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Population Trends of Large Carnivores in the Benoue Ecosystem, a Savannah Landscape of Central Africa (Cameroon)

Serge A. Kamgang[1,2,3,4] | Romaric P. Tegang[3,5] | Iris Kirsten[6] | Paul J. Johnson[5] | Justin G. Didolanvi[3] | Serge P. Tadjo[7] | Achille M. Goue[8] | Awe Central[9] | Pricelia N. Tumenta[10] | Elise Bakker[11] | Michel Babale[2] | Saleh Adam[12] | Hans de Iongh[13,14] | Claudio Sillero[5] | Hans Bauer[5,14,15]

[1]German Development Cooperation, BSB Yamoussa, Garoua, Cameroon | [2]Garoua Wildlife College, Ministry of Forestry and Wildlife, Garoua, Cameroon | [3]Biodiversity-Environment & Sustainable Development, Garoua, Cameroon | [4]ERAIFT-UNESCO, Kinshasa, Democratic Republic of the Congo | [5]Wildlife Conservation Research Unit, Department of Biology, the Recanati-Kaplan Centre, University of Oxford, Oxford, UK | [6]Africa Parks, Zakouma National Park, Djamena, Chad | [7]Bouba Ndjidda National Park, Ministry of Forestry and Wildlife, Koum, Cameroon | [8]Benoue National Park, Ministry of Forestry and Wildlife, Banda, Cameroon | [9]Faro National Park, Ministry of Forestry and Wildlife, Voko, Cameroon | [10]Department of Forestry, University of Dschang, Dschang, Cameroon | [11]Leo Foundation, Wageningen, the Netherlands | [12]North Regional Delegation, Ministry of Forestry and Wildlife, Garoua, Cameroon | [13]Institute of Environmental Sciences, Leiden University, Leiden, the Netherlands | [14]Evolutionary Ecology Group, Department of Biology, University of Antwerp, Wilrijk, Belgium | [15]African Parks, Gambella National Park, Gambela Region, Ethiopia

Correspondence: Serge A. Kamgang (sergekamgang@gmail.com) | Paul J. Johnson (paul.johnson@biology.ox.ac.uk)

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ABSTRACT

Large carnivores play a vital role in ecosystem functioning, yet their populations are increasingly threatened by habitat loss, human–wildlife conflict and declining prey availability. The Benoue ecosystem in Cameroon, one of the last strongholds for lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyaenas (*Crocuta crocuta*) in Central Africa, is experiencing significant conservation challenges. This study assessed spatiotemporal trends in large carnivore encounter rates in the Benoue ecosystem, Cameroon, from 2014 to 2023. We used repeated spoor counts as a proxy for inferring population trends and assessing the impacts of land cover changes. We found significant declines across species and blocks. Lion declines were similar between blocks (substrates are similar and detection therefore unlikely to be affected by this source of bias). Spoor encounter rates were significantly higher in the National Park (NP) compared with the surrounding Hunting Zones (HZ) in the Bouba Ndjidda block, whereas the reverse was true in the Benoue block; there was no significant effect in the Faro block. Leopard spoor encounter rates were highest in the Bouba Ndjidda block and in the NP within the block. Spotted hyaena spoor encounter rates decreased over time across the ecosystem (and were lowest in the Benoue block). These trends can be linked to trends in vegetation dynamics across the three blocks, with the highest habitat loss recorded in the Benoue block, compared to the more stable habitat conditions in Bouba Ndjidda and Faro. These differences are likely influenced by variations in conservation investments, habitat degradation, and anthropogenic pressures, which were not fully assessed during the study. The findings emphasise the urgent need for increased conservation efforts in the Benoue block to mitigate further population declines and habitat fragmentation. Effective management strategies, including enhanced anti-poaching efforts and habitat restoration, are likely to be crucial for maintaining viable carnivore populations in the region.

1 | Introduction

The persistence of large carnivore populations is increasingly threatened worldwide, with implications for ecosystem stability and biodiversity conservation (Ripple et al. 2014; Wolf and Ripple 2016; Riggio et al. 2013). In the Benoue ecosystem of Cameroon, a critical stronghold for large carnivores in Central Africa, understanding population trends is essential for guiding conservation strategies in the face of habitat degradation, prey depletion and human–wildlife conflict (Lindsey et al. 2017; Green et al. 2018; Everatt et al. 2019). Human populations have grown rapidly in the last century, which has been the root cause of drastic reductions in both distributional range and numbers of large carnivores throughout the continent (Hofer and Mills 1998; Riggio et al. 2013; Jacobson et al. 2016).

The monitoring of large carnivore populations is essential for assessing their status and population trends and for evaluating conservation interventions. However, long-term repeated surveys to monitor trends in density over large spatial scales are costly and rare (Bauer, Chapron, et al. 2015; Bakker et al. 2020). Spoor surveys have been widely used as an alternative method that can be applied over large areas to generate indices of large carnivore abundance and distribution (Funston et al. 2001; Stander 1998; Winterbach et al. 2016). Spoor surveys consist of counting the number of tracks (spoor) of a target species along predefined transects (Funston et al. 2001). Dröge et al. (2020) pointed out that the conversion to carnivore abundance produced results of doubtful precision and this has been abandoned by most practitioners. Therefore, we assess only trends in our spoor count index, calculated as the number of spoors per 100 km of transect, as a proxy (Bakker et al. 2020). The usefulness of this proxy depends on some assumptions concerning variation in detection (Anderson 2003), and we discuss how this affects our findings concerning different hypotheses.

The Benoue ecosystem in North Cameroon is one of the last strongholds for large carnivores in Central Africa, hosting the regionally Critically Endangered northern lion (*Panthera leo leo* Linnaeus, 1758), leopards (*Panthera pardus*) and spotted hyaenas (*Crocuta crocuta*) (Tumenta et al. 2010; Bauer, Kamgang, et al. 2015; Bakker et al. 2020; Croes et al. 2011; Nicholson et al. 2023). However, the Benoue ecosystem is also facing multiple threats, such as poaching, habitat loss, human encroachment, livestock grazing, bushfires and climate change, that may affect the viability of large carnivore populations and their prey base (Tumenta et al. 2010; Bauer, Kamgang, et al. 2015; Bakker et al. 2020). In support of conservation activities by government conservation services and local stakeholders, international Non-Governmental Organisations (NGOs) have been active in the area. The Leo Foundation, and the German Development Cooperation have been active in Bouba Ndjidda since 2014 and the African Wildlife Foundation and Conserve Global in Faro since 2019.

The main objective of this study was to determine spatiotemporal trends in lion, leopard and spotted hyaena abundance using repeated spoor counts on transects from 2014 to 2023 across the Benoue ecosystem. Our main research questions focused on trends in large carnivores. We expected to observe an overall temporal effect, with declining trends over time linked to our knowledge of increasing threats in the area.

We also hypothesised that trends in large carnivore spoor abundance would vary according to land management type, with higher maintenance of populations expected in national parks compared with hunting zones. Specifically, we addressed the following questions:

1. Do encounter rates of large carnivores (lion, leopard, spotted hyaena) show significant temporal trends from 2014 to 2023 across the study area?
2. How do these trends vary among management types (National Parks vs. Hunting Zones) and ecological blocks?
3. What is the relationship between observed carnivore trends and land cover changes over time?
4. Which species and locations should be prioritised for conservation interventions based on these results?

2 | Material and Methods

2.1 | Study Area

The Benoue ecosystem is located in North Cameroon between latitudes 8°30′ N and 10°30′ N and longitudes 13°30′ E and 15°30′ E. It covers an area of about 30,000 km^2 within the Sudanian savanna biome, characterised by a mosaic of wooded grasslands, shrublands and gallery forests along rivers. The climate is semi-arid, with a mean annual rainfall of about 900 mm and a mean annual temperature of about 27°C. The rainy season lasts from May to October and the dry season from November to April. The ecosystem is drained by the Benoue River and its tributaries, which provide permanent water sources for wildlife and humans. The ecosystem harbours a rich diversity of wildlife, including elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), buffaloes (*Syncerus caffer*), antelopes and primates, as well as several endemic and endangered species, such as the giant eland (*Taurotragus derbianus*) and the red-fronted gazelle (*Eudorcas rufifrons*) (Tumenta et al. 2013; Bakker et al. 2020).

The landscape comprises three national parks (NPs): Benoue, Bouba Ndjidda and Faro. The national parks are under the jurisdiction of the Ministry of Forestry and Wildlife (MINFOF) and are strictly protected from illegal human activities. However, the level of law enforcement and anti-poaching patrols varies among the parks, with Bouba Ndjidda being the most effectively managed, followed by Faro and Benoue (Bakker et al. 2020). Surrounding the NPs are 28 hunting zones (HZs), allocated to private safari operators who pay concession fees to MINFOF to operate. The operators are also expected to contribute to wildlife conservation and community development in their areas of operation, but the extent and quality of their interventions differ among the HZs (Bauer et al. 2017). Some HZs on the northern and southern edges of the ecosystem have been fully encroached; larger wildlife is no longer resident, and these were not considered in this study. Our study area thus comprises three NPs and 12 HZs with a total area of 17,044 km^2 (Figure 1).

Human population density in the Benoue ecosystem is low, with on average approximately 10 people per km^2, concentrated in villages and settlements along the main roads and rivers. The main human activities include agriculture, livestock rearing, fishing, hunting, logging and mining, which may have negative impacts on wildlife habitats and populations (Tumenta et al. 2010; Bakker et al. 2020).

2.2 | Data Collection

We followed the protocol described by Funston et al. (2010) for conducting spoor surveys in the Benoue ecosystem. The transects were stratified according to management type (national park or HZ) and block (Benoue, Bouba Ndjidda or Faro), resulting in six strata with at least two transects per stratum. The transects were also georeferenced using GPS devices and were maintained over the years as a semi-permanent monitoring tool.

We surveyed large carnivores by counting their spoor (footprints) on 25 km segments of roads across the sampled area of the Benoue ecosystem (Funston et al. 2010). Substrate was similar across the ecosystem, unpaved and poorly maintained car tracks with no substantial differences between management units, mostly laterite but with patches of sand and clay. The spoor count index was then calculated as the number of spoors per 100 km of transect. Under some circumstances, the encounter rate can be usefully correlated with the density of the species. Winterbach et al. (2016) estimated *r*-squared values of between 43% and 97% for predictions of carnivore density using spoor counts in sandy and clay soils.

The use of abundance indices in wildlife monitoring has been heavily criticised. The problem lies with variability in detection. Anderson (2003) goes so far as to say that 'Unless detection probabilities are known or estimated from the data, index values reveal nothing about the parameter of interest'. It is therefore important to consider how such variation affects our ability to test different hypotheses. The transects were located along existing roads or tracks with suitable substrates for spoor detection and identification. We photographed each pugmark three times and recorded key details including species, GPS position, track age, time, road condition, and observer information. To minimise observer bias, all photographs were first verified by an independent expert and then cross-checked by the entire research team, with reclassification applied when necessary (Funston et al. 2010). Knowledge regarding interspecific variation in spoor detectability remains limited; therefore, comparisons between species should be interpreted with caution. Analyses were conducted separately for each species. Observed trends are considered to provide more reliable insights. There was no trend

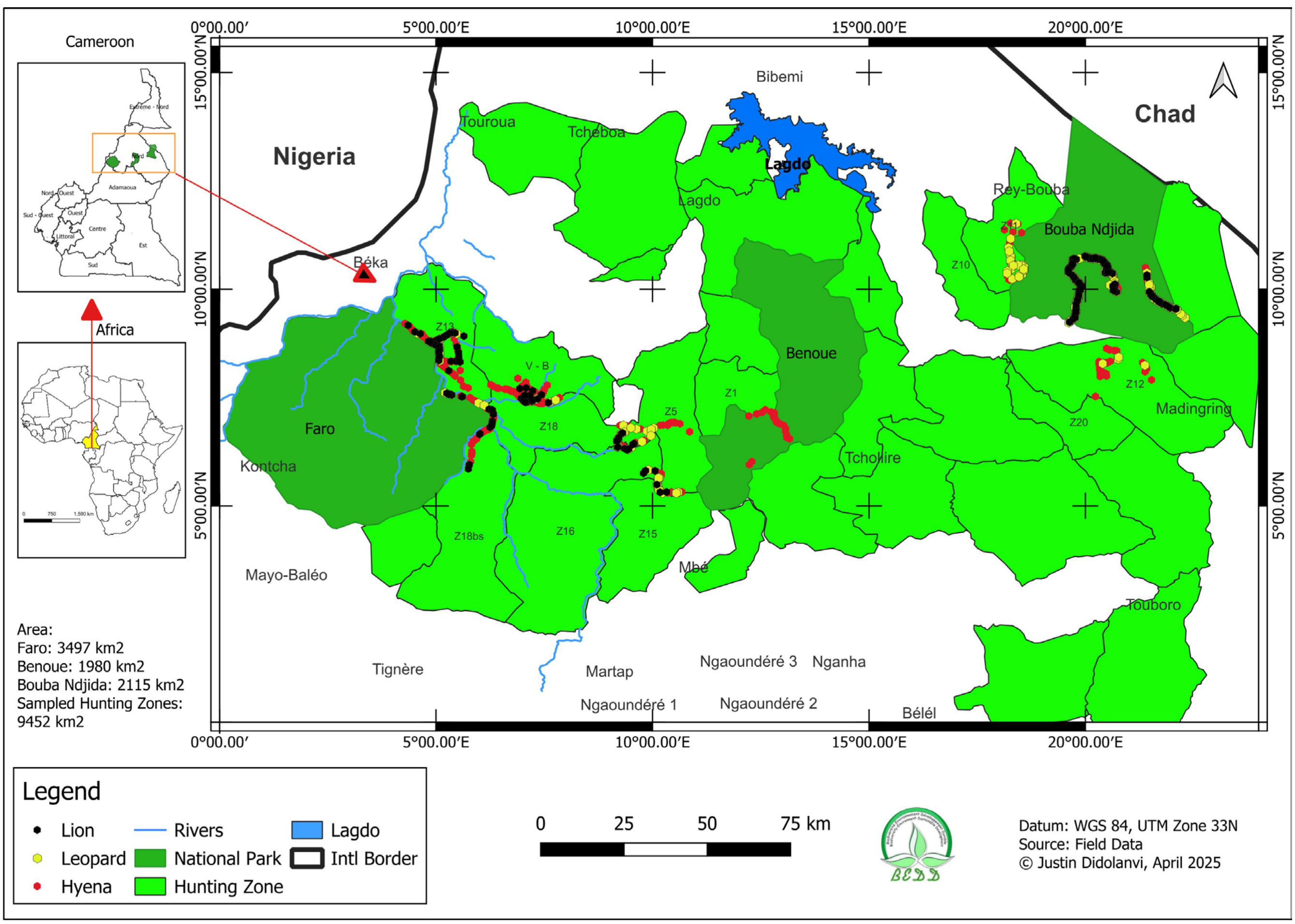

FIGURE 1 | The study area highlighting the spoors' position of large carnivores' species.

in substrate type for transects at any location. In addition, each data point used was a summary of many sampling events for combinations of location and year and may be less susceptible to short-term changes in detectability, caused by weather for example. The reported long-term changes in land use are unlikely to affect observed trends as a result of detection changes; the surrounding vegetation does not affect spoor detection; spoors are located by searches at short distances. We did, however, have a strong a priori expectation that land use might affect trends in encounter rate caused by loss of predators. For these reasons, we focus on observations on trends in this manuscript. We report the area effects from our models for completeness; their veracity depends on some assumptions concerning the effect of substrate on spoor detectability.

We conducted spoor surveys annually from 2014 through 2023, except in 2018 and 2019 when security issues prevented data collection in some areas. The surveys were carried out during the dry season (January–May), when spoor visibility is optimal. Each transect was surveyed at least twice per month. The surveys were conducted by two trained observers (local lion guards) who drove along the transects on motorbike at a speed of 15 km/h to record all large carnivore spoor using CyberTracker on a smartphone, datasheets, a numeric camera and GPS devices.

To evaluate spatiotemporal dynamics in land use, we used Landsat 8–9 OLI/TIRS satellite images captured in February and March for the years 2015 and 2022. Images from paths 184 and 185 and rows 054 and 055 were selected to ensure complete coverage of the study area. The early dry season was chosen for image acquisition due to the superior quality of the data, as this period provides optimal conditions for observing land cover. All satellite images were sourced from the United States Geological Survey (USGS) Earth Explorer platform (https://earthexplorer.usgs.gov/).

2.3 | Data Analysis

To analyse spoor count data across different blocks in the Benoue ecosystem, we follow a structured approach. Statistical analyses were performed using (R Core Team 2023), to assess spatial and temporal trends. We fitted linear models (using the base R 'lm' command). Spoor count indices, calculated as spoor counts encountered per 100 km, were used as proxies for abundance (Stander et al. 1997; Bakker et al. 2020). We counted each spoor encountered in combinations of year, Block and date which defined a sampling event. These encounter rates were square root transformed to improve adherence to the assumptions of glm modelling. The glm model included a continuous predictor defining the temporal trend, as well as Block and land management type, a variable with two levels: National Park (NP) and Hunting Zone (HZ). Interactions were included to test the null hypotheses that any temporal trends were the same in each block and land management type. A further interaction term between area type and block tested the null hypothesis that the effect of management type was constant across blocks. Effects were visualised using the R 'interactions' package (Long 2019) Tukey's means comparison procedure was carried out using the R 'emmeans' package (Lenth 2024). Inspection of patterns in model residuals provided no evidence for non-linear temporal trends.

For our exploration of land use, the initial step in image processing involved creating false-colour composites by combining the red and near-infrared bands (5R/3V/2B) to improve vegetation differentiation across both time periods. Using visual interpretation, expert knowledge of the Benoue Ecosystem, and existing land cover data, we identified and classified various land cover types (Figure 4). Spatial analysis was performed in QGIS using the Semi-Automatic Classification Plugin (SCP) to preprocess, classify, and analyse land cover changes over time. We evaluated the surface areas occupied by different land cover classes for each year and estimated land use changes between 2015 and 2022. To assess vegetation cover dynamics, we calculated the overall rate of change using the methodology outlined by Tapobda et al. (2008) and Arouna et al. (2009).

3 | Results

3.1 | Hyaena

There was no evidence that encounter rate declined over the study period (Figure 2a, $F_{1,35} = 2.73$, $p = 0.11$), and no evidence that this varied with block ($F_{2,35} = 0.42$, $p = 0.62$). There was strong evidence for variation in encounter rate between blocks ($F_{2,35} = 9.8$, $p < 0.001$) and no evidence that encounter rate differed overall with land management (National Park or Hunting Zone, $F_{1,35} = 0.02$, $p = 0.91$), The land management effect did not vary with year ($F_{1,35} = 1.92$, $p = 0.16$, respectively).

The overall block effect was accounted for by the consistently low encounter rates in the Benoue block—these were significantly

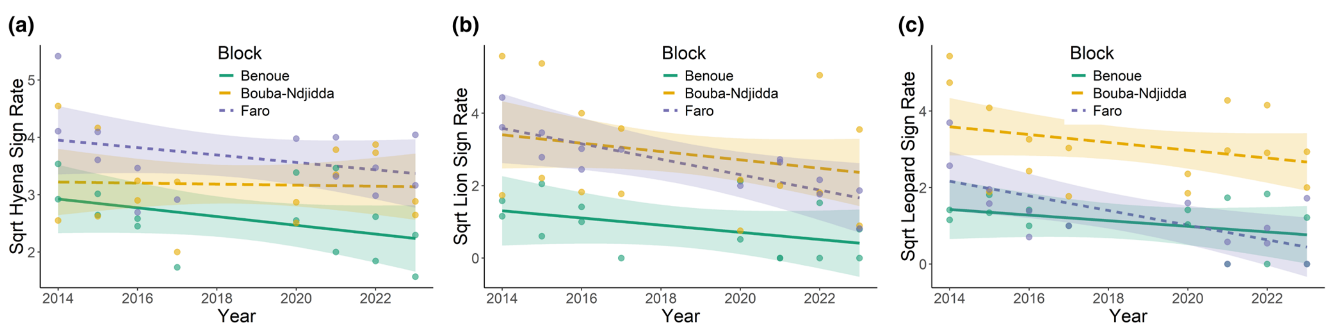

FIGURE 2 | Trends in large carnivore spoor encounter rate (encounters per 100 km of transect). Model marginal means with confidence intervals.

lower than in either of the other two blocks (Tukey's mean separation procedure). The average encounter rate there per 100 km was 6.76 (SE = 0.24) compared with 14.8 (SE = 1.20) in Faro and 10.52 (SE = 0.88) in Bouba Ndjidda.

3.2 | Lion

There was strong evidence for an overall negative trend (Figure 2b, $F_{2,35} = 21.66$, $p < 0.001$). There was also strong evidence for variation in encounter rate between blocks ($F_{2,35} = 41.0$, $p < 0.001$). There was no evidence that the trend varied between blocks ($F_{2,35} = 1{,}39$, $p = 0.26$). There was limited evidence that encounter rate differed overall with land management (National Park or Hunting Zone, $F_{2,35} = 6.8$ $p = 0.01$). There was no evidence that the land management effect varied with year ($F_{1,35} = 0.52$, $p = 0.47$).

As for hyaena encounters, the overall block effect was attributable to low encounter rates in Benoue Tukey means separation procedure: the average encounter rate there per 100 km was 1.48 (SE = 0.24) compared with 4.0 (SE = 0.60) in Faro and 10.48 (SE = 0.92) in Bouba Ndjidda. The land management effect differed across blocks: there was a significant interaction between management type and block (block × management type interaction, $F_{1,35} = 27.6$, $p < 0.0001$) The management effect was strongest in Bouba Ndjidda, where encounter rates were substantially higher in National Parks compared with Hunting Zones (Figure 3b, Tukey contrast for Bouba Ndjidda, $p < 0.001$). In Benoue, the opposite was observed: encounter rates were significantly higher in hunting zones compared with National Parks (Figure 3b, Tukey contrast, $p = 0.04$). There was no evidence for an effect in Faro (Figure 3b, Tukey contrast, $p = 0.25$).

3.3 | Leopard

The results for leopards mirrored those for lions, with strong evidence for a downward temporal trend (Figure 2c, $F_{1,35} = 12.2$, $p < 0.001$). There was also strong evidence for a block effect ($F_{2,35} = 33.0$, $p < 0.001$) and no evidence that the temporal trend differed between blocks ($F_{2,33} = 1.03$, $p = 0.36$). Unlike the pattern for the other large carnivores, the average encounter rate was clearly higher in the Bouba Ndjidda block compared with the other two blocks (Tukey's means separation procedure, $p < 0001$ for both), while there was no evidence for a difference between Faro and Benoue (Tukey: $p = 0.8006$). However, the block effect was not consistent for management types (block × management type interaction, $F_{2,35} = 6.28$, $p = 0.004$, Figure 3c). The encounter rate difference between Bouba Ndjidda and the other two blocks was more marked in National Parks (Figure 3c). A difference between management types was apparent only in Bouba Ndjidda where encounter rates were clearly higher in National Parks (Tukey contrast, $p = 0.0061$).

Land cover changes in the landscape between 2015 and 2022 vary between the three different blocks (Figure 4a–c). There are only minor changes in the Bouba Njidda Block, but there is clear evidence of degradation in the Faro Block with agricultural expansion and forest clearance (gallery forest was completely removed). Shrubland savannah also declined markedly. There was also evidence of degradation in the Benoue Block with an increase in bare soil and loss of clear forest. These changes are quantified in Table 1.

Table 1 Land cover categories by % over time.

A summary of all main statistical effects by species is presented in Table 2 to facilitate interspecific comparison.

4 | Discussion

Our main research questions centred on temporal trends in large carnivores. The results of this study reveal declines in large carnivore spoor densities across the Benoue ecosystem: leopards and lions both showed strong evidence of declining prevalence There was also limited evidence for land management effects, though little indications that trends were influenced by management type. We speculate that conservation efforts, habitat changes and anthropogenic pressures are at least partly responsible for the observed patterns. The observed declines are consistent with previous studies (Bakker et al. 2020; Bauer, Chapron, et al. 2015; Croes et al. 2011).

Our findings confirm to some extent that areas with stronger conservation interventions, such as Bouba Ndjidda NP have significantly higher encounter rates than Benoue NP. This spatial comparison is subject to the usual concerns regarding detection effects, but substrate conditions did not differ substantially. Our prior assessment that National Park management was more effective in Bouba Ndjidda was supported

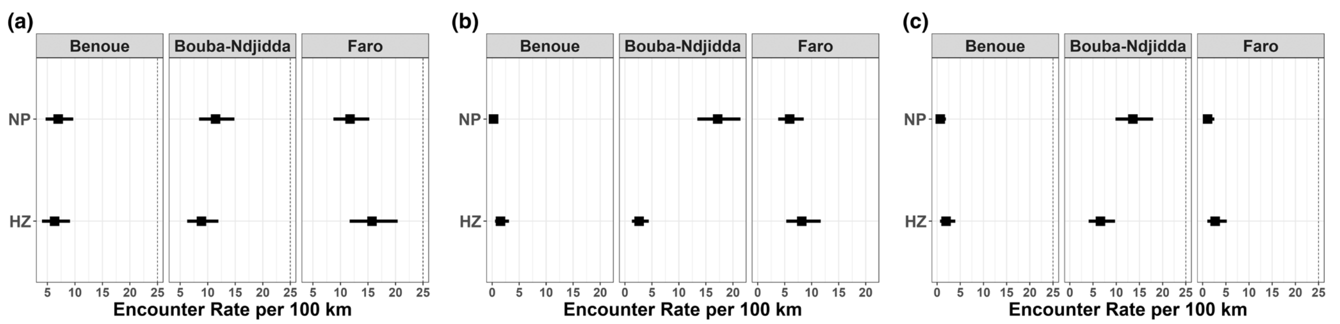

FIGURE 3 | Land management and block effects on spoor encounter rates. Model marginal means with confidence intervals. NP = National Parks, HZ = Hunting Zones.

TABLE 1 | Land cover change Matrix of Benoue Ecosystem (2015–2022).

	Land cover							
Landscapes	**Bare soil (%)**	**Clear forest (%)**	**Field crop (%)**	**Shrubland savannah (%)**	**Woody savannah (%)**	**Water (%)**	**Gallery forest (%)**	
Bouba Ndjidda	15.7	31.97	6.95	28.12	17.25	—	—	2015
	15.61	30.68	7.89	26.55	19.26	—	—	2022
Faro	22.44	9.31	0	25.12	21.47	—	21.66	2015
	22.1	18.06	17.4	18.43	24.01	—	0	2022
Benoue	16.38	25.74	5.9	24.96	25.42	1.61	—	2015
	23.17	15.03	8.09	30.4	22.56	0.76	—	2022

Note: — indicates that the land cover class is not present in the classification map.

by the results (Figure 3). This mirrors broader patterns across Africa, where well-managed protected areas provide better conditions for large carnivore persistence (Lindsey et al. 2017). However, declines were observed in both National Parks and Hunting Zones. There is no evidence of greater protection arresting a downward trend. We cannot exclude the possibility that higher encounter rates predate the establishment of the Parks' status, and that current management is no more effective than that in Hunting Zones.

The decline in spoor densities in Benoue is concerning, given its strategic location within the ecosystem. This decline, as also observed by Bakker et al. (2020), appears to be ongoing and has not been reversed. In their study, Bakker et al. (2020) assessed spatiotemporal trends in the abundance of lions (*P. leo*), leopards (*P. pardus*), and spotted hyaenas (*C. crocuta*) based on repeated spoor counts conducted along transects from 2007 to 2015. Their temporal analysis revealed a consistent decrease in lion and spotted hyaena populations across the entire complex, while leopard numbers declined only during the final 2 years of the study, mainly within the Faro Block.

Continued declines could lead to population fragmentation, reducing genetic connectivity and increasing the risk of local extirpations, a phenomenon observed in other carnivore populations facing similar pressures (Jacobson et al. 2016; Riggio et al. 2013). The absence of spoor from cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*) suggests that these species may already be locally extirpated, as they are particularly sensitive to habitat fragmentation and human–wildlife conflict (de Iongh et al. 2011; Woodroffe et al. 2005).

Carnivore spoor encounter rates are also declining in Bouba Ndjidda and Faro, which highlights the need for more effective conservation investments. Bakker et al. (2020) also found that spoor abundances varied across different areas within the Benoue Complex and among management types, reporting a particularly high spoor encounter rate in Bouba Ndjidda National Park and in the hunting zones surrounding Faro. Organisations such as the Wildlife Conservation Society and the African Wildlife Foundation have played a crucial role in supporting anti-poaching measures and habitat management activities that have likely contributed to maintaining higher carnivore populations in these areas. Similar conservation models have proven effective elsewhere, where sustained funding, law enforcement, and community engagement have stabilised or increased carnivore populations (Estes et al. 2011; Dröge et al. 2020; Boronyak et al. 2022).

Land cover changes between 2015 and 2022 further contextualise these findings and highlight spatial and temporal variation among the three blocks. While Bouba Ndjidda maintained relatively stable habitats, there was considerable degradation in both Faro and Benoue. In Benoue, there was an increase in bare soil and a reduction in forest cover. These changes are likely contributing to carnivore declines by reducing prey availability and increasing human–wildlife conflict (Durant et al. 2022; Green et al. 2018, 2024). However, land cover change alone cannot explain the declines. We also observed reductions in Bouba Ndjidda where land cover remained stable. The combined impacts of habitat loss, poaching, and encroachment emphasise the need for urgent, ecosystem-wide conservation action.

Given their extensive spatial requirements and sensitivity to disturbance, large carnivores serve as effective umbrella species (Roberge and Angelstam 2004). Maintaining landscape connectivity and minimising conversion are critical to sustaining both apex predators and the broader biodiversity they support. Recent findings on lion movement patterns underscore how spatial ecology can inform conservation planning for wide-ranging species (Kamgang et al. 2025). Overall, the land cover matrix provides a clear visualisation of the spatial trends, helping identify priority areas for conservation interventions and reinforcing the importance of long-term monitoring to inform adaptive management strategies.

Finally, this study reaffirms the value of spoor count indices for monitoring large carnivore trends. While spoor surveys do not provide absolute density estimates, they remain useful for assessing population changes over time (Funston et al. 2010; Winterbach et al. 2016). In line with recent recommendations (Dröge et al. 2020), we did not attempt to convert spoor counts into absolute numbers. Nevertheless, observed changes in encounter rates offer valuable insights into carnivore distribution and habitat use.

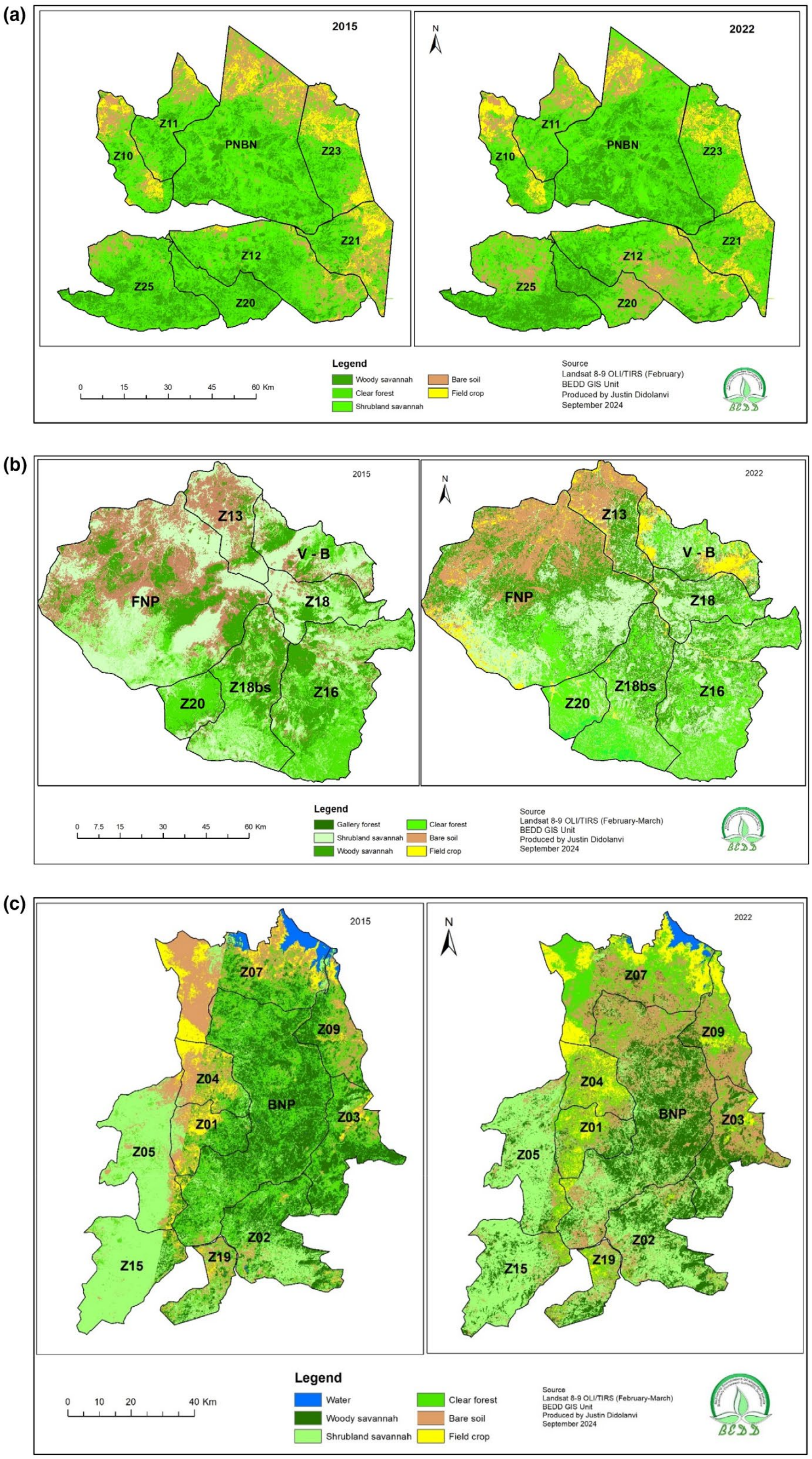

FIGURE 4 | Land cover changes across the Benoue blocks between 2015 and 2022.

Future conservation efforts should prioritise strengthening anti-poaching patrols, restoring degraded habitats, and improving management strategies. Integrating prey monitoring in future studies will provide a more comprehensive understanding of the ecological drivers shaping large carnivore populations in the Benoue ecosystem.

5 | Conclusion

The findings of this study underscore the urgent need for targeted conservation interventions to safeguard large carnivore populations within the Benoue ecosystem. The observed decline in Benoue not only endangers local populations but also threatens the broader connectivity of carnivore populations across Central Africa, heightening the risk of genetic isolation and local extirpation.

To counter these trends, conservation strategies should focus on reinforcing anti-poaching efforts, enhancing habitat restoration, and improving the overall effectiveness of park management. Building on the proven success of conservation initiatives in Bouba Ndjidda and Faro, replicating similar approaches in Benoue through increased support from both governmental and non-governmental actors will be essential. Equally important is the collaboration with local communities to reduce human–wildlife conflict, foster coexistence, and secure key habitats, ensuring the long-term survival of large carnivores in the region.

In addition, long-term monitoring programs should continue to use spoor count indices as a cost-effective means of assessing population trends, maintaining consistency through standardised methodologies. Complementary techniques, such as camera trapping and prey abundance surveys, should also be integrated to provide a more comprehensive understanding of the ecosystem dynamics.

TABLE 2 | A comparative summary of effects by species.

Species	Overall temporal trend	Block effect	Management effect (NP vs. HZ)	Interaction (block × management)	Observation
Hyaena	No significant trend ($P=0.11$)	Significant ($p<0.001$)	Not significant ($p=0.91$)	Not significant ($p>0.05$)	Stable overall; lowest in Benoue block
Lion	Decline ($p<0.001$)	Significant ($p<0.001$)	Significant ($p=0.01$)	Significant ($p<0.001$)	Strong declines; highest in Bouba Ndjidda NP
Leopard	Decline ($P<0.001$)	Significant ($p<0.001$)	Not significant overall	Significant ($p=0.004$)	Higher in Bouba Ndjidda NP; similar in others

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

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