Disentangling the effects of human pressures and available resources on

critically endangered lion space use in a protected area complex of West Africa

by

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ABSTRACT

African lions reside primarily in protected areas, both of which are increasingly threatened by human pressures and subsequent depletion of natural resources and suitable habitat. Management of protected areas as hunting concessions often results in higher revenues and smaller areas compared to national parks, allowing for high quality habitat and stronger regulation of illegal activity. The successful conservation of lions in protected areas where both management types are implemented could depend on the extent to which lions avoid the risks associated with human encounters, which likely depends on distribution of high-quality habitat, water availability and prey resources. We conducted the first camera survey of lions in the W-Arly-Pendjari (WAP) protected area in West Africa, a 26,620-km^2 complex which has two primary management types: national parks (NPs) and hunting concessions (HCs). We combined occupancy modeling, which accounts for imperfect detection of lions, and structural equation modeling to disentangle the relative effect sizes (ES) of environmental, ecological, and anthropogenic variables expected to influence lion space use. Lion occupancy (ψ) did not show a response to management type ($\psi_{NP} =$ 0.56; $\psi_{HC} = 0.58$), exhibiting no spatial avoidance of hunting concessions. Water availability was higher and habitats were more diverse in hunting concessions, which may negate mortality risks from trophy hunting and higher human occupancy ($\psi_{NP} =$ 0.49; $\psi_{HC} = 0.61$). Lion occupancy was strongly driven by prey availability (ES = 0.219), which was influenced by edge effects and water availability. Cues of high-quality habitat combined with increased human pressures may indicate hunting concessions functioning as ecological traps for lions in WAP. We recommend management interventions (e.g., increasing water availability and patrols near park edges) to provide refuge for lions in national parks by reducing the intersection of lion space use and the risk of human encounters.

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INTRODUCTION

African lions (*Panthera leo*) fundamentally shape ecosystems as a selective force in nature of both evolutionary and ecological significance. Through consumptive and non-consumptive pathways, they influence the spatio-temporal dynamics of sympatric species to structure communities[1–6]. The loss or decline of lions can reduce diversity and cascade to impact ecosystem processes across scales, such as disease dynamics and carbon storage[7–10]. And yet, African lions remain vulnerable and face numerous threats including human-induced mortality, habitat loss, and displacement of prey by livestock. Human-induced mortality from trophy hunting, poaching, and retaliatory killings devastates lion populations by affecting abundance, behavior, and demographic structure[11–17]. The loss of suitable habitat and increased human activities also depletes prey [8,12,18,19], which in turns induces increased spatial overlap and exploitative competition with other large predator species[1,16,20,21]. Their ability to avoid these threats is hampered by limited habitat refuges as well as slow life histories, low population densities, and wide home ranges[8,22–24]. As such, lion populations have declined by 43% over the last two decades and now occupy only 10% of their historic range in Africa[8]. While threats are ubiquitous across the range of lions, they are often locally varied in degree and exacerbated by a range of management strategies within protected areas[25,26].

Despite the role of trophy hunting in lion population declines across their range, the sport is permitted in many protected areas throughout Africa[14,27]. Trophy hunting often occurs in private protected areas, which are recognized for their contributions to increasing the global conservation estate [28,29]. Hunting-related tourism can provide revenue for conservation and socio-economic benefits to communities, while incorporating additional stakeholders with vested interests in the conservation of species[29,30]. Unfortunately, offtake quotas for target species like lions

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are not often well-supported by ecological evidence and sometimes rely on subjective opinions of government agencies[27]. Though difficult to accurately identify, setting proper hunting quotas for lions is essential to avoid harmful population effects and reap long-term benefits from hunting[27,29].

The trophy hunting debate is particularly pronounced in the transboundary W-Arly-Pendjari (WAP) protected area complex, comprised of both hunting concessions and national parks with the largest population of lions in West Africa (Fig. 1)[12,30,31]. Hunting of lions is permissible within designated zones in Burkina Faso and Benin, but illegal throughout Niger and all national parks in WAP. Burkina Faso hunting concessions have among the highest levels of lion offtake per area in Africa (~15 lions killed per year) compared to exceptionally low offtake or lack of lion hunting altogether in the rest of the region (1-1.5 lions killed per year in Benin, Chad, and Senegal)[27,29,30]. The dearth of research into the effects of hunting on lion population distributions, demographics, and persistence challenges the sustainability, profitability, and long-term conservation goals of trophy hunting in this system[29–31] . WAP holds almost 90% of this critically endangered subpopulation at less than half of its potential carrying capacity, indicating the delicacy of ensuring proper management decisions that lead to increases in the population instead of a heighten threat of extirpation in this region altogether[12,15,32].

WAP is a heterogeneous landscape in which anthropogenic pressures interact within a finite amount of suitable habitat and resources in national parks and privately-owned hunting concessions that buffer them. Separate management schemas across 20 different sites within WAP generate inconsistencies in management priorities, resources, and the ability to regulate illegal activity that likely influence the effectiveness of lion conservation across the complex[12,26]. Human populations have been increasing around WAP, putting pressure on the borders of the

protected area, leading to increased poaching, natural resource extraction, and livestock encroachment[33,34]. In addition to human pressures, lions compete with hyenas and leopards for limited prey and available habitat within this system [12]. Such dynamic coupled human-natural processes induce tradeoffs between resources and risks that could create ecological traps where high-quality habitat coincides with human-induced mortality[35]. Large carnivores such as lions are especially vulnerable to ecological traps due to large home ranges and high intake levels that require leaving protected areas to find adequate resources, generating little to no avoidance of risky areas when resources area scarce[36–40]. Lions utilize well-protected areas as refuge from human pressures, but the risks associated with those protected areas are not always as straightforward as their designations imply[40]. National parks may not sufficiently combat poaching and habitat degradation due to lower budgets and staffing. While, in hunting concessions, revenues from trophy hunting allow for improved regulation of illegal activity and infrastructure[12,33,41]. The extent to which lion populations, especially those that are most vulnerable, spatially respond to the threats of mortality associated with trophy hunting and poaching may depend on the quality and availability of resources[35,36]. A necessary precursor to discerning whether hunting concessions or national parks create ecological traps with source-sink dynamics operating on lion demography is to first determine whether this heterogeneity in land management results in differential space use.

Mitigating detrimental effects of lion mortality in both management types is complicated by the combination of ecological and environmental factors that drive lion space use that are interacting with variable mortality risks across the WAP complex[42,43]. Therefore, high-quality and locally-specific information about the relationships between lion space use, the human pressures that threaten them, and the

ecological and environmental resources upon which they rely can enable effective management decisions that conserve lions[31].

Here we aim to understand how the risks of ecological and human pressures and the benefits of high-quality habitat interact to influence the space use of the critically endangered lions in WAP. We combined occupancy modeling, which accounts for imperfect detection, and structural equation modelling (SEM) to disentangle effects of management type (national parks vs. hunting concessions), indicators of habitat quality, and ecological and human pressures on lion space use. We conduct the first extensive camera survey within national parks and adjacent hunting concessions within the WAP complex[44]. Specifically, we determine: 1) the direct and indirect effects of management as well as environmental, ecological, and anthropogenic variables on lion occupancy; 2) if lion space use, ecological (e.g., competitors, prey) variables, and anthropogenic (e.g., humans, livestock) variables vary by management type; and 3) whether responses to management and humans observed in lions are consistent with other large predators in the system. Our results will elucidate the effects of management on lion space use and its drivers, and thus provide insight into the risks and benefits of hunting concessions and national parks for the conservation of the critically endangered West African population.

METHODS

Study area

      The W-Arly-Pendjari (WAP) protected area complex is primarily comprised of 4 national parks (NPs, 54% of total area) and 14 hunting concessions (HCs, 40% of total area) that are government and privately-owned, respectively (hereafter referred to as 'management types'). WAP encompasses over 26,500 km^2 and lies at the transboundary area of Burkina Faso, Niger, and Benin in West Africa (0.514ºE-3.224º E, 10.62ºN-12.817ºN; Fig. 1).

      WAP supports a diverse mammal community with several competing carnivore species and many species of potential prey for lions. Four large predator species occur within WAP: lions (*Panthera leo*), hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and cheetahs (*Acinonyx jubatus*), though cheetahs occur at low abundances and are unlikely to interact with other apex predators in the system[45]. Potential prey items include many medium to large-sized ungulate species, most commonly roan antelope (*Hippotragus equinus koba*), West African savanna buffalo (*Syncerus caffer brachyceros*), bushbuck (*Tragelaphus sylvaticus*), common warthog (*Phacochoerus africanus*), Western Buffon's kob (*Kobus kob kob*), Bohor reedbuck (*Redunca redunca*), oribi (*Ourebia ourebi*), and red-flanked and common duiker (*Cephalophus rufilatus* and *Sylvicapra grimmia*)[45].

      We conducted our study in the dry season (January to June), during which average monthly precipitation throughout WAP ranges from 0-4 mm in February and from 44mm-101mm in June (WorldClimv2.0; Fick & Hijmans 2017). WAP climate is mostly arid, with expansive Sudanian and Sahel savannahs. The drier northeast area consists largely of open grasslands, bushlands, and woodlands, but transitions gradually towards denser woodlands in the southwest region of the complex[45].

Camera survey

We implemented systematic camera trap surveys within WAP in both Niger and Burkina Faso from February to June of 2016-2018. Our efforts represent the first camera trap survey conducted in WAP, and more broadly the countries of Burkina Faso and Niger with relatively few studies conducted in West Africa (Agha et al. 2018). Over the course of 3 years, we deployed 250 white-flash and infrared, remotely-triggered cameras (Reconyx© PC800, PC850, PC900) to sample across 204 square cells of a 10x10-km grid within 3 NPs and 11 HCs in WAP (Fig. S2; Tab. S1). A 10-km^2 grid size was chosen as the sampling unit size to ensure accurate detection at scales relevant for both small and large species in the WAP mammal community. The same sites were not surveyed each year, due to a limited number of cameras. One camera was placed within 2-km of the grid centroid for each sampled grid cell to attain near-uniform camera dispersal and adequate coverage of the complex. Camera locations within this radius were chosen in the field to maximize trap success based on animal sign, the presence of game trails and direction of nearby water sources. Cameras were attached to a tree c. 50-cm above the ground to maximize detection and identification success of small- to large-sized vertebrates. Cameras were programmed to rapid-fire capture 3 images when triggered (adjusted to capture 5 images in 2017) with no delay between triggers and high sensitivity. We checked cameras 2-4 weeks after deployment, and adjusted placement or settings as necessary. Cameras that malfunctioned were removed and replaced by new cameras at that location, while cameras that were tampered with (e.g. burned) were removed and not replaced.

Within each grid cell, the number of days that cameras were operational were summed to provide a measure of grid-cell sampling effort for each survey season. In

this way we were able to account for grid cells with multiple cameras, which occurred during the 2016 pilot survey, camera replacements/relocations, and in two locations where additional cameras were placed outside of the centroid buffer in 2017.

Image processing

Our camera trap survey captured c. 1.7 million images over three sampling seasons. Every photo captured by camera traps in WAP was visually examined and classified according to species for all species in the image set by at least two members of the Applied Wildlife Ecology at University of Michigan. False triggers where no animal was captured as well as true triggers where the species was unidentifiable (2.9% of true triggers) and when photos captured park staff (0.2% of true triggers) were removed from analyses. Pictures were then aggregated using R package 'camtrapR' to determine individual trigger events using a 30-minute quiet period to create independence in capture histories for species.

Occupancy models

We constructed single-season, single-species occupancy models to estimate occupancy probabilities of lions as well as competitor species (hyenas and leopards), humans, and livestock (cattle and goats) in each sampled grid cell, while accounting for imperfect detection using repeated survey periods[46]. We separated presence-absence data at each grid cell into 2-week survey periods, changing 96 independent triggers into 64 detections for lions used in analysis. Through occupancy modeling, we account for imperfect detection by first modeling presence-absence data with covariates expected to influence detection, the output of which was then modeled with covariates expected to influence occupancy[46].

We estimated cell-specific detection (p) and occupancy (Ψ) probabilities for all combinations of the global detection and occupancy models. Covariates present in

the global models to explain grid-level detection probabilities included: management

type (MGMT), year (YR), trap-nights (TN), camera type (CAM), and site (i.e.,

individual parks or concessions; SITE). Cell-specific human occupancy (HUM) was

also included as a covariate for detection of lions and competitor species. If

management type is included in the top detection models, it would indicate

behavioral differences in lions between the hunting concessions and national parks

that produce unequal probabilities of detecting lions when they are present.

Occupancy (Ψ) for each group was modeled with all combinations of the grouping

variables: management type (MGMT), year (YR), and site (SITE). The inclusion of

management type in the final model set is indicative of difference in occupancy

between national parks and hunting concessions. All other covariates that are

expected to influence lion occupancy are included in structural squations modeling

described later in the Methods. Because our sampling units were smaller than the

home ranges of the species surveyed, our occupancy models do not meet the

assumption of closure and are thus interpreted as probabilities of occurrence rather

than true occupancy[46]. We used the Akaike Information criterion corrected for small

sample sizes (AICc) for model selection to assess support of all combinations of

detection and occupancy covariates. In doing so, we assumed that all covariates

included have an impact on detection and occupancy of the target species to some

degree, but we excluded covariates that did not significantly improve model fit to

maximize accuracy of the latent occupancy estimates. We assessed goodness-of-fit of

the top models with ΔAICc < 2 for each group using 1,000 parametric bootstraps of a

χ^2 test statistic appropriate for binary data[47]. We determined final model selection

from the top model sets by choosing the model that maximized spatial heterogeneity

of latent occupancy estimates without significantly changing the overall occupancy

estimates based on a Wilcoxon signed-rank test for non-normal data. All detection

and occupancy models were created using the 'unmarked' R package and model selection was conducted using the 'MuMIn' R package.

Covariate development

Several extrinsic factors could influence lion occupancy, especially in such a heterogeneous landscape of our study area (Tab. S4). We expect effects from anthropogenic variables to be amongst the most pronounced due to implications of risks. Human and livestock occupancy were expected to elicit a finer-scale spatial response in lions, though to varying degrees between groups. For example, large livestock herds could provide an additional source of prey for lions (possible positive effect) and likely differ from the impacts of humans gathering materials and travelling in small groups (possible negative effect). Road density within each grid cell provides easier access to those areas for humans; thus, enhancing human pressure and subsequent habitat degradation. Edge effects should reduce lion occupancy due to human pressures surrounding the complex and particularly in national parks because they are buffered by hunting concessions where mortality risks are expected to be higher.

We also explored effects of four ecological variables on lion occupancy: wild prey availability, competitor occupancy, fire pressure, and savanna land cover. Here, we considered wild prey to be any prey species lions potentially hunt including baboon, aardvark, and all ungulate species observed in the camera survey except for elephant and hippopotamus. We considered the log-transformed capture rate of wild prey (camera triggers/number of trap-nights x 100) during the camera survey to be an index of prey availability within each grid cell. We expect occupancy of competitor species to correspond with lion occupancy, due to reliance on similar resources and habitat that may not be plentiful enough to facilitate spatial partitioning. Fire pressure was measured as the average fire radiative power of fire detected within a grid cell,

obtained from NASA VIIRS active fire detection data for the duration of our three year study[48]. We consider fire pressure to be an ecological variable because we are unable to discern from our data whether fire occurrences are the product of natural fires or illegal poaching strategies. The percentage of savanna habitat, which is the primary habitat of lions, within a grid cell was extracted from USGS land cover time series data from 2013[49].

In addition to anthropogenic and ecological variables, it is important to consider the impacts of environmental factors that regulate the system through bottom-up processes and may provide insight into the effects of global climate changes on lion populations. Thus, we considered the influence of availability of drinking water lion occupancy using density of rivers and average precipitation. River spatial data was obtained from the USGS HydroSHEDS program dataset[50]. Rainfall data was extracted from WorldClim v2.0 for each month of January-April and averaged first temporally at a ~5-km^2 resolution then averaged spatially across each 10-km^2 grid cell (mm/km^2)[51]. We tested lion occupancy and each of the above anthropogenic, ecological, and environmental covariates for differences between national parks and hunting concessions using a one-tailed Mann-Whitney U test with significance evaluated at $\alpha = 0.05$.

Structural equation modeling (SEM)

We used SEM to disentangle the relative direct and indirect effects of the aforementioned covariates on lion occupancy at the grid level. SEM assumes causal relationships between variables, which enables effect sizes to be interpreted literally and assumes *a priori* knowledge of directionality of those effects[52]. We first evaluated the pair-wise correlations of all hypothesized covariates using Pearson's correlation coefficient (r), to ensure that all pairs of covariates for which $r > |0.6|$ were included in the SEM model when causal pathways were supported. Based on

our hypothesized relationships, we constructed a global model that includes both direct and indirect effects of the final set of covariates on lion occupancy (Fig. 3). To assess indirect effects of the human pressures on lion occupancy, we measured the influence of human and livestock occupancy on both competitor occupancy and wild prey availability. Road density was also considered as an indirect effect via its effect on prey availability, because prey species might benefit from easier movement throughout the park. We further assessed indirect effects of all environmental variables mediated by prey availability as such factors bottom-up regulate the system. We calculated indirect effects by multiplying the coefficients of direct pathways to lion occupancy and found the total effects for each covariate on lion occupancy by adding the direct and indirect path coefficients. We used a global estimation approach, maximum likelihood methods, and 10,000 bootstraps of the standard errors to estimate standardized path coefficients (i.e. effect sizes) and 95% confidence intervals for each modeled pathway. The significance of path coefficients was evaluated at $\alpha = 0.05$. Our global a priori model had a sufficient ratio of sample units per paths estimated (10.2) to ensure model explanatory power[53,54]. We further ensured adequate model specification by confirming model power (probability of accurately rejecting null hypothesis) ~0.8 according to the root mean squared error of approximation[55]. We assessed model fit using a Pearson's χ^2 test in which $P > 0.05$ indicates that the modeled covariance matrices adequately fit the observed data. We used the 'lavaan' package in R for all SEM analyses.

Group SEM

We then conducted a multi-group SEM model, in which path coefficients were evaluated independently for national parks and hunting concessions, to further understand the effects of management type on the relationships between the variables and lion occupancy in WAP. Grouping the data by national park (n = 118) and

hunting concession (n = 86), we included only significant paths from the final full

model to ensure the ratio of samples per estimated pathway is greater than 10 for both

groups (NPs = 14.75, HCs = 10.75)[54].

Patterns in lion occupancy in W-Arly-Pendjari (WAP)

From the largest camera study in West Africa, we captured only 96

independent lion triggers over 21,430 trap-nights (Tab. S1). Accounting for imperfect

detection of lions allowed us to estimate of lion occupancy (ψ) in WAP ($\bar{\psi} = 0.57$,

SE ± 0.05), a value much higher than would be assessed based on observation alone

(naïve $\psi = 0.27$). Occupancy estimates for each 10-km grid cell that was surveyed

allow for fine-scale understanding of the heterogeneity in lion space use within the

complex, which exhibited consistency in overall occupancy among the 15 sites

surveyed but with large variation in the spread of grid-level estimates (Fig. 2).

Overall lion occupancy estimates in WAP were comparable to other lion populations

throughout Africa[41,56,57]. However, national parks that were sampled consecutive

years showed a decline over time; in contrast to an increase in occupancy in hunting

concessions (Fig. S1).

The global SEM model showed adequate performance overall (Model fit: χ^2

$= 10.67$, df $= 7$, $P = 0.15$), but best explained competitor occupancy ($R^2 = 0.21$) and

prey availability ($R^2 = 0.28$) with lower explanatory power for lion occupancy ($R^2 =$

0.13). Analysis of 204 total sample units revealed lion occupancy was primarily

driven by prey availability (standardized path coefficient (SPC) = 0.219) and the

occupancy of hyenas and leopards (SPC = 0.157; Fig. 3, Tab. S2). Lion occupancy

did not show a response to management type ($\psi_{NP} = 0.56$; $\psi_{HC} = 0.58$) or any other

anthropogenic variable (Tab. S2). Lions did not exhibit spatial avoidance to hunting

concessions, human pressures, or competitors. Instead, space use was governed by

the distribution and availability of prey, indicating a strong preference for areas

where food is abundant. If lions are disregarding mortality risks and antagonistic

interactions to satisfy consumptive needs, it may suggest prey depletion in WAP similar to trends observed in other West African protected areas[12,15,18,19].

Risks and benefits of management types in WAP

We found no spatial response of lions to the management type in WAP (Fig. 4). Possible explanations include: 1) lions are not responding to risks of human encounters altogether, 2) risks from trophy hunting in concessions may be comparable to mortality risks in national parks, or 3) the risks in hunting concessions are outweighed or balanced by the relative benefits of suitable habitat and resources.

While indiscriminate use across management types could plausibly be attributed to a lack of response altogether to humans, it is unlikely because lions have consistently shown spatial responses to humans in other systems[40,42,56,58,59]. Despite increased human pressure due to higher road density and human occupancy (ψ_{HC} = 0.72 vs. ψ_{NP} = 0.19), lions continue to exploit hunting concessions to a similar extent as national parks (Fig. 4). Furthermore, such differential levels of human pressures suggest the risks associated with hunting concession exceed that of national parks, if only due to greater likelihood of human encounters that may result in lion killings. As such, comparable risks of mortality between management types are not supported by our results. However, lion conservation in WAP would benefit from a study of cause-specific lion mortality to assess the distribution and cause of mortality across management types.

In contrast to significantly higher levels of human pressure (human occupancy, $P = 0.006$; road density, $P = 0.005$), resource availability was also greater in hunting concessions than national parks (average precipitation, $P < 0.001$; river density, $P = 0.034$; non-savanna habitat, $P = 0.004$; Fig. 4). Lion occupancy was primarily driven by prey availability (SPC = 0.218; Tab. S2), which did not differ between management types (Figs. 3, 4) and likely contributed to similar patterns in

lions. We hypothesize that ecological cues indicating high-quality habitat, e.g., plentiful water resources and comparable available prey (Fig. 4), are negating the expected negative response to the risks associated with human encounters. Significantly higher detection rates in hunting concessions reflect increased movement activity for lions likely induced by human presence ($p_{HC} = 0.089$ vs $p_{NP} = 0.079$; Mann-Whitney U test, $P < 0.001$), which suggests finer scale spatio-temporal avoidance behaviors in lions that we are not able to discern in our current occupancy/SEM model framework. While this pattern supports higher costs to lions in hunting concessions (in this case increased energy requirements from avoidance behaviors), confirmation of higher mortality rates from empirical investigations is necessary to verify that hunting concessions represent ecological traps in this system. Our results highlight the intersection of human pressures and high-quality habitat that could be detrimental to the persistence of the critically endangered lion population in WAP.

SEM further revealed prey availability was influenced by multiple ecological and environmental variables including edge effects, available water, and habitat variability (Fig. 3, Tab. S2). Because lions respond primarily to prey at a fine scale, these results provide insight into management interventions that could stimulate lion occupancy in low-risk areas of WAP.

Revenue generated from trophy hunting provides funds that allow increased patrol staff and better regulation of illegal human activities compared to national parks[41,60]. The advantages of higher revenues and staffing are bolstered by smaller areas over which resources and patrols must be dispersed. In WAP, hunting concessions are almost 4 times smaller on average (mean size: 567.94-km^2) than national parks (mean size: 2,265.68-km^2). Such disparities are important to note

when considering conservation effectiveness in WAP and could be contributing to the patterns of lion space use observed in this study.

Competing large predators' response to management

In contrast to lions, hyenas (*Crocuta crocuta*) and leopards (*Panthera pardus*) have significantly higher occupancy in hunting concessions than in national parks ($P = 0.001$, Fig. 4). Trophy hunting induces differential pressure across the carnivore guild, which we suspect resulted in lower sensitivities to hunting concession management for competitor species. Therefore, we hypothesize that these non-target species can take better advantage of the enhanced infrastructure (e.g., more available drinking water) in hunting concessions with less demographic consequences. Competitors showed a stronger response to prey availability in hunting concessions ($SPC_{HC} = 0.475$) than in national parks ($SPC_{NP} = 0.319$; Tab. 2) compared to a similar response in lions between management types ($SPC_{NP} = 0.266$, $SPC_{HC} = 0.296$; Tab. 2). A weaker effect of humans on the detection of competitor species ($\beta = 0.37$) compared to lions ($\beta = 0.47$, Tab. 1) can be attributed to lower changes in competitor activity when humans are present, indicating reduced responses to human-associated risks. Lion association with other large predators in the system also differed between management types, in that lions showed a positive spatial response to competitor occupancy only in national parks with no significant response in hunting concessions (Tab. 2). Higher occupancy of competitors in hunting concessions accompanied by lower spatial overlap with lions indicates higher levels of spatial partitioning between species than occurs in national parks. Therefore, hunting concessions may serve as a competitive refuge for subordinate predator species in multi-management systems such as WAP.

Management priorities to enhance habitat suitability in national parks

We demonstrated that there is a disparity in resources and habitat between management types in WAP, and that lion space use is primarily driven by bottom-up regulation from prey availability. Small sizes of hunting concessions allow for revenue generated from trophy hunting to be dispersed more effectively to improve infrastructure and patrolling, while national parks receive drastically lower tourism income that limit management and capacity to deter illegal human activities[41]. Lions did not directly respond to any of the variables representing human pressure in our study, and thus exhibit no avoidance human-induced mortality. We recommend prioritizing the reduction of edge effects and increasing water availability throughout the system to increase suitable habitat for prey and thus lions. Such efforts will likely require increased patrol staff near park edges and where poaching is common to deter illegal activities that degrade habitat. Influencing lion occupancy in WAP with management decisions can help to minimize risks of human-lion conflict that arise from spatial overlap in both parks and concessions. Across their range, lions reside in national parks that are often abutted by hunting concessions[32,61,62], and assessing the existence of similar spatial patterns in other protected areas may be important in improving conservation outcomes for the species.

By conducting the first ever camera trap survey to systematically monitor wildlife of WAP, we demonstrated that lions are not spatially avoiding human pressures or the mortality risks associated with them at both the landscape and finer scales[44]. Prey availability is the primary driving factor in lion space use, which can be manipulated through management interventions to reduce human-lion conflict and total lion mortality. Effective conservation of lions in WAP should consider incorporating these spatial patterns to influence lion occupancy within the complex and reduce the intersection of mortality risks and high-quality habitat.

TABLES

TABLE 1: Model averaged coefficients of lion detection and occupancy from the

top candidate models of ΔAICc < 2.

|	β coefficient (standard error)		*P*	Importance	N-containing models
Detection (*p*)					
CAM				1.00	10
Both types	-1.41	(0.64)			
Infrared	-2.36	(0.75)	0.00		
White Flash	-1.86	(0.78)	0.06		
MGMT				0.50	5
HC	-1.10	(0.50)	0.03		
NP	-1.32	(0.63)	0.04		
HUM	0.47	(0.36)	0.20	0.33	3
TN	0.00	(0.01)	0.59	0.13	2
Occupancy (Ψ)					
Intercept	0.31	(0.52)	0.55		
MGMT				0.23	3
HC	0.10	(0.72)	0.89		
NP	0.64	(0.94)	0.50		
YR				0.06	1
2016	0.86	(1.03)	0.41		
2017	-0.19	(0.50)	0.70		
2018	-0.58	(0.78)	0.45		

TABLE 2: Standardized effect coefficients of the group SEM path analysis, in which separate path coefficients were measured for each of the two management types for all pathways found to be significant in the full SEM (see Fig. 3, Tab. S2). Differences in the effects of each pathway between each management type were evaluated based on 95% confidence intervals; negative difference indicate lower effect sizes in national parks. Significant standardized paths: $*P < 0.05$; $+P < 0.1$

|	National Park				Hunting Concession				NP-HC
	Std. effect	P	95% CI		Std. effect	P	95% CI		
Lion occupancy ~									
Competitor occupancy	0.100*	<0.001	0.049	0.150	0.111	0.200	-0.059	0.280	-0.011
Prey availability	0.266*	<0.001	0.131	0.402	0.296*	0.001	0.116	0.475	-0.030
Prey availability ~									
% savanna	-0.418*	<0.001	-0.550	-0.286	-0.088	0.346	-0.272	0.096	-0.330*
River density	0.079	0.316	-0.075	0.232	0.193+	0.091	-0.031	0.417	-0.114
Road density	0.158+	0.054	-0.003	0.320	0.250*	0.021	0.039	0.462	-0.042
Distance to edge	0.149*	0.044	0.004	0.294	0.233*	0.041	-0.010	0.457	-0.084
Competitor occupancy ~									
Prey availability	0.319*	<0.001	0.286	0.561	0.475*	<0.001	0.316	0.635	-0.156
Livestock occupancy	-0.144	0.125	-0.035	0.284	0.005	0.958	-0.184	0.194	-0.149

FIGURE 1: Location of the W-Arly-Pendjari (WAP) complex in Africa, and the constituent parks, concessions, and reserve boundaries: (1) Tapoa-Djerma hunting concession; (2) Park W-Niger; (3) Park W-Benin; (4) Djona hunting concession; (5) Tamou reserve; (6) Park W-Burkina Faso; (7) Kourtiagou hunting concession; (8) Koakrana hunting concession; (9) Mekrou hunting concession; (10) Pendjari National Park; (11) Arly National Park; (12) Pagou hunting concession; (13) Ouamou hunting concession; (14) Singou Septentrional hunting concession; (15) Pama Nord hunting concession; (16) Pama Centre Nord hunting concession; (17) Konkombouri hunting concession; (18) Pama Centre Sud hunting concession; (19) Pama Sud hunting concession; (20) Pendjari hunting concession. Dark gray shading indicates sites where our camera survey took place in at least one survey year (see Tab. S1).
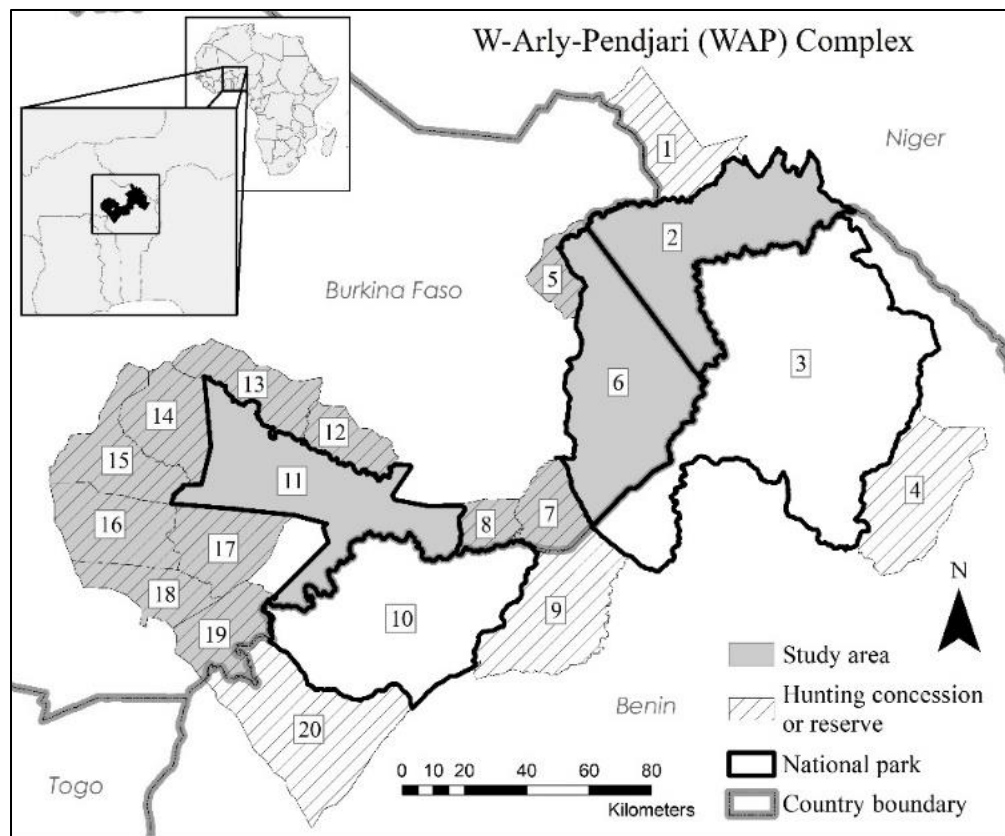
FIGURE 2: Cell-specific occupancy probabilities of lions in WAP study area, averaged by years surveyed. Occupancy values are based on the latent occupancy estimates of the final chosen model (Tab. S3). Boxplots show average lion occupancy estimates each national park and hunting concession surveyed.
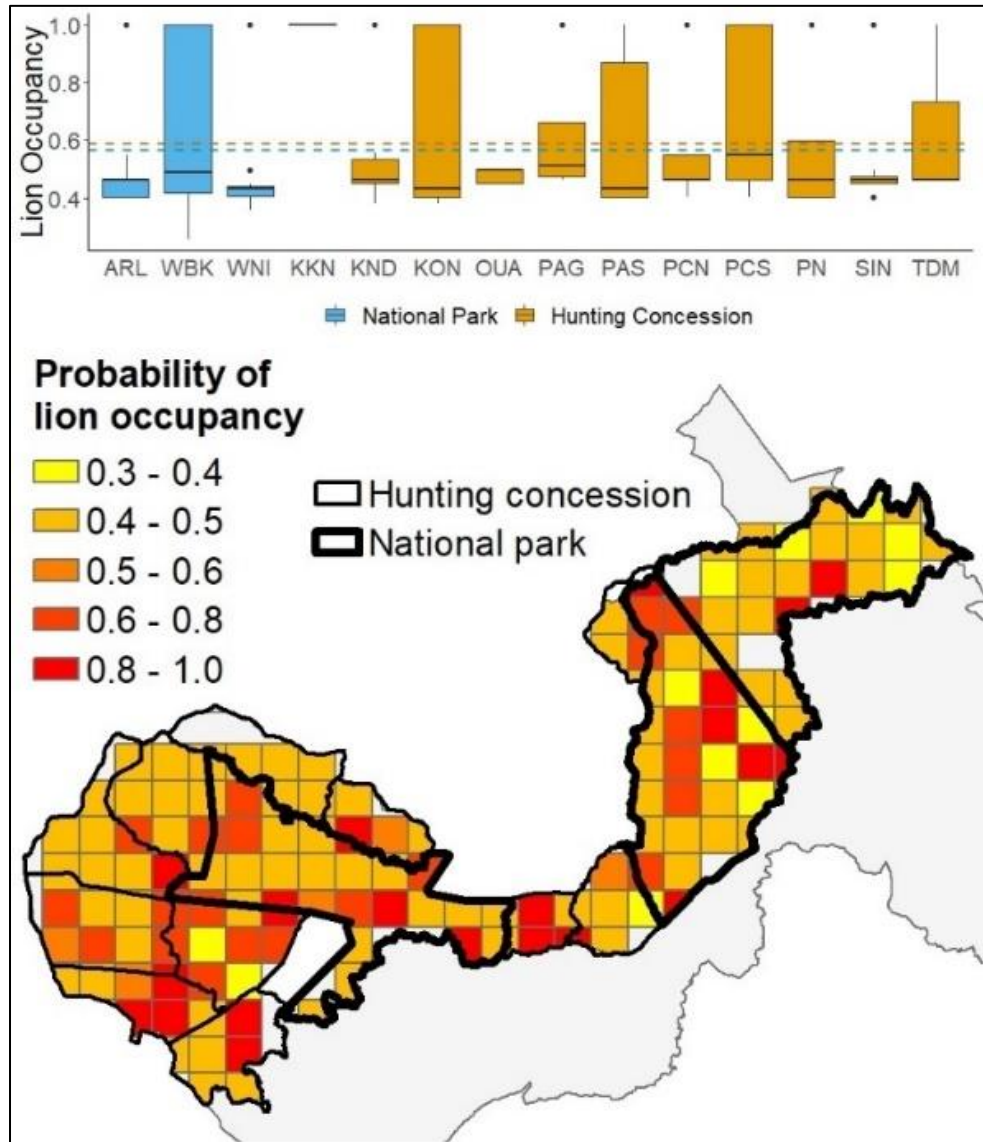
FIGURE 3: Results of the global SEM path analysis evaluating the effects of variables on lion occupancy. All significant (black) and insignificant (grey) direct pathways are shown, but only significant path coefficients are displayed (see Tab. S3 for all path coefficients, including indirect). Displayed path coefficients are significant at level α = 0.05, except for coefficients with asterisks which are significant at level α = 0.1. Arrow sizes represent standardized effect sizes of direct effects. Variables outline types indicate category: dotted = environmental, dashed = ecological, solid = anthropogenic. Variables in rectangles were obtained via occupancy modeling of camera trap data, while those in ovals were obtained from other sources or estimates directly from camera trap data (e.g. prey availability).
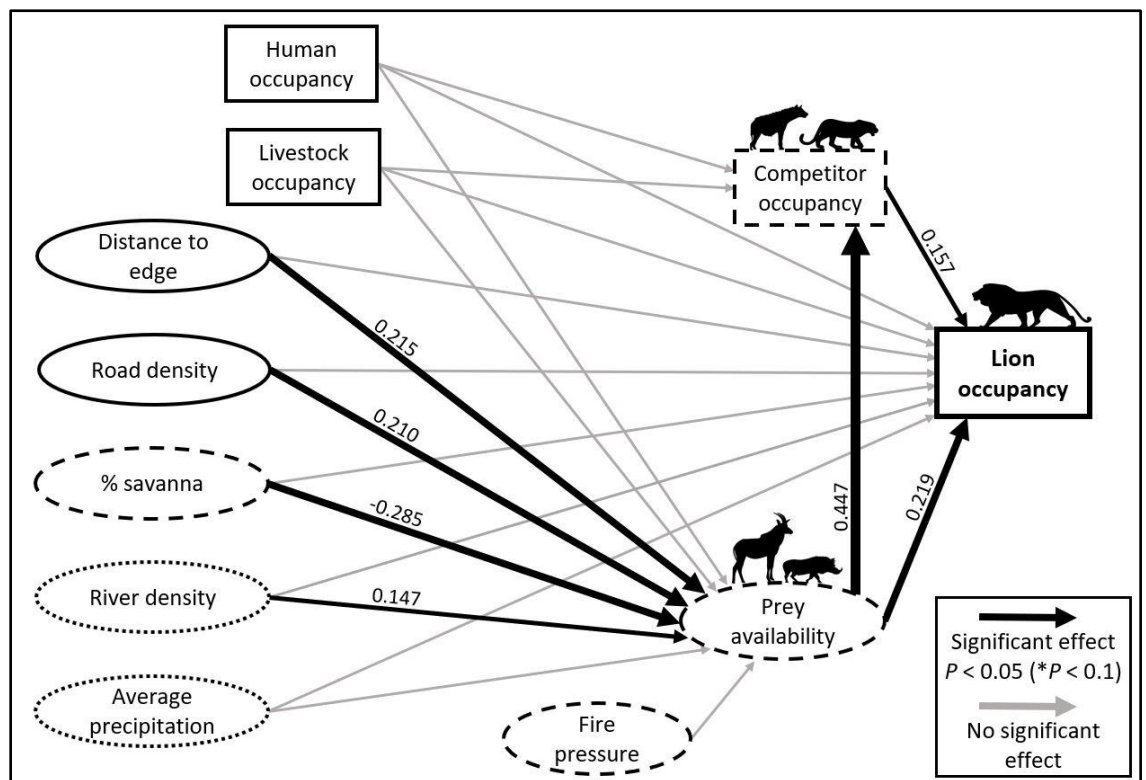
FIGURE 4: Differences in distributions between national parks (n = 118) and hunting concessions (n = 86) for all variables included in the SEM analysis. Occupancy estimates are based on the final chosen occupancy model for each group (Tab. S3). Significance is indicated in the top-left of each individual plot. Significance in differences between management types were tested using a Mann-Whitney U test for non-normally distributed data for all variables except for prey availability, which was normally distributed (Shapiro-Wilk test $P < 0.05$) and for which a t-test was used.
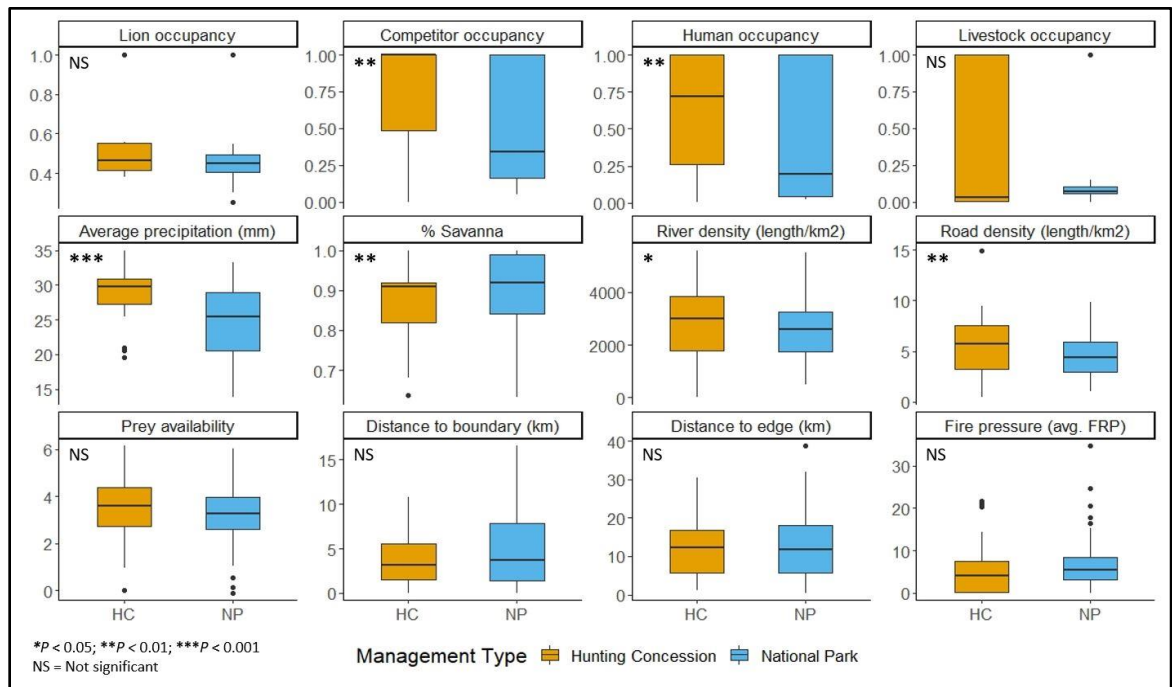
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SUPPLEMENTARY MATERIALS

Results on prey availability and livestock encroachment

Prey availability, a primary driver of occupancy for lions (0.218) and other large predators (0.373; Tab. S2), was driven by many environmental and ecological factors. Fire, which is an illegal hunting technique to flush out animals by poachers, negatively affected prey distribution (-0.111; Fig. 3, Tab. S2). Although livestock did not show any significant direct impacts on prey distribution, prey avoided edge areas (0.218) likely due to encroachment of illegal human activities as livestock occupancy was higher near WAP edges (linear regression, $P = 0.04$). Because we aggregated prey availability, we are unable to discern species-specific responses of prey that may lead to a stronger indirect effect of livestock on lions. Diet analysis of lions in WAP would enable us to determine more specifically the prey that are most important to lions and the effects of livestock on those preferred prey. It is possible, however, that illegal livestock encroachment is restructuring herbivore community composition and distributions in WAP because large-bodied ungulates are more likely to be displaced by livestock (Bouché et al, 2004). Unfortunately, mitigation of livestock encroachment and illegal hunting activities in WAP to promote prey populations is probably easier to achieve in hunting concessions that have higher revenues and smaller areas to cover. This would further increase the likelihood that lions would utilize hunting concession habitat as an ecological trap resulting in increased mortality.

TABLE S1: Camera trap survey summary table showing sampling effort for all sites
surveyed over three field seasons. Lion detections represent the number of presence
detections in 2-week detection histories.

Site	Abbv.	Area (km^2)	Years surveyed	Trap-nights	Lion detections
National Parks					
Arly National Park	ARL	2227.45	2017,2018	4,268	10
Park W-Burkina Faso	WBK	2344.04	2016,2017	6,886	23
Park W-Niger	WNI	2225.54	2017	2,461	3
Hunting Concessions					
Koakrana	KKN	270.24	2018	233	1
Konkombouri	KON	733.58	2017,2018	1492	7
Kourtiagou	KND	474.56	2018	612	1
Ouamou	OUA	639.44	2017	335	0
Pagou Tandougou	PAG	402.83	2018	317	1
Pama Centre Nord	PCN	824.66	2017,2018	1060	6
Pama Centre Sud	PCS	508.87	2018	673	3
Pama Nord	PN	786.63	2017	686	4
Pama Sud	PAS	597.44	2018	659	2
Singou Septentrional	SIN	721.74	2017,2018	1409	1
Tapoa-Djerma	TDM	287.36	2018	339	2
Total		**13,046.38**		**21,430**	**64**

TABLE S2: SEM standardized path coefficients for direct, indirect, and total effect sizes (direct*indirect). Significant standardized paths: $*P < 0.05$; $^+P < 0.1$

	Direct Effects			Indirect effects	Total effects
	Lion occupancy	Competitor occupancy	Prey availability	Lion occupancy	Lion occupancy
Average Precipitation	-0.006	…	-0.005	-0.001	-0.007
% Savanna	0.040	…	-0.285*	-0.062*	-0.023
River density	0.014	…	0.147*	0.032	0.046
Road density	0.077	…	0.210*	0.046+	0.123
Distance to edge	0.026	…	0.215*	0.046*	0.073
Fire pressure	…	…	-0.105	-0.023	-0.023
Prey availability	0.219*	0.447*	…	0.070*	0.289*
Competitor occupancy	0.157*	…	…	…	…
Human occupancy	0.076	0.002	0.102	0.023	0.098
Livestock occupancy	-0.081	0.123*	-0.025	0.014	-0.067

TABLE S3: Final candidate model set of all lion, competitor, human, and livestock occupancy models of ΔAICc < 2 compared to the top performing model for each group. The bolded model indicates the model from which latent occupancy estimates were obtained for use in SEM model. The model for which latent occupancy

estimates showed highest variability without being significantly different from the
top performing model was chosen as the final model. We tested differences in latent
occupancy estimates compared to the top model using a paired Wilcoxon signed rank
test for non-normally distributed data, in which $P < 0.05$ indicates significant
differences in median occupancy estimates. CAM = camera type, MGMT =
management type (NP, HC), HUM = human occupancy, TN = trap-nights, SITE =
site, YR = survey year.

Candidate Models	AICc	ΔAICc	AICc weight	χ^2 Goodness-of-fit P-value	Occupancy Estimates		
					Mean	Var.	P
Lions							
P (CAM) **Ψ (.)**	**513.34**	**0.00**	**0.17**	**0.879**	**0.572**	**0.060**	
P (MGMT + CAM) Ψ (.)	513.44	0.10	0.16	0.907	0.577	0.059	0.004
P (CAM + HUM) Ψ (.)	513.87	0.53	0.13	0.743	0.581	0.058	<0.001
P (CAM + HUM + MGMT) Ψ (.)	513.98	0.64	0.12	0.809	0.578	0.059	0.010
P (MGMT + CAM) Ψ (MGMT)	514.79	1.46	0.08	0.895	0.599	0.068	0.005
P (MGMT + TN + CAM) Ψ (.)	514.94	1.61	0.07	0.841	0.577	0.060	0.015
P (CAM + HUM + MGMT) Ψ (MGMT)	514.98	1.64	0.07	0.802	0.606	0.074	<0.001
P (CAM) Ψ (MGMT)	515.00	1.67	0.07	0.916	0.586	0.059	<0.001
P (CAM) Ψ (YR)	515.26	1.92	0.06	0.459	0.554	0.074	0.005
P (CAM + TN) Ψ (.)	515.33	2.00	0.06	0.806	0.571	0.061	<0.001
Competitors							
P (SITE + HUM + MGMT + TN) **Ψ (MGMT)**	**1373.94**	**0.00**	**0.66**	**0.783**	**0.659**	**0.165**	
P (SITE + MGMT + TN) Ψ (MGMT)	1375.35	1.41	0.34	0.765	0.653	0.170	0.004

|							
Humans							
P (YR + SITE) **Ψ (YR)**	**834.53**	**0.00**	**0.32**	**0.227**	**0.540**	**0.156**	
P (YR + SITE + CAM) Ψ (YR)	834.72	0.18	0.29	0.242	0.536	0.158	<0.001
P (YR + SITE) Ψ (MGMT)	835.10	0.57	0.24	0.261	0.569	0.154	0.002
P (YR + SITE + TN) Ψ (YR)	836.18	1.65	0.14	0.205	0.540	0.156	0.021
Livestock							
P (YR + MGMT) **Ψ (YR + MGMT)**	**421.51**	**0.00**	**0.51**	**0.290**	**0.342**	**0.200**	
P (YR + TN + CAM + SITE) Ψ (.)	422.09	0.57	0.26	0.246	0.369	0.008	0.014
P (YR + MGMT + CAM + TN) Ψ (YR + MGMT)	422.72	1.21	0.10	0.283	0.355	0.194	0.044
P (YR + CAM + MGMT) Ψ (YR + MGMT)	423.19	1.68	0.08	0.198	0.353	0.194	<0.001
P (CAM + SITE) Ψ (YR + MGMT)	423.46	1.94	0.05	0.095	0.442	0.161	<0.001

TABLE S4: Covariates and hypothesized relationships with lion occupancy within

WAP

Variable	Code	Hypothesis	Data source
Environmental			
River density (km/km^2)	RIV	+	USGS HydroSHEDS (Lehner et al. 2006)
Average precipitation (mm/km^2)	PRC	+	WorldClim v2.0 (Fick & Hijmans 2017)
Anthropogenic			
Human occupancy	HUM	-	Camera survey
Livestock occupancy	LVS	-	Camera survey
Road density (mm/km^2)	RD	-	
Distance to unprotected edge (km)	EDG	+	UNEP WDPA
Ecological			
Wild prey availability (detections per 100 trap-nights)	PRY	+	Camera survey
Competitor occupancy	CMP	+	Camera survey
Fire pressure (mean FRP/ km^2)	FIR	-	NASA VIIRS (Schroeder et al. 2014)
Savanna land cover (% savanna/km^2)	SAV	+	USGS (Tappan et al. 2016)

FIGURE S1: Trends in average lion occupancy between national parks and hunting concessions. Only sites that were surveyed in consecutive years are included (National parks: WBK, ARL; Hunting concessions: KON, PCN, SIN).
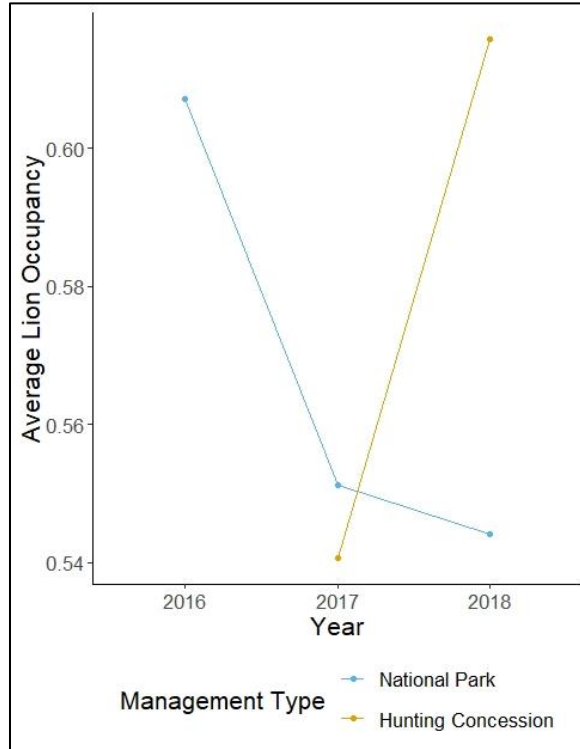
FIGURE S2: Camera placement for three survey years. 50 cameras were deployed in 2016, 115 cameras in 2017, and 73 cameras in 2018.