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RESEARCH ARTICLE

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Community knowledge on factors behind extirpation of lion *Panthera leo* in Comoé National Park, Côte d'Ivoire (West Africa)

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Abstract

A rise in human disturbance in Comoé National Park (CNP) has led to lion (*Panthera leo*) extirpation. After the crisis, there have been numerous efforts to restore this ecosystem and CNP's management authority is considering reintroducing lions. This ideally requires an understanding of the earlier process of lion extirpation. We assessed the causes of lion extirpation through semi-structured questionnaires to 307 volunteer participants in surrounding 23 villages. Respondents reported that lions were extirpated two decades ago (19.75 years ± 8.15). Bouna was the sector that lions seem to have disappeared first (mean = 23.61 years ± 9.14) and recently on Nassian and Téhini sectors (mean = 18.43 years ± 8.17 and 18.74 years ± 6.74 respectively). People identified civil war from 2002 as the main facilitator of lion extirpation (85%; $n = 261$), which led to the abandonment of CNP, and opened the way for all forms of anthropogenic pressures including illegal hunting and prey depletion (70%; $n = 216$), illegal gold mining (74%; $n = 227$), direct lion killing due to transhumance and human-wildlife conflict (15%; $n = 45$), and wildfires (23%; $n = 72$). Historically, prey density curves show a progressive decrease with a drastic drop during the civil war period before a post-crisis recovery from 2016 to 2022. We recommend intensifying CNP monitoring and local measures to limit anthropogenic disturbances and improve indigenous communities' involvement to ensure the success of potential lion reintroduction.

KEYWORDS
anthropogenic pressures, conservation of lion, prey baseline, species reintroduction

Résumé

Une augmentation des perturbations anthropiques dans le parc national de la Comoé (PNC) a engendré la disparition locale du lion (*Panthera leo*). De nombreux efforts pour conserver et restaurer cet écosystème et sa biodiversité ont été faits et l'autorité de gestion envisage la réintroduction des lions. Ce retour des lions nécessite idéalement une compréhension des processus antérieurs de la disparition. Nous avons évalué les causes de la disparition des lions au moyen de questionnaires semi-structurés adressés à 307 participants volontaires dans les 23 villages riverains.

Les personnes interrogées ont déclaré que les lions ont disparu il y a deux décennies (19,75 ans ± 8,15). Bouna est le secteur où les lions semblent avoir disparu en premier (moyenne = 23,61 ans ± 9,14) et plus récemment par les secteurs de Nassian et Téhini (moyenne = 18,43 ans ± 8,17 et 18,74 ans ± 6,74 respectivement). Les enquêtés ont identifié la guerre civile de 2002 (85%; $n = 261$), qui a conduit à l'abandon du PNC, et a ouvert la voie à toutes les formes de pressions anthropiques telles que la chasse illégale et l'épuisement des proies (70%; $n = 216$), l'orpaillage illégal (74%; $n = 227$), la chasse directe de lions du fait de la transhumance et aux conflits homme-faune (15%; $n = 45$), et les feux de végétation (23%; $n = 72$). Chronologiquement, les courbes de densité des proies montrent une diminution progressive avec une chute drastique pendant la période de la guerre civile avant une reprise post-crise de 2016 à 2022. Nous recommandons l'intensification de la surveillance du parc et des mesures riveraines en vue de limiter les perturbations anthropiques et d'améliorer l'implication des communautés autochtones pour garantir le succès à la réintroduction potentielle des lions.

1 | INTRODUCTION

Recent decades have been marked by habitat degradation and the rapid loss of biodiversity across West and Central Africa despite conservation efforts (Mallon et al., 2015; Sarrazin & Barbault, 1996). Wildlife is mostly confined to protected areas, but even there, conservation is not always effective (Brashares et al., 2001; Brugière et al., 2015). Of great concern is West Africa, where many species, including carnivores like the lion, *Panthera leo* (Linnaeus, 1758), are increasingly threatened by anthropogenic pressures (Bauer et al., 2015; Henschel et al., 2010; IUCN SSC Cat Specialist Group, 2018).

The critical situation of West Africa's lion population has led to their classification as Critically Endangered, while the species *Panthera leo* is more widely classified as vulnerable due to the loss of at least 75% of their original habitat (Barnett et al., 2009; Henschel et al., 2014; IUCN SSC Cat Specialist Group, 2018).

Comoé National Park (CNP), located in northeastern Côte d'Ivoire, was inhabited by lions until at least the late 1990s (Bodendorfer et al., 2006). Because lion numbers are closely dependent on healthy ungulate populations, lion conservation has faced difficulty in CNP since the 1980s, when the population of several key prey species suffered great losses (Lauginie, 2007). The overall biomass loss of five prey species over this period was at least 60% in CNP (Lauginie, 2007), which did not bode well for the future of CNP's lions. Bauer and Van Der Merwe (2004) indicated an estimated number of 30 (minimum of 15 and a maximum of 45) lions in CNP. Similarly, Bodendorfer et al. (2006) later confirmed that there were no more than 30 lions, with the last sighting dating back to the late 1990s, tracks, and traces rarely found. These authors reported that three lions were heard roaring simultaneously in spring 2002, close to the research station in CNP, but later, (Henschel et al., 2010) reported that lions no longer occur within CNP, concluding that the last observations of lions dated to 2004.

During Côte d'Ivoire's civil war from 2002, an influx of refugees led to severe degradation in CNP and the listing of the park on the World Heritage in Danger List in 2003 (Badman et al., 2009). The extirpation of lion in this protected area (PA) occurred during the same period and we hypothesise that this is likely associated with the civil war. As shown by Bauer et al. (2022), most local extirpations of lions were associated with civil wars, but it is currently unclear whether any specific threat drives these declines faster than others. However, two threats emerged as affecting both the number of lion populations and numbers within them: livestock depredation leading to retaliatory killing of lions and bushmeat poaching leading to prey depletion (Bauer et al., 2022).

CNP's biodiversity has in recent years experienced a positive trend due to current conservation efforts and Côte d'Ivoire's socio-political stability (Bouché, 2016; Linchant et al., 2022; Viljoen, 2019). Studies have clearly demonstrated that ecological and environmental conditions in CNP are improving and CNP's management authority is now considering the reintroduction of lions (Bouché, 2016; Djafarou & Kalpers, 2013; Linchant et al., 2022; OIPR, 2015; Viljoen, 2019). To reduce the extinction risk and improve the conservation status of lions, their reintroduction into former natural habitats, based on the Guidelines for Reintroductions of the International Union for Conservation of Nature, is recommended (IUCN SSC Cat Specialist Group, 2018; IUCN/SSC, 2013; Mechin, 2012; Paquette-Boisclair, 2019; Seddon & Van Heezik, 2013). Thus, it is fundamental to understand the causes of CNP's lion extirpation and assess the availability of suitable prey, habitat, and the acceptance of lion reintroduction by local populations, all crucial to ensure the existence of large carnivores such as lions (Karanth et al., 2004). Therefore, one of the most important actions to undertake is updating the risks of decline and the status of causes behind extirpation (IUCN/SSC, 2013; UICN/SSC, 1998) through local community perceptions (Ma et al., 2021).

Considering the potential reintroduction of lions to CNP, we aim to (1) assess the estimated year of lion extirpation according to local community knowledge; (2) evaluate potential anthropogenic causes of lion extirpation from CNP; and (3) determine whether the civil war and illegal hunting affected the pattern of prey density. Hypotheses related to these objectives are as follows: (1) the main causes of lion extirpation from CNP are anthropogenic in nature; (2) more than 80% of local people believe that prey poaching and poisoning by pastoralists led to lion extirpation; and (3) prey populations were expected to decline significantly during the civil war as disturbances within CNP increased, before their post-crisis recovery. This study, which is part of a greater feasibility study, will contribute to guide authorities in making appropriate decisions to minimise post-reintroduction problems (IUCN/SSC, 2013). The management system should integrate activities to deter indiscriminate killing of future re-introduced lions, including improved coverage of patrols.

2 | MATERIALS AND METHODS

2.1 | Study area

CNP is located in the northeast of the Republic of Côte d'Ivoire, between latitudes 8°30′–9°36′ North and longitudes 3°6′–4°25′ West, covering an approximate area of 11,500 km^2 (Figure 1). The major watercourse for which CNP is named is the Comoé River, which crosses the park in its western part from north to south. The climate is tropical with a rainy and a dry season; the latter can last up to 8 months and covers the period from October to May. This is the period for development and management activities in CNP. The rainy season runs from June to September and the park is mostly inaccessible during this period. March is the hottest month, with temperatures around 37°C, while January is the coolest with an average temperature of around 15°C. Annual precipitation ranges from 900 to 1200 mm with an average of 1084 mm per year (Fischer et al., 2002). The average annual temperature ranges from 26 to 27°C (OIPR, 2015). There are four main vegetation types in CNP; gallery forests, forest patches, tree savannah, and grassy savannah. Savannah formations occupy more than 80% of the total area of the park (Poilecot et al., 1991; Schweter, 2016). As Comoé National Park is located in the savannah-forest transition zone, it hosts both savannah and forest species, including the chimpanzee *Pan troglodytes* and forest elephant *Loxodonta cyclotis* (Lauginie, 2007; OIPR, 2015), and various species of antelope. Despite the fact that the secondary streams and most pools dry up for several months of the year, the Comoé, Iringou and Kongo Rivers, along with some other tributaries, provide wildlife with ample access to water. Several saltpans allow the animals to meet their mineral requirements. Recent work in CNP, including the last aerial census, identified 19 mammal species, with Western hartebeest (*Acelaphus buselaphus major*), African buffalo (*Syncerus caffer*), Buffon's kob (*Kobus kob*) and roan antelope (*Hippotragus equinus*) the most common (Atta et al., 2020; Bouché, 2016; Linchant et al., 2022; Viljoen, 2019).

The main ethnic groups around CNP are Koulango, Lobi, and Malinké called Dioula, Djimini, and Lohron (Figure 2), who settled in successive waves between the 16th and 19th centuries (Djafarou & Kalpers, 2013). In addition to these four main communities, there are Fulfulde nomads. Fulfulde were already present around the CNP but their population was increased with the droughts in Sahel between period of 1971 and 1973, and period of 1982 and 1984. Finally, there are a few groups that have arrived from three neighbouring countries (Lobi from Burkina Faso, Bozo from Mali, Awlan from Ghana). The main activities carried out around CNP are agriculture, done by 90% of the population; livestock raising, most often with transhumance movements; agro-food processing, and illegal artisanal gold panning (OIPR, 2015). The high rate of human population growth, combined with difficulties in accessing alternative sources of income, has resulted in increasing anthropogenic pressure on arable land, animal resources and forest products around and within CNP (OIPR, 2015; UNEP-GEF Volta Project, 2011).

2.2 | Methods of data collection

2.2.1 | Sampling and survey techniques

Our survey was carried out among local populations from September to November 2022. The socio-professional groups within local villages were farmers, agro-pastoralists, housewives, former hunters, traditional healers, influential people, livestock breeders, and others (drivers, students, traders). Since hunting is illegal, the use of "former hunters" is a locally conventional way to allow for uncontroversial dialogue with people that may, in fact, still hunt. Participants were selected from twenty-three main villages bordering CNP (Figure 1). The choice of surveyed villages was based on the criteria of accessibility, proximity to CNP (villages less than or equal to 1 km from CNP), characteristics of socio-cultural groups and security of the area (Atta et al., 2021).

This study combined a quantitative and qualitative approach given the nature of the information sought. Semi-structured interview guides and photo support sheets designed on the lion and its potential prey were used (Dickman, 2008). In each of the villages, with the agreement and presence of the village chief and the youth president, twenty-three focus groups were carried out in the communities for a brief presentation of the project to participants, followed by individual interviews (Koue Bi et al., 2017). In view of the low literacy among participants, respondents were those who had given verbal prior informed consent, and interviews were carried out anonymously. The service of an interpreter was used for translations into the main local languages during the surveys. We interviewed 307 respondents from the five main ethnic groups: Lobi, Koulango, Dioula (Malinké) Djimini, and Fulfulde.

The questionnaire covered socio-demographic variables such as province, village, ethnic groups, age, gender, religion, profession, and the perception of local communities of the timing and causes of lion extirpation in CNP.

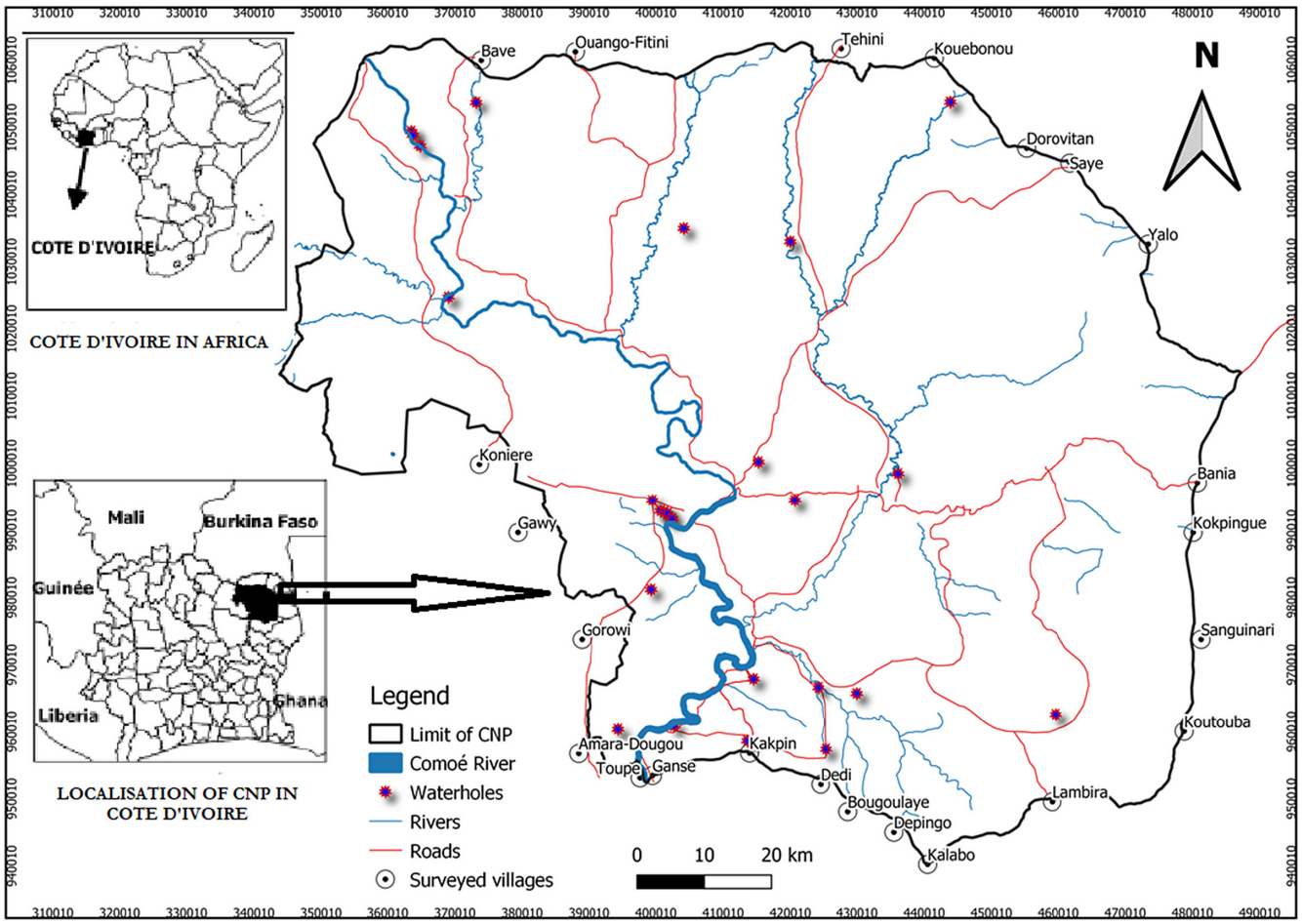

FIGURE 1 Geographic location of Comoé National Park and distribution of surveyed villages.

2.2.2 | Trends of potential lion prey

We combined data from literature (scientific articles and aerial census reports) to obtain statistics regarding the trends of prey densities in CNP before and after the civil war period. These data come from Fischer and Linsenmair (2001) and aerial censuses in CNP in 2016 (Bouché, 2016), 2019 (Viljoen, 2019) and 2022 (Linchant et al., 2022). The methods for data collection and analysis tools of individual counts are described in the respective sources (Bouché, 2016; Fischer & Linsenmair, 2001; Linchant et al., 2022; Viljoen, 2019). Here, we describe our method of meta-analysis. We tabulated density and biomass data for nine potential small, medium and large prey species to generate mean prey density and prey biomass, which were then used to create prey biomass curves for the given surveys.

2.2.3 | Statistical analysis

Globally and at the level of five zones surrounding CNP, descriptive statistics were performed to estimate the average year of lion extirpation, along with the standard deviation, minimum and maximum years of extirpation, and the variance. With the analysis of variance (ANOVA), we explored the significance of differences in the average year of lion extirpation at the level of the five surrounding zones, and pairwise between two zones with the Student's *t*-test and *F*-test (Hanson et al., 2009; Student, 1908; Warner, 2013). We also performed Pearson's correlation tests to assess the relationship between the age of respondents and the estimated year of lion extirpation in CNP (Pearson, 1895). The rates (frequencies %) of respondents indicating each cause were subsequently determined (Mouzoun, 2018). The non-parametric chi-square test assessed the significance ($p < 0.05$) of differences between frequencies of suspected lion extirpation causes among ethnic groups and socio-professional categories. Finally, we assessed the significance of differences in prey biomass between years using Chi-square tests. All statistical analyses were performed with SPSS *v2022.4.1*.

3 | RESULTS

3.1 | Sociodemographic characteristics of the respondents

We surveyed 307 respondents consisting of 212 (69%) men and 95 (31%) women, aged 33–94 through 23 focus groups and a questionnaire filled in by respondents. Our sample was composed of 61%

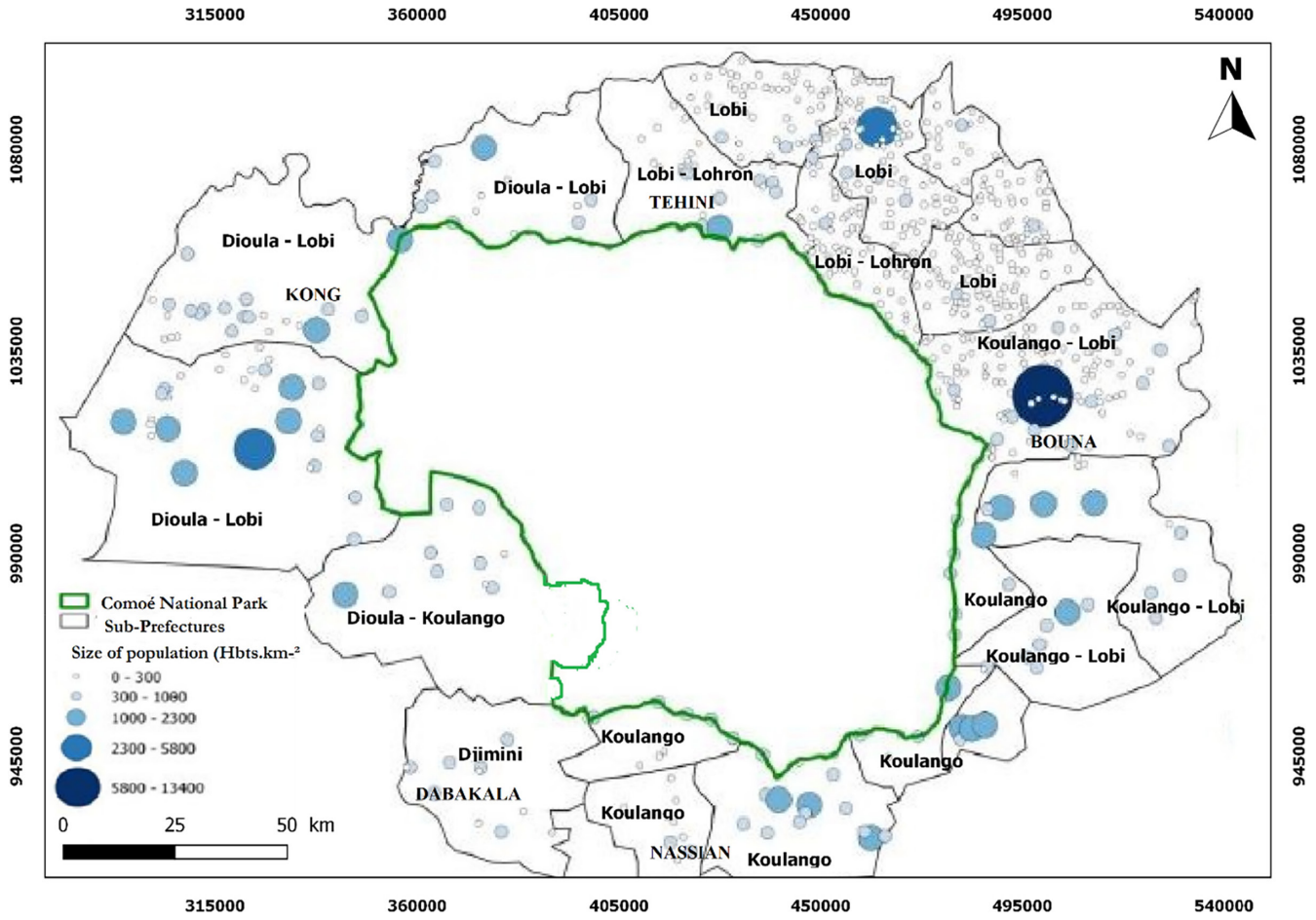

FIGURE 2 Map of human settlement surrounding the CNP (OIPR, 2015).

TABLE 1 Ethnic groups and socio-professional composition of respondents with number of respondents in a given ethnic group or profession, and relative percentages.

Variables	Terms	*n*	%
Ethnic groups	Koulango	153	50
	Dioula (Malinké)	77	25
	Lobi	40	13
	Djimini	23	07
	Fulfulde	14	05
Total		307	100
Profession	Farmers	150	49
	Housewives	38	12
	Agro-pastoralists	36	12
	Former hunters	22	07
	Traditional healers	20	06
	Influential people	17	06
	Livestock breeders	14	05
	Other (students, drivers, traders)	10	03
Total		307	100

TABLE 2 Descriptive statistics with groups, number of respondents (*n*), and accumulation of different number of years mentioned globally and at the level of each zone (sum), average of estimated year (mean) and standard deviation (SD).

Groups	N	Sum	Mean ± SD	Variance
Global	307	6064	19.75 ± 8.15	66.44
Bouna	52	1228	23.61 ± 9.14	83.53
Dabakala	30	605	20.16 ± 9.57	89.38
Kong	30	602	20.06 ± 8.41	68.34
Nassian	85	1567	18.43 ± 8.17	65.94
Téhini	110	2062	18.74 ± 6.74	45.09

(*n* = 188) Muslims, 21% (*n* = 65) Christians and 18% (*n* = 54) Animists. The ethnic groups and socio-professional distributions of the sample are summarised in Table 1. Our sample had significantly more respondents from the regionally dominant ethnic group, the Koulango ($\chi^2 = 31.92$; Df = 5 and *p*-value < 0.05), and significantly more respondents from the main profession, farmers ($\chi^2 = 36.71$; Df = 7 and *p*-value < 0.05).

TABLE 3 Analysis of variances in the estimated year of lion extirpation in Comoé National Park with source of variation, sum of squares, degree of freedom (Df), mean of square, value of *F*, probability, and critical value of *F*.

Source of variations	Sum of squares	Df	Mean of squares	*F*	Probability	Critical value for *F*
Between groups	1043.08	4	260.77	4.08	0.003	2.40
Within groups	19,288.11	302	63.87			
Total	20,331.18	306				

TABLE 4 Pearson's correlation matrix with variables, number of respondents (*n*), minimum (min) and maximum (max), mean and standard deviation (SD).

Variable	*n*	Min	Max	Mean	SD
Estimated year of lion extirpation in Comoé National Park	307	5.00	40.00	19.75	8.15
Age of respondents	307	33.00	94.00	51.23	12.79
	Age of respondents		**Estimated year of lion extirpation in Comoé National Park**		
Age of respondents	1		0.10		
Estimated year of lion extirpation in Comoé National Park	0.10		1		

3.2 | Year of lion extirpation from CNP

Table 2 shows the descriptive statistics about the estimated number of years since lion have been extirpated from CNP. The average year of lion extirpation in CNP was estimated at 19.75 ± 8.15 with a minimum of 5 and maximum of 40 years. Our survey suggests that the last sightings of lions by local people dated back to approximately late 2002, that is, before the civil war period. Respondents who mentioned dates after the civil war assumed that lions would still be in the park, even if they were not observed. Based on the average dates, the oldest observations were made in the Bouna sector (mean = 23.61 years ± 9.14) while the most recent were located in the Nassian and Téhini sectors (mean = 18.43 years ± 8.17 and 18.74 years ± 6.74 respectively).

The year of lion extirpation in CNP varied significantly either between sectors of Nassian and Bouna or between Bouna and Téhini P (Table 3; $F = 4.08$ Critical $F = 2.40$; $p < 0.05$). The estimation of the year of lion extirpation in CNP was weakly correlated with the age of respondents (Table 4; Pearson's $\alpha = 0.01$).

3.3 | Direct and indirect causes of lion disappearance to CNP

Local people identified five groups of potential indirect and direct causes of lion extirpation. The majority of respondents pointed out the civil war and CNP abandonment as the main indirect cause of lion extirpation in CNP (85%; $n = 261$), followed by direct causes, that is, illegal gold mining (74%; $n = 227$), and illegal hunting and prey depletion (70%; $n = 216$). Wildfires were cited by 23% ($n = 72$) of respondents, while 15% ($n = 45$) mentioned direct lion killing due to transhumance and human-wildlife conflicts (Table 5).

Within ethnic groups and socio-professional categories, the respondents were almost unanimous citing the civil war and the abandonment of CNP, illegal gold mining, and excessive wildlife poaching (Figure 3). However, the Fulfulde, who are livestock breeders, had a higher citation rate for the direct lion killings ($\chi^2 = 41.44$; p-value < 0.05; $\chi^2 = 39.42$; p-value < 0.05; Figure 4). In addition, for notables and traditional healers, the main cause was wildfires ($\chi^2 = 24.07$; p-value < 0.05; Figure 3).

3.4 | Trend of ungulate densities through three last aerial censuses in CNP

Figure 5 shows the decreasing densities of key prey species in CNP from 1995 to 2022, spanning Côte d'Ivoire's civil war which took place between 2002 and 2011. All prey species experienced significant anthropogenic pressure during the civil war period with the most abundant species, Buffon's kob, decimated. The African buffalo, the most abundant large ungulate, also suffered a great population decline. Small, less abundant herbivores including duikers and oribi were severely impacted as well. Barring hartebeest and roan antelope, rampant illegal poaching during the civil war period targeted many species, including Buffon's kob, the African buffalo and small herbivores such as the red flanked duiker (*Cephalophus rufilatus*), the oribi (*Ourebia ourebi*), the bushbuck (*Tragelaphus scriptus*), Maxwell's duiker (*Cephalophus maxwelli*) as well as species of pigs such as warthog (*Phacochoerus africanus*; Figure 5). For all these prey species, mean biomass (kg/km^2) started declining around 1995–1998 before a drastic drop during the civil war. After the civil war, we observed a significant increase in prey biomass for all species from 2016 to 2022 (Figure 6; $\chi^2 = 9.48$; Df = 4 and p-value < 0.05). As shown in Figure 7, the species' contributing most to this increase were hartebeest, buffalo and roan antelope, followed by waterbuck and Buffon's kob.

4 | DISCUSSION

Traditional cultural practices are widely practised in this region, and each person is necessarily rooted in tradition irrespective of their religious affiliations. Clearly, CNP management appeared already

TABLE 5 Different causes identified by local people, with number of respondents per cause (*n*) and percentage (P).

Civil war and park abandonment		Illegal hunting and prey depletion		Illegal gold mining		Lion killing due to transhumance and human-wildlife conflicts		Wildfires	
N	P	*N*	P	*n*	P	*n*	P	*n*	P
261	85.02	216	70.36	227	73.94	45	14.66	72	23.45

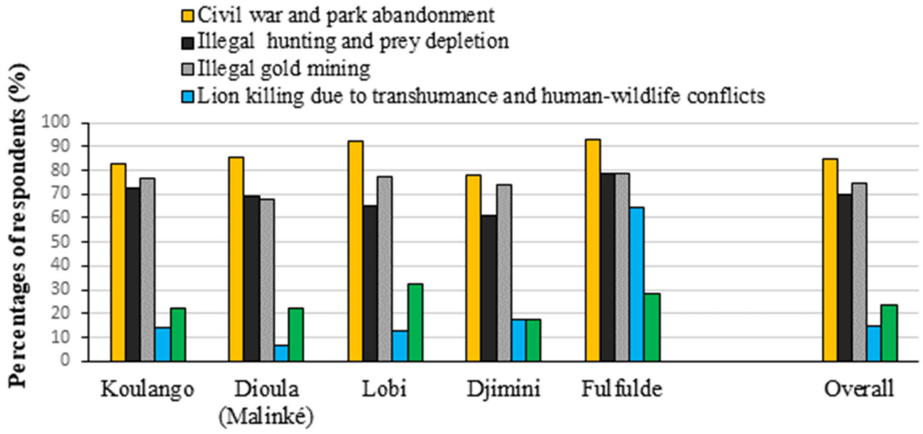

FIGURE 3 Potential anthropogenic indirect and direct causes of lion extirpation in Comoé National Park identified by local ethnic groups.

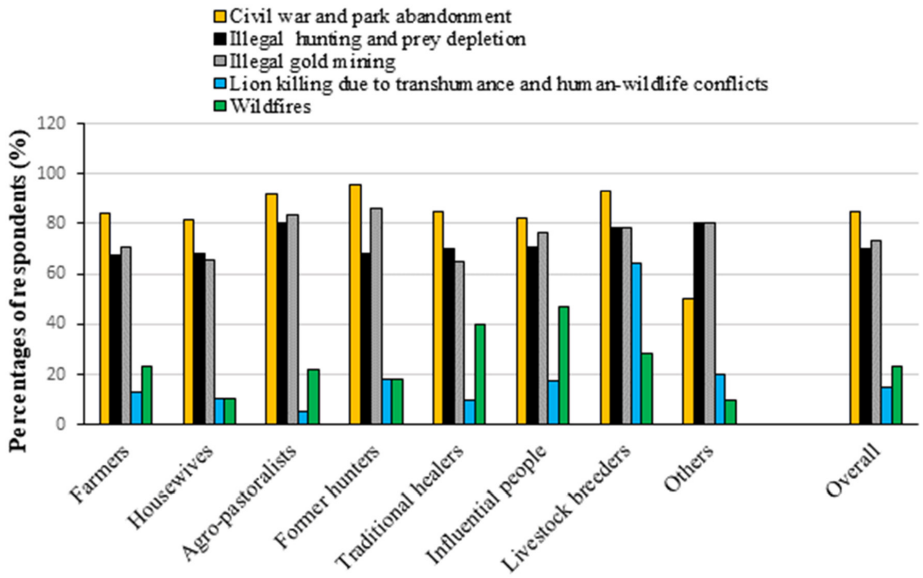

FIGURE 4 Potential anthropogenic indirect and direct causes of lion extirpation in Comoé National Park identified by professional categories.

problematic before the advent of the civil war, as the densities of two of the lion's main prey species, cob and buffalo, were almost halved between 1995 and 1998, and lions were already considered very rare before the 2000s (Bauer & Van Der Merwe, 2004; Fischer & Linsenmair, 2001). The civil war appears to have been the straw that broke the camel's back in accelerating the extirpation of the lion in Côte d'Ivoire. Indeed, armed conflicts are widely distributed in Africa, having occurred in 71% of all Afrotropical protected areas and over 80% of biodiversity hotspot areas between 1946 and 2010 (Daskin & Pringle, 2018; Hanson et al., 2009). Armed conflicts and civil strife throughout the world's biodiversity hotspots are typically associated with detrimental effects on wildlife and their habitats, posing a critical threat to conservation (Daskin & Pringle, 2018; Gaynor et al., 2016). Some studies indicate that Côte d'Ivoire's socio-political crisis caused many difficulties for the management and losses in biodiversity of CNP (Dudley et al., 2002; Gaynor et al., 2016). CNP was abandoned

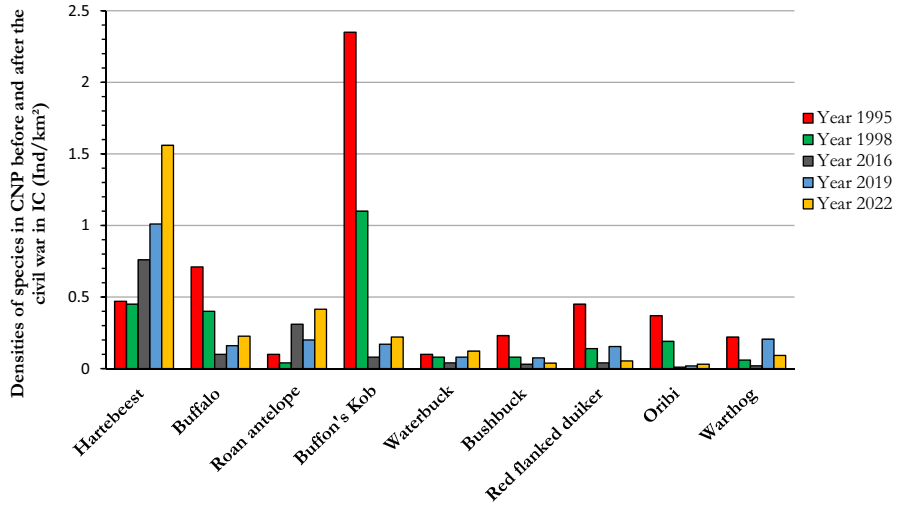

FIGURE 5 Densities of the main prey species of Comoé National Park in 1995, 1998, 2016, 2019 and 2022. The red and green bands indicate the densities estimated by some authors before the crisis period (Fischer & Linsenmair, 2001) and the black, blue and orange bands reflect the densities resulting from the three aerial censuses carried out by Office Ivoirien des Parcs et Réserves (OIPR) in post-crisis period in 2016 (Bouché, 2016), 2019 (Viljoen, 2019) and 2022 (Linchant et al., 2022).

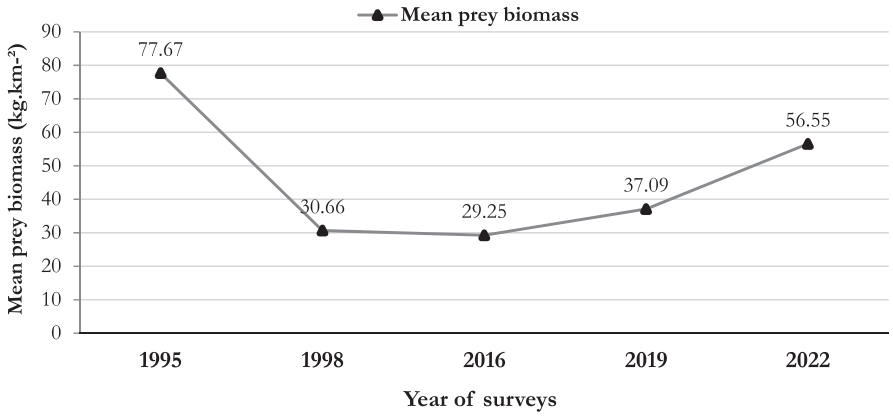

FIGURE 6 Trend of mean prey biomass in Comoé National Park from 1995 to 2022. Source of data: Studies by Fischer and Linsenmair (2001) before the civil war and aerial censuses in post-civil war period (Bouché, 2016; Linchant et al., 2022; Viljoen, 2019).

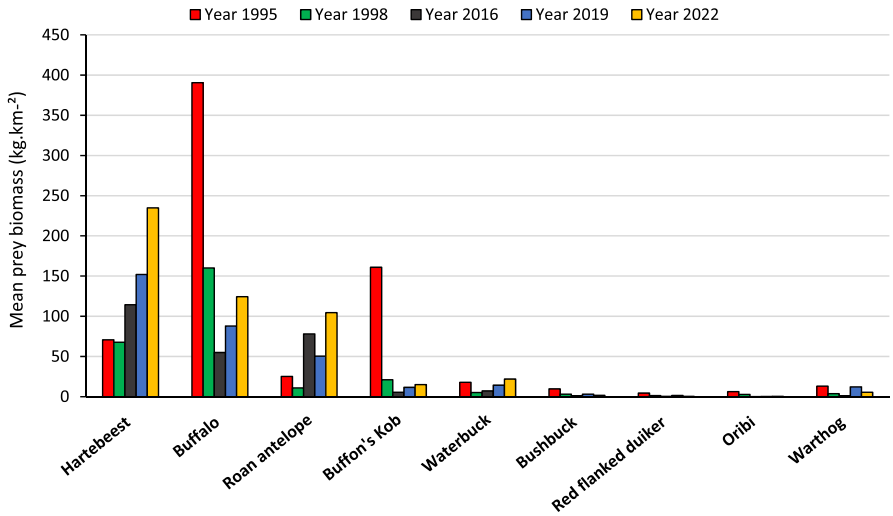

FIGURE 7 Biomass of the main prey species of Comoé National Park in 1995, 1998, 2016, 2019 and 2022. Fischer and Linsenmair (2001) determined only prey biomass for 1995 and 1998. The prey biomass for 2016, 2019 and 2022 were estimated based on prey densities resulting from the three aerial censuses carried out by Office Ivoirien des Parcs et Réserves (OIPR) in post-crisis period in 2016 (Bouché, 2016), 2019 (Viljoen, 2019) and 2022 (Linchant et al., 2022).

during this crisis as a significant portion of the park was, like the rest of the country, under the sway of rebellion (Fischer, 2004). CNP represented for rebels both shelter and pantry, with subsequent great declines in prey species (Fischer, 2004). We found that almost all of CNP's natural resources were the targets of excessive exploitation during the war, notably with intense illegal gold mining and excessive hunting. Our findings showed that the extirpation of lions in this PA dates back some twenty years to this period of civil war, which represents the precursor to the outbreak of pressure on CNP's resources. Therefore, with the prior prey decreasing and low population of lion (Bauer & Van Der Merwe, 2004; Fischer & Linsenmair, 2001), the extirpation of lions here is thus further evidence of the devastating impacts that armed conflicts can favour on biodiversity. This was the case in Quiçama National Park and Quiçama Game Reserve in

Angola, where the populations of 20 out of 26 assessed mammals, especially large-bodied species in open savannah environments were reduced during the war from 1975 to 2002 with declines up to 80% for some species (Braga-Pereira et al., 2020). We found that excessive prey hunting and direct lion killing were threats during the civil war period. According to (Bauer et al., 2022), livestock depredation leading to the retaliatory killing of lions, and bushmeat poaching leading to prey depletion, represent the two most common threats that could affect both the number and size of lion populations. Therefore, the overharvesting of wildlife and vegetation in conflict zones exacerbates existing constraints on access to natural resources, threatening both the resource base and the livelihoods of local communities dependent on these resources (Dudley et al., 2002).

In CNP, we found that small- and medium-sized prey suffered excessive overharvesting during the civil war, in contrast to large-sized prey (with the notable exception of buffalo). It was shown that lions in CNP preyed predominantly upon small to medium-sized ungulates, while large ungulates (hartebeest, buffalo and warthog) made up a surprisingly small proportion of their diet and were not preferentially killed as recorded for Eastern and Southern Africa (Bodendorfer et al., 2006). These authors suggested that the preference of lions for small prey in CNP may have been an indicator of a dwindling lion population in which the social system and communal hunting mode may have broken down due to human persecution. However, lion diet in Pendjari National Park was also predominantly composed of medium-sized prey (average of 60%) while large-sized prey comprised approximately 32% of diet (Sogbohossou, 2011). The prey preference of lions in West Africa seemed converging to small- and medium-sized prey probably because these are the most abundant prey species in protected areas of the region (Bauer et al., 2008). Accordingly, the lion's preferential prey in CNP was overharvested and depleted through the civil war period. Concomitantly, CNP's lion population was already low before the civil war; approximately 30 individuals, with a minimum of 15 and a maximum of 45 lions (Bauer & Van Der Merwe, 2004). Although these figures were absolute guestimates, which were not based on any field survey work, these authors still gave an idea on the presence of lions in pre-crisis period. There was no targeted lion survey using appropriate field survey techniques, or even using other methods in CNP to highlight the actual lion population size or lion density in CNP in pre-strive. However, this is evidence that a low population size, compounded by the effects of the various anthropogenic pressures in CNP, increased the vulnerability of the lions and hastened their decline. Slow-breeding large animals, such as great apes, elephants, and lions, are particularly vulnerable to hunting because of their low potential for population recovery over short time scales (Cardillo et al., 2004; Sodhi et al., 2014; Trinkel & Angelici, 2015). A lack of monitoring and research can lead to undetected local extirpations. Probably lion extirpation in CNP took place prior to the onset civil war and being undetectable. This was the case in some other sites in West Africa during the same period (Henschel et al., 2014), including in countries without civil strive (e.g. the local extirpation of lions in Ghana's Mole NP in the same wider landscape around the same period) (Angelici et al., 2015).

After the civil war the facilitator of effects, the country recovered a socio-political stability and many efforts had been undertaken to mitigate sources of pressures. There is thus a positive trend in prey density and biomass from 2016 to 2022 resulting in effective management system (Bouché, 2016; Linchant et al., 2022; Viljoen, 2019). On the another hand, as the civil war was a facilitator instead of a direct cause, all sources of threats to wildlife in CNP could not be mitigated despite the end of civil strife. As pointed out by some authors, direct causes of lion extirpation in CNP such as poisoning by pastoralists and direct killing for body parts were confirmed after the socio-political crisis (Henschel et al., 2010, 2014).

We conclude that various factors, including the civil war as indirect determinant, cessation of management activities in CNP, anthropogenic pressures on habitat, prey depletion, and direct lion killing, were conducive to the extirpation of lions in CNP from 2002 to 2011. Côte d'Ivoire has now been stable for at least a decade and prey densities and biomass are on the rise, the return of lions to this CNP may be possible if the entire park is properly controlled with effective management that mitigate the direct causes of earlier extirpation. Our study is part of a larger feasibility project inspired by IUCN Guidelines that focused on many other aspects including the community perspective on the prospect of lion reintroduction (Aglissi et al., submitted), prey base and spatio-temporal patterns of larger competitors (Aglissi et al. in prep) as well as the current threats on wildlife populations in CNP. A potential reintroduction should also be based on implementing the combination of approaches explored by Dickman et al. (2011) that promote human-lion coexistence. According to these authors, the best way of "payments to encourage coexistence" might be a combination of compensation payments, revenue sharing, and conservation payments. In addition, Lindsey et al. (2013) suggest that payments to encourage human-wildlife coexistence could also be a useful tool to decrease the hunting of wildlife.

The research project on the lion reintroduction in CNP, of which the present paper is a first outcome, complies with the capital steps of the IUCN Guidelines for Reintroductions and Other Conservation Translocations. Indeed, as required by these Guidelines, the knowledge of earlier processes behind the species disappearance is a priority. Thus, our present study highlighted the main causes of lion extirpation in CNP, but other major components focused on the carrying capacity, the spatio-temporal dynamic of large competitors, the current threats on wildlife populations, and the local communities' perceptions towards the lion return in CNP. Based on our assessment that unsustainable hunting during the civil war period resulted in prey depletion and the extirpation of lions in CNP, we recommend intensifying monitoring and local measures to limit anthropogenic disturbance and improving the involvement of indigenous communities. This could improve the effectiveness of the management system and contribute to the success of the potential reintroduction of lions in CNP.

AUTHOR CONTRIBUTIONS

Janvier Aglissi is the designer of the study. He was responsible for the data collection, data processing and data analysis, and the manuscript writing. **Etotépé A. Sogbohossou** and **Hans Bauer** contributed to the design of the study, data analysis, and the manuscript writing. **Jamie Bolam** was in charge of the language editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request at aglissi@hotmail.fr

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