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Cost effective assessment of human and habitat factors essential for critically endangered lions in West Africa

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Conflict with humans and habitat fragmentation are major threats to large carnivores in Africa, and transboundary protected areas may ease some of the space requirements for individual countries. The W-Arly-Pendjari complex (WAP) in West Africa sits across Benin, Burkina Faso and Niger and is the last regional stronghold for many species, including the regionally critically endangered lion *Panthera leo*. However, variation in monitoring efforts, limited resources and imperfect coordination confound their conservation.

We demonstrate a cost-effective and scalable design to effectively identify the landscape-level factors that limit the distribution and abundance of large carnivores and their preferred prey. We used an occupancy framework for a combination of spoor and line transect data. We found a high degree of variation in prey density, strongly related to evapotranspiration. Lion occupancy increased in areas of high riparian forest cover, far from hunting concessions and with more pastoralist activities. Hyaena occupancy was inversely related to anthropogenic pressures, and positively related to dense vegetation and overall prey density. We discuss conservation challenges such as illegal hunting and grazing in the context of transboundary management.

Keywords: apex predator occupancy, habitat, hunting, pastoralism, Spotted hyaena, W-Arly-Pendjari, West African lion

Large carnivores are keystone species and their extirpation can have cascading effects across ecosystems (Estes et al. 2011, Ripple et al. 2014). In Africa, declines have been described for lion *Panthera leo*, cheetah *Acinonyx jubatus* (Durant et al. 2017), leopard *P. pardus* (Jacobson et al. 2016), wild dog *Lycaon pictus* (Nicholson et al. 2020) and spotted hyaena *Crocuta crocuta* (Somerville 2021). These species were all present in West Africa's largest and most intact savannah ecosystem, the W-Arly-Pendjari Ecosystem (WAP), but wild dog has apparently been extirpated and leopard and cheetah occur at low densities (Henschel et al. 2016). Declines in wildlife are acute across West Africa (Mallon et al. 2015) and especially large carnivores are under continued threat of local extirpation (Brugiere et al. 2015, Bauer et al. 2020), leading to a critically endangered status of the lion (Henschel et al. 2014). In fact, the WAP hosts 90% of the region's lions and is an important stronghold for the northern subspecies *P. leo leo* (Bertola et al. 2016).

Large carnivores have large ranges and many populations extend across national boundaries; lion and leopard were recently listed under the international Convention on Migratory Species (Hodgetts et al. 2018). The WAP extends across Benin, Burkina Faso and Niger. Concerns have been expressed about the potential negative consequences on carnivore conservation of the diverse management philosophies across the WAP's international boundaries (Sogbohossou et al. 2014, Henschel et al. 2016, Mills et al. 2020). In such circumstances, effective collaboration across international boundaries is fundamental to the conservation of large carnivores (Plumptre et al. 2007, Hodgetts et al. 2018). Without coordinated transboundary management efforts across the WAP, the long term conservation of both lions

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and hyenas will be hampered (Harris et al. 2019). Therefore, a robust transboundary monitoring protocol is vital to guide and evaluate the management actions for large carnivores.

Large carnivores are hard to count, and monitoring is therefore costly (Elliot and Gopalaswamy 2017, Braczkowski et al. 2020, Dröge et al. 2020). Additionally, financial resource allocation to conservation and lack of local capacity among the three different nations in the WAP are factors associated with variation in monitoring effort. For instance, WAP countries not only have unequal sizes of the complex but the management budget per km^2 is also vastly different, e.g. Niger: US$5 km^{-2} year^{-1}; Benin: US$627 km^{-2} year^{-1} (Henschel et al. 2016). As a result, even baseline data on carnivore ecology are lacking for certain parts of this system; certainly at the time of our fieldwork which predates the 2-year University of Michigan study in Burkina Faso and Niger (Harris et al. 2019). Given the challenges of surveying large carnivore populations across a network of transboundary PAs, approaches to data collection must be not only expeditious but also cost-effective, sustainable and scalable. If monitoring schemes fail in any one of these respects, then they are unlikely to be adopted in any rigorous way (McComb et al. 2010).

Recognizing that this may not be achievable with abundance-based surveys, we offer insight and direction into data collection protocols, modeling techniques and collaborative strategies that can: 1) map the occurrence of carnivores and the relative abundance of their primary prey, 2) identify the landscape-level factors correlated with carnivore occurrence, 3) inform management on the influence of human activities on carnivore occupancy in the WAP complex and 4) inform transboundary strategies intending to conserve carnivore populations. Specifically, we test the hypothesis that lion and hyena respond to patterns in the presence of prey, people and livestock. Furthermore, we hypothesize that covariates include rainfall, evapotranspiration, habitat type, management type (e.g. with or without trophy hunting) and distance to water or to human settlement.

Via a proof of concept approach, we demonstrate how cost-effective solutions for multi-species monitoring can be validated in one country and then scaled up to other countries across transboundary PAs. Within this guiding framework, we make recommendations for how our results can inform progressive policies intended to conserve lions and spotted hyenas across transboundary areas in West Africa with implications for carnivore conservation more broadly.

Methods

Study area

The WAP extends over 27 000 km^2 across the border region of Benin (48.4%), Burkina Faso (40.3%) and Niger (11.3%), and comprises a network of national parks (54%), hunting concessions (43%) and wildlife reserves (3%; Fig. 1). Like most PAs in West Africa, the WAP is surrounded by areas of high human population density, with most people maintaining an agro-pastoral lifestyle. Livestock production is more prevalent than agriculture in

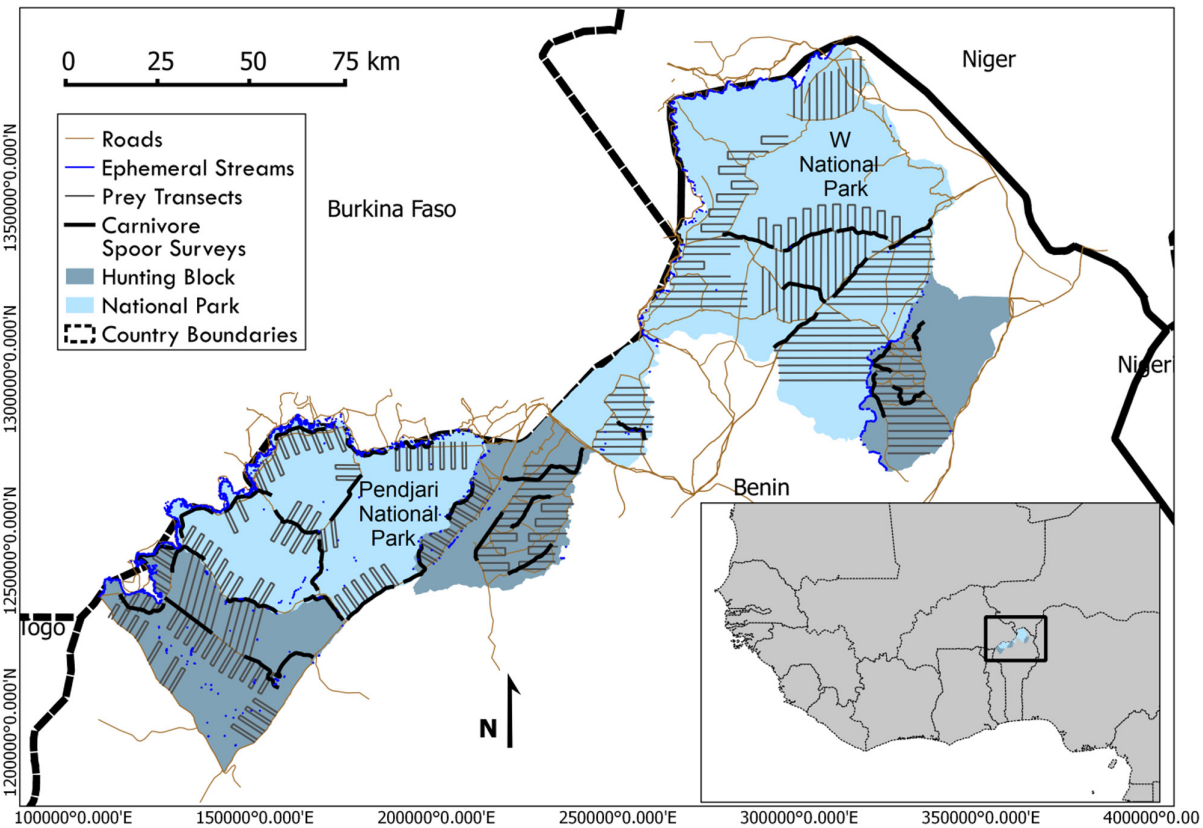


Figure 1. The distribution of carnivore spoor survey routes and primary prey line transects in the southern W-Arly-Pendjari complex of West Africa, (2013–2014).

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this arid savannah system given that the climate tends to be less-suited for crop cultivation. Livestock graze within the WAP particularly at the end of the dry season (February–May) during the seasonal migration of cattle by Fulani pastoralists exploiting available pastures and water resources (Baudron et al. 2009). In some parts of the WAP, livestock density is higher than that of wild ungulates (Bouché et al. 2012), which can exacerbate human–carnivore conflict.

Sub-standard equipment, limited funding, institutional and cultural differences and the need for transboundary coordination complicates the management of carnivore populations in the WAP. As a consequence, intensity of anti-poaching and livestock encroachment prevention patrols varies spatially. Limited funding available in Burkina Faso and Niger at the time of our fieldwork meant that we were able to deploy our experimental design only on the Benin side (16 480 km^2) of the WAP. Thus, our study area extends over two Benin management sectors; the eastern containing W National Park and the western containing Pendjari National Park (Fig. 1), with the western sector having an operational budget five times larger than the eastern one (Henschel et al. 2016).

Data collection

Lions and hyenas have high dietary overlap throughout their range (Hayward 2006). In the WAP, four ungulate prey species account for approximately 60% of lion diet (Sogbohossou et al. 2011); buffalo *Syncerus caffer*, roan antelope *Hippotragus equinus*, kob *Kobus kob* and warthog *Phacochoerus africanus*. Bohor reedbuck is abundant in the area but we did not include it as a preferred prey species since Sogbohossou (2011) found that it was present in only 2.1% of scats and contributed only 0.4% to diet biomass. Livestock are also an important component, but difficult to quantify as predator access to livestock varies in space and time due to semi-nomadic pastoralism. The rest of the lion's diet is composed of a wide variety of food items. In collaboration with Benin's Wildlife Authority we evaluated the relative habitat selection of these species as well as the spatial prevalence of anthropogenic disturbances to wildlife – namely illegal hunting and livestock grazing. We surveyed 509 line transects in the study area, each between 4.5 and 25.9 km long (12.9 ± 2.3 km; Fig. 1). Twenty-two teams of three members each walked these foot-transects in April 2013, always starting at around 7 a.m. When ungulates were detected, the teams recorded the number of individuals of each species encountered, and, using a Global Positioning System (GPS) receiver, the coordinates of that observation. Signs of illegal hunting recorded included snares, hunting camps, spent ammunition and direct sightings of hunters. Signs of livestock grazing included cattle tracks and direct sightings of livestock and herdsmen. Both sectors were divided into blocks of known areas. Using the Distance ver. 6.0 program (Buckland et al. 2015) we calculated the density of each prey species using the following formula: $D = \frac{n}{2\mu L}$ where n is the sampling size and L the total length of the transects and μ is the effective strip width.

We surveyed for lion and hyena spoor across the study area, a method that is efficient, cost-effective and scalable for studying large carnivore occurrence at the landscape level using occupancy models accounting for imperfect detection (Thorn et al. 2010). Evidence of carnivore spoor included scats and footprints. We divided our study area into eighty 200-km^2 grid cells, based on the average home range size (200 ± 141 km^2) of lions in this region (Sogbohossou et al. 2011), in view of the assumption of independent detections across survey sites in single-season occupancy models (Karanth et al. 2011, MacKenzie et al. 2017). Between March and April 2014, we surveyed these grid cells for spoor, driving 15-km sections of the dirt road network each morning with two experienced trackers on the front of the vehicle; details in Bouché et al. (2016). When carnivore spoor was detected, we identified the responsible species, recorded the coordinates and photographed the spoor; photographs were later independently evaluated to confirm the species identification. We also recorded the road substrate at 500 m intervals as it has been previously suggested to affect the probability of carnivore spoor detections (Funston et al. 2010).

Predictor variables

We fit binomial Resource Selection Functions (RSF) to predict the relative intensity of habitat use for each of the four primary prey species (buffalo, roan, kob, warthog). The RSF models compared used locations, at which prey species were detected, to randomly-generated available locations along the surveyed transects, where prey were not observed. The ratio of used to available locations was 1:4 as recommended in the literature (Boyce 2006, Millspaugh et al. 2019). We used distance to water, distance to human settlements, percent tree cover (VCF), rainfall, evapotranspiration and proportion of habitat type as possible covariates in the RSFs (Supporting information). Each covariate was incorporated in the RSFs at the scale of 500 m, by averaging all values available for that covariate at a 500 m radius. Prior to model fitting, we assessed the covariates for collinearity and excluded the least informative from each pair of covariates ($|r| > 0.7$), as determined from the performance of their univariate models (Menard 2002) (Supporting information). We considered models with all remaining covariate combinations and ranked them using Akaike information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002). We used the parameter estimates from the model with the lowest AICc value to develop predictive maps of the relative intensity of habitat use across the WAP, which can serve as a proxy for prey availability. In addition to developing species-specific RSFs for consideration in carnivore occurrence models, we also considered the composite effect of all primary prey species hypothesizing that lions and spotted hyenas may respond to spatial patterns of prey availability at an aggregate level (Petrunenko et al. 2016).

With the same RSF procedures as for prey species, we used the data on evidence of illegal hunting and livestock grazing from the line transect surveys to predict the relative probability of these disturbances across our study area. We used the top models' covariate coefficients to estimate the relative probability of illegal hunting and illegal grazing

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across the WAP, and considered them as carnivore occupancy model covariates.

We used the statistical software R ver. 2.14 and the MuMIn R package ver. 1.10 (MuMIn 2016). Each covariate was averaged at the survey grid level (200 km^2) for inclusion in the carnivore occupancy models.

Based on a priori rationale, we considered a set of environmental/anthropogenic covariates that could affect the occurrence of carnivores. We developed these covariates as geospatial layers using QGIS ver. 2.2/GRASS ver. 6.4.3 (see the Supporting information for each variable's data source, resolution and development steps). Specifically, we calculated the Euclidean distance to: a) nearest dry season water bodies (water holes or major rivers), as several species of lion and hyena prey are water-dependent (Valeix et al. 2010), b) nearest human settlement, as a proxy of human disturbance and c) nearest hunting reserve, as protection level is different from that in NP (inside hunting reserves, values were negative). We created habitat layers for riparian forest, grassland, shrub savannah and woodland by reclassifying remotely-sensed landcover data provided by the Panthera Foundation's Landscape Lab (30 m resolution; accuracy 84.2% across all classes; Supporting information). Using a moving window analysis in GRASS, we generated final grid layers for each habitat type whose cells reflected the proportion of that habitat within a circular area of 30 arc (930 m) radius centred on any given focal cell.

The different road substrate types recorded during the carnivore spoor surveys were assigned a track suitability value based on a scale of 1 'ideal' (e.g. fine sand) to 4 'inappropriate' (e.g. exposed rock). We considered as a detection probability covariate in the carnivore occupancy models the mean of all substrate values per road segment.

Carnivore occupancy models

We fit likelihood-based single-season occupancy models to the carnivore spoor survey data to estimate the probability of lion and hyena occurrence (ψ) in the WAP accounting for imperfect detection probability (p), following published examples (MacKenzie et al. 2002, 2017, Hines et al. 2010). Since the duration of the spoor survey period was two months and within a single season (dry), we consider that the population closure assumption of single-season models was met. Occupancy analysis requires multiple surveys to estimate the detection probability of a species. Since all roads were surveyed only once, we split each 15-km road in five 3-km segments, using the pooled spoor observations within each segment (0 absence/1 presence) as spatial survey replicates of the encompassing grid cell (site); a cost-effective and practical survey design that is used for large carnivore studies (Karanth 2011, Henschel et al. 2016). A caveat of the design is that it can introduce spatial dependence between spoor sign detections, as the detection of a species in adjacent segments may be correlated if a carnivore was moving along the surveyed road. To test for such Markovian dependence, we compared single-season occupancy models that assume spatial independence (MacKenzie et al. 2002) to models which account for spatial dependence (Hines et al. 2010). The spatial dependence model adds three additional parameters, θ_0, θ_1 and $\theta_0\pi$ where θ_0 is the species' detection probability at a road segment given non-detection in the previous one, θ_1 is detection probability at a segment given detection in the previous one, and $\theta_0\pi$ is detection probability at the transect's first segment when we do not know whether the preceding (unsurveyed) segment would have resulted in a sign presence or not. For both species, the non-Markovian (MacKenzie et al. 2002) single season models performed better than the Hines et al. (2010) spatial dependence models (Supporting information). So, we assumed spatial independence of detections in adjacent 3-km segments and considered models that accounted for heterogeneity in detection and occupancy (MacKenzie et al. 2002). We fit all models using the software PRESENCE ver. 8.4 (Hines 2006) and ranked candidate models using AICc (Burnham and Anderson 2002).

We standardized all continuous covariates using a normal z-transformation to stabilize the numerical optimization algorithm of the models (Fiske and Chandler 2011), and checked for collinearity among covariate pairs, retaining in cases of correlation $|r| > 0.7$ only the most informative covariate as determined from the performance of their univariate models (Menard 2002). This way, we reduced the final set of occupancy covariates considered in multivariate models, decreasing the risk of model overfitting and excessive model testing which can lead to the inclusion of spurious variables (Burnham and Anderson 2002).

We used a two-step modelling approach in which we first considered the variables hypothesized to affect a species' detection probability at site level – namely WAP sector (Sec) and road substrate (Sub) – while keeping constant across sites the state process (occupancy) component of the hierarchical model (Long et al. 2011). Sector was considered as a detection covariate to see if the management philosophy in eastern and western WAP, respectively, has resulted in differential use of roads by carnivores and hence a spatial variation in the species' detection probability. The second step was to use the detection variables of the first step's best model as a fixed covariate set in models with occupancy covariates. We considered candidate models representing all possible occupancy covariate combinations as equally likely and biologically plausible to describe the underlying ecological process resulting in the study area's site-level occupancy probabilities (Long et al. 2011). We used information-theoretic approaches for model selection of candidate models (Burnham and Anderson 2002), and ranked all models using AICc values, and considered models with $\Delta AICc \leq 2$ as supported by our data. We tested the effect among the covariates in the top model by examining whether the 95% confidence intervals of the beta coefficients contained zero or not (Zeller et al. 2011). We tested for goodness of fit of each species' top model with a Mackenzie–Bailey's goodness of fit test, using 10 000 parametric bootstraps. In the event that the goodness of fit test showed evidence of data overdispersion (i.e. $\hat{c} > 1$), we used the quasi-likelihood AICc (QAICc) to inflate a model's standard errors of covariate beta coefficients and for model selection instead of AICc (MacKenzie and Bailey 2004). We then generated predictive maps depicting lion and hyena occupancy in our study area from these top models, using occupancy estimates conditional on the detection/non-detection data for surveyed cells and unconditional estimates for unsurveyed ones (Midlane et al. 2014).

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Finally, using methods described in Guillera-Arroita and Lahoz-Monfort (2012) we calculated the power of our survey design to detect significant ($\alpha \leq 0.05$) differences in occupancy of lions and hyenas in future surveys, given the current survey effort (number of sites and transect segments) and the average landscape-level estimates of occupancy and detection probability reported in this study. Dröge et al. (2020) proposed 30% as a useful threshold for population change in view of criteria commonly used to assess threat status. Based on these findings, we developed recommendations on the number of sites that would need to be surveyed across the WAP in Benin, Burkina Faso and Niger to reliably (80% probability) detect a 30% decrease in the overall occupancy of the two carnivores.

Results

Prey species

We covered a total cumulative foot transect distance of 3193 km covering over 54 carnivore survey grid cells as part of our prey surveys. In total, we recorded 968 detections of 11 medium to large ungulate species (Supporting information). The most-frequently encountered primary prey species were buffalo (n = 65 encounters, resulting density 9.65 individuals km^{-2}) and kob (n = 116 encounters, 5.91 individuals km^{-2}) in the Pendjari NP sector and warthog (n = 55 encounters, 1 individual km^{-2}) and roan antelope (n = 53 encounters, 1 individual/2 km^2) in the 'W' NP sector. The encounter rate of all prey species except waterbuck and western topi were higher in the western sector (Pendjari NP). In the eastern sector (W NP), the most frequently encountered prey species were warthog and roan. Large carnivores were not detected.

The top performing RSF models (ΔAIC < 2) of each of the four primary prey species included as covariates evapotranspiration, percent tree cover (except roan), percent of riparian forest habitat (except buffalo), grassland, and shrub savannah, rainfall and distance to human settlements, hunting concessions and water (except roan; Supporting information). Evapotranspiration was the only parameter present in all four species' top models used to calculate the composite primary prey RSF estimate. This covariate had a significant (95% CI range of beta coefficient not including zero) and consistently positive relation to all four prey species' probability of relative intensity of habitat use (Supporting information). All species with top models including distance from human settlements showed an increased selection for areas further away from human settlements (Table 1). Furthermore, buffalo also showed increased selection for areas further away from hunting reserves (Table 1). Although values were not high, all species showed some selection for areas close to permanent water sources (Table 1). Areas with higher tree cover were selected by buffalo and kob (Table 1).

The predicted relative intensity of habitat use for buffalo, kob and roan was higher in the western (0.25 ± 0.13; 0.20 ± 0.18; 0.21 ± 0.05) than the eastern sector (0.07 ± 0.04; 0.06 ± 0.01; 0.16 ± 0.04), where as it did not differ significantly between sectors for the warthog (western: 0.17 ± 0.09; eastern: 0.15 ± 0.05; estimate ± SE). Across the WAP, buffalo and kob showed a more pronounced and clustered intensity of habitat use compared to a more evenly distributed and variable intensity of habitat use predicted for warthog and roan (Supporting information).

Human activities

We recorded evidence of human activity in 82 (16%) of the transects surveyed (162 illegal hunting signs; 94 illegal grazing signs). The predicted relative hunting intensity was similar across WAP sectors (western: 0.21 ± 0.05; eastern: 0.23 ± 0.30) (Supporting information). There was a positive relationship of hunting with riparian forest (0.25 ± 0.13) and distance to interior roads (0.24 ± 0.11), reflecting a tendency of poachers to avoid roads where they might be detected by patrols. The predicted relative grazing intensity was higher in the eastern (0.30 ± 0.04) than the western sector (0.09 ± 0.04; Supporting information which is opposite to what was estimated for the relative intensity of habitat use of most prey species. There was a significant positive relationship of grazing with riparian forest habitat and distance to ephemeral streams and waterholes, and a significant negative relationship with distance to human settlements.

Table 1. The top modelcoefficients (β) and standard errors (SE) describing the predicted relative intensity of habitat use for buffalo *Syncerus caffer*, roan antelope *Hyppotragus equinus*, kob *Kobus kob* and warthog *Phacochoerus africanus* in the southern W-Arly-Pendjari complex, West Africa (2013–2014). The Rel. column represents the relative importance of each covariate and was calculated as the sum of 0.95 AICc weights of all models containing the covariates. *Cover*: tree cover (%); *Dhu*: distance to hunting concessions; *Fores*: proportion riparian forest habitat; *Grass*: proportion grassland habitat; *Pet*: potential evapo-transpiration (mm); *Rain*: rainfall (mm); *Sav*: proportion shrub savannah habitat; *Dset*: distance to human settlements (m); *Dwa*: distance to water (m).

	Buffalo			Roan			Kob			Warthog		
Parameters	β	SE	Rel.	B	SE	Rel.	β	SE	Rel.	β	SE	Rel.
Intercept	−1.785	0.177		−1.039	0.13		−2.397	0.198		−1.547	0.127	
Cover	0.631	0.202	1	–	–	–	0.370	0.174	1	–	–	–
Fores	–	–	–	0.281	0.119	0.86	−0.591	0.182	1	–	–	–
Grass	–	–	–	–	–	–	−0.221	0.143	0.74	0.186	0.097	0.9
Dhu	0.63	0.241	1	–	–	–	−0.976	0.268	1	–	–	–
Pet	0.66	0.183	1	0.340	0.117	1	2.03	0.201	1	0.427	0.145	1
Rain	0.85	0.240	1	–	–	–	−0.775	0.269	1	−0.326	0.149	1
Sav	–	–	–	0.236	0.124	0.75	−0.593	0.158	1	–	–	–
Dset	0.34	0.24	1	–	–	–	0.298	0.174	0.78	0.246	0.13	0.9
Dwa	−0.35	0.24	0.64	–	–	–	–	–	–	−0.28	0.158	0.89

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Carnivores

We surveyed for carnivore spoor across a total of 540 km of roads. Within this network we surveyed 36 road segments covering 42 of the 80 200-km^2 grid cells (mean 10.07 ± 5.57 km/grid cell) in the study area. We recorded a total of 85 lion spoor and 131 hyena spoor. Naïve occupancy was 54% (23 cells) for lions and 74% (31 cells) for hyenas. Road substrate was the most informative covariate for modelling heterogeneity in detection probability of both carnivores and was therefore included in all occupancy models. The detection probability of the baseline ψ(.)p(.) model was higher for hyenas (0.77 ± 0.07) than lions (0.61 ± 0.09).

According to the top model, lion occurrence was greatest in areas of high riparian forest cover (> 25–30%) located away from hunting concessions (> 10 km; Table 2, Fig. 2, 3a–b). The top model had a good fit (p = 0.28) and there was little evidence of data overdispersion (c-hat = 1.08). While illegal grazing did not feature in the final multivariate models, it was the parameter with the highest ΔAICc value among the univariate models we run in the first step of the analysis, showing a positive relation with lion occupancy (Supporting information). Using conditional occupancy estimates for surveyed grid cells and unconditional estimates for unsurveyed cells, the predicted occupancy probability for lions across the WAP was spatially variable across the landscape (0.69 ± 0.30), with the eastern sector having more areas of uniformly high probability of lion occurrence (Fig. 2).

According to the top hyena model, which also had a good overall fit (p = 0.48) and no evidence of overdispersion (c-hat = 0.99), the species' occurrence was substantially lower in areas of high illegal hunting intensity (but not affected by proximity to hunting reserves, suggesting rather an indirect effect of hyenas not selecting areas with very large prey, in contrast to poachers and lions), approaching zero when probability of illegal hunting use was higher than 20% (Table 2, Fig. 4a–c). Illegal hunting was also clearly the parameter with the lowest ΔAICc value among the univariate models considered (Supporting information). Hyena occupancy probability seems to be influenced by overall prey availability (composite prey index) and to some extent – but not significantly so – proportion of woodland habitat (Table 2). Increased illegal grazing also has a negative effect on hyena occupancy as seen by the presence of the parameter in one of the top models (ΔAICc = 1.31; Table 2). Combining conditional and unconditional predicted occupancy estimates, hyenas had spatial variation in occupancy probability across the landscape (0.74 ± 0.35), with highest occupancy probability in the western sector (Fig. 2).

The power of the survey effort employed as part of this study (i.e. sites 42, survey replicates/road segments 4) would have an 80% chance of detecting as significant (α = 0.05) a change in hyena and lion landscape-level occupancy of 39% and 42.9% respectively in a future survey (Supporting information). This calculation is based on the assumption that the detection probability of the two species does not change over time in regards to the survey protocol and survey grid cell size used. Thus, future surveys would have to be undertaken also in the dry season. The probability of detecting with confidence as significant a 30% occupancy decline for either species – which was an original goal of the study – is only 57.7% and 49.1% for hyenas and lions with the current design. Increasing the number of 3-km transects (survey replicates) from four to eight would only marginally increase the power to 57.9% and 50.1%, so it would not be an advisable investment of extra human and financial resources. However, if each of the three WAP countries coordinated to run a similar survey in their respective management areas, effectively tripling the number of survey cells to 126, the power of the suggested monitoring methodology would be

Table 2. Ranking of candidate models developed to understand the environmental covariates affecting estimated occupancy (ψ) for lion *Panthera leo* and spotted hyena *Crocuta crocuta* in the W-Arly-Pendjari complex, West Africa, 2013–2014. Akaike information criterion scores corrected for small sample sizes (AICc), AICc weights and evidence ratios are presented. *Prey*: the predicted relative intensity of composite prey habitat use (buffalo + roan + kob + warthog); *Hunt*: the predicted relative probability of illegal hunting; *Pasto*: the predicted relative probability of illegal pastoralism/grazing; *Dhu*: distance to hunting concessions; *Fores*: proportion riparian forest habitat; *Wood*: proportion woodland habitat; *Roan*: the predicted relative intensity of roan antelope habitat use; *Kob*: the predicted relative intensity of kob habitat use; *Sub*: roads substrate.

Species	Models	AICc	ΔAICc	AICc wgt	ERatio	no.Par.
Lion	ψ(*Fores* + *Dhu*)*p*(*Sub*)	171.73	0	0.2269	1	5
	ψ(*Fores*)*p*(*Sub*)	172.72	0.99	0.1380	1.6	4
	ψ(*Fores* + *Dhu* + *Kob*)*p*(*Sub*)	173.66	1.93	0.0863	2.6	6
	ψ(*Fores* + *Dhu* + *Roan*)*p*(*Sub*)	174.02	2.29	0.0721	3.1	6
	ψ(*Fores* + *Dhu* + *Kob* + *Roan*)*p*(*Sub*)	174.27	2.55	0.0635	3.6	7
	ψ(*Fores* + *Dhu* + *Hunt*)*p*(*Sub*)	174.32	2.59	0.0621	3.7	6
	ψ(*Fores* + *Hunt*)*p*(*Sub*)	174.77	3.04	0.0496	4.6	5
	ψ(*Fores* + *Kob*)*p*(*Sub*)	174.79	3.06	0.0491	4.6	5
	ψ(*Fores* + *Roan*)*p*(*Sub*)	175.29	3.56	0.0383	5.9	5
	ψ(*Dhu*)*p*(*Sub*)	176.07	4.34	0.0259	8.8	4
Hyena	ψ(*Hunt* + *Prey* + *Wood*)*p*(*Sub*)	217.1	0	0.2544	1	6
	ψ(*Hunt* + *Prey*)*p*(*Sub*)	217.90	0.80	0.1708	1.5	5
	ψ(*Hunt* + *Pasto*)*p*(*Sub*)	218.41	1.31	0.1324	1.9	5
	ψ(*Hunt*)*p*(*Sub*)	218.97	1.87	0.0998	2.5	4
	ψ(*Hunt* + *Wood*)*p*(*Sub*)	219.38	2.28	0.0815	3.1	5
	ψ(*Hunt* + *Pasto* + *Wood*)*p*(*Sub*)	219.46	2.36	0.0782	3.3	6
	ψ(*Hunt* + *Pasto* + *Prey* + *Wood*)*p*(*Sub*)	219.93	2.83	0.0617	4.1	7
	ψ(*Hunt* + *Pasto* + *Prey*)*p*(*Sub*)	220.04	2.94	0.0585	4.3	6
	ψ(*Pasto* + *Wood*)*p*(*Sub*)	222.18	5.08	0.0201	12.7	5

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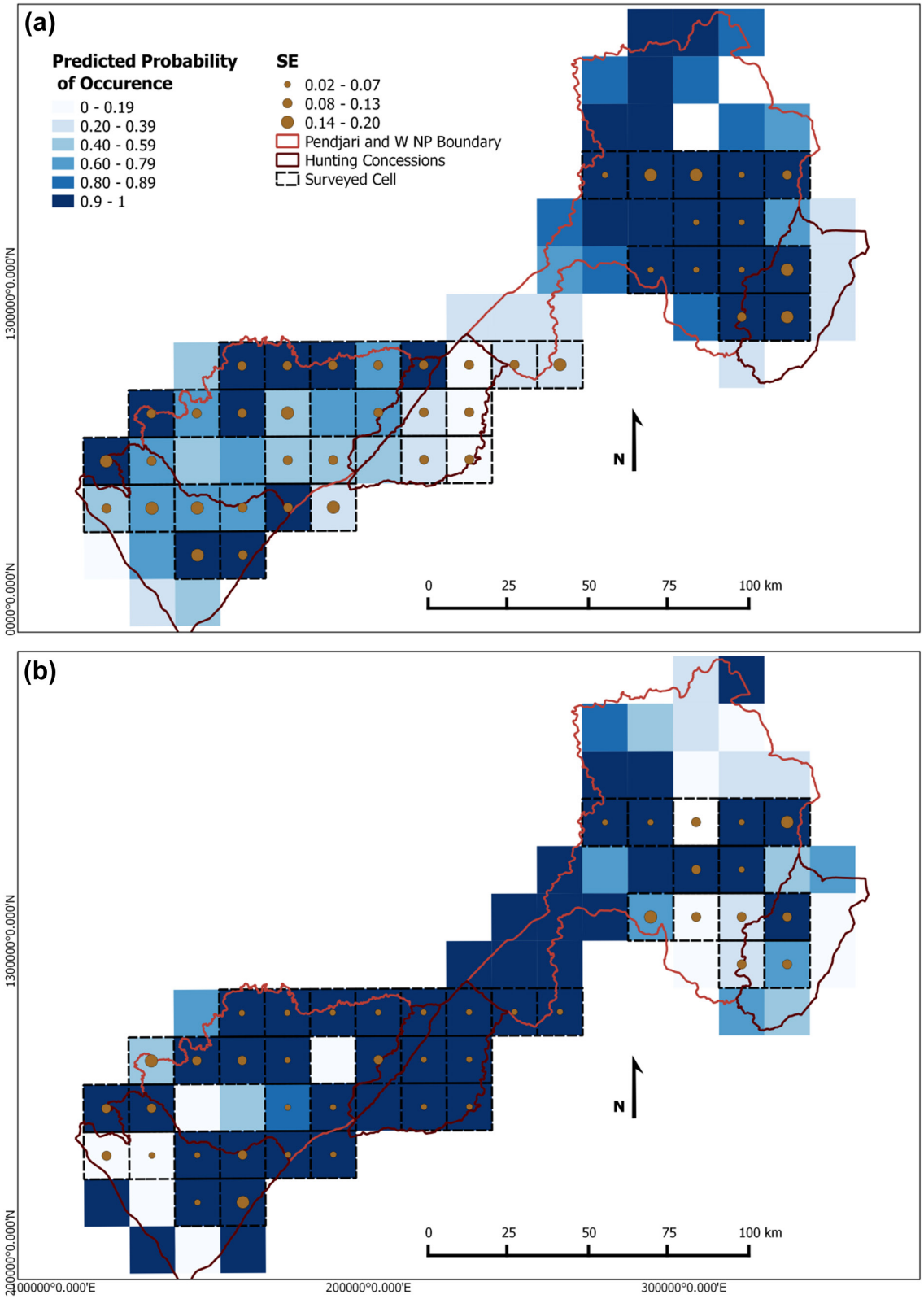


Figure 2. The predicted probability of (a) lion *Panthera leo* occurrence and (b) spotted hyena *Crocuta crocuta* occurrence in the southern W-Arly-Pendjari complex, West Africa, (2013–2014).

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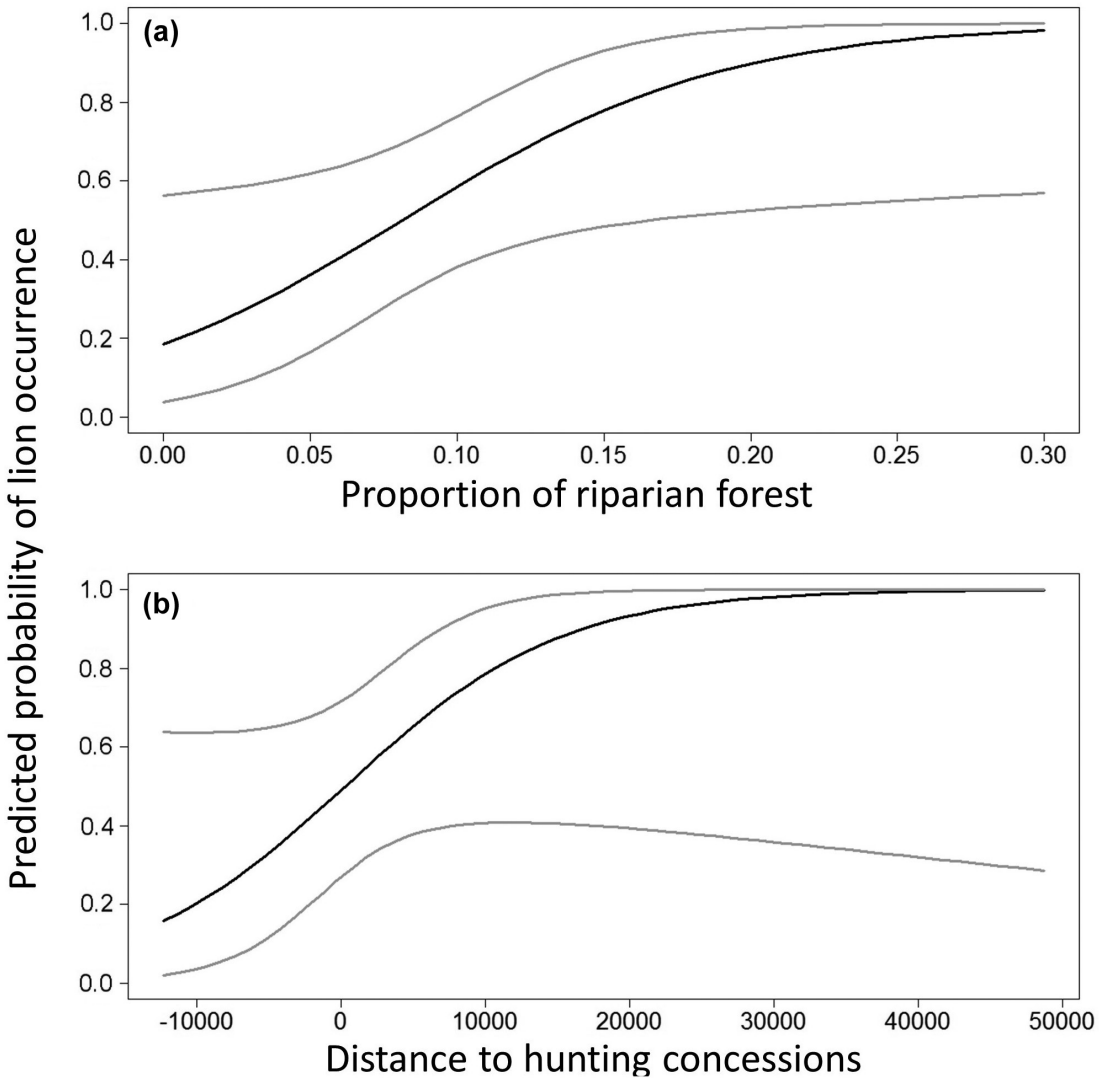


Figure 3. The effect of proportion riparian forest habitat (a) and the effect of distance to hunting concessions (b) on the predicted probability of lion *Panthera leo* occupancy in the southern W-Arly-Pendjari complex, West Africa, (2013–2014). The fitted lines are represented in black with the 95% confidence intervals of the estimates represented as gray lines.

sufficient to detect a 30% occupancy decline 77.8% of the times for hyenas and 67.6% for lions (increasing to 86% and 78% at a significance level of 0.1 instead of 0.05).

Discussion

While carnivore surveys based on occupancy modelling frameworks are becoming increasingly popular (Karanth 2011, Long et al. 2011, Midlane et al. 2014) they often consider only landscape and environmental parameters for the state process component of the models. Our study incorporated parameters on prey availability and levels of human disturbance which are often unavailable for inclusion in models (Ripple et al. 2014, Bauer et al. 2015a, 2020), despite their known importance for carnivore persistence (Soofi et al. 2019). Importantly, the prey availability and human disturbance parameters considered were developed using comparable landscape-wide data collection protocols, suggesting that our inferences could hold across the WAP.

Our results confirm that the WAP remains one of the last strongholds for large carnivores in West Africa, even if we don't present new estimates of abundance. Research deriving abundance estimates tend to be resource-intensive (Braczkowski et al. 2020); we demonstrate that affordable methods can also be informative for management at the landscape level. Cost-effectiveness in data collection and analysis is key for the adoption and sustainability of monitoring programs in areas where resources are limited; making monitoring more accessible to more actors actually increases the potential number of actors involved and the potential for collaboration to cover entire landscapes. We are not advocating the use of spoor surveys for abundance estimates, following concerns raised recently by Dröge et al. (2020). The potential dependence of data between adjacent cells is a potential caveat for the analysis of our data, but one for which we tested for by comparing the models used against Markovian models developed exactly for data collection protocols as ours (Hines et al. 2010). Moreover, our fieldwork was performed at a time when spoor surveys were widely used across the continent (Bauer et al. 2015b,

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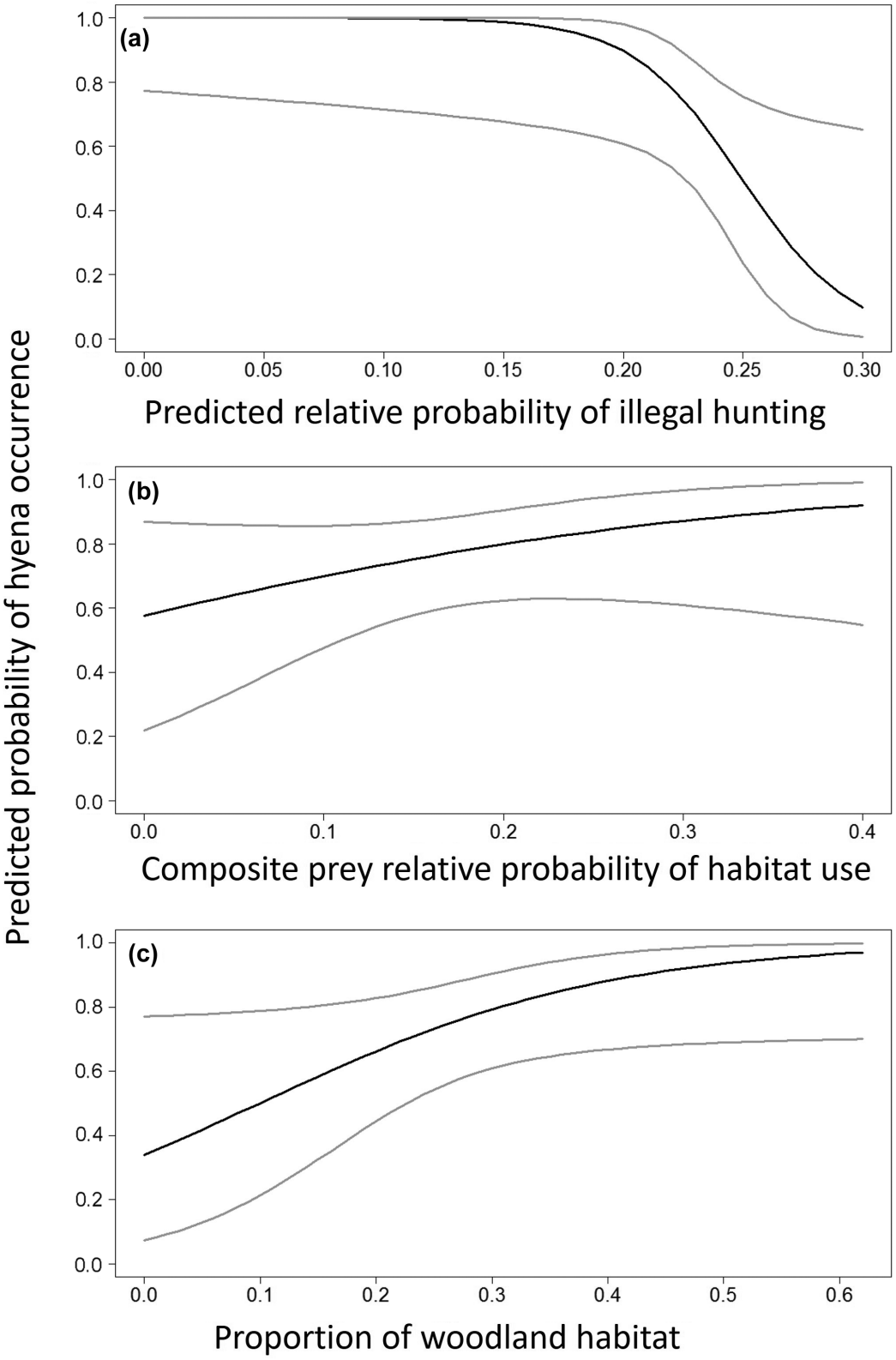


Figure 4. The effect of the predicted relative probability of illegal hunting (a), composite prey relative probability of habitat use (b) and proportion of woodland habitat (c) on the predicted probability of spotted hyena *Crocuta crocuta* occupancy in the southern W-Arly-Pendjari complex, West Africa, (2013–2014). The fitted lines are represented in black with the 95% confidence intervals of the estimates represented as gray lines.

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Bouché et al. 2016, Winterbach et al. 2016, Henschel et al. 2020). Considering the difficulty to train and retain personnel within protected area management teams, spoor surveys continue to be widely used despite the methodological concerns. In our framework, we at least avoid the problems related to the regression between spoor and carnivore density (Dröge et al. 2020), making better use of available data.

While similar approaches have been used to study predator occupancy (Karanth et al. 2011, Henschel et al. 2016, 2020), we also used it to assess the power of a spoor-based survey design to detect changes in lion or hyena probability of occurrence. As far as we know this has previously only described in East Africa (Henschel et al. 2020). Such sensitivity analysis is recommended for occupancy surveys of low-density carnivores (Linden et al. 2017), and in our opinion is essential for deciding whether a survey design is only good for rapid baseline surveys or if it can also serve as a long-term monitoring plan. Our survey design would detect as significant a 30% change in lion and hyena occurrence four out of five times, but only if it was extended to the scale of the entire WAP. Ideally, management would benefit from detection of small changes in population densities, rather than relatively large changes in occupancy, but in view of a balance in cost-effectiveness we assessed our performance against the 30% population change threshold proposed by Dröge et al. (2020).

Our analysis also showed that investing resources in surveying more than four 3-km road segments per grid cell would be inefficient as the increase in the overall power of the design is insignificant. This is because of the high overall detection probability of both lions and hyenas. If the monitoring was to incorporate additional species with a lower detection probability, increasing the number of road segments per cell could be advisable. A coordinated survey across the tri-border area would further reduce costs per unit as teams, equipment and costs of analysis could be shared. Over the last few years, similar work has been done in the WAP components in Burkina Faso and Niger (Harris et al. 2010, 2019, Mills et al. 2020), and we will investigate the possibility of pooling data. After our fieldwork, management on the Benin side was delegated to the NGO African Parks and this NGO has considerably increased the frequency and performance of activities such as law enforcement patrols. This management model is increasingly advocated (Lindsey et al. 2021), and if it would be applied across the entire WAP, it would increase scope for harmonisation and coordination. Lion occurrence was higher in riparian forests, such as those along the Niger and Pendjari rivers that form the natural and administrative boundary between Benin to the south and Burkina Faso and Niger to the north, which underscores the need for transboundary collaboration in these frontier zones.

Lion selection for riparian forests, but not in general for areas near water, suggests that the selection is for the habitat type and not – solely at least – for its association with water. In fact, WAP streams in some riparian forests are dry in the dry season. A study in Kenya (Schuette et al. 2013) also reported no evidence of lion selection for areas near water. A study in Zambia (Midlane et al. 2014) did report distance to water being included in the top model, but in that model it was not significant. More important may be the riparian forests' vegetation that provides cover to increase hunting success (Van Orsdol 1984). In fact, Hopcraft et al. (2005) reported increased lion selection for sites with high prey accessibility due to habitat structure rather than just high prey availability. Given that roan and kob also prefer riparian forests, this habitat appears to provide lions with both available and vulnerable prey. However, since our study reflects lion selection for environmental parameters at home range scale, it is possible and indeed likely that finer scale analysis would show that lions do show a preference for sites with water in the dry season, where prey may aggregate around water holes (Valeix et al. 2010, Davidson et al. 2013).

Considering that riparian forests are not only preferred by lions and wild ungulates, but also by poachers and herdsmen grazing their livestock, human and lions overlap in space at these areas at least during the dry season. Livestock predation is the principal cause of human–carnivore conflict and thereby, human-induced mortality for large carnivores and is a critical threat for their populations (Sogbohossou et al. 2011, Bauer et al. 2020). In addition to a call for increased law enforcement in these areas, especially in the dry season, there is scope for local studies on possible conflict mitigation measures such as the adoption of animal husbandry techniques that would reduce attacks (e.g. use of guard dogs, lion warning systems, mobile bomas) (Petracca et al. 2019, Jablonski et al. 2020, Sibanda et al. 2020).

Several things have changed since we did our fieldwork. We already mentioned the delegation of management to African Parks, and some of the observed patterns may have already changed. However, a new threat emerged over the last few years; jihadist insurgencies are spreading across West Africa and are paralysing management in parts of the region's protected areas (Bauer et al. 2020, 2021b). This makes cross-border mobility of people and livestock of special concern, and authorities are critically looking at corridors that were historical transhumance routes for the local communities. The riparian forests along the border rivers are thus flashpoints of attention, leading to deployment of armed forces and changing land use patterns. The area is rapidly changing and our observations may no longer be the most pressing concern for the border areas. However, it remains of vital importance to protect the critically endangered West African lion population in the WAP in the long term.

The hyena's wider and less clustered distribution in the WAP compared to that of the lion and the species' lack of selection for water or riparian forests is in accordance to previous reports for the WAP (Henschel et al. 2012, Sogbohossou et al. 2018). Nevertheless, hyena preference for areas near water has been reported in other areas (Kolowski and Holekamp 2009, Mhlanga et al. 2018). The aforementioned studies also agree on hyena selection for dense vegetation, but there is less convergence on the role of humans (Yirga et al. 2017, Green and Holekamp 2019, Harris et al. 2019).

The poor performance of prey covariates in hyena occupancy models is not surprising given the species' opportunistic nature and broad and adaptable diet (Hayward 2006). Considering the broad diet of hyenas, the reported lower probability of occurrence in areas with high levels of hunting may not be due to low prey availability but rather due to direct pressure on the species. Persecution by humans is also a possible explanation for the negative relationship between hyena probability of occurrence and that of grazing livestock.

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An alternative explanation for the different response of lions and hyenas to human disturbance may be an increased ability of lions to temporally – and on fine scale spatially – avoid encounters with humans. Such spatiotemporal avoidance of humans by large carnivores has been reported previously (Kolowski and Holekamp 2009, Schuette et al. 2013, Oriol-Cotterill et al. 2015, Suraci et al. 2019). Answering this question would require fine scale movement data from both livestock and predators, and therefore we recommend additional monitoring effort using GPS collars on multiple species in the area.

In conclusion, our findings show that spoor-based surveys of large carnivores in the WAP can be used in combination with occupancy data on prey for a trans-boundary monitoring protocol, but we recommend replicate transects in future to account for detection probability. Occupancy modelling not only provides improved landscape-wide estimates of the species distribution by accounting for imperfect detection, but it also permits – via the inclusion of relevant parameters – the identification of priority areas for conservation action and targeted research. We emphasize the need to recognize the effect of scale when interpreting the results, as all parameters were considered at the level of a lion home range. It is clear from our findings, however, that illegal hunting and grazing should be addressed, as the potential for human–carnivore conflict within the WAP is high.

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Supplementary information (available online as Appendix wlb-00848 at <www.wildlifebiology.org/appendix/wlb-00848>).

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