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The Impact of West African Trade on the Distribution of Chimpanzee and Elephant Populations (Guinea, Guinea-Bissau, Senegal, 19th–20th Century)

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Abstract This article elaborates a relational historical geography of human, chimpanzee and elephant populations, working mainly from precolonial and early colonial (nineteenth and twentieth century) narratives by travellers to regions now corresponding to parts of Guinea, Guinea-Bissau and Senegal. It then compares a global 'West African trade' model of human and animal population's spatial distribution with elements of an 'East African settlement colony' model drawn from other historical research. This perspective balances mainstream evolutionary approaches to animal biogeography with the human history, ecology and the geopolitics of their habitats. Taking such historical processes into account helps to unravel contrastive spatial and temporal dynamics of large mammal populations and to raise new questions about the anthropogenic causes of present-day population distributions.

Keywords Historical ecology · Human/animal interactions · West Africa · Colonial trade · Chimpanzee · Elephant

Introduction

Over the past 15 years field primatology, like other areas of animal ecology, has increasingly addressed biodiversity conservation issues in relation to human environmental practices and perceptions. In particular, a sub-field labelled "ethnoprimatology" focuses on the long history of nonhuman primate (thereafter primate) coexistence with modern humans in various regions of the primate order's range, dealing with the impact of hunting, agriculture, and other human activities on the behaviour and ecology of primates (e.g., Fuentes and Wolfe 2002; Fuentes and Hockings 2010; Yamakoshi 2011; Fuentes 2012). However, this research has usually concentrated on these historical processes' present-day outcomes rather than on the processes per se and the kind of historical data and methods needed to understand them (see Anderson *et al*. 2007; also Baker 1992; Sept and Brooks 1995 for early appraisals). Recently, following ethnoprimatological research, some elephant scholars have begun to address issues of conservation and coexistence with humans (Locke 2013; but see Leblan 2013, for a survey of the problematic range of meanings implied in adding the "ethno" prefix to "primatology").

It is worth noting that the use of *nonhuman ecology* criteria to elaborate the biogeography of primates was initially motivated through evolutionary approaches to facts of distribution. Arguments connect population distributions to bioclimatic areas, among other factors. For example, in Africa it has been established that the distribution of chimpanzee populations does not exactly coincide with the limits of the vegetation belts which divide the continent into ever-drier gradients as one moves away from the equator (Kortlandt 1983). The last decade has witnessed the development of "phylogeographic" approaches, often motivated by conservationist research into the genetic viability of ape populations (Fischer *et al*. 2006), or generated by biomedical investigations into the history of the simian immunodeficiency virus (Gonder *et al*. 2011). These recent studies link ape populations' phylogenetic distance, as inferred from molecular data, to the alternating sequences of forest cover shrinkage and expansion during the Quaternary period. Cartographic representations of these historical processes consist of wide biogeographic regions separated by vegetation (e.g., the Dahomey Gap) or fluvial barriers (e.g., the Sanaga River).

Scaling up to the other extremity of apes' biogeography, maps have been developed representing the very localized and tenuous knowledge of population distribution derived from field surveys and behavioral studies, many published in

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policy-oriented documents (Kormos *et al.* 2003; Caldecott and Miles 2005). Graphic translations of these surveys as dots within populations, whose limits actually remain poorly known, contrast sharply with the representation of species' and sub-species' supposedly natural, and therefore expected, distribution areas. But they also omit the representation of human presence and activities, except for protected areas. Overall, we are often left with little more than speculative models about the putative consequences of farming, hunting, and other human activities on the geography of primate population distributions (Tutin and White 1999).

This article elaborates a relational historical geography of human, chimpanzee and elephant populations, working mainly from precolonial and early colonial narratives by late nineteenth- and early twentieth-century European travellers to regions now corresponding to parts of Guinea, Guinea-Bissau and Senegal. On the one hand, this perspective balances mainstream evolutionary approaches to animal biogeography with the human history, ecology and geopolitics of their habitats. On the other, it addresses issues that the social and historical sciences have often left aside as well, when dealing with ecological issues. Indeed, these disciplines have mainly historicized the plant kingdom, working from a combination of ethnographic research and written sources, and sometimes resorting to naturalistic observations (e.g., floristic data, diachronic remote sensing analyses). Considering forest-savanna cover dynamics as much the expression of changing social and political relationships as the outcome of unpredictable ecological transformations has allowed social scientists and historians to discuss the unverified narratives of linear deforestation that often underpin western-based conservation programs in the 'Global South' (for West African examples, see Fairhead and Leach 1996; Basset and Zuéli 2000; Nyerges and Green 2000; Temudo 2009; Leblan 2012). However, these studies have left aside the animal populations inhabiting these environments, while the processes they analyze presumably have major consequences for these populations' demography and distribution.

Thus, after describing the region and time frame of this study, I present a comparison of models of elephant/human and chimpanzee/human space use dynamics. On this basis I discuss a global 'West African trade' model of human and animal population spatial distribution, as compared to elements of an 'East African settlement colony' model. I conclude with considerations on interdisciplinary and inter-specific comparisons and about the usefulness of these historical models in understanding the recent dynamics of human, elephant and chimpanzee populations' current coexistence on the Guinea-Liberia border.

Study Region and Time Frame

Field observations (12 months between 2003 and 2012) were conducted in a 560 km^2 area located between the Rio Nunez and Cogon rivers (Fig. 1). This rural area is inhabited by Landuma and *runndebe* Fula people who subsist mainly on the products of swidden agriculture. Fula pastoralists also practice bovine transhumance, travelling seasonally between the Fouta Djallon highlands and the maritime plains. The topography is characterized by maritime plains and lateritic plateaux, having a maximum difference in altitude of 150 m. The treeless plateaux, dominated by herbaceous vegetation in the rainy season, usually extend across a whole inter-fluvial area. Their slopes are covered with woodland, patches of closed-canopy forest which may be opened for agriculture, and fallow vegetation. Fields are also set up adjacent to streams, along which they alternate with gallery forest ranging from a few meters to several tens of meters wide, vegetation at various stages of regrowth into shrubs, and more rarely woodland and savanna. The maritime plains are covered by shrub savanna and woodland, interspersed with dense forest patches, sizeable ones being cleared for agriculture.

The historical field observations are taken from the period between 1880 and 1910, along with a critical examination of the sporadic twentieth-century evidence. Precolonial Boké, which was the Landuma political centre located on the Rio Nunez, had been one of the main trading posts with Europeans on the Guinean coast, along with Boffa on the Rio Pongo and Benty on the Mellacoree during the nineteenth century. In these localities, palm oil, pelts, ivory, and wax, among other natural products, as well as slaves, were exchanged with Europeans for manufactured commodities (Goerg 1986:40–42). With the establishment of the Rivières du Sud colony in the early 1880s, becoming Guinée Française in 1891, explorations and natural resource inventories published by local colonial administrators and doctors provide us the first repeated observations of chimpanzees and elephants in the hinterland of this region. During the decade 1900–1910, publications concerning the resources of the north of the colony drastically diminish as trade was increasingly directed towards Conakry, the political centre of the colony established 300 km to the south in the 1880s. Another cause for this decrease in number of publications during this decade is the administration's reduced interest in exploration and inventories once military conquest was completed (Bonneuil 1997:91–93). I also describe population dynamics in the area to the north of the Fouta Djallon highlands, now corresponding to southeastern Senegal, where the context for naturalistic observations at the end of the nineteenth century was somewhat different. At this time, the region was already dominated by the French administration, forming the base for the last military expeditions aimed at the conquest of the upper Niger Sudanian savannas controlled by Samori Touré (Goerg 1986:225–236). This situation allowed the region to be explored by naturalists from the Museum of Natural History in Paris.

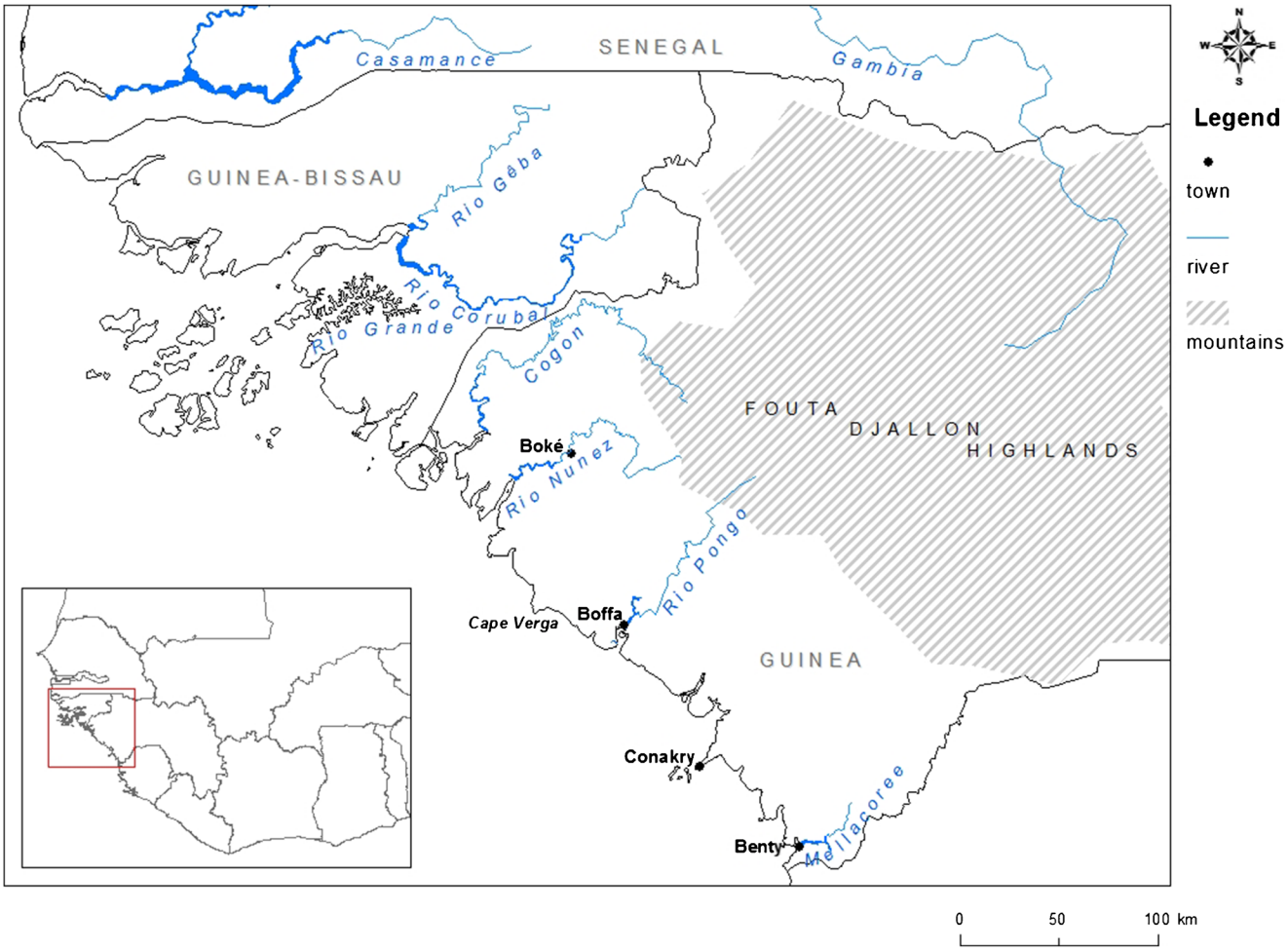

Fig. 1 Extent of study and places mentioned in the text

Materials and Methods

Personal observations consist of chimpanzee traces (nests, faeces, feeding remains) tracked in the company of local hunters. Most of the historical data analysed in this article are extracted from texts published in the journal of geographic societies, whose goal was to promote profitable observations for European traders and industrialists (Lejeune 1993:150–151). As European presence increased in the 1880s and 1890s, colonial administrators relied heavily on naturalistic research, both as a means to legitimize the colonial project and to produce knowledge that would attract investors in the newly-conquered territories. For their part, scientists from the Museum of Natural History in Paris took advantage of colonial expansion to increase their collections and consolidate their naturalistic disciplines, which at that time were losing institutional influence in favour of experimental biology (Bourguet and Bonneuil 1999; Bonneuil 1999). A variety of people with different backgrounds: doctors, pharmacists, colonial entrepreneurs, soldiers, and diplomats tracing the frontier with Portuguese Guinea, some of them in correspondence with the Natural History museum, produced sometimes detailed resource inventories as they settled in and travelled through the Boké region. However, distinguishing between their first-hand observations and second or third-hand reports they pass on is a difficult exercise (Chouin 2001). In this study, I use only what can be established as direct observations by the authors in order to filter out the difficulties inherent in assessing the ecological significance of the reported observations, such as those of local inhabitants, which appear throughout their writings.[1] However, the majority of observations were made in situ by these travellers seeking legitimacy within the interdependent worlds of colonial administration and natural scientific circles, and direct observation was central to their field practices, as much for scientific reasons as for the prestige it brought them back in their home country.

[1] With the exception of Anonymous 1903 and Lemoine 1903, which are reviews of travellers' conversations by other authors.

Results

Chimpanzees

The military medical doctor Vigné, who lived and conducted various missions in the colony between 1883 and 1886, spent his free time investigating a variety of local issues, such as traditional customs (Brunschwig 1974), and produced a census of the colony's vertebrates (Vigné 1888). He mentions the presence of chimpanzees thus :"in the gallery forests of river basins' upstream sections and in Fouta Djallon's western hills," he observed "a certain number of individuals which all featured the external characteristics of the type *Troglodytes niger*"[2] (Vigné 1888:637). Chimpanzees were also present in the downstream sections of at least some of the region's large rivers, including an area between the Rio Nunez and the Rio Pongo travelled on foot by Laumann (1894:216).

A naturalist working for the Museum of Natural History in Paris also reported the presence of chimpanzees on the northern periphery of the Fouta Djallon highlands:

> "Globally speaking, the Senegambian mammal fauna is characterized by the considerable development of the monkey family (…). These animals are usually confined to the forests of the upper basin, as much as in those of coastal areas; anthropoid forms appear there as well (…)." (de Rochebrune 1883:54)

De Rochebrune's description of "the uppers basins of the rivers flowing towards the coast" in the Fouta Djallon foothills reasonably allows us to deduce that his "anthropoid" observations took place near the Gambia River. They suggest that chimpanzees were present in the 1870s–1880s at a similar latitude to that of present-day Niokolo-Koba National Parc (Senegal), although "the (*Troglodytes niger*) is very rare in Senegambia. It goes back up the Gambia and Casamance river, where it is sometimes reported" (de Rochebrune 1883:65). This is the earliest record of chimpanzee presence encountered in French published sources from the colonial period.

Fras (1891:302) defines the category "monkeys" as comprising "animals nearly as big as orang-utans, a few dogheads or gorillas, (…) down to very little animals, similar to marmosets," suggesting that chimpanzees might have been reported under the *monkey* label by other travellers. However, this would bring us only two extra early accounts of chimpanzee presence, one near Boké in the 1870s by the Major of Boké's military post (Guichon de Grandpont 1879) and one in the late 1880s by Rançon (1894: 374), a doctor travelling in the northern Fouta Djallon with objectives similar to de Rochebrune.

With the decline of exploration policies in the early twentieth century and the estuary trading posts' marginalization in favour of Conakry, published observations about chimpanzee presence in western Guinea are even fewer. The next available report is the much later chimpanzee field survey carried out on the periphery and inside the Fouta Djallon highlands by the naturalist de Bournonville, as part of Adrian Kortlandt's "Rift hypothesis" research program, with the aim of establishing whether the species was or was not better adapted to humid tropical forests than to the Sudano-Guinean savannas (Kortlandt 1983). His results, based on nest observations and local inhabitants' and missionaries' accounts, indicate that chimpanzees were frequently seen and heard to the northwest of Boké, as well as on the left bank of the Rio Nunez, with groups comprising as many as 30 individuals. A few kilometers from the chimpanzee ranging areas surveyed in detail in 2003–2005 for this study, de Bournonville (1967) reported chimpanzees to be numerous and "heard at least once a week." They were also regularly reported by members of the forest administration near the village of Silikonko, just 2 k from our 2005 population density transects which indicated a mean chimpanzee (*Pan troglodytes*) population density varying from 0.15–0.28 to 0.37–0.67 ind/k^2 (Leblan in press). Overall, the chimpanzees are nowadays nearly unnoticeable to the farmers. They seldom come out in grassy environments and often forage in the dense fallow vegetation people cannot see through or enter without revealing their presence. The most continuous human presence in areas between village spaces is nomadic pastoralists, but since they focus on the most herbaceous components of the landscape for pasturing their herds, they tend to range away from chimpanzees.

Elephants

Elephants were encountered in somewhat more localized areas of the western and northern Fouta Djallon regions. Having published observations about local customs and natural resources in the recently established colony, on behalf of the Ministry of Colonies and the Museum of Natural History, Doctor Maclaud (1899a, b) was entrusted with a diplomatic and reconnaissance mission to trace the frontier between French and Portuguese Guinea during which he reported that the Rio Corubal region was characterized by countless numbers of elephants, buffaloes, and antelopes (Anonymous 1903). George Paroisse, an explorer whose solid training at the Museum of Natural History (Bonneuil 1997:122–129) and regular travels in western Guinea for more than a decade attest to the reliability of his observations, wrote that "the ivory coming from elephants still wandering the Cogon river's deserted areas is subject to an insignificant traffic" (Paroisse

[2] All translations from the French are by the author.

1908:698). The species was also reported in the downstream region of the Cogon River (Brosselard 1889). However, elephants had already disappeared from the coastal regions of western Guinea by the time of Paroisses's explorations (Paroisse 1892), presumably as a consequence of the ivory trade in Boké during the preceding decade (Polliart 1883).[3]

The Monographie du Cercle de Boké, an ethnographic, historical and economic synthesis compiled by local colonial administrators to report on the territories falling under their jurisdiction (Wooten 1993), contains quantified ivory exports from the Rio Nunez customs office between 1901 and 1911 (Figarol 1911:77): they range from 673 units in 1901 to 288 units in 1906, and oscillate between 11 and 294 units between 1907 and 1911 (unfortunately, the size of a unit is unspecified). Available economic data indicate that this does not appear to be a result of an overall reduction in ivory trade from Africa: annual exports from French West Africa rise spectacularly from approximately 110 to 380 t during the same time-period (Barnes 1999), 160 to 275 annual tons in the Belgian Congo, and remain considerable in French Equatorial Africa despite a decrease from 200 to 130 annual tons (Barnes 1996). In addition, while Boké was becoming progressively marginalized compared to Conakry during this decade, exports of other products such as palm oil, wax, or pelts, remained comparatively stable (Figarol 1911:77). Thus, the decline in ivory exports from the Rio Nunez region may reasonably be ascribed to a local reduction in elephant numbers, an interpretation supported by data from the French West Africa archives which indicate, to the contrary, an overall gradual increase in ivory exports from French Guinea between 1898 and 1912 (Roth and Douglas-Hamilton 1991).

There is also evidence of specialized hunting practices in the area, probably in order to supply European trading posts. Members of the 1889 French/Portuguese Guinea frontier commission reported on a Fula chief who "possessed" several villages inhabited by ivory and hide hunters (Machat 1906:196). This notion of *possession* undoubtedly reflects the spatial and social segregation between masters and captives in Fula-dominated land. The former, usually pastoralists, occupied *misside* or *fulaso*, settlements characterized respectively by the presence and absence of a mosque, while their captives lived in a separate nearby settlement (*runnde*) (Diallo 1972:106–110). Hence, it is plausible that specialized commercial hunting was integrated into one of the region's dominant social organization patterns, which in turn suggests that it was a common and regular activity rather than a marginal one in the northwest of the Fouta Djallon highlands.

Elephant hunting was at times motivated by other non-exclusive factors such as subsistence production, although the sources are not very precise about them. The only mention of other motives concern the Bassari area to the north of the Fouta Djallon, where Dr Rançon (1894:62, 313) reported elephants were hunted both for meat, which was consumed locally, and for the tusks, which were exchanged on the downstream section of the Gambia river for salt, kola nuts and fabrics, among other items.[4] The possibility of elephant hunting as a means of preventing crop damage, which is documented in many parts of the continent from colonial times onwards (Sukumar 2003:299), is not mentioned in the travel accounts. However, it is indirectly suggested by the absence of elephants from coastal regions in the late 1880s reported by Paroisse (1892), as this area was extensively cultivated for the peanut trade between 1850 and 1880 (Leblan 2012). Elephant hunting may certainly be understood as an opportunistic activity fulfilling interrelated objectives: social (master-captive relationships, and perhaps inter-group conflicts), political and economic (long distance trade of local groups with Europeans), and ecological (protection of crops). However, the ivory trade was undoubtedly the main factor behind the species' regional decline.

In the twentieth century, a published inventory of Bissau-Guinean mammals lists elephant observations between the Rio Corubal and Cogon rivers every 10 to 30 years from the 1930s to the 1990s (Reiner and Simoes 1998:148). A 1950s' ungulate census conducted by a zoologist quotes the observation of about a hundred individuals reported to him by local residents (Sa e melo Cristino 1958). Some 50 years later, a 2003–2004 census reported the near-absence of elephants (4–10 individuals across the Guinea/Guinea-Bissau frontier), illustrating the scale of reduction of elephant populations in this region. Brugière *et al.* (2006) describe elephants as having been gradually confined from the northwest to the south of the country since the 1950s.

Discussion

The historical sources described two direct observations of chimpanzees to the west of the Fouta Djallon (Vigné and Laumannn) and one to the north (de Rochebrune). By contrast, they report four observations of elephants (or their footprints) to the west of the Fouta Djallon (Brosselard, Maclaud, Paroisse) and three to the north (de Rochebrune, Chautard, Rançon).

[3] In fact, the trade in elephant ivory is documented over a much longer timescale than this study addresses. Ivory was one of the main items traded with Europeans in many parts of the coast of Guinea, including between the Rio Nunez and Cape Verga regions, since the seventeenth century (Rodney 1970:154–155).

[4] Elephants are also reported to the north of the Fouta Djallon by de Rochebrune (1883: 55) and Chautard (1905: 162).

Chimpanzees

One conclusion concerning population numbers for chimpanzees in the area in the nineteenth century may be drawn from these meagre bibliographic results: as Europeans in those times of intense ivory trade systematically provided more detailed information about elephants, one may reasonably assume that the relative rarity of allusions to chimpanzees results from their marginal economic status in precolonial and early colonial trade, rather than from low population densities. Altogether, these sporadic data testify to chimpanzees continuous presence in western Guinea since the end of the nineteenth century, and even indicate more precisely some features of their past distribution: they seem to have been easily noticeable in the forests along the rivers' upper sections, around lateritic plateaux (i.e. the "western hills" mentioned by Vigné 1888), as well as in downstream sections. Peanuts, one of the main products supplied to Europeans during the second half of the nineteenth century, were at times intensively cultivated in the latter areas (Leblan 2012). This suggests that chimpanzees already inhabited a highly heterogeneous environment resulting from swidden agriculture, as they do today.

Local residents in agricultural areas reported to the ecologist de Bournonville in the 1960s that they could hear chimpanzees regularly. A comparison with my own recent observations in the same localities suggests that population numbers have been more or less stable over the past 50 years. Furthermore, de Bournonville's (1967) reliance on local residents' *hearing* rather than *vision* in order to estimate the presence of chimpanzees indicates a continuously similar style of human-chimpanzee spatial interactions during this time-period, as both farmers and pastoralists still find it difficult to *see* them today. This hypothesis of chimpanzee population stability gains partial confirmation through a larger regional survey spanning the Guinea/Guinea-Bissau frontier according to which chimpanzees are present in the vicinity of nearly all villages (Brugière *et al.* 2009).

Policy-oriented documents often refer to humans encroaching on animal habitat (e.g., Kormos *et al*. 2003). However, in line with the more relational perspective recently adopted in field primatology (Fuentes and Hockings 2010), the data presented here show no evidence of an original spatial segregation between humans and chimpanzees evolving towards increased population overlapping. This situation raises the issue of the ecological relevance of protected areas for chimpanzee conservation in Western Guinea: this research together with another study conducted in south-eastern Guinea on one of the most-studied chimpanzee communities (Yamakoshi and Leblan 2013) suggest that the thick fallow vegetation may actually act as a more efficient buffer between humans and chimpanzees than any park limit.

Elephants

In contrast, elephants are hunted mainly for the value of their tusks, for meat, and probably in some circumstances to prevent crop damage, and their regional numbers have regularly dwindled both to the west and to the north of the Fouta Djallon from the 1880s to the present. Nevertheless, all late nineteenth- and early twentieth-century travellers (de Rochebrune, Rançon, Chautard) to the northern region indicated that they could still be seen frequently, even if they often mentioned them in the context of hunting. Elephants were at the time also considered as abundant to the west and to the northwest of the Fouta Djallon, particularly in the Cogon basin area (Brosselard, Maclaud, Paroisse). It is thus surprising that Vigné, an experienced and wide-ranging traveller in the Rivières du Sud region between 1883 and 1886, does not mention them in his census of the colony's most-frequently encountered vertebrate fauna (Vigné 1888).

A piece of evidence from the 1906 geography thesis of Jules Machat enables us to propose a hypothesis for this apparent contradiction. Machat never travelled to Guinea, but relied exclusively on his own analysis of travellers reports and sources (Nordman 2008). Machat reports late nineteenth-century observations of elephants by two travellers to the west of the Kuranko country and in the Sankaran and Sulima regions of southeast Guinea. This was accounted for by an engineer on the Conakry-Niger railroad in the late 1890s as the outcome of a severe drop in human population density following the recent military conflicts between Samori Touré and the French Army (Machat 1906:201).

Recent ecological studies on the interlinking of human and elephant spatial dynamics in northeastern Gabon (thus involving forest elephants) support this interpretation: the distribution of dung piles along a series of transects indicates that elephant population density rises as one moves away from main roads and settlements, and that it is higher in areas which were inhabited 30 or 40 years earlier (Barnes *et al*. 1991). Other studies also indicate that a rise in elephant numbers in any given region may result from movements towards uninhabited or less farmed regions, rather than from population increase (Spinage 1973; Verschuren 1982), thereby strengthening the nineteenth-century interpretation of the evidence.

This movement of elephants in reaction to human population density and distribution may help in understanding why the species was 1) not listed in a 1880s vertebrate census of the colony and 2) reported by 1890s travelers to the Rio Nunez and Cogon river basins. In the early 1890s, a mission sponsored by the governor of French Guinea to explore the Rio Grande and Cogon river courses found that these regions already supported small human populations (Madrolle 1895:274) as a consequence of "an atrocious war provoked by the invasion of Foulah hordes"[5] (Brosselard 1889:113). The final demarcation of the French/Portuguese frontier a decade later (Lemoine 1903) further intensified migration

[5] A reference to the slave raids conducted by the Fouta Djallon Empire on its margins.

from the Cogon region towards the political centre of the territory placed under Portuguese rule (Paroisse 1908). In light of the above evidence, it is plausible that the elephants occupied from the 1890s onwards this area progressively deserted by humans.

In the twentieth century, the most recent census documenting a progressive confinement of elephant populations from the northwest to the south of the country (Brugière *et al*. 2006) treats Guinea-Bissau as a vast ecological reserve rather than a political space whose inhabitants experienced 11 years of anti-colonial struggle (1963–1974) and one year of civil war (1998). The National Director of the Bissau-Guinean forestry administration had already suggested in the early 1980s that the anti-colonial war had had a harmful effect on elephant numbers (Roth and Douglas-Hamilton 1991). In light of the nineteenth-century data concerning the interlocked movements of human and elephant populations in unstable geopolitical contexts, it seems plausible that the 1998 civil war triggered a second wave of elephant displacements and population reductions, reducing to a few individuals a population that perhaps had been as many as 35 individuals in the early 1990s, according to Sournia (Barnes *et al*. 1999:207).

The distribution of the few remaining elephants is now limited to an area overlapping the frontier with Guinea. Interestingly, this is not the only Guinean elephant population whose distribution is tightly related to the State's frontiers. A map (Fig. 2) compiling evidence from two recent documents dealing with elephant distribution and conservation (Blanc *et al*. 2003; Brugière et al. 2006) shows that all observations of elephant populations linked to the Guinean territory since the mid-1990s (N=9) took place on or near the State frontiers, and of those, only three took place inside protected areas (Niokolo-Koba, Ziama, Outamba-Kilimi). An analysis of the locations of these elephant populations taking into account the complex historical, ecological and geopolitical processes that relate them to human settlements is beyond the scope of this article. However, this initial study spanning the borders of Guinea with Guinea-Bissau and Senegal, as well as the evidence gathered for the map in Fig. 2, suggest that politics of State formation have played and continue to play a crucial role in the distribution of elephant populations.

Humans and Large Mammals in Territories of West African Trade

This study shows that a better understanding of the history of human conflict and human migration is crucial to analyzing the present-day spatial distribution of large mammal populations. While conservation-driven research on contemporary elephant populations (Barnes *et al*. 1991; Barnes 1996, 1999) could support this observation, few studies have sought to investigate the historical dimension of these spatial processes.

A study of nineteenth- to twentieth-century hunting and conservation practices in the British colonies of east Africa revealed that contemporary animal population distributions inside National Parks are the product of a voluntary policy of human and animal separation following European game overexploitation *circa* 1850-1900. Indeed, big game and particularly elephant hunting was a source of prestige for colonial administrators, of subsistence and personal wealth for settlers, of entertainment for soldiers who made little distinction between warfare and sports hunting, and of income for the funding of diverse businesses such as religious missions, railway construction, or gold prospecting expeditions. The creation of reserves after decades of high settler-driven hunting pressure then led to the fauna's reconstitution and relocation to those areas (Mackenzie 1988:120–146 and 256; see also Steinhart 2006:99).

The situation in West Africa differs in the near-absence of settlement colonies, since European commercial activities took place in coastal posts to which African traders transported resources. The production of trade products (ivory, pelts, wax, etc.) was controlled by the dominant social groups inland and apparently well integrated into patterns of labor division. Since elephants were likely to move into areas depopulated by warfare in the context of the slave trade (and later on by geopolitical processes linked to the establishment of the colonies), the establishment of specialized hunting villages in areas under the control of indigenous slave owners was perhaps conceived as part of the same economic process of trading both humans and subsequently the products of the animals remaining or settling in their wake.

Benoît (2003) already suggested that it was violence against people through warfare and the slave trade which led to high animal numbers in West Africa's early colonial period. Colonial authorities later took control of the large tracts of "no man's land" created by these sociopolitical dynamics and their ecological consequences in order to establish the first areas of animal protection in the 1920s. The elephant-chimpanzee comparison I have outlined here adds a layer of complexity to this 'West African trade' model of human-animal relationships by emphasizing species' differential adaptive capacities: while elephant occupation of a transborder region between Portuguese and French Guinea is modeled as a systematic permutation with human land occupation and use, chimpanzees are, as far as the sources suggest, able to thrive alongside human populations in a swidden agriculture environment for long periods.

Local sociopolitical and ecological conditions determine variations in this model. In the humid tropical forest zone of interior Liberia for instance, according to Yves Person elephant ivory was bartered for weapons and ammunition by the Samori Touré Empire in the late nineteenth century (Fairhead *et al*. 2003:323). However, this did not immediately lead to the species' extinction throughout the region. The naturalist and

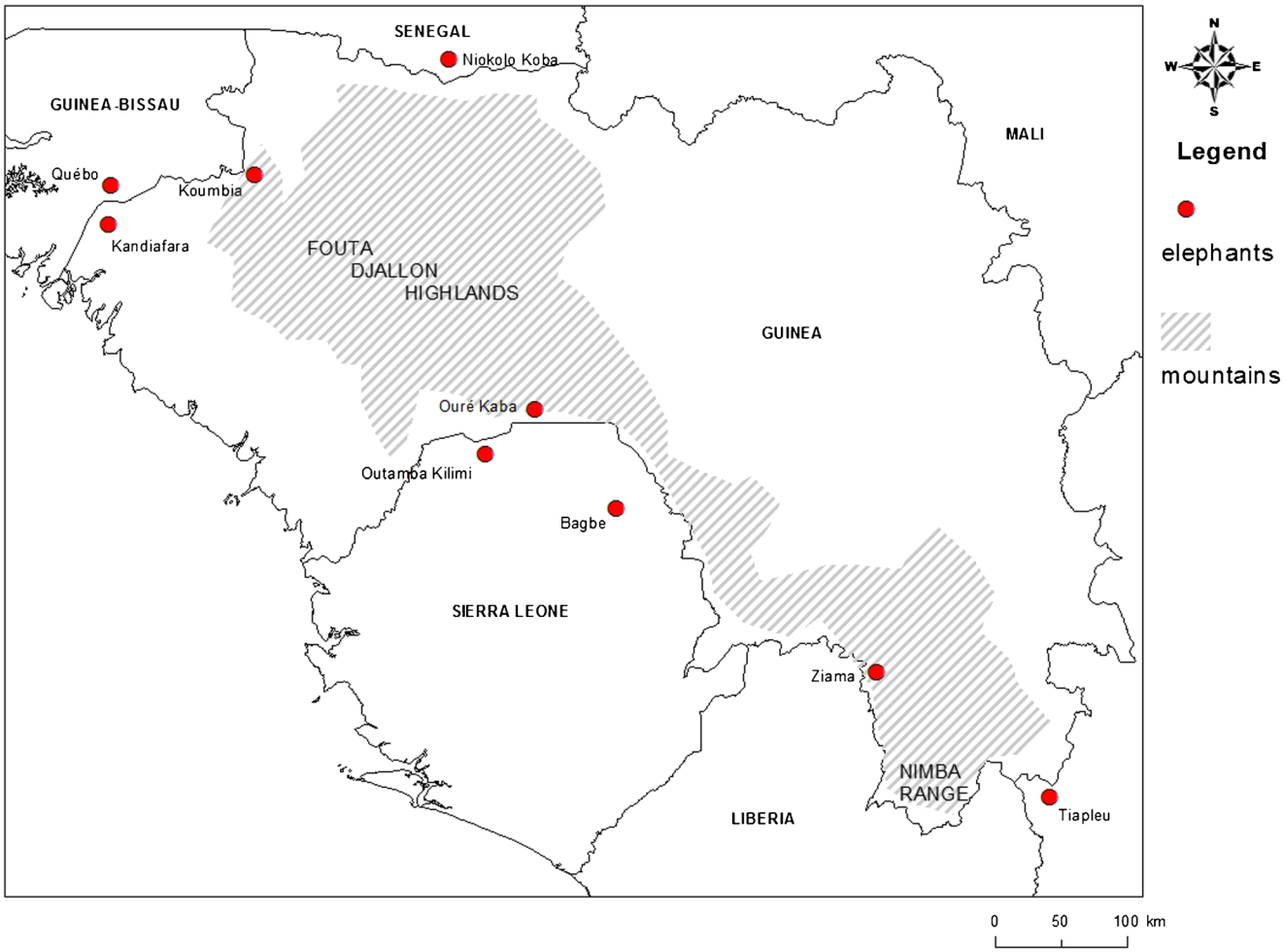

Fig. 2 Distribution of recent elephant observations in relation to the frontiers of the Guinean State (sources compiled from Blanc *et al.* 2003; Brugière *et al.* 2006)

British colonial administrator Sir Harry Johnston visited Liberia on five occasions between 1882 and 1906 and reported that elephants in areas located some 70 miles inland were a real threat to commercial caravans heading towards the coast (Johnston 1906:427). He further reported that "many of the paths [used by humans] appear to have been elephant-tracks in origin" (ibid.), an observation confirmed by the disappearance of elephant tracks after their sharp decline inside the neighbouring Taï Park in Ivory Coast (Boesch and Boesch-Achermann 2000:12). Hence, the ecology of population interactions between humans on one hand, and forest and savanna elephants (respectively browsers and grazers)[6] on the other, may vary according to different agricultural and population distribution patterns in different regions of West Africa.

Conclusion

Emphasizing the social and political context of the distribution of chimpanzee and elephant populations alerts us to potential interpretive traps resulting from insufficient methodological collaboration between the social/historical and the ecological sciences. For, on the one hand, there is always a possibility that local social and political meanings given to animals permeate the writings of nineteenth- and early twentieth-century Europeans travelling across unfamiliar regions, with the effect of misleading contemporary readers about the actual ecological and political significance of the second-hand observations they report. On the other hand, knowledge of animal population spatial ecology is also a prerequisite for the interpretation of past observations, as the sighting of elephants, for instance, does not certify their permanent presence in any given region, and vice versa.

Chimpanzee sightings by French traders and colonizers of the Northern Rivers, along with more recent censuses and field observations, testify to the species' continuous presence

[6] The taxonomy of African elephants has been regularly discussed over the last 15 years with respect to the species status of "forest" vs "savanna" elephants (Sukumar 2003:52–54; Ishida *et al.* 2011). Here, the distinction between forest and savanna elephants refers to their feeding behaviour (Sukumar 2003:45).

in agricultural landscapes of present-day northwestern Guinea and southeastern Senegal for over a century. Even if these animals' lack of economic value usually caused nineteenth-century European travellers to ignore them (at least in published reports), there is enough evidence to infer a past range as diversified as today's: from the dry savannas to the north of the Fouta Djallon highlands, to the more wooded savannas on their western margins and all the way down French Guinea's rivers and interfluvial spaces.

Elephants, on the other hand, were one of the most prized and thus most frequently-reported species in precolonial and early colonial resource inventories. They offer us a radical contrast on dynamics of regional space occupation by humans and animals. This study has retraced some aspects of elephant and human population movements, the former preferentially inhabiting spaces depopulated by wars in the context of the slave trade and by migrations linked to the demarcation of the colonial frontier between French and Portuguese Guinea. The present distribution of elephant populations examined at a larger scale, in relation to the frontiers of the Guinean State, clearly suggests that it is not independent from processes of State formation. This human-elephant model based on comparatively abundant data is also a means to assess the significance of fewer references to chimpanzees in late nineteenth-century travellers' reports. As such, it may be considered a heuristic device to more confidently infer knowledge about the long-term geographical relationships of human and chimpanzee populations. These analyses show that interspecific comparisons provide an efficient framework for the study of human and primate populations' relationships in space and time. They open up a new avenue for the development of a relational historical geography of animal populations calling for collaboration across academic disciplines such as ecology and history.

Finally, I use the human and animal population interactions analyzed in this article to interpret those reported more recently on the Guinea-Liberia frontier in the region now known as the Ziama forest reserve (Fig. 2). On the one hand, late twentieth-century conservation documents indicate that elephants were unknown inside the reserve before 1996, but in 1997 numbered 108 individuals, estimated from dung counts (Blanc *et al.* 2003:219). At the same time, it contained an estimated 300 chimpanzees (Kormos *et al.* 2003:63). It is notable that these elephant population movements coincide with times of intense (civil) warfare and refugee movements in neighbouring Liberia and across the border with Guinea. On the other hand we also know from a nineteenth-century traveller's account that large parts of the present-day reserve were at that time covered by fields and fallow vegetation rather than today's dense semi-deciduous forest. The development of dense forest is the consequence of an extreme human population decline linked to warfare, slavery, and sickness (Fairhead and Leach 1994). Under these conditions, two possibilities may be posited: that this area was only recently populated by chimpanzees, or that the species adapted to these abrupt human and vegetation changes, permanently inhabiting the area throughout this period. The evidence I present here strongly supports the second option.

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