First insights into the spatio-temporal ecology of sympatric large carnivores in Niokolo-Koba National Park, Senegal

ROBIN HORION*[1], ZOE WOODGATE[2] and MARINE DROUILLY[1,3,4]

Abstract Large carnivores play a crucial role in their native ecosystems, but their populations are rapidly declining across the African continent. West Africa is no exception, with large protected areas often forming the last strongholds for these species. Little is known about the population status and ecology of large carnivores in the region, hampering the design and implementation of effective conservation strategies. We conducted a camera-trap survey during the dry season in Niokolo-Koba National Park, the largest terrestrial protected area in Senegal and the second largest in West Africa, to investigate the spatio-temporal ecology of the four large carnivores inhabiting the Park: the spotted hyaena *Crocuta crocuta*, leopard *Panthera pardus*, West African lion *Panthera leo leo* and African wild dog *Lycaon pictus*. Spotted hyaenas and leopards had the widest spatial distribution and highest probability of site use. Spotted hyaena site use was positively associated with leopard relative abundance index and negatively associated with normalized difference vegetation index, whereas only distance to the nearest road influenced leopard site use. Distance to the Gambian River was the most important covariate positively affecting site use by lions. African wild dog site use was negatively associated with the relative abundance indices of lions and leopards. Lions, spotted hyaenas and leopards showed strong overlap in their activity patterns. By providing new information on the ecology of large carnivores in West Africa, including where they range and which habitats are critical for their survival, our study will facilitate conservation planning. Our findings lay the foundations for future research to conserve these threatened species in West Africa effectively and to guide ranger patrol efforts, which are key for their long-term survival.

Keywords Activity pattern, African wild dog, large carnivores, leopard, lion, occupancy, Senegal, spotted hyaena

*Corresponding author, robin.horion@gmail.com
[1]Panthera, Tambacounda, Senegal
[2]Institute for Communities and Wildlife in Africa, University of Cape Town, Cape Town, South Africa
[3]Panthera, New York City, New York, USA
[4]Centre for Social Science Research, University of Cape Town, Cape Town, South Africa

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Introduction

Protected areas are crucial for biodiversity conservation (Osipova et al., 2020), especially for large carnivores, which are acutely sensitive to anthropogenic impacts (Wolf & Ripple, 2014). Large carnivores are key species for successful protected area management as they occupy the highest trophic levels within ecosystems (Woodroffe, 2000), shaping community structure by controlling mesopredator (Soulé et al., 1988) and prey populations (Creel et al., 2018). In addition to their important ecological roles, charismatic carnivore species raise public awareness of protected areas and conservation efforts, indirectly protecting other species by helping to generate tourism income, funding opportunities and conservation actions (Carignan & Villard, 2002).

West African protected areas suffer from a lack of baseline research in comparison to those in East and Southern Africa (Bauer et al., 2021), largely because of limited financial support from governments and international donors, lack of private-sector investment and minimal tourism opportunities (Lindsey et al., 2017). Funding difficulties, combined with inconsistent management, hinder basic management practices such as long-term monitoring and law enforcement (de Boissieu et al., 2007), reducing the conservation effectiveness of protected areas in the region. As a result, some protected areas have been classified as so-called paper parks (Lindsey et al., 2018), which, despite their official protected status, lack effective management and fail to achieve desired conservation outcomes. These deficiencies are directly affecting populations of large carnivores, which have suffered significant declines in the region for several decades (Brugière et al., 2015). African wild dogs *Lycaon pictus* have been extirpated from the W–Arly–Pendjari Complex, leaving the last remaining West African population in Niokolo-Koba National Park in Senegal (Woodroffe & Sillero-Zubiri, 2020). The Park also harbours one of the four remaining populations of the West African lion *Panthera leo leo*, which is categorized as Critically Endangered on the IUCN Red List (Henschel et al., 2014). Although a large population is located in Pendjari National Park, this faces significant threats heightened by the rise of terrorism (Lhoest et al., 2022). The situation for the leopard *Panthera pardus* is also serious; this species has been described as the most persecuted felid globally (Hunter & Balme, 2004) and has lost 86–95% of its historic West African distribution since 1750 (Jacobson et al., 2016). In contrast, the spotted hyaena *Crocuta crocuta* has a broader regional distribution and persists in some of the human-altered landscapes of Senegal (Mills & Hofer, 1998). Many large carnivores are the target of the illegal trade in skins and body parts, which are used for cultural practices in line with various local belief systems (Adeola, 1992). Retaliatory persecution by herders because of real or perceived predation on livestock is also driving carnivore declines (Gueye et al., 2022).

West African large carnivores are generally geographically isolated from the rest of the continent and are (or are suspected to be) distinct subspecies (Henschel et al., 2010; Anco et al., 2018; Woodroffe & Sillero-Zubiri, 2020), except for the spotted hyaena, for which data on its genetic status are lacking (Gueye et al., 2022). Niokolo-Koba National Park holds a nearly intact guild of large carnivores—only missing the historically present Northwest African cheetah *Acinonyx jubatus hecki*—which makes it a crucial landscape for the conservation of these species in West Africa. Yet little is known about the population status and ecology of large carnivores within the Park, and in the region more broadly.

We present the first insights into the distribution and spatio-temporal interactions of the sympatric large carnivores occurring in Niokolo-Koba National Park. Our specific aims were to identify factors driving spatial use by large carnivores within the study area, explore how these species spatially coexist and determine their activity patterns and overlaps. Robust data on the ecology and distribution of large carnivores in Niokolo-Koba National Park could inform conservation planning and management efforts by providing insights into which habitats and resources are crucial to their persistence. This baseline information could then be used to develop conservation strategies including restoration and management of habitats and prey populations, targeted anti-poaching patrols and conflict mitigation measures (Ripple et al., 2014). Our work thus forms the basis to improve our knowledge of large carnivores in Niokolo-Koba National Park and guide the long-term conservation and monitoring of these species in the region (Bauer et al., 2021).

Study area

Niokolo-Koba National Park, the largest terrestrial protected area in Senegal, covers c. 9,130 km² in the Western Sudanian savannah ecoregion (Fig. 1) and has monthly temperatures ranging from 28.0 °C in December to 34.5 °C in April (Arbonnier et al., 2019). Annual rainfall is 900–1,200 mm, with 78% falling during the rainy season (June–October; Dagorne et al., 2020). The Gambian River is the largest and only permanent river in the Park, but waterholes can be found in its two tributaries (Niokolo-Koba and Koulountou) during the dry season. The landscape comprises a mosaic of habitats such as grassy savannahs, shrub savannahs, wetlands, dry forests, gallery forests and bamboo groves (Arbonnier et al., 2019). The terrain is largely flat, except in the south-west, where Mont Assirik, the highest point in the Park, culminates at an elevation of 310 m.

Methods

Camera-trap survey

We conducted a camera-trap survey during the 2021 dry season (12 March–27 June), with the primary objective of estimating leopard density and the secondary objective of obtaining baseline information on the distribution of key species in the National Park. We used 139 cameras (44 PantheraCam V6 and 94 PantheraCam V7, Panthera, USA; and one infra-red Browning BTC-6HDX, Browning Trail Cameras, USA) deployed in 72 stations, 63 of which were paired. The survey covered just under one-fifth of the National Park (1,523 km²). We used a grid of 5-km² cells and deployed a camera-trap station within each cell (mean inter-station distance = 3 km). We selected macro-placement remotely through satellite imagery, focusing on the road network (Fig. 1), gallery forests and proximity to permanent water sources (Tanwar et al., 2021). We chose micro-placement to maximize large carnivore detection by identifying areas with large carnivore spoors, scats and prey carcasses, amongst other factors. When no sign of presence could be found, we deployed cameras along vehicle tracks and at the intersections of wildlife trails (Kolowski & Forrester, 2017). We placed the camera traps c. 30–45 cm above the ground on trees, orientated perpendicular to animal tracks (TEAM Network, 2011). We programmed the cameras to take a single picture each time the sensor was triggered by movements, with a 1-s delay between triggers. We treated photographs of the same carnivore species at the same station as independent events if they were separated by at least 30 min (Meek et al., 2014).

Data analyses

Relative abundance index and non-metric dimensional scaling analysis To visualize dissimilarity amongst species based on their presence or absence at different camera-trap stations, we used non-metric dimensional scaling (nMDS; Woese et al., 1990). We computed nMDS from the relative abundance index (RAI) of each species at each station

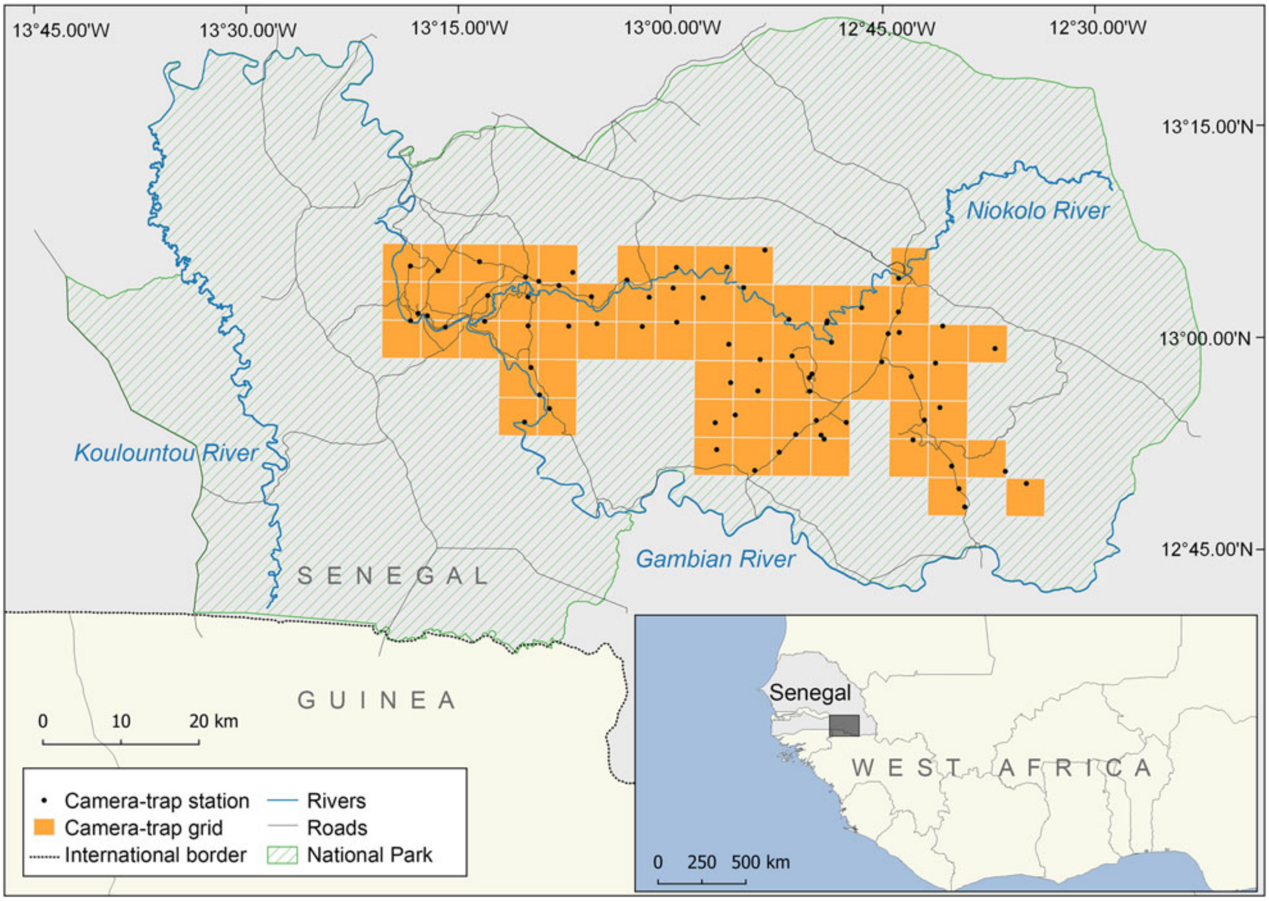

FIG. 1 Niokolo-Koba National Park in Senegal, with the survey area where we conducted camera trapping during March–June 2021.

(Fonteyn et al., 2021). We calculated RAI as the number of independent images for each species divided by the total number of trap-days multiplied by 100 (O'Brien et al., 2003). Although RAIs do not incorporate detection heterogeneity between species, they can be useful for species-level comparisons within single surveys (Royle & Nichols, 2003). We pooled our data into a relative abundance matrix for each species, thereafter fitting the nMDS with 10,000 random starts using the Bray–Curtis distance dissimilarity measure. We used covariates, which we selected based on a priori hypotheses (Table 1). We also included all mammal species (with a body mass $\geq$ 0.5 kg) detected, to determine similarities between carnivores and the terrestrial mammal community of the Park. In this ordination, the closer two points are, the more similar the corresponding species are with respect to the covariates (derived at the camera-station level) used in the nMDS plot. We checked nMDS distortion using the stress value, with values $<$ 0.3 indicating that the ordination is arbitrary (Legendre & Legendre, 1991). We conducted the nMDS calculations using the *vegan* package (Oksanen et al., 2022) in *R 4.1.1* (R Core Team, 2022).

Occupancy We fitted single-season, single-species occupancy models (MacKenzie et al., 2002) using the *R* package *unmarked* (Fiske & Chandler, 2011) to investigate the patterns of habitat use in the Park for each large carnivore (lion, leopard, spotted hyaena and wild dog). Occupancy models utilize binary detection/non-detection data (a site-by-occasion matrix, where 1 represents a presence and 0 an absence) to estimate the probability of detection (ρ) and occupancy (ψ). In this study, because all target species have home ranges larger than our grid cells, we use the term 'site use' rather than occupancy (Choki et al., 2023), which represents the percentage of the study area used by the species (Tobler et al., 2015). We employed a data-driven approach to mitigate zero inflation and improve model fit, as suggested previously (Broekhuis et al., 2022). To enhance modelling accuracy, we pooled detection histories into 9-day sampling occasions for leopard and spotted hyaena and 11-day occasions for wild dog and lion. After testing various durations (7–15 days), we selected the best-fit pooling duration for each species. Detection probability (ρ) and occupancy (ψ) can be modelled as functions of site-specific covariates (MacKenzie et al., 2002), and we used the same covariates as for the nMDS (Table 1) and standardized them to z-scores. We used the Spearman correlation coefficient (r) to assess multicollinearity amongst chosen covariates, and removed covariates with the least explanatory

Table 1 Covariates used to model site use (occupancy; ψ) and detection probabilities (ρ) of the four large carnivore species (West African lion *Panthera leo leo*, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta* and African wild dog *Lycaon pictus*) occurring in Niokolo-Koba National Park, Senegal (Fig. 1), associated hypotheses and predicted signs of influence. We derived all covariates at the camera-trap station level.

Process	Covariates	Description	Hypotheses	Predicted sign of influence	Source of the data
ρ	Effort	Number of trap-days at the station level	Survey effort impacts detection of studied species (Combe et al., 2019)	(+) Longer survey duration increases the likelihood of large carnivores being detected (Dröge et al., 2020)	This study
	Type	Type of camera used (PantheraCam V7, V6 or Browning BTC-6HDX)	Difference between camera brand & models could impact detection	(+ or −) Large carnivores are more likely to be detected with more sensitive cameras & vice versa	This study
	Presence of sympatric species (i.e. leopard, lion, hyaena, wild dog)	Detection history (presence, absence) for each sympatric large carnivore	Detections of sympatric carnivores at the same station may affect the detection of other carnivores (Creel et al., 2001)	(−) For leopards & African wild dogs because of subordinate relation with lions (Darnell et al., 2014); (+) for lions & spotted hyaenas because of scavenging &/or dominant relationships with other carnivores (Swanson et al., 2014)	This study
ψ	NDVI	Normalized difference vegetation index	NDVI has been shown to influence site use of large carnivores in West Africa (Pettorelli et al., 2011)	(+) During the dry season, NDVI is a proxy for resources (water & primary productivity; Santin-Janin et al., 2009)	GEE Landsat 2020–2021 (resolution: 30 m)
	Dist_Gambie Dist_Niokolo Dist_River	Distance to the Gambian River, the Niokolo-Koba River or the main river of the National Park: Niokolo-Koba, Koulountou or Gambian Rivers (km). We separated the two rivers as the Gambian River is considerably larger than the Niokolo River, containing more water & waterholes	Distance to water influences site use of large carnivores (Kittle et al., 2016)	(+) During the dry season, large carnivores are more likely to use areas near water sources (Valeix et al., 2010)	This study
	Dist_Road	Distance to the nearest road (km)	Large carnivores are affected by the presence of roads & vehicle tracks (Tanwar et al., 2021)	(+) Large carnivores favour roads for travel (Stander, 1998)	This study
	Dist_Edge	Distance to the edge of the National Park (km)	Distance to the edge of the protected area affects carnivore species (Murcia, 1995)	(+) Illegal activities such as hunting are often carried out by communities around national parks & decrease with the distance to the edge of the park. Therefore, large carnivores' site use should increase with the distance to the edge (Woodroffe & Ginsberg, 1998)	This study

TABLE 1 (*Cont.*)

Process	Covariates	Description	Hypotheses	Predicted sign of influence	Source of the data
	RAI of sympatric species (i.e. RAI_Leopard, RAI_Lion, RAI_Hyaena, RAI_Wild_dog)	Relative abundance index for each of the sympatric large carnivore	Interactions between sympatric carnivores affect their site use (Creel et al., 2001)	(−) Higher local abundance of sympatric carnivores may increase competition & decrease subordinate species' site use (Sarmento et al., 2011); (+) higher local abundance of sympatric carnivores may increase scavenging opportunities &/or dominant relationships with other carnivores (Swanson et al., 2014)	This study

power if $r > 0.6$ (Burnham et al., 2002). We followed a two-step procedure to select covariates that best explained model heterogeneity. Firstly, we modelled the influence of four covariates on ρ (effort, presence of leopard, presence of lion and presence of African wild dog) whilst keeping ψ constant. Then, we modelled the influence of nine covariates on ψ (distance to the Gambian River, distance to the Niokolo River, distance to the nearest river, distance to the nearest road, distance to the edge of the Park and the RAIs of each of the four sympatric large carnivores) whilst keeping detection constant (Strampelli et al., 2022). We ranked models using the Akaike information criterion corrected for small samples (AICc; Burnham et al., 2002), and we considered models with ΔAICc < 2 to be equally plausible. Finally, we assessed the goodness of fit of each top model based on Pearson's χ^2 test (MacKenzie & Bailey, 2004). Values of the overdispersion parameter $\hat{c} > 1$ were interpreted as overdispersion and $\hat{c} > 4$ as a lack of fit, with $\hat{c}$ values near 1 representing models with the best fit (Mazerolle, 2020).

Daily activity patterns We used a kernel density function to analyse timestamp data from independent capture events of each of the four carnivore species (Meredith & Ridout, 2024), to determine the extent of their temporal activity overlap. Non-parametric coefficient of overlap values (Δ_4) range from 0 (no overlap) to 1 (uniformly distributed and 100% overlap). We followed previous recommendations (Ridout & Linkie, 2009) for the choice of operators and worked with Δ_4 when samples were larger than 50 observations and Δ_1 otherwise. We generated 1,000 bootstrap estimates for each comparison to extract confidence intervals (Schmid & Schmidt, 2006). We considered the overlap to be low when $\Delta_x \leq 0.50$, moderate when $0.50 < \Delta_x \leq 0.75$ and high when $0.75 < \Delta_x \leq 1.00$ (Monterroso et al., 2014). Temporal overlap was calculated using the *R* package *overlap* (Meredith & Ridout, 2024).

Results

Camera-trap data

Six cameras experienced substantial data loss (primarily because of human interference, destruction or software malfunction) and thus did not contribute any data. The final dataset comprised a total of 121,282 images from 11,082 trap-days, of which 26% (n = 31,845) were blank (no species recorded) and 59% (n = 70,991) showed wild mammals (40 species; Supplementary Table 2). The most frequently detected large carnivore was the spotted hyaena (453 images, of which 278 were independent images), followed by leopard (168 images, 106 independent), lion (165 images, 59 independent) and African wild dog (114 images, 22 independent).

Data analyses

Relative abundance index and non-metric dimensional scaling analysis Computation of the nMDS resulted in a stress value of 0.09, suggesting that the representation was a good fit for the data. All large carnivores were widely spread in the low dimensional space (Fig. 2), indicating a strong dissimilarity between them. Large carnivores were mostly differentiated through the horizontal axis (MDS1), but lions and African wild dogs were also separated through the vertical axis (MDS2). Only four covariates were significant ($P < 0.05$) and were therefore represented. The Spearman test of correlation showed a significant correlation ($\hat{c} = 0.75$) between the distance to the Niokolo River and distance to the nearest river. Consequently, the distance to the

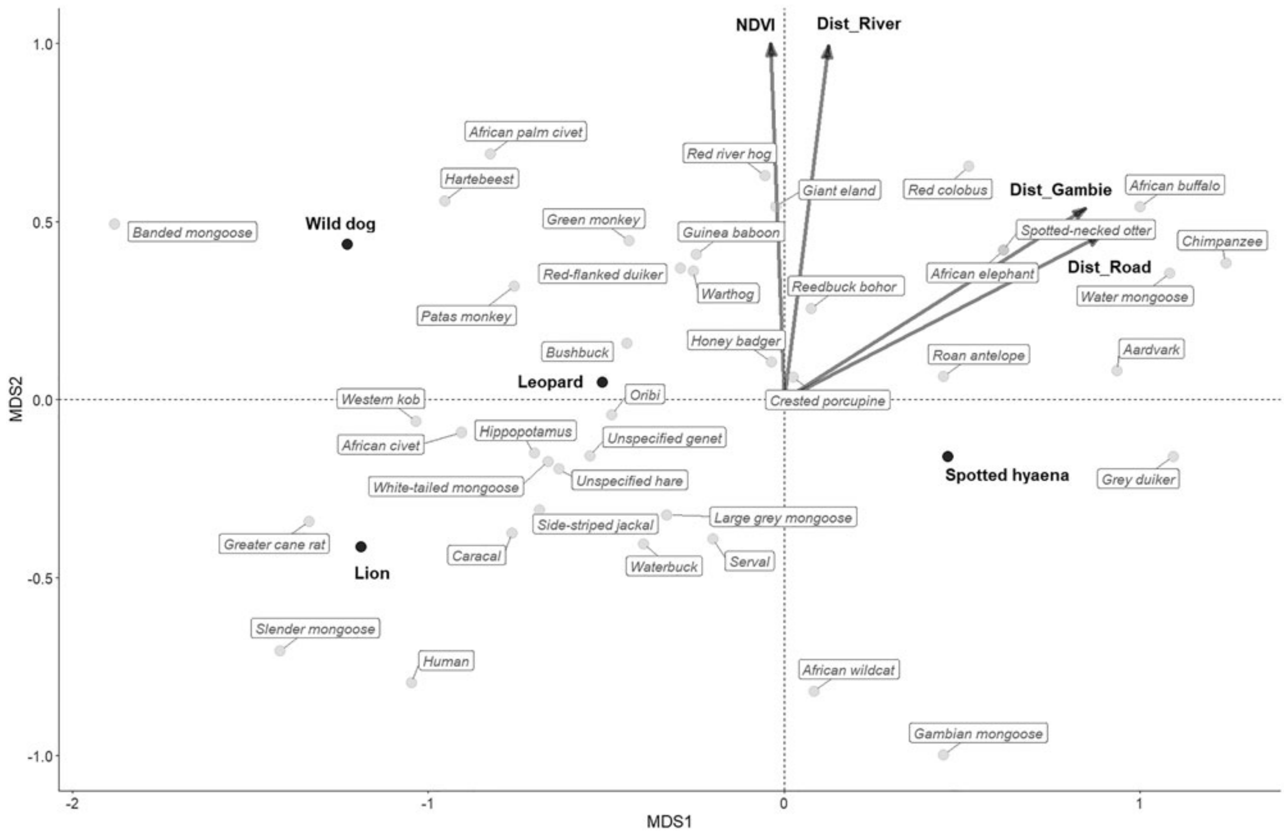

FIG. 2 Non-metric dimensional scaling plot representing the pairwise dissimilarities between the four species of large carnivores (West African lion *Panthera leo leo*, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta* and wild dog *Lycaon pictus*) and other mammal species detected during the camera-trap survey in Niokolo-Koba National Park during the dry season (March–June) of 2021. The scientific names of the other species are listed in Supplementary Table 2. MDS, metric dimensional scale; NDVI, normalized difference vegetation index.

Niokolo River was removed from further analyses. The best covariate was the distance to the nearest road, contributing slightly more to the MDS1 axis than to the other axis ($R^2 = 0.29$, MDS1 = 0.78, MDS2 = 0.62). Distance to the main rivers of the National Park ($R^2 = 0.22$, MDS1 = 0.01, MDS2 = 0.99) and normalized difference vegetation index (NDVI; $R^2 = 0.15$, MDS1 = −0.09, MDS2 = 0.99) were both strongly associated with MDS2. Distance to the Gambian River was the weakest of the significant covariates ($R^2 = 0.06$, MDS1 = 0.93, MDS2 = 0.36). Lion RAI was negatively related to the distance to the nearest road and the Gambian River, and to NDVI (Fig. 2). Leopard RAI was positively associated with NDVI, and wild dog RAI was positively associated with NDVI and distance to the nearest river. Finally, the representation of spotted hyaena in the nMDS was near zero, indicating almost no influence of covariates.

Occupancy Spotted hyaenas had the highest predicted detection probability ($\rho = 0.31$; range 0.25–0.38), followed by lions ($\rho = 0.27$; range 0.20–0.36), leopards ($\rho = 0.19$; range 0.14–0.25) and African wild dogs ($\rho = 0.12$; range 0.05–0.27). Spotted hyaenas also had the highest probability of site use ($\psi = 0.79$; range 0.59–0.90), followed by leopards ($\psi = 0.60$; range 0.43–0.76), lions ($\psi = 0.26$; range 0.13–0.46) and African wild dogs ($\psi = 0.21$; range 0.03–0.70; Figs 3 & 4). The top-ranked model for the spotted hyaena (Table 2) included all four detection covariates and two covariates influencing site use, namely NDVI (negative association) and leopard RAI (positive association). The presence of spotted hyaenas influenced the detection of leopards, and only the distance to the nearest road influenced the probability of site use for leopards (Table 2). We included no detection covariates in the best models for lion and African wild dog. Distance to the Gambian River was the most important covariate affecting lion site use, amongst two other covariates (NDVI and leopard RAI). African wild dog site use was negatively associated with the RAIs of the two felids (Table 2). The results of the goodness-of-fit tests for the best models indicated no evidence of a lack of fit for spotted hyaena, leopard and wild dog (Supplementary Table 1). By contrast, the

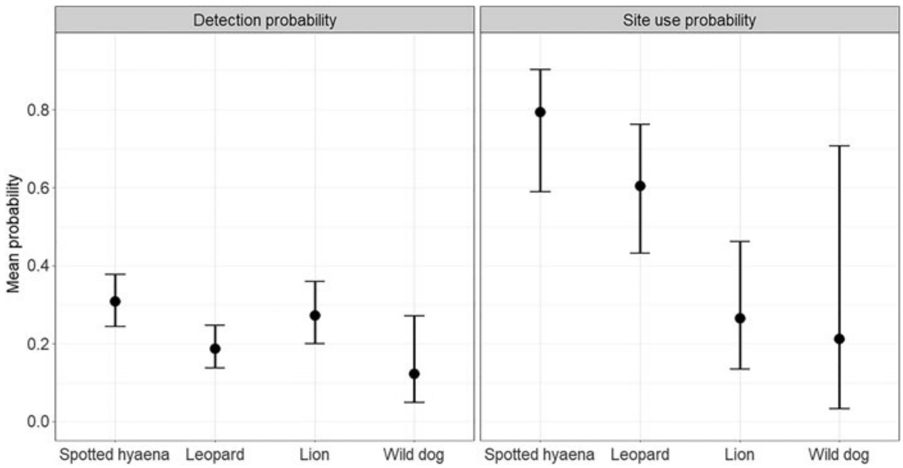

FIG. 3 Mean probabilities of (a) detection and (b) site use for the four sympatric large carnivore species in the study area in Niokolo-Koba National Park, Senegal, during the dry season of 2021. Error bars represent the standard errors.

goodness-of-fit test result for the top lion model indicated overdispersion of the data ($\hat{c}$ = 2.17).

Daily activity patterns Spotted hyaenas had the highest percentage of independent detections at night-time (96%; n = 221), followed by leopards (92%; n = 91), lions (78%; n = 39) and African wild dogs (24%; n = 4). Leopards had a strong crepuscular bimodal activity (Fig. 5), with a clear morning peak (at c. 05.30) and an evening peak (at c. 20.10). Spotted hyaenas were largely nocturnal, being active between 19.30 and 09.00. Lions were less restricted to nocturnal activities, with records from 15.10 to 10.00. African wild dogs were cathemeral, with a bimodal activity pattern occurring at night (peak at 03.30) and during the day (more significant peak at 08.30). Activity patterns of lions, spotted hyaenas and leopards strongly overlapped, whereas African wild dogs displayed little overlap with all of the other species (Fig. 5). Leopards and spotted hyaenas showed the strongest overlap of their activity patterns, whereas spotted hyaenas and African wild dogs had the least overlap (Table 3).

Discussion

Our study is the first to focus on large carnivores in Niokolo-Koba National Park, Senegal, and is one of few such studies in West Africa. We found that the Park hosts four species of threatened large carnivores. We highlight some important drivers of their site use, as well as spatial and temporal aspects of their ecology that allow them to coexist.

In line with their generalist behaviour (Watts & Holekamp, 2007; Athreya et al., 2013), both leopards and spotted hyaenas had high occurrences across the study area. Both species appeared to co-occur spatially and temporally, corroborating findings of earlier studies (Davis et al., 2021). Leopard detection probability was positively related to spotted hyaena presence, whereas spotted hyaena detection and site use probability were positively linked to

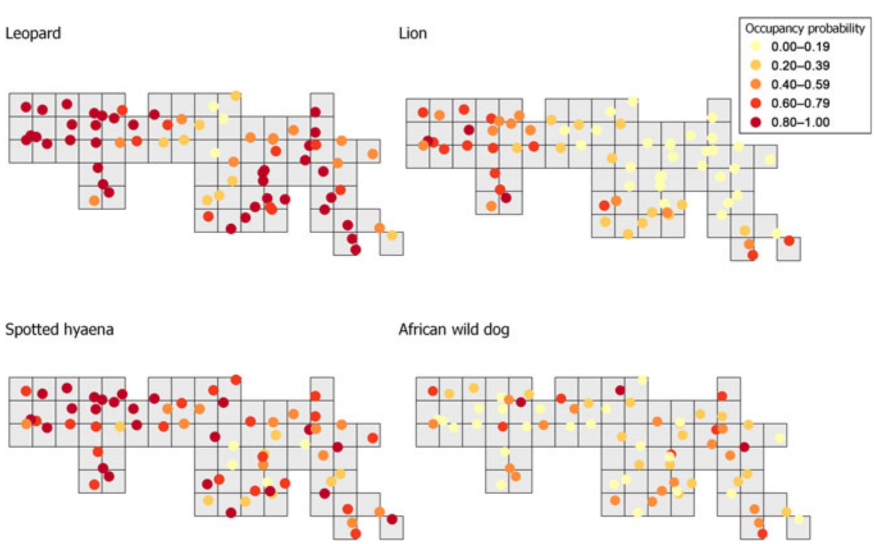

FIG. 4 Site use (occupancy) probabilities for the four large carnivore species at the camera-trap station level in the study area in Niokolo-Koba National Park, Senegal, during the dry season of 2021.

TABLE 2 Parameter estimates, standard errors and P-values for detection probability (ρ) and site use (ψ) for the best model for each species of large carnivore surveyed in Niokolo-Koba National Park, Senegal, during the dry season of 2021.

Species		Parameters[1]	Estimate ± SE	P
Spotted hyaena	ρ	Effort	0.108 ± 0.041	7.87×10^{-3}
		Leopard	0.618 ± 0.253	1.48×10^{-2}
		Lion	0.606 ± 0.350	8.32×10^{-2}
		Wild dog	1.286 ± 0.606	3.37×10^{-2}
	ψ	NDVI	−0.999 ± 0.388	1.01×10^{-2}
		RAI_Leopard	0.975 ± 0.534	6.80×10^{-2}
Leopard	ρ	Hyaena	0.641 ± 0.260	1.39×10^{-2}
	ψ	Dist_Road	−1.083 ± 0.363	0.002
Lion	ψ	NDVI	−0.910 ± 0.418	0.029
		Dist_Gambie	−1.006 ± 0.443	0.023
		RAI_Leopard	0.494 ± 0.339	0.145
Wild dog	ψ	Dist_Road	−0.743 ± 0.645	0.249
		RAI_Hyaena	1.542 ± 0.765	0.043
		RAI_Lion	−2.856 ± 2.292	0.212
		RAI_Leopard	−0.693 ± 0.891	0.437

[1]NDVI, normalized difference vegetation index; RAI, relative abundance index.

leopard presence and RAI, respectively (Table 2). Despite their hunting skills (Kruuk, 1972), spotted hyaenas are well-known for their kleptoparasitism (Périquet et al., 2015), which could explain the positive association of their detection with the presence of leopards, lions and African wild dogs (Table 2). However, despite evidence of positive spatio-temporal interactions, the occupancy probabilities of leopards and spotted hyaenas were driven by different habitat characteristics. Our results suggest that spotted hyaenas preferred open, less vegetated habitats (probably related to their prey searching behaviour; Watts & Holekamp, 2007), whereas leopards were more likely to occur on roads, corroborating findings of earlier studies (Mann et al., 2014; Cusack et al., 2015).

Lion site use was concentrated in the core area of the Park, close to the Gambian River. Prior research found that lions tend to use areas near water sources during the dry season, probably because of the higher prey biomass and water availability in these areas (Valeix et al., 2010; Kittle et al., 2016). This relationship between prey biomass and lion site use has been observed previously in Pendjari National Park (Henschel et al., 2016). Poachers often target areas near permanent water, with most such poaching activity occurring during the dry season when surrounding crop fields lie fallow and people are thus not occupied with farming work, and because accessibility of the Park and visibility across the terrain are improved during this period relative to the wet season (Compaore et al., 2020). These findings emphasize the need to focus anti-poaching patrols around the Gambian River and other riverine areas in the Park during the dry season to better protect lions and their prey species. However, although these results were corroborated by the nMDS analyses (Fig. 2), limited data availability and poor model fit hinder further interpretation, and we recommend further research on lion occupancy in the Park.

African wild dogs are the smallest and most subordinate species amongst the four large carnivores in Niokolo-Koba National Park (Darnell et al., 2014). We showed that they had a low overall site use probability that was negatively associated with distance to roads and leopard and lion RAIs, a finding that is widely attested to in the literature (Darnell et al., 2014; Henschel et al., 2020; Madsen & Broekhuis, 2020). The low detection rates for both lions and African wild dogs may be linked to their low densities in the Park, resulting in large confidence intervals for site use, overdispersion for the lion model and potentially biased activity patterns (Ridout & Linkie, 2009). However, our results match the literature (Saleni et al., 2007; Darnell et al., 2014) and are the first to be published for these emblematic species in Niokolo-Koba National Park.

Providing baseline information on the spatio-temporal ecology of threatened large carnivores is crucial to identify key habitats that are important for their long-term survival, notably for the species with low site use (lion and African wild dog) in a context of recovery; ongoing surveys suggest that the lion population has doubled since the first survey conducted in the Park in 2011 (P. Henschel, pers. comm., 2021). We show that leveraging data from camera trapping designed for a single species (i.e. leopard) can be used successfully to explore the spatio-temporal patterns of so-called bycatch (i.e. non-target) species. It is important to note that when using such data in the study of wide-ranging species, particularly those with large home ranges that encompass multiple camera-trap stations, there is an increased probability of spatial autocorrelation (Guélat & Kéry, 2018). Therefore, it is important to exercise caution when interpreting our results. Furthermore, the size of the Park and limited accessibility by road presented logistical challenges, so we focused on the core area, which is better protected and where carnivores are most likely to be detected. Thus, our results only apply to the study area and should not be extrapolated to the entire Niokolo-Koba National Park.

In the present context of lion recovery, it is crucial to monitor interactions between species. Co-occupancy models (Rota et al., 2016) are generally recommended for this purpose, but because of data scarcity (MacKenzie et al., 2002) we opted to use single-species occupancy models to compare our results to the existing literature (Everatt et al., 2014; Spencer et al., 2020; Broekhuis et al., 2022).

The results of our study provide insights into the ecological needs of the large carnivores in the study area, enabling authorities to prioritize anti-poaching efforts within the Park. Specifically, we recommend strengthening anti-poaching patrols around waterholes and the Gambian

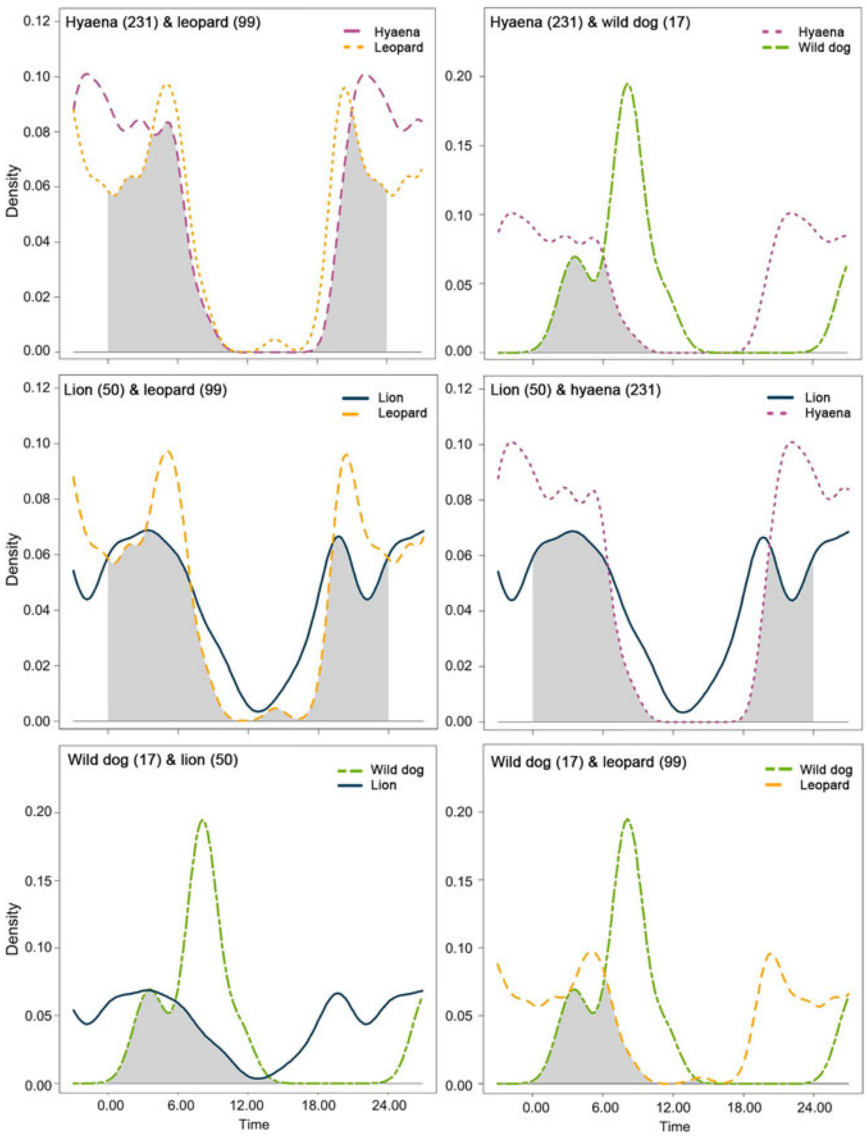

FIG. 5 Activity patterns and overlaps between the four large carnivore species in Niokolo-Koba National Park, Senegal, during the dry season of 2021 (Table 3), with the number of independent images captured for each species shown in parentheses.

TABLE 3 Activity pattern overlaps between each pair of large carnivores (with confidence intervals in parentheses) in Niokolo-Koba National Park, Senegal, during the dry season of 2021 (Fig. 5).

	Leopard	Lion	Wild dog
Spotted hyaena	$\Delta_4 = 0.84$ (0.75–0.92)	$\Delta_4 = 0.75$ (0.63–0.85)	$\Delta_1 = 0.36$ (0.19–0.51)
Leopard		$\Delta_4 = 0.83$ (0.70–0.92)	$\Delta_4 = 0.41$ (0.21–0.54)
Lion			$\Delta_4 = 0.44$ (0.27–0.61)

River during the dry season. Collecting and analysing data on patrols and illegal activities within the Park (Burton et al., 2012; Everatt et al., 2015) could further help to determine the impact of patrols and where they should be focused.

It is crucial to prioritize the conservation of large carnivores in West Africa, yet this is hampered by a lack of knowledge regarding their local ecology. Robust baseline data are needed on the population sizes, distributions and ecological roles of large carnivores in this region, as well as the potential threats that they face. This information could then be used to develop targeted conservation strategies and construct successful recovery programmes for carnivores, their prey and their habitats (IUCN SSC, 2012). Given the potential ecological, cultural and economic benefits of conserving large carnivores (Ripple et al., 2014; Gebresenbet et al., 2018), there is an urgent need for more research on these species in West Africa.

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Conflicts of interest None.

Ethical standards This study abided by the *Oryx* guidelines on ethical standards and followed strict guidelines provided by Panthera. The fieldwork and camera deployment are conducted as part of a long-term agreement (Memorandum of Understanding 2017 and 2023) between the Direction des Parcs Nationaux of Senegal and Panthera within the Niokolo-Koba National Park.

Data availability Data are available from the corresponding author upon reasonable request.

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