local inhabitants suggesting that maintaining populations of primates is important not only for forest regeneration, but also for human populations that rely on forest resources. The conservation of primate species is a critically important goal in itself, but by working to ensure their protection in forest fragments, we certainly protect indirectly the seed dispersal of important human resources in these fragments as well.

Key Words: Conservation, forest fragments, forest regeneration, Taï National Park, primate seed dispersal, useful plants

Resume

Suite à la dégradation des forêts, les primates se retrouvent à dépendre de plus en plus de fragments de forêts. Il en est de même des populations humaines qui par le passé trouvaient leur moyens de subsistance dans des forêts continues. Il est de plus en plus reconnu que la dispersion des graines par les primates à un effet significatif unique sur la démographie et la régénération de la forêt. Le but de cette étude était d'explorer le potentiel des singes à queue pour maintenir l'utilité des fragments forestiers pour les humains à travers la dispersion des graines dans la région de Taï à l'ouest de la Côte-d'Ivoire. Pour cela, nous avons d'abord établi une liste des espèces des fruits dont les graines sont dispersées par sept des huit espèces de singes à queue dans le Parc National de Taï en utilisant des données d'observations personnelles ainsi que des données publiées par d'autres auteurs. Nous avons ensuite déterminé l'abondance, dans les fragments forestiers de la région de Taï, des espèces d'arbres dont les graines sont dispersées par les singes à queue en mettant l'accent sur les plantes utilisées par les humains. Les singes à queue frugivores du Parc National de Taï ont consommé les fruits de 75 espèces d'arbres dont 52 (69%) produisaient des graines dispersées de façon quasi exclusive par les singes et se rencontraient aussi dans les fragments forestiers voisins de ce parc. Au total, 25 (48%) de ces 52 espèces d'arbres étaient d'utilité pour les communautés locales suggérant que le maintien des populations de primates dans les fragments est important non seulement pour la régénération de ces fragments, mais aussi des populations humaines qui vivent au dépens des ressources forestières. La conservation des espèces de singes est un but essentiel en soi, mais en assurant leur maintien dans les fragments forestiers, l'on maintient aussi la dispersion des graines de ressources importantes pour les humains dans ces fragments.

Mot Clefs: Conservation, dispersion des graines par les primates, fragments forestiers, Parc National de Taï, plantes utiles, régénération de la forêt

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Introduction

An estimated 95% of tree species in the tropics produce seeds that are dispersed by frugivorous animals, and the role of vertebrates in dispersing these seeds is increasingly understood to have significant effects on plant demography and forest regeneration [1-10]. Because of their high density in some habitats, along with high rates of frugivory and relatively large body size, primates have been argued to be a particularly important faunal group in the effective dispersal of seeds both in the Neo- and Paleotropics and have also been demonstrated to impact tree species reproduction [11-14]. Moreover, recent work has demonstrated that the seed dispersal services provided by primates are generally unique and cannot be compensated for by any other taxa (Cameroon: [15]; Taï National Park, Côte-d'Ivoire: [16]).

Yet, relationships between plants and animals are increasingly being interrupted and altered as a consequence of acute anthropogenic impact natural habitat. Ninety percent of all primate species are found in tropical regions and most depend upon forest [17], and modification to tropical forests results in forest area reduction and fragmentation [18]. Forest fragments are hence increasingly common, and forest-adapted primate species, in turn, increasingly must rely on fragments to meet their nutritional requirements. Yet, most forest fragments are not legally protected; they are on land held by citizens or local communities that depend on them for valuable sources of income, fuel, charcoal, food, fodder, building materials, and many household tools [18-20]. Despite the lack of legal protection, the sustainable use of forest fragments is increasingly viewed as a way of diminishing human pressure upon protected areas. For example, in Côte-d'Ivoire the World Wildlife Fund (WWF) strongly encourages the maintenance of village-owned forest fragments for participatory, sustainable use to reduce communities' dependence on forest resources from the Taï National Park (pers. comm. with Nandjui -WWF officer).

In order for fragments to remain viable and useful to the goals of protecting more intact forest areas and providing important resources for human populations, they must maintain important plant-animal interactions [21]. Our aim in this paper is thus to explore the potential for primate seed dispersers to maintain the utility of these forest fragments through seed dispersal. We have few data on the cultural and economic value of primate seed dispersal and the ways in which the role of primates may be considered in building sound management strategy for forest resources. These limited data are known from only two sites in Uganda: Budongo Forest Reserve [19], and the Kibale National Park [20]. Such connections among primates, their frugivory and seed dispersal, and the reliance of humans on primate-dispersed forest resources are not available for most of the forested regions of Equatorial Africa.

The Taï National Park, Côte-d'Ivoire, is of key conservation concern: it is the largest remaining tract of Guinean forest and is home to 12 primate species (three prosimian species, eight monkey species, and one ape species - chimpanzee [*Pan troglodytes*]), several of which are endangered. In addition, as with most tropical forest, much of the surrounding forest is fragmented. Of note is that since forest fragmentation in this area is relatively recent (20 years at most), the floristic composition of forest fragments in the greater Taï region is still largely similar to that of the protected areas [22]. Both colobine and cercopithecine monkeys, but not chimpanzees are repeatedly reported by villagers to occur in many of these fragments. These anecdotal observations were recently confirmed by recent

surveys conducted by a research team from the *Centre Suisse de Recherches Scientifiques en Côte-d'Ivoire* (CSRS) that included two of the authors (Koné, Bakayoko; unpub).

Our specific aims in this paper are to: (1) evaluate the total set of fruit species in the Taï National Park whose seeds are dispersed by monkeys, (2) establish a list of the human uses of monkey-dispersed tree species in the greater Taï region at the western side of the Taï National Park (i.e., the National Park and surrounding, unprotected fragments), and (3) determine the abundance of monkey-dispersed tree species in forest fragments at the western periphery of the Taï National Park.

Methods

Study site

We conducted the study in the Taï National Park (TNP) and its western periphery in the South Western corner of Côte-d'Ivoire, West Africa. The TNP is located between 5°10' to 6°20' N and 4°20' to 6°20' W (Figure 1); it has an area of 4,570 Km² and is extended to the North by the N'zo Wildlife Reserve (NWR: 790 Km²). The Taï forest is the largest evergreen lowland moist forest under protection in West Africa. It achieved the status of National Park in 1972 and that of World Heritage Site in 1982. The larger Taï region comprises the TNP-NWR complex, four gazetted forests: *Forêt Classée de la Haute Dodo* (1,150 Km²), *Forêt Classée des Rapides Grah* (3,150 Km²), *Forêt Classée du Cavally* (520 Km²), the *Forêt Classée du Goin-Débé* (1,333 Km²), and numerous forest fragments (Fig. 1). Forest fragmentation in the Taï region resulted essentially from agricultural clearings intensified in the 1980s when the government encouraged an influx of people in the region to stimulate local development [23]. Many of the forest fragments are relatively close to the TNP or to the Cavally and Goin-Débé forests (table 1) and separated from these protected forest blocks by small fallow lands that can be easily crossed by many animal species including monkeys. The Taï region is a biodiversity hotspot within the upper Guinean forest region [24]. Annual rain fall averages 1800 mm and daily temperature averages 24 °C. The climate is characterized by four seasons: two rainy seasons (March to June, and September to November) and two dry seasons (December to February and July to August). Human population size at the periphery of the TNP increased from 113, 000 in 1992 to 527, 000 in 1998 [25]. Native peoples living at the western periphery of the TNP are the *Guéré*, the *Oubi* and the *Kroumen* who strongly still rely on forest resources in their daily life.

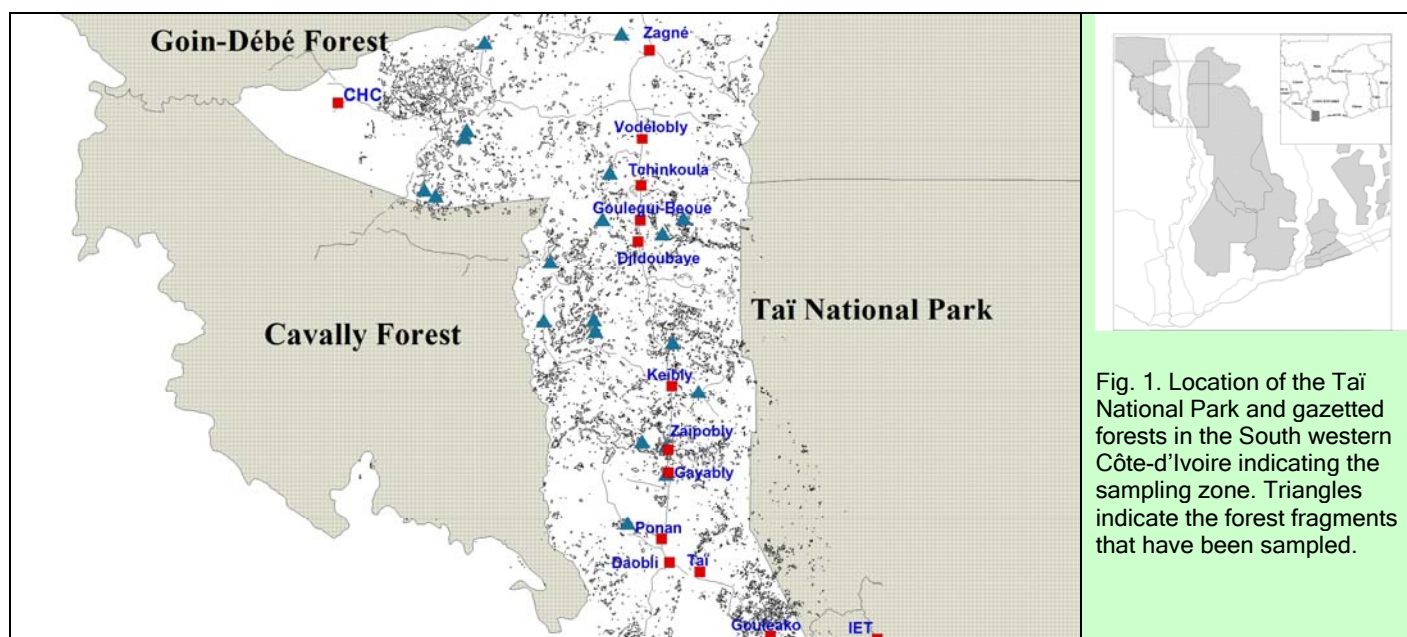


Fig. 1. Location of the Taï National Park and gazetted forests in the South western Côte-d'Ivoire indicating the sampling zone. Triangles indicate the forest fragments that have been sampled.

Data collection

We compiled an exhaustive list of all fruit species known to be consumed by the Taï forest monkeys using data collected by two of the authors (Koné, Refisch) between 1997 and 2000 and by the Taï Monkey Project between 1991 and 1998 (unpublished data). We also included data from published accounts [16,26,27]. Of the eight monkey species occurring in the TNP, only the frugivory of the greater spot-nosed monkey (*Cercopithecus nictitans*) has not been well documented although Eckardt and Zuberbühler [28] found that its diet is similar to that of the Diana monkey (*Cercopithecus diana*) (Fig. 2a). Thus, we include here all known information on the frugivory of seven monkey species occurring in the TNP: Diana monkey, lesser spot-nosed monkey (*Cercopithecus petaurista*) (Fig. 2b), greater spot-nosed monkey (*Cercopithecus nictitans*), Campbell monkey (*Cercopithecus campbelli*), black-and-white colobus (*Colobus polykomos*), red colobus (*Procolobus badius*), olive colobus (*Procolobus verus*), and sooty mangabeys (*Cercocebus atys*) (Figure 2c). Data on the potential alternative dispersers for primate-dispersed seeds are essentially from published accounts compiled by Chatelain *et al.* 2001 [27]. We excluded data on seed dispersal by animals such as elephants that are not found in the surveyed forest fragments.

Table 1: characteristics of forest fragments considered in the present study

Forest Fragment	Area of fragment (ha)	Distance from closest continuous forest (m)	Age of fragment (year)	UTM Coordinates of reference point	
				LAT	LONG
A	6,52	913,12	17	644317	676735
AC	9,84	1812,60	17	643113	675029
AD	4,52	1778,57	17	643324	676742
AG	33,21	4299,76	17	666116	669097
B'	5,80	1501,44	17	676977	651582
C'	31,85	1235,77	17	676544	652383
F'	10,60	5977,31	17	678166	664656
G	2,24	6047,57	20	688120	665505
G'	5,12	5711,23	30	673894	668382
I	21,89	4538,27	17	653206	665923
I'	8,76	1101,50	17	667624	660019
L	26,25	6085,32	17	659000	666940
M	20,12	4927,47	17	658690	668630
M'	4,12	4149,64	20	656742	668666
Pt1	26,05	2990,66	17	662602	670924
Pt8	13,40	1002,47	17	671869	660462
Pt80	11,72	3843,73	20	674999	669861
T	16,36	1840,10	17	680714	654387
T'	17,20	4507,66	17	667718	663537
U	12,48	1823,97	17	681278	654573
U'	13,16	4633,20	17	666933	663646
W	11,84	1379,64	17	687483	655827
Z	6,17	4252,99	20	674898	664146

Unpublished data on diet were collected parallel to behavioral data from direct field observations using hourly-based group scan samplings (15 min each) during all-day follows of monkey troops from dawn to dusk [29]. Koné and Refisch focused on *Cercopithecus diana* (four troops), *C. petaurista* (one troop), *C. campbelli* (one troop) and *Procolobus badius* (four troops); dung was collected opportunistically and sieved for seeds between 1997 and 1998 and were then identified by specialists. Three troops of *Cercopithecus diana*, one troop of *C. petaurista*, one troop of *C. campbelli*, two troops of *Procolobus badius*, three troops, *P. verus*, three troops of *Colobus polykomos*, and one troop of *Cercocebus atys* were under permanent study by the Taï Monkey Project in the period 1996-2000.

For each monkey troop under study, the field assistants of the TMP made an average of 9 group scan samplings per day during 240 days per year for a total of 2400 scans per year.

We categorized seed-handling behavior as either spit, probably spit, swallow, abandon or destroy. We considered seeds to have been probably spat when cercopithecines were observed to consume fruits containing those seeds and no data on seed-handling was available. Indeed previous studies characterized cercopithecines as seed-spitting monkeys [30, 31]. We considered seeds to have been abandoned when lost by monkeys while opening dry fruits or dropped after monkeys have consumed the pulp of fleshy fruits. We considered seed that were either spat, swallowed, or abandoned to have been dispersed by the monkeys, whereas those seeds that were destroyed by the primates were considered dead and therefore not dispersed.

From direct field observations, dung samples, and published accounts, we compiled and evaluated a list of seed-handling techniques by these seven frugivorous monkey species (whether opportunistically or not) to determine whether seeds were dispersed or destroyed during feeding. We then evaluated the human use of plant species whose seeds are dispersed by Tai monkeys by examining reports published in Chatelain *et al.* [27], Kasperek [32], and Téré [33].

We compared the list of monkey-used tree species with that of the tree species inventoried by Bakayoko [22] in 63 forest fragments at the western periphery of the Tai National Park in 2000-2002 using the line transect method of Gautier *et al.* [34]. We restricted that comparison to 22 forest fragments that were larger than 4 hectares as such forest fragments are most likely to house monkey species as observed during the above-mentioned recent survey carried out in the region (unpublished data). The 22 forest fragments are located between the Zagné and Paulé-Oula villages at the western periphery of the TNP and cover 4-33 hectares.

Results

Between 1997 and 2000, Refisch and Koné observed frugivorous monkeys to consume 25 species of Tai forest trees. The Tai Monkey Project database contributed another 50 species. Of this total set of 75 species, 23 (31%) were destroyed by the monkeys either because seeds were broken open and the endosperm purposely consumed, or because seeds were broken open in the process of consuming fruit pulp. The remaining 52 species (69%) were dispersed by either one, two, three, four, five, six, or all seven of the frugivorous monkey species considered. Only six (i.e. 12%) of these 52 plant species were dispersed by other animals likely to be found in the forest fragments of the region (Appendix 1).

In general, this dispersal either took place via seed swallowing and defecation some distance away from the parent tree, or, in the case of the cercopithecines, also through cheek-pouching fruit and spitting unwanted seeds some distance away from where fruits were removed. In some cases, fruits were carried over some distance and seeds were lost during the process of opening dry fruits or dropped once the pulp of fleshy fruits had been consumed.

We found that 25 (48%) of the 52 fruiting forest tree species that are dispersed by Tai monkeys, have some utility to local inhabitants. Table 2 details the subset of species that are both dispersed by monkeys and have some economic/cultural value.

The categories employed here include "Wood", "Food", "Medicinal", "Environmental", "Ritual" and "other" uses. By far the most common use of these 25 forest tree species was "Food" use. Indeed, 16 species (64%) are being used for fruit and/or seed direct consumption and also for oil extraction and sauce cooking from either seeds or leaves. The next two most common uses of these 25 species are "household utility" and "medicinal" uses, with seven (28%) and 6 (24%) species, respectively. "Household utility" uses include house construction, manufacturing furniture, canoes and accessories, charcoal production, utensil repair, torch and incense uses. Plant parts are used for their purgative, antiseptic and healing properties and also for their curative properties against toothache and tiredness. Three (12%) of the monkey-dispersed tree species have resources that fall under the

category “Environmental” uses including rodent poisoning, shade production and increasing rice farms’ productivity. Finally uses of three (12%) of the monkey-dispersed tree species fall under the category “Ritual” - a category which includes evaluation of witch/sorcerer identity, magic spells, and the manufacture of supernatural masks. It should be noted that seven tree species had resources whose uses fall under multiple (2-3) categories.

Table 2. List of human uses of tree species whose seeds are dispersed by primates in the Taiï region.

Tree species	Food	Medicinal	Household utility	Environ mental	Ritual
<i>Bussea occidentalis</i>	seed consumption (almond)		house construction, manufacturing furniture		
<i>Canarium schweinfurthii</i>	fruit consumption, oil extraction		Incense, torch, utensil repair		
<i>Chrysophyllum taiense</i>	fruit consumption (chewing-gum)				
<i>Coelocaryon oxycarpum</i>		healing, antiseptic			
<i>Coula edulis</i>	seed consumption (almond)		house construction		
<i>Dacryodes klaineana</i>	fruit consumption				
<i>Dialium aubrevillei</i>	seed consumption				
<i>Dialium dinklagei</i>	fruit consumption				
<i>Erythrophleum ivorense</i>					Determining witch/sorcerer identity
<i>Lannea welwitschii</i>		healing			
<i>Maesobotrya barteri</i>	fruit consumption				
<i>Oldfieldia africana</i>	fruit consumption	healing			mysticism, supernatural masks
<i>Pachypodanthium staudtii</i>		tiredness			
<i>Parinari excelsa</i>	fruit consumption		charcoal	rice farm	
<i>Pentaclethra macrophylla</i>	seed consumption				magic spell
<i>Piptadeniastrum africanum</i>				shade	
<i>Pycnanthus angolensis</i>		toothache			
<i>Sacoglottis gabonensis</i>	fruit consumption				
<i>Spondianthus preusii</i>				rodent poison	
<i>Strombosia pustulata</i>			house construction		
<i>Uapaca esculenta</i>	fruit consumption				

Bakayoko did not make an exhaustive inventory of the studied fragments but could find a total of 487 tree species in 22 considered forest fragments including all of the monkey-dispersed tree species except *Spondianthus preusii* and *Uapaca paludosa*. The monkey-dispersed tree species that are most often found in forest fragments are *Strombosia pustulata*, *Maesobotrya barteri* (Fig. 2d), *Dialium aubrevillei*, *Chrysophyllum taiense*, *Dacryodes klaineana*, *Uapaca guineensis*, *Coula edulis* and *Pycnanthus angolensis* (Table 3). These tree species are used for food except *Pycnanthus angolensis* that is a medicinal plant. In addition to being used for food, *Strombosia pustulata* and *Coula edulis* have some household utility.

Table 3. Abundance of monkey-dispersed tree species in 23 forest fragments sampled at the western periphery of the Taï National Park. Includes total number of fragments in which tree species occur.

Tree species	Total number of individual trees in 23 fragments	Number of forest fragments in which the species occurs
<i>Strombosia pustulata</i>	338	23
<i>Maesobotrya barteri</i>	122	20
<i>Dialium aubrevillei</i>	102	20
<i>Chrysophyllum taiense</i>	84	22
<i>Dacryodes klaineana</i>	74	18
<i>Uapaca guineensis</i>	73	15
<i>Coula edulis</i>	64	21
<i>Pycnanthus angolensis</i>	55	20
<i>Dialium dinklagei</i>	32	5
<i>Piptadeniastrum africanum</i>	26	12
<i>Parinari excelsa</i>	26	8
<i>Uapaca esculenta</i>	25	12
<i>Xylopia villosa</i>	22	15
<i>Bussea occidentalis</i>	14	8
<i>Pentaclethra macrophylla</i>	13	3
<i>Pachypodanthium staudtii</i>	12	6
<i>Oldfieldia africana</i>	9	4
<i>Xylopia aethiopica</i>	5	4
<i>Canarium schweinfurthii</i>	4	4
<i>Sacoglottis gabonensis</i>	4	3
<i>Lannea welwitschii</i>	2	2
<i>Coelocaryon oxycarpum</i>	1	1
<i>Erythrophleum ivorense</i>	1	1

Discussion

Although hunting is currently prohibited in Côte-d'Ivoire, wildlife continues to experience extreme hunting pressure [35]. After duikers, primates are the most affected taxon in the Taï region, where subsistence and/or commercial hunting are common in both rural and protected areas [25]. Harvest level in the TNP and adjacent continuous forests exceeds sustainability for most monkey species [36,37]. Indeed, it is likely that some monkey species are already - or soon will be - hunted to local extinction in most rural areas of the Taï region where cropland continues to replace tropical forest [38] and where primates are hunted both for food and to reduce their role as agricultural pests (Nandjui A., unpublished data collected for Conservation International).

The cost of losing monkeys extends beyond the loss of the animals themselves. Indeed, the local extinction of frugivorous primates is predicted to have deleterious consequences for forest regeneration and/or tree species community composition [16,39,40]. Quantification of primate seed dispersal in Kibale, Uganda, indicates that, in a single day, monkeys can disperse 33, 800 fruits Km^{-2} ; such dispersal has direct consequences for forest regeneration dynamics and plant reproduction [12-14,30].

Perhaps most importantly, researchers have demonstrated that in many forests including the Taï forest, monkeys disperse more seed species than any other taxon and that the dispersal service of monkeys cannot be compensated for by other taxa including large birds [15,16].

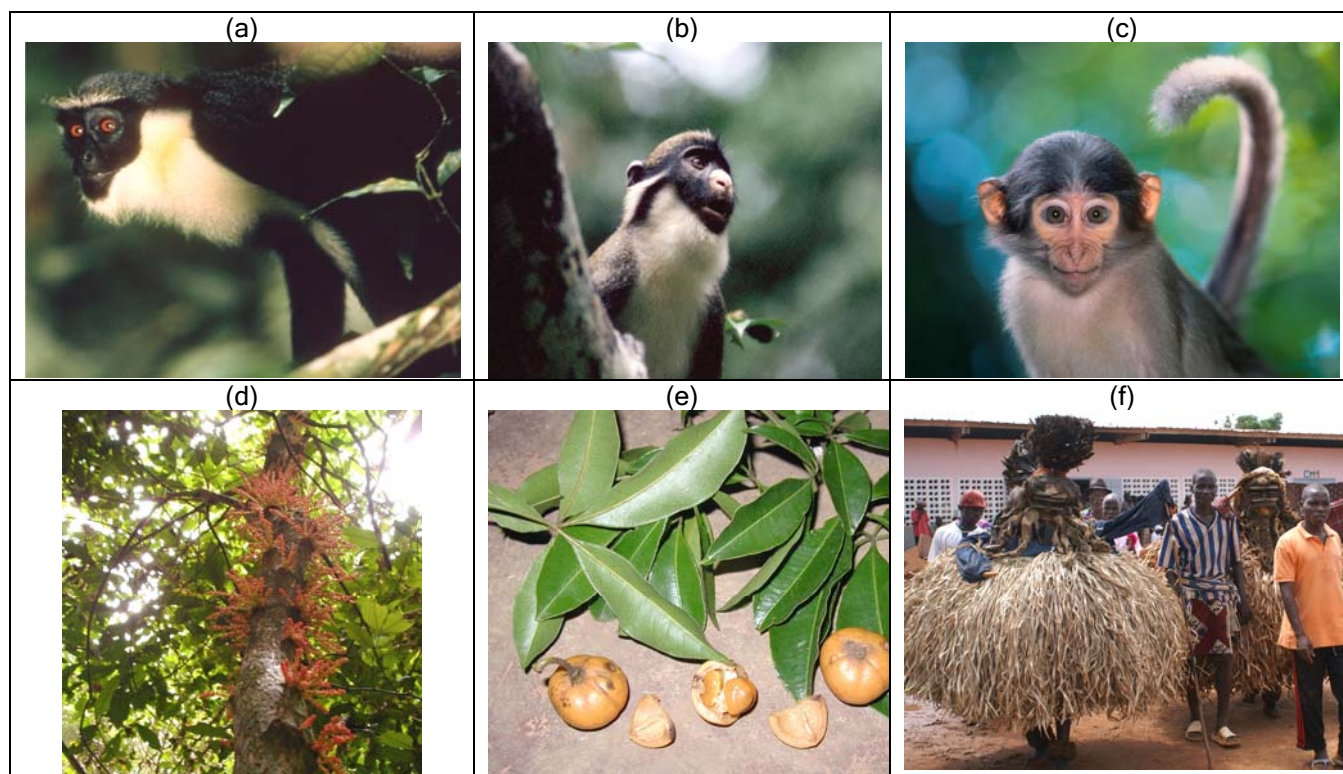


Fig. 2. Selected photos showing some of the monkeys of the Taï region (*Cercopithecus diana* (a); *C. petaurista* (b); *Cercocebus atys* (c)), some fruit species consumed by both humans and monkeys (*Maesobotrya barteri* (d) and *Oldfieldia africana* (e)) and supernatural masks during a mask festival (f). Photos (a-c) by F. Möllers. Photos (d-e) by A. Bakayoko. Photo (f) by I. Herbinger

In addition to the ecological importance of seed dispersal, many monkey-dispersed tree species have some economic and/or cultural value to humans living in or near forested regions. Most of the plant uses described in this paper are still widespread. This is not an insignificant finding as it suggests that local knowledge of plant value still exist. For example, some medicinal and food plant resources (Medicinal: *Pycnanthus angolensis*; Food: *Carnarium sweinfurthii*, *Coula edulis*, *Dialium aubrevilei*, *D. dinklagei*, *Oldfieldia africana* - Fig. 2e) are still found in local Taï region markets and are sometimes exported toward larger markets in urban areas such as Guiglo, Duekoué, Issia and Soubré (Koné, pers. obs.). Of note is that the seeds of these tree species are potentially exclusively dispersed by monkeys in fragments with the exception of *Carnarium sweinfurthii* which is also possibly dispersed by birds.

Rituals are an important component of the cultural life of the *Guéré* and *Oubi* people living at the western periphery of the TNP, and mask festivals are organized there on a yearly basis (Fig. 2f). The diversity of ceremonial masks and costumes are constructed using forest resources (e.g., supernatural masks are made of wood derived from a monkey-dispersed tree species, *Oldfieldia africana*), suggesting links among plants/dispersers and the human populations that rely on forest fragment habitats.

The number of monkey-dispersed tree species in the TNP is somewhat smaller than those of Lambert [20] but certainly represents an underestimate. Indeed, the same monkey species occurring in the TNP are reported elsewhere (i.e. in Gabon) to disperse the seeds of other tree species occurring in the Taï forest and adjacent forest fragments and some of these monkey-dispersed tree species have some utility to humans [41,42].

Implications for Conservation

Results of this study suggest that maintaining populations of monkeys is important not only for forest regeneration, but also for human habitat use. The conservation of primate species is a critically important goal in itself [20]; by working to ensure their protection in forest fragments, we protect indirectly the seed dispersal of important human resources in these fragments as well. Protection of monkeys and seed dispersal systems outside protected areas is particularly relevant in this context, since it is in these areas (the “matrix”, *sensu* Cowlshaw and Dunbar [43]) that primates are most at risk, and also where people are allowed to exploit forest plant resources [20].

A recent survey carried out at the periphery of the TNP highlighted extensive habitat losses and/or depletion of forest resources due to various uncontrolled exploitation forms including hunting, logging and agriculture even in gazetted forests [44]. The authors concluded that this may impact the TNP in two ways if no urgent measure is taken to stop the trend: (i) human pressure over the park will increase if forest resources at its periphery become insufficient for the local communities depending on such resources, (ii) the TNP might become ecologically isolated. This demonstrates the importance of maintaining forest fragments over the long term in the Taï region. To achieve that goal, it is essential to determine sustainable harvest rates but also to maintain seed dispersal services provided by monkeys. Promoting community-based management of forest fragments and their resources at the periphery of the TNP is currently envisaged. This is no doubt feasible if awareness is increased within human communities and the economic value of some of the forest resources enhanced through appropriate marketing systems. As many forest fragments in the Taï region are small in size and isolated [38], it may be necessary to establish biological corridors between them in order to facilitate their re-colonization by monkeys and other arboreal mammals and/or to increase the survival chance of these animals.

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References

- [1] Howe, H.F. and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- [2] Levey, D. J., Silva, W. R. and Galetti, M. 2002. *Frugivory and Seed dispersal and frugivory: ecology, evolution and conservation*. CABI Publishing, Wallingford, Oxfordshire, UK.
- [3] Terborgh, J., Pitman, N., Silman, M., Schichter, H. and Nunez, P.V. 2002. Maintenance of tree diversity in tropical forests. In: *Frugivory and Seed dispersal and frugivory: ecology, evolution and conservation*. Levey, D. J. Silva, W. R. and Galetti, M. (Eds), pp 351-364. CABI Publishing: Wallingford, Oxfordshire.

- [4] Beckman, N.G., Muller-Landau, H.C. 2007. Differential Effects of Hunting on Pre-Dispersal Seed Predation and Primary and Secondary Seed Removal of Two Neotropical Tree Species. *Biotropica* 39(3): 328-339.
- [5] Dirzo, R., Mendoza, E., Ortíz, P. 2007. Size-Related Differential Seed Predation in a Heavily Defaunated Neotropical Rain Forest. *Biotropica* 39(3): 355-362.
- [6] Nuñez-Iturri, G., Howe, H.F. 2007. Bushmeat and the Fate of Trees with Seeds Dispersed by Large Primates in a Lowland Rain Forest in Western Amazonia. *Biotropica* 39(3): 348-354.
- [7] Stoner, K.E., Riba-Hernandez, P., Vulinec K., Lambert, J.E. 2007. The Role of Mammals in Creating and Modifying Seedshadows in Tropical Forests and Some Possible Consequences of Their Elimination. *Biotropica* 39(3): 316-327
- [8] Wang, B.C., Sork, V.L., Leong, M.T., Smith, T.B. 2007. Hunting of Mammals Reduces Seed Removal and Dispersal of the Afrotropical Tree *Antrocaryon klaineum* (Anacardiaceae). *Biotropica* 39(3): 340-347.
- [9] Wright, S.J., Hernández, A., Condit, R. 2007. The Bushmeat Harvest Alters Seedling Banks by Favoring Lianas, Large Seeds, and Seeds Dispersed by Bats, Birds, and Wind. *Biotropica* 39(3): 363-371.
- [10] Stevenson, P.R. and Aldana, A.M. 2008. Potential Effects of Ateline Extinction and Forest Fragmentation on Plant Diversity and Composition in the Western Orinoco Basin, Colombia. *International Journal of Primatology* 29(2): p365
- [11] Lambert, J.E. and Garber, P.A. 1998. Evolutionary and Ecological Implications of Primate Seed Dispersal. *American Journal of Primatology* 45: 9-28.
- [12] Kaplin, B.A. and Lambert, J.E. 2002. A review of seed dispersal effectiveness by Cercopithecus monkeys: Implications for seed input into degraded areas. In: *Frugivory and Seed dispersal: ecology, evolution and conservation*. Levey, D. J., Silva W. R. and Galetti M. (Eds). CABI Publishing, Wallingford, Oxfordshire.
- [13] Lambert, J.E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and *Strychnos mitis*: Evidence for plant benefits beyond seed dispersal. *International Journal of Primatology* 22 (2): 189-201.
- [14] Lambert, J.E. 2002. Exploring the link between animal frugivory and plant strategies: the case of primate fruit-processing and post-dispersal seed fate. In: *Frugivory and Seed dispersal: ecology, evolution and conservation*. Levey, D. J., Silva W. R. and Galetti M. (Eds), pp 365-379. CABI Publishing: Wallingford, Oxfordshire.
- [15] Clark, C.J., Poulsen, J.R. and Parker, V.T. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* 33(4): 606-620.
- [16] Refisch, J. and Koné, I. 2001. *Influence du braconnage sur les populations simiennes et effets secondaires sur la végétation : un exemple tiré d'une région forestière à régime pluvieux en Côte-d'Ivoire*. GTZ, Eschborn.
- [17] Mittermeier, R.A. and Cheney, D.L. 1987. Conservation of primates and their habitats. In: *Primate societies*. Smuts B.B., Cheney D.L., Seyfarth, R.M., Wrangham R.W. and Struhsaker, T.T. (Eds), pp 477-490. University of Chicago Press, Chicago.
- [18] Chapman, C.A., Chapman, L.J., Vulinec, K., Zanne, K. and Lawes, M.J. 2003. Fragmentation and alteration of seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* 35: 382-393.
- [19] Bakuneeta, C., Johnson, K., Plumtre, R. and Reynolds, V. 1995. Human uses of tree species whose seeds are dispersed by chimpanzees in the Budongo Forest, Uganda. *African Journal of Ecology* 33: 276-278.
- [20] Lambert, J.E. 1998. Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. *African Journal of Ecology* 36 (3): 234-240.
- [21] Didham, R.K., Ghazoul, J., Stork, N.E. and Davis, A.J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11: 255-260.
- [22] Bakayoko, A. 2005. *Influence de la fragmentation forestière sur la composition floristique et la structure végétale dans le Sud-Ouest de la Côte-d'Ivoire*. PhD Dissertation, University of Cocody, Abidjan, Côte-d'Ivoire.
- [23] Koch, V. 1994. Peuplement et ethnies. In: *Le Parc National de Tai- Côte-d'Ivoire ; Synthèse des connaissances*. Riezebos, E.P., Vooren, A.P., & Guillaumet, J.L. (Eds), pp 94-100. Tropenbos Series 8, Wageningen.

- [24] Conservation International 2001. *De la forêt à la mer : les liens de biodiversité de la Guinée au Togo*. Conservation International, Washington.
- [25] Caspary, H.-U., Koné, I., Prouot, C. and De Pauw, M. 2001. *La chasse et la filière viande de brousse dans l'espace Taï, Côte-d'Ivoire*. Tropenbos Côte-d'Ivoire série 2, Abidjan.
- [26] Bergmüller, R. 1998. *Nahrungsökologie der rauchgrauen magabe (Cercopithecus torquatus atys). Ein schlüssel zur sozialen organisation?* Msc thesis, Nürnberg Friedrich Alexander University, Germany.
- [27] Chatelain, C., Kadjo, B., Koné, I. and Refisch, J. 2001. *Relations faune-flore dans le Parc National de Taï: une étude bibliographique*. Tropenbos Côte-d'Ivoire série 3, Abidjan.
- [28] Eckardt, W. and Zuberbühler, K. 2004. Cooperation and competition in two forest monkeys. *Behavioural Ecology* 15 (3): 400-411.
- [29] Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior* 69:227-263.
- [30] Lambert, J.E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): Implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology* 109:365-386.
- [31] Lambert, J.E. 2005. Competition, predation and the evolution of the cercopithecine cheek pouch: the case of *Cercopithecus* and *Lophocebus*. *American Journal of Physical Anthropology* 126: 183-192.
- [32] Kasperek, M. 2000. *Flore du Parc National de Taï, Côte-d'Ivoire*. Ksperek Verlag, Heidelberg.
- [33] Téré, H. 2001. *Signification des noms vernaculaires des plantes chez les Guéré, Côte-d'Ivoire*. Sempervira 7, CSRS, Abidjan.
- [34] Gautier, L., Chatelain, C. and Spichiger R. 1994. Presentation of a releve for vegetation studies based on high resolution satellite imagery. In : *Comptes rendus de la treizième réunion plénière de l'AETFAT*, pp 1339-1350. Zomba. Malawi.
- [35] Caspary, H.-U. and Momo, J. 1998. *La chasse en Côte-d'Ivoire - résultats dans le cadre de l'étude "filiale viande de brousse" (Enquêtes chasseurs)*. Preliminary report for the World Bank. Abidjan.
- [36] Refisch, J. and Koné, I. 2005a. Impact of commercial hunting on monkey populations in the Taï region, Côte-d'Ivoire. *Biotropica* 37 (1): 136-144.
- [37] Refisch, J. and Koné, I. 2005b. Market hunting in the Taï National Park, Côte-d'Ivoire and its implications for monkey populations. *International Journal of Primatology* 26 (3): 621-629.
- [38] Chatelain, C., Gauthier, L. and Spichiger, R. 1996. A recent history of forest fragmentation in southwestern Ivory Coast. *Biodiversity Conservation* 5:37-53.
- [39] Chapman, C.A. and Chapman, L.J. 1995. Survival without dispersers: seedling recruitment under parents. *Conservation Biology* 9: 675-678.
- [40] Chapman, C.A. and Onderdonk D.A. 1998. Forests without primates: Primate/Plant Codependency. *American Journal of Primatology* 45:127-141.
- [41] Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Emmons, L., Dubost, G.C., Hechestweiler, P., Mounqazi, P., Roussillon, C. and Thiollay, J.M. 1985. Fruit as basis of fruit and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.
- [42] White, L.J. and Abernethy, K. 1996. *Guide de la végétation de la Réserve de la Lopé*. ECOFAC, Libreville.
- [43] Cowlshaw, G. and Dunbar, R. 2000. *Primate conservation biology*. University of Chicago Press: Chicago.
- [44] Adou-Yao, C. Y., Koné, I., Béné K. J-C., Bakayoko, A., Kouassi K.E., Akpatou K.B. (2008). Evaluation de l'état de conservation des ressources naturelles dans l'espace Taï et leur mode d'exploitation : propositions pour une gestion durable. Report for WWF Côte d'Ivoire : Abidjan.

Appendix 1. List of tree species whose seeds are dispersed by monkeys in the Taï National Park, Côte-d'Ivoire with details on seed handling by different monkey species. Monkey species: C.c.: *Cercopithecus campbelli* ; C.d.: *Cercopithecus diana*; C.p.: *Cercopithecus petaurista* ; C.a. ; *Cercocebus atys* ; P.b. : *Procolobus badius* ; P.v. : *Procolobus verus* ; Cb.p. : *Colobus polykoma*. Sources: 1: Taï Monkey Project (unpublished); 2: Chatelain *et al.* (2001); 3: Refisch and Koné (2001); 4: Koné (unpublished)

Fruit species	Monkey species which swallowed seeds	Monkey species which spat seeds	Monkey species which probably spat seeds	Monkey species which abandoned seeds	Alternative faunal group which disperse seeds
<i>Aidia genipflora</i>	C.d. (2)		C.d. (1)		
<i>Aphantostylis leptantha</i>	C.d. , C.c. (3)	C.c. (3)	C.d. (1)		
<i>Baphia bancoensis</i>	C.c. (3), C.p. (3), Cb.p. (3)				
<i>Berlinia grandifolia</i>				P.b. (1,4)	
<i>Brieya fasciculatum</i>	C.d. (3)		C.d. (1)		
<i>Bussea occidentalis</i>				Cb.p. (1,4)	
<i>Canarium schweinfurthii</i>				P.b. (4)	birds
<i>Chrysophyllum taiense</i>	C.c. (3), Cb.p. (1)	C.c. (3)	C.d., C.p. (1)		
<i>Coelocaryon oxycarpum</i>	C.d. (3), Cb.p. (3)		C.d., Cb.p. (1)		
<i>Coula edulis</i>				P.b. (1,4)	
<i>Dacryodes klaineana</i>	C.p. (2,3), C.c. (2,3), C.d. (2), P.b. (1,2)	C.p. (3), C.c. (3)	C.p., C.d. (1)		birds
<i>Dialium aubrevillei</i>	C.c., C.d., C.p., C.a. (3), P.b. (1), Cb.p. (1)	C.c. (3)	C.d., C.p., C.a. (1)		
<i>Dialium dinklagei</i>	P.b. (1)				
<i>Diospyros mannii</i>	C.d. (2,3), C.p. (2), P.b. (1,2)		C.d., C.p. (1)		
<i>Diospyros sanza-minika</i>	C.d. , C.p. (2), P.b. (1,2)		C.d., C.p. (1)		
<i>Diospyros soubreana</i>	C.d., C.p. (2), P.b. (1,2)		C.d., C.p. (1)		
<i>Drypetes pellegrini</i>	P.b. (1,3)				
<i>Duboscia viridiflora</i>				P.b. (1,3)	
<i>Erythrophleum ivorense</i>				C.d. (1,4), P.b. (1,4)	
<i>Garcinia gnetoides</i>	P.b. (1,3)				
<i>Hirtella spp</i>				C.a. (3)	
<i>Hugonia platysepala</i>		Cb.p. (2,3)			
<i>Hugonia rufopilis</i>		Cb.p. (2,3)			
<i>Lanea welwitschii</i>		C.d. (1,3)			
<i>Maesobotrya barberi</i>	C.p. (2,3,4)		C.p. (1)		
<i>Memecylon afzelii</i>	C.p. , C.c. (3), C.d., P.b., Cb.p., P.v. (1)	C.p. (3), C.c. (3)	C.p., C.d. (1)		
<i>Memecylon lateriflorum</i>	C.p. (3), P.b. (1)		C.p., C.d. (1)		
<i>Memecylon polyanthemos</i>	C.d. (3)		C.d. (1)		
<i>Napoleona leonensis</i>	C.d. (3)		C.d. (1)		
<i>Oldfieldia africana</i>	C.c., C.a., C.d., C.p. (3), P.v., Cb.p. (1), P.b. (1,4)	C.c. (3)	C.a., C.d., C.p. (1)		
<i>Ongokea gore</i>	P.b. (1,2)				
<i>Pachypodanthium staudtii</i>	C.a. (3), P.b. (1)		C.a. (1)		
<i>Parinari excelsa</i>	C.d. , P.b., C.a. (2)		C.d., C.a. (1)		

Appendix 1 continued

Fruit species	Monkey species which swallowed seeds	Monkey species which spat seeds	Monkey species which probably spat seeds	Monkey species which abandoned seeds	Alternative faunal group which disperse seeds
<i>Parkia bicolor</i>	C.d. , C.p. (2), Cb.p. (1,2), P.b. (1,2)		C.d., C.p. (1)		
<i>Pentaclethra macrophylla</i>			C.d., C.p., C.c. (1)	C.a. (3), P.b. (1,4), Cb.p. (1) P.b. (1,4)	
<i>Piptadeniastrum africanum</i>					
<i>Pycnanthus angolensis</i>	C.d. (2,3), C.a., C.p. (2), Cb.p. (1,2)		C.d., C.a., C.p. (1)		birds, squirrels
<i>Raphia africana</i>	C.p. (3)	C.p. (3)			
<i>Sacoglottis gabonensis</i>				C.a. (3), C.c. (1,2), C.p. (1,2), P.v. (1,2), Cb.p. (1,2), C.d. (1,2), P.b. (1,2)	
<i>Scytopetalum tieghemii</i>	C.d. (1,3), C.p. (1,3), C.c. (1,3), C.a. (1,3), P.v. (1), Cb.p. (1), P.b. (1)	C.d. (3), C.p. (3)	C.c., C.a. (1)		
<i>Spondianthus preusii</i>				C.d. (1,3), P.b. (1,3)	
<i>Strombosia pustulata</i>				C.d. (1,3), P.b. (1,3)	
<i>Trichoscypha arborea</i>	C.d. (2), P.b. (1,2)		C.d. (1)		
<i>Trichoscypha beguei</i>	C.d. , P.v., C.p. (2)		C.d., C.p. (1)		
<i>Uapaca esculenta</i>	C.c. (2,3), C.p. (2,3), C.d. (2,3), C.a. (2,3), P.b. (1,4)	C.p. (3), C.c. (3), C.d. (3)			
<i>Uapaca guineensis</i>	C.p. (2,3), C.d. (2), P.b. (1,2), C.a. (2)	C.p. (3)	C.d., C.a. (1)		duikers
<i>Uapaca paludosa</i>	C.a. (2,3)		C.a. (1)		
<i>Xylopiacutiflora</i>		Cb.p. (2,3)			
<i>Xylopiacutiflora</i>	C.d. (2)		C.d. (1)		duikers
<i>Xylopiaparviflora</i>	C.d. (2)		C.d. (1)		birds
<i>Xylopiacutiflora</i>	Cb.p. (2,3), C.a. (2,3), C.d. (2), C.p. (2)		C.a., C.d., C.p. (1)		
<i>Xylopiavillosa</i>	P.b. (1,2), C.p. (2,3), C.d. (2,3), C.c. (2,3)				