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Assessing the impacts of oil exploration and restoration on mammals in Murchison Falls Conservation Area, Uganda

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Abstract

Global energy demand has driven expansion of oil and gas extraction into African protected areas, raising concern about potential deleterious impacts on wildlife. Efforts aim to restore extraction sites to their original condition, but may take many years to be successful. We analysed the impact of human disturbance (road density, distance to border, sound levels and the presence of restored oil drill pads) on mammal distributions in Murchison Falls Conservation Area (MFCA), Uganda. We detected 27 mammal species using camera trap surveys within three disturbance-related strata: restored (<500 m from a restored drill pad), disturbed matrix (within the disturbed landscape but >1 km from a disturbance feature) and remote (>3 km from any disturbance). Herbivore species richness was greater within the disturbed matrix and at restored sites compared to remote areas, whereas species richness did not vary by strata for other guilds. Occupancy models fit for 15 relatively common species indicated no difference in occupancy probability across the three strata, but giraffe occupancy was higher at sites with more restored drill pads. Most species did not avoid areas of high human disturbance in this study, and new vegetation growth may attract some herbivores to restored oil sites.

Résumé

La demande mondiale en énergie pousse l'expansion de l'extraction de pétrole et de gaz jusque dans les aires protégées africaines, suscitant des inquiétudes quant aux impacts potentiellement délétères sur la nature. Des efforts visent à restaurer les sites d'extraction pour leur rendre leur état d'origine, mais cela peut prendre des années avant d'être atteint. Nous avons analysé l'impact de perturbations humaines (densité de routes, distances jusqu'aux frontières, niveau de bruit et présence de sites de forage pétrolier restaurés) sur la distribution de mammifères dans l'Aire de Conservation des Chutes de Murchison (MFCA), en Ouganda. En utilisant des pièges photographiques, nous avons détecté 27 espèces de mammifères dans trois strates de perturbation : restauré à moins de 500 m d'un site de forage ; matrice perturbée à l'intérieur du paysage perturbé mais à plus d'un km d'un élément de perturbation et ; distant, à plus de 3 km de toute perturbation. La richesse en espèces d'herbivores était plus grande dans la matrice perturbée et sur les sites restaurés que dans les zones distantes, tandis que la richesse en espèces ne variait pas selon les strates pour d'autres guildes. Des modèles d'occupation convenant à 15 espèces relativement fréquentes n'indiquaient aucune différence de probabilité d'occupation pour les trois strates, mais le taux d'occupation des girafes était plus élevé là où les sites de forage étaient plus restaurés. La plupart des espèces n'évitaient pas les lieux de fortes perturbations humaines de cette étude, et la croissance d'une nouvelle végétation pourrait attirer certains herbivores sur les sites de forage pétrolier restaurés.

KEYWORDS
camera trap, human disturbance, large mammals, occupancy modelling, oil exploration, protected area

1 | INTRODUCTION

Few ecosystems are entirely devoid of human activity, and as the global human population continues to grow, the extent and frequency of human disturbances are increasing (Geldmann, Joppa, & Burgess, 2014; Gill, Sutherland, & Watkinson, 1996; Green, Cornell, Scharlemann, & Balmford, 2005; Gutzwiller, 2002). Protected areas are established to protect wildlife from deleterious human impacts, but many suffer from human disturbances within and just outside their borders, with 33% of protected land worldwide influenced by intense human activity (DeFries, Karanth, & Pareeth, 2010; Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008; Geldmann et al., 2013, 2014 ; Jones et al., 2018). African protected areas, in particular, are increasingly isolated by rapidly growing human populations (Newmark, 2008; Population Reference Bureau, 2014; Salerno et al., 2017). Habitat loss, roads, fences, overhunting and illegal resource extraction restrict wildlife movements outside of reserves in Africa and result in edge effects that encroach on protected areas and threaten the viability of wildlife populations (Brashares, Arcese, & Sam, 2001; Fuda, Ryan, Cohen, Hartter, & Frair, 2016; Newmark, 2008; Tucker et al., 2018). Within protected areas, there are additional sources of disturbance such as roads and infrastructure for wildlife-based tourism, a vital revenue source for many African protected areas and economic driver (Newsome & Moore, 2012). More recently, global economic development and demand for energy have led to an expansion in oil and gas exploration, and oil and gas reserves in many cases overlap with protected areas and biodiversity hot spots (Harfoot et al., 2018). In Africa, oil exploration has occurred in protected areas in Gabon, the Democratic Republic of the Congo and Uganda (Coghlan, 2014; Dowhaniuk, Hartter, Ryan, Palace, & Congalton, 2018; Prinsloo, Mulondo, Mugiru, & Plumptre, 2011; Rabanal, Kuehl, Mundry, Robbins, & Boesch, 2010).

The impacts of human disturbances on wildlife have long been of interest to conservationists (Carney & Sydeman, 1999; Cole, 1991; Coleman, Schwartz, Gunther, & Creel, 2013; Dyer, O'Neill, Wasel, & Boutin, 2002; Forman & Godron, 1986; Gill et al., 1996; Madsen, 1995; Sanei & Zakaria, 2011). Human disturbance affects wildlife at multiple scales (Leblond et al., 2011). At a landscape level, disturbance may affect the distribution and persistence of wildlife populations and alter the structure and composition of wildlife communities (Duerksen, Elliott, Hobbs, Johnson, & Miller, 1997; Nellemann, Vistnes, Jordhøy, Strand, & Newton, 2003; Patten & Rotenberry, 1998; Turner, Gardner, & O'Neill, 2001; Vistnes & Nellemann, 2008; Wassenaar, Aarde, Pimm, & Ferreira, 2005). At a finer scale, individual animals may exhibit a variety of direct responses to human activity: behavioural responses such as flight (Glover, Weston, Maguire, Miller, & Christie, 2011; Stankowich, 2008), increased vigilance (Manor & Saltz, 2003), avoidance (Courbin, Fortin, Dussault, & Courtois, 2009; Dyer et al., 2002; Leblond et al., 2011) and habituation (Baudains & Lloyd, 2007); physiological responses such as heightened stress (Wasser, Keim, Taper, & Lele, 2011); and demographic responses such as decreased survival rates (Nielsen, Stenhouse, & Boyce, 2006) and reduced fecundity (Ellenberg, Mattern, Seddon, & Jorquera, 2006).

Oil and gas development involves several stages that may take decades to complete. Once potential production areas are identified, seismic surveys are used to obtain details of subsurface geological structures (Borasin et al., 2002). Following seismic testing, exploration wells are drilled to determine commercial viability of the reserve (PA Resources, 2015). Four to ten years following a discovery, the production phase begins, which may involve construction of additional wells, pipelines and refineries (Borasin et al., 2002; PA Resources, 2015). Each of these phases can impact wildlife in a variety of ways.

Short-term impacts associated with oil development include increased human presence and traffic, as well as increased generation of anthropogenic noise. During seismic surveys, large crews of workers operate vibrating and recording vehicles and explosives. During the exploration and production phases, noise is generated by construction of roads, pads and fences as well as operation of drilling equipment. Recently, researchers have begun to recognise the importance of understanding noise impacts on wildlife (Barber et al., 2011). Anthropogenic noise such as traffic or industrial noise is often both louder and more frequent than natural sounds and can have a variety of deleterious impacts on wildlife (Patricelli & Blickley, 2006), including communication disruption (Bee & Swanson, 2007; Brumm, 2004; Habib, Bayne, & Boutin, 2007; Rheindt, 2003), startling (Harrington & Veitch, 1991), avoidance (Landon, Krausman, Koenen, & Harris, 2003) and an increase in perceived predation risk (Blickley & Patricelli, 2010; Gavin & Komers, 2006; Quinn, Whittingham, Butler, & Cresswell, 2006). However, some species may habituate to noise that is not associated with dangers; for example, mule deer in Alberta habituated to highway traffic noise (Yarmoloy, Bayer, & Geist, 1988), and crop-raiding elephants may become habituated to loud noises produced by farmers attempting to deter them (Osborn & Parker, 2003). The majority of research on wildlife response to energy development has been conducted in North America, and most studies on anthropogenic noise impacts have focused on birds or marine mammals (Northrup & Wittemyer, 2012); therefore, our understanding of the potential impacts of these disturbances on large mammals in Africa is limited.

In addition to the ephemeral impacts associated with increased human activity and noise, oil activities can have longer-term impacts on wildlife. Clearing of vegetation along seismic lines and pipelines can fragment habitat and alter predator–prey interactions (Borasin et al., 2002; Dyer et al., 2002; McKenzie, Merrill, Spiteri, & Lewis, 2012), However, newer cableless seismic techniques minimise surface footprint and vegetation clearing and require less manpower (Cardama, Sanchez, & Mougenot, 2014; Ocowun & Okethwengu, 2013). Construction of drill pads and new roads and fences results in habitat loss and exacerbates fragmentation (Uganda Wildlife Authority, 2012). Additionally, improved access to remote areas can increase poaching (Northrup & Wittemyer, 2012) and oil spills can have devastating effects on entire ecosystems (Johnson, 2007; Rwakakamba, Mpiira, & Turyatemba, 2014).

Following cessation of an anthropogenic disturbance, wildlife may not immediately return to a site. In the US state of Wyoming, elk (*Cervus canadensis*) were displaced during seismic activity and for up to two weeks after surveys were completed (Gillin, 1989). Likewise, in the state of Montana, elk continued to avoid a drill pad even after drilling had ceased (Dyke & Klein, 1996). A disturbed site may be restored in an effort to expedite recolonisation by flora and fauna, but the timeline for recovery may vary by taxa and level of disturbance (Nichols & Nichols, 2003; Walker & Moral, 2003). For example, bird species richness and abundance in the state of California were lower than predisturbance levels 4 years following the restoration of flood control structures (Patten & Rotenberry, 1998). In the state of Virginia, reclaimed coal mining sites had fewer salamanders compared to mature forest sites (Carrozzino, 2009), and some salamander species took 40 years to return to predisturbance abundance at reclaimed sites (Crawford & Semlitsch, 2008). However, some species favour restored sites. For example, elk in the state of Colorado used newly reclaimed coal mining sites in proportion to their availability in spring and summer and preferentially selected for them during fall and winter (Johnson, 1990).

Occupancy modelling is useful for studying the impacts of disturbance on wildlife distribution because it facilitates investigation of relationships between species occurrence and site-specific covariates without estimating abundance, which often requires more intensive and often expensive surveys (MacKenzie et al., 2002). Occupancy models use detections from repeated surveys to simultaneously estimate species occurrence (ψ) and detection probabilities (p), thus producing unbiased parameter estimates by accounting for the confounding effects of imperfect detection (MacKenzie et al., 2006). The occupancy framework has been widely adopted for analysis of data from camera trap surveys (O'Connell, Nichols, & Karanth, 2010). Camera traps are a cost-effective and non-invasive means of studying wildlife that can detect multiple species at once (Rowcliffe & Carbone, 2008; Vermeulen, Huynen, Trolliet, & Hambuckers, 2014), including rare or nocturnal species that may be missed by other survey methods (Pettorelli, Lobora, Msuha, Foley, & Durant, 2010; Sollmann, Azlan, & Kelly, 2013).

In this study, we used camera traps and occupancy models to quantify the potential effects of anthropogenic disturbance on mammal distribution in Murchison Falls Conservation Area (MFCA), Uganda, a protected area where oil exploration was recently completed and exploratory drill pads and access roads were restored. We examined both the effects of past oil-related disturbance, measured as the density of restored oil drill pads, and ongoing human disturbance/features, measured as road density, distance to protected area border and sound levels, on mammal occupancy and detection probabilities. Understanding the effects of past and present disturbance, and evaluating effectiveness of restoration strategies, is essential to shaping successful mitigation strategies for energy extraction activities in African protected areas.

2 | MATERIALS AND METHODS

2.1 | Study area

Murchison Falls Conservation Area, in northwest Uganda (Figure 1), is located within the Albertine Rift biodiversity hot spot and protects 144 species of mammals and 556 bird species (Plumptre et al., 2003; Plumptre, Ayebare, Mugabe, Ayebare, & Mudumba, 2015). It is the county's largest (5,595 km^2) and most visited protected area, with more than 70,000 visitors in 2014 (Uganda Bureau of Statistics, 2015).

Murchison Falls Conservation Area comprises Murchison Falls National Park, where our camera sites were located, and three surrounding reserves: Bugungu Wildlife Reserve (336 km^2), Budongo Forest Reserve (817 km^2) and Karuma Wildlife Reserve (574 km^2) (Prinsloo et al., 2011) (Figure 1). Elevation in MFCA ranges from 619 to 1,271 m, and temperature ranges from 22 to 29°C (Olupot, Parry, Gunness, & Plumptre, 2012). Average annual rainfall ranges from 1,100 mm to 1,500 mm and occurs in a bimodal seasonal pattern (Laws, Parker, & Johnstone, 1975; Mann, 1995; Prinsloo et al., 2011). Major vegetation types in the national park and the two wildlife reserves include grassland, woodland and swamps, while Budongo Forest Reserve is made up of semi-deciduous forest (Ayebare, 2011; Nampindo, Phillipps, & Plumptre, 2005; Olupot et al., 2012).

The first exploratory well within MFCA was drilled in 2008 (Total E&P Uganda, 2013), and subsequently, 32 exploratory drill pads (approx. 100 × 100 m) were constructed inside MFCA, entailing removal of vegetation in drill pads, construction of access roads and fences, and movement and operation of drilling equipment (M. Dhabasadha, oil warden, *pers. commun.*). Drilling activity was concentrated in the Nile Delta region, an area also popular for wildlife

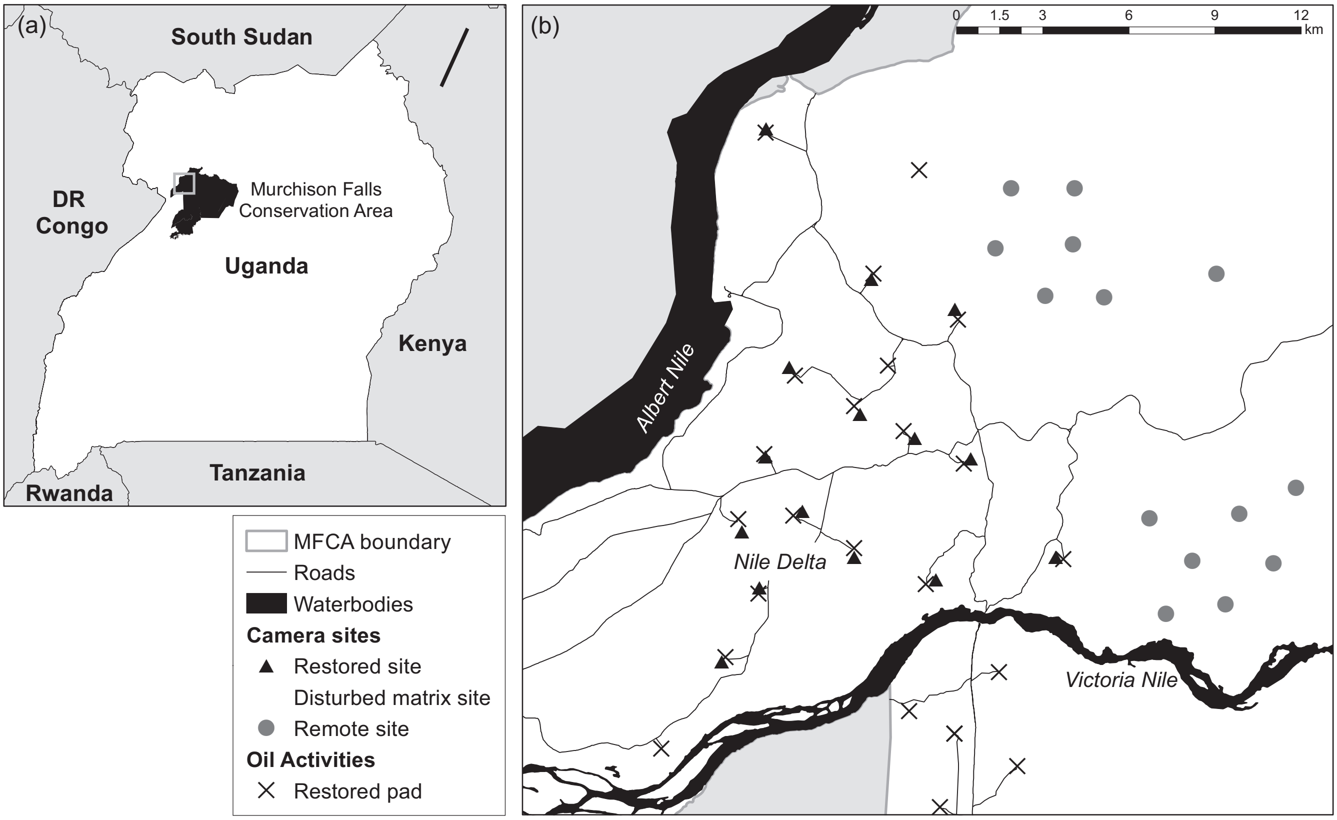

FIGURE 1 (a) Location of Murchison Falls National Park in northwest Uganda, (b) Study area in 2014 with camera trap sites in three strata: restored (<500 m of restored drill pad), disturbed matrix (>1 km from disturbance) and remote (>3 km from disturbance)

tourism (Kityo, 2011, Figure 1). Upon completion of the appraisal period in early 2014, all drill pads and pad access roads north of the Nile were restored. Restoration involved removal of all equipment and murram (a laterite soil used for building roads in East Africa) at the site, scarification of subsoil, reinstatement of topsoil and translocation of native grasses from nearby areas to the decommissioned access road and pad footprint (Total E&P Uganda, 2013). There was no replanting of native trees or shrubs, which resulted in restored sites being more heavily dominated by grasses, compared to surrounding areas (*pers. obs.*).

2.2 | Camera trap survey

From May to August 2014, we surveyed the Nile Delta area of MFCA and the area to the east using 15 infrared motion-triggered camera traps (Figure 1). To maximise the number of sites and improve precision (Guillera-Arroita, Ridout, & Morgan, 2010), we moved cameras twice during the study period creating a total of 45 sites with 15 sites each within three disturbance strata. During each subsurvey period, cameras were placed at five sites in each stratum. All sites were >2 km apart. Two strata occurred within the delta area, where both oil and tourist activities were concentrated: *restored sites* and *disturbed matrix sites*. Restored sites were located <500 m from a restored drill pad while disturbed matrix sites were located >1 km from any drill pads, roads, protected area boundary or other human infrastructure. We established a third stratum, *remote*, to the east and northeast of the delta region, an area with relatively few roads and little infrastructure. Remote sites were >3 km from roads, the protected area boundary, or other human disturbance, and within 9 km from the nearest restored or disturbed matrix site. We randomly located sites using the above criteria in ArcGIS and, upon arrival at the site, secured cameras on the nearest suitably sized tree using a locking cable at a height of 40 cm, to facilitate detection of both large- and medium-sized mammals (Ancrenaz, Hearn, Ross, Sollmann, & Wilting, 2012). To measure sound levels, we concurrently deployed Convergence Instruments Noise Sentry RT sound level metres at each site and recorded sound levels for up to 7 days (due to limitations on battery life).

2.3 | Site covariates

Since both occupancy (ψ) and detection probabilities (p) are related to local abundances (MacKenzie et al., 2006; Royle & Nichols, 2003; Royle, Nichols, & Kéry, 2005), we hypothesised that covariates affecting ψ may also affect p (Table 1, Lewis et al., 2015). We investigated the effects of two environmental and five anthropogenic covariates on species occupancy and detection. Environmental covariates included distance to water and land cover type. Land cover type was either grassland (tree/shrub cover <10%) or shrub (tree/shrub cover >10% and <50%). Anthropogenic covariates included

TABLE 1 Mammal species detected by camera trap survey with total number of detections (# det) and number of sites with at least one detection (# sites)

					Hypothesised relationships: ψ and p		
Common name	**Scientific name**	**# det**	**# sites**	$\hat{c}$	**dw**	**shrub**	**ant**[a]
Common warthog	*Phacochoerus africanus*	294	41	1.00	ψ(-) p(-)	ψ(-) p(-)	ψ(-) p(-)
Uganda kob	*Kobus kob*	252	25	2.93	ψ(-) p(-)	ψ(-) p(-)	ψ(-) p(-)
Hartebeest	*Alcelaphus buselaphus*	244	31	1.11	NA	ψ(-) p(-)	ψ(-) p(-)
Oribi	*Ourebia ourebi*	172	26	1.02	NA	ψ(-) p(-)	ψ(-) p(-)
Buffalo	*Syncerus caffer*	148	26	1.05	ψ(-) p(-)	ψ(NA) p(-)	ψ(-) p(-)
Defassa waterbuck	*Kobus ellipsiprymnus*	109	24	1.90	ψ(-) p(-)	ψ(NA) p(-)	ψ(-) p(-)
Elephant	*Loxodonta africana*	97	35	5.51	ψ(-) p(-)	ψ(NA) p(-)	ψ(-) p(-)
Rothschild's giraffe	*Giraffa camelopardalis rothschildi*	97	31	0.87	NA	ψ(NA) p(-)	ψ(-) p(-)
Common hippopotamus	*Hippopotamus amphibius*	67	13	1.51	ψ(-) p(-)	ψ(-) p(-)	ψ(-) p(-)
Olive baboon	*Papio anubis*	51	21	1.23	ψ(-) p(-)	ψ(NA) p(-)	NA
Spotted hyaena	*Crocuta crocuta*	45	20	2.35	NA	ψ(NA) p(-)	ψ(-) p(-)
Crested porcupine	*Hystrix cristata*	39	12	1.34	NA	ψ(NA) p(-)	ψ(-) p(-)
Bushbuck	*Tragelaphus scriptus*	38	15	0.95	ψ(-) p(-)	ψ(+) p(+)	ψ(-) p(-)
Patas monkey	*Erythrocebus patas*	33	13	0.78	ψ(-) p(-)	ψ(-) p(-)	ψ(-) p(-)
Aardvark	*Orycteropus afer*	27	13	1.31	NA	ψ(NA) p(-)	ψ(-) p(-)
Leopard	*Panthera pardus*	14	12				
Common duiker	*Sylvicapra grimmia*	5	4				
Bunyoro rabbit	*Poelagus marjorita*	4	2				
Rusty-spotted genet	*Genetta maculata*	4	4				
Bushpig	*Potamochoerus larvatus*	3	3				
White-tailed mongoose	*Ichneumia albicauda*	3	2				
Striped ground squirrel	*Xerus erythropus*	2	1				
Lion	*Panthera leo*	2	2				
Reedbuck	*Redunca redunca*	2	2				
Gambian pouched rat	*Cricetomys gambianus*	2	1				
Large grey mongoose	*Herpestes ichneumon*	1	1				
Black-backed jackal	*Canis mesomelas*	1	1				

Note. Shaded rows represent species with adequate detections for occupancy models, species with <27 detections failed to converge. Also listed are hypothesised relationships for occupancy (ψ) and detection probability (p) with distance to water (dw), shrub land cover type and anthropogenic disturbance covariates (ant).

[a]Anthropogenic covariates included equivalent average sound level (LEQ), distance to MFCA border, road density within 5 km of site and number of restored oil drill pads within 5 km of site

stratum (restored, disturbed matrix, or remote), distance to protected area border, road density within 5 km of site, number of restored drill pads within 5 km of site and equivalent average sound level LEQ—a measure of ambient sound (Pater, Grubb, & Delaney, 2009). We tested for differences in sound levels among strata using a one-way analysis of variance (ANOVA). We measured road density and number of restored drill pads within 5 km of the site because Benítez-López, Alkemade, and Verweij (2010) found that human disturbance could negatively impact mammal densities for up to 5 km. We z-standardised all covariates and examined correlation among covariates using Pearson's correlation coefficient (r). Covariates were not strongly correlated ($|r|<0.6$); therefore, we retained all covariates in the global model (Dormann et al., 2013).

2.4 | Data analysis

We identified all mammals in photographs to species. To determine whether sampling effort was adequate, we constructed mean species accumulation curves by feeding guild, adding camera trap days in random order with 1,000 permutations (Gotelli & Colwell, 2001; Oksanen et al., 2015). We assigned species to one of four feeding guilds (herbivore, carnivore, omnivore or insectivore) and compared

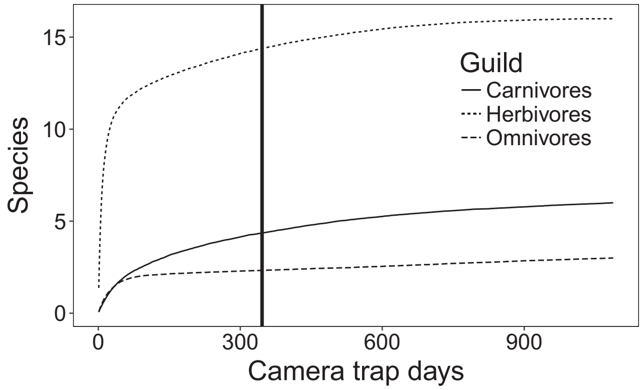

FIGURE 2 Species accumulation curve by feeding guild for mammals detected by a 2014 camera trap study in Murchison Falls National Park, Uganda. Bolded vertical line indicates the minimum number of camera trap nights per stratum (346). A curve for insectivores could not be calculated, because only one insectivorous species was detected

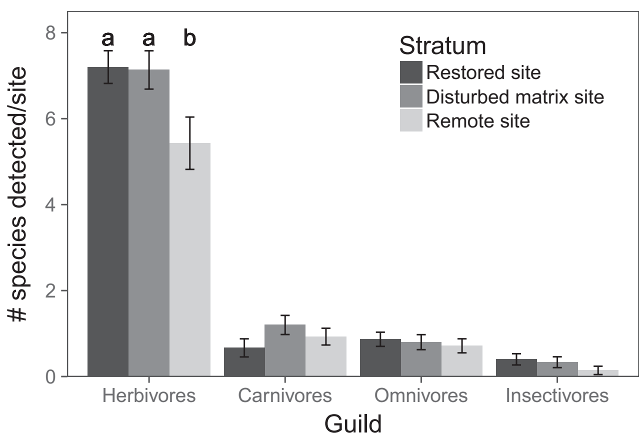

FIGURE 3 Average number of mammal species detected per camera trap site (±standard error) in Murchison Falls National Park, Uganda, by feeding guild in 2014. Means with the same lower case letters are not significantly different (Kruskal–Wallis test with post hoc Dunn's test)

the average number of species detected/site in each stratum by guild using non-parametric Kruskal–Wallis one-way ANOVA tests.

We recorded encounter histories for each species at each site. We defined sampling occasions as three consecutive sampling days to increase detection probabilities and reduce variance in parameter estimates (Cruz, Paviolo, Bó, Thompson, & Bitetti, 2014; Gantchoff & Belant, 2015; Jennings et al., 2015; MacKenzie & Royle, 2005; Ramesh & Downs, 2015). We tested the goodness of fit of each species' global or subglobal occupancy model (when the global model did not converge) using the Pearson chi-square statistic and 1,000 parametric bootstrap simulations (MacKenzie & Bailey, 2004; Mazerolle, 2015). When overdispersion was detected ($\hat{c} > 2$), we inflated standard errors by a factor of $\sqrt{\hat{c}}$. We developed a set of 40 candidate models for occupancy and detection, each representing the possible effects of either environmental covariates, anthropogenic covariates, or a combination of both. We used a multi-stage approach, first running candidate models for p in the R package *unmarked* (Fiske & Chandler, 2011), while holding the global model for ψ constant, and compared models using Akaike's information criterion corrected for small sample size (AIC_c), or quasi-likelihood AIC_c ($QAIC_c$), in the case of overdispersion (Burnham & Anderson, 2002). Second, we held the best detection model for each species constant in subsequent comparisons of candidate models for ψ (Schuette, Wagner, Wagner, & Creel, 2013; Widdows, Ramesh, & Downs, 2015). We identified the top model set (ΔAICc < 2 or ΔQAICc < 2) for each species, excluding models equivalent to a higher-ranked model except for the addition of uninformative parameters (Arnold, 2010; Burnham & Anderson, 2002).

3 | RESULTS

We removed one site from the analysis due to camera damage by spotted hyaena (*Crocuta crocuta*) shortly after deployment, leaving 44 sites across the three strata. We achieved 1,089 total trap nights, with ≥346 trap nights/stratum, and an average of 24.75 ± 0.77 *SE* trap nights/site. Photos yielded 1,756 detections of 27 mammal species (Table 1). Species accumulation curves revealed that 346 trap nights was adequate to detect at least four of the six carnivores (67%), 14 of the 16 herbivores (88%) and all three of the omnivores detected over the full course of our study (Figure 2). Species richness differed among strata only for herbivores (Kruskal–Wallis $H_c = 6.08$, $p = 0.05$, Figure 3), with the number of herbivores being 33% and 31% higher at restored sites and within the disturbed matrix, respectively, than at remote sites (post hoc Dunn's test, $p = 0.02$). Herbivore richness did not differ between restored sites and the disturbed matrix ($p = 0.50$).

3.1 | Occupancy models

Models failed to converge for 12 species having ≤14 detections (Table 1). For another 12 species, models indicated adequate fit ($\hat{c} \approx 1$). Models for spotted hyaena ($\hat{c} = 2.35$) and Uganda kob (*Kobus kob thomasi*, $\hat{c} = 2.93$) indicated overdispersion, and, for spotted hyaena, the null model without covariates for both ψ and p had the most support ($w_i = 0.28$, Table 2). We excluded the model for elephant (*Loxodonta africana*) because $\hat{c} = 5.51$, which may indicate poor specification leading to inaccurate inferences (MacKenzie & Bailey, 2004).

3.2 | Environmental covariates

Land cover type was a problematic covariate, as only five sites were located in shrub (all others were in grassland) and only four species had >6 total detections at shrub sites: bushbuck (*Tragelaphus scriptus*), common hippopotamus (*Hippopotamus amphibius*), common warthog (*Phacochoerus africanus*) and waterbuck (*Kobus ellipsiprymnus*). We excluded land cover from candidate models for all other

TABLE 2 Top-ranked occupancy models (ΔAICc < 2 or QAICc < 2) for mammal species by guild detected in a 2014 camera trap study in Murchison Falls National Park, Uganda

				Occupancy covariates					Detection covariates						
Guild	Species	ψ	p	Distance to water[a]	LEQ	Distance to border	Road density	# of restored pads	Distance to water[a]	Land cover[b]	LEQ	Distance to border	Road density	# of restored pads	w_i
browser	gira	0.90 (0.09)	0.25 (0.03)					**2.09 (0.98)**		NA		**0.60 (0.20)**	**0.54 (0.20)**		0.14
		0.87 (0.08)	0.24 (0.03)			**−1.50 (0.61)**				NA		**0.63 (0.20)**	**0.60 (0.19)**		0.12
browser	bshb	0.49 (0.11)	0.14 (0.03)						**−0.72 (0.27)**						0.17
grazer	buff	0.70 (0.10)	0.40 (0.04)	**2.30 (0.70)**	**1.18 (0.58)**					NA				**0.55 (0.14)**	0.58
grazer	hart	0.76 (0.08)	0.49 (0.03)	0.90 (0.47)						NA				**0.59 (0.13)**	0.24
grazer	hipp	0.54 (0.13)	0.10 (0.04)				**−1.39 (0.65)**		**−2.48 (0.52)**			**0.77 (0.21)**			0.16
		0.53 (0.14)	0.08 (0.03)		1.37 (0.80)				**−2.66 (0.52)**			**0.86 (0.21)**			0.08
grazer	kob	0.59 (0.08)	0.51 (0.04)							NA		**−0.89 (0.29)**			0.22
grazer	orib	0.76 (0.10)	0.35 (0.04)	**2.00 (0.70)**						NA		−0.39 (0.22)	**0.48 (0.21)**	**0.36 (0.15)**	0.27
grazer	wabu	0.59 (0.09)	0.26 (0.04)[b]	**−0.90 (0.40)**						**1.19 (0.38)**				**−0.46 (0.19)**	0.10
grazer	wart	0.96 (0.04)	0.48 (0.03)	NA	NA	NA	NA	NA					0.17 (0.11)		0.12
rooter[c]	porc	0.32 (0.08)	0.24 (0.05)							NA	**0.78 (0.33)**				0.27
insecti-vore	aard	0.51 (0.15)	0.10 (0.03)		−1.17 (0.67)				**−0.65 (0.28)**	NA		**−0.94 (0.34)**			0.35
omni-vore	babo	0.59 (0.11)	0.18 (0.03)		**0.98 (0.47)**				**−0.68 (0.34)**	NA		**0.66 (0.27)**		**0.59 (0.39)**	0.32
omni-vore	pata	0.51 (0.17)	0.04 (0.02)				1.19 (0.77)			NA		**−2.11 (0.49)**			0.16
		0.66 (0.14)	0.03 (0.02)									**−2.23 (0.47)**			0.12
carni-vore	hyen	0.58 (0.11)	0.17 (0.03)												0.28

Note. Indicated are estimates of occupancy (ψ, with standard error) and detection probabilities (p, with standard error), parameter estimates (with standard error) for occupancy covariates, parameter estimates (with standard error) for detection covariates, and Akaike weights (w_i). Parameter estimates in bold are significant at $\alpha = 0.05$.

aard: aardvark; babo: olive baboon; bshb: bushbuck; buff: African buffalo; gira: Rothschild's giraffe; hart: hartebeest; hipp: common hippopotamus; hyen: spotted hyaena; kob: Uganda kob; orib: oribi; pata: patas monkey; wabu: Defassa waterbuck.

[a]For common hippopotamus, distance to water measured distance to the Nile River only, as this was the only river in the study area large enough to support hippopotamuses. [b]Reference land cover type was grassland. [c]The diet of crested porcupine consists of roots, bulbs, bark and fruit.

species because models including this covariate either failed to converge or failed to provide meaningful parameter estimates.

Environmental covariates were included in top models for detection probability for several species. The top model for waterbuck indicated that waterbuck were more likely to be detected in shrubland than grassland. Detection rate declined with increasing distance to water for four species: hippopotamus, olive baboon (*Papio anubis*), bushbuck and aardvark (*Orycteropus afer*). Top models did not indicate a significant effect of land cover on occupancy for any species. Distance to water was included as an occupancy covariate for four species, with occupancy probability declining with distance to water for waterbuck while increasing for buffalo (*Syncerus caffer*), hartebeest (*Alcelaphus bucelaphus*) and oribi (*Ourebia ourebi*; Table 2).

3.3 | Effect of anthropogenic covariates

Although we expected covariates representing anthropogenic disturbance to negatively affect occupancy for most species, responses varied considerably among species (Table 2). Stratum was not retained in any top models, indicating that neither ψ nor p differed among restored sites, the disturbed matrix and remote sites.

In terms of species detection probability, responses to disturbance covariates were more prevalent (Table 2). The number of restored drill pads within 5 km decreased detection probability for waterbuck, but increased detection probabilities for buffalo, hartebeest, oribi and baboon. Likewise, giraffe, oribi and warthog were more likely to be detected at sites with higher road densities. Distance to protected area boundary affected detectability of seven species: with three species showing a lower detection probability (giraffe, baboon and hippo) and four species showing a higher detection probability (kob, oribi, aardvark and patas monkey) at sites closer to the border. Finally, noise levels were positively associated with p only for crested porcupine (*Hystrix cristata*).

Occupancy of most species (10 of 14) showed no response to distance from the protected area border, density of roads or the number of restored drill pads within 5 km (Table 2). However, giraffe (*Giraffa camelopardalis rothschildi*) was more likely to occupy sites with higher restored drill pad densities or sites closer to the protected area boundary (Table 2). Patas monkey (*Erythrocebus patas*) was more likely and hippopotamus less likely to occupy sites as the density of roads increased. Noise level did not differ significantly among strata (ANOVA: $F_{2, 41} = 0.2$, $p = 0.82$), but was negatively

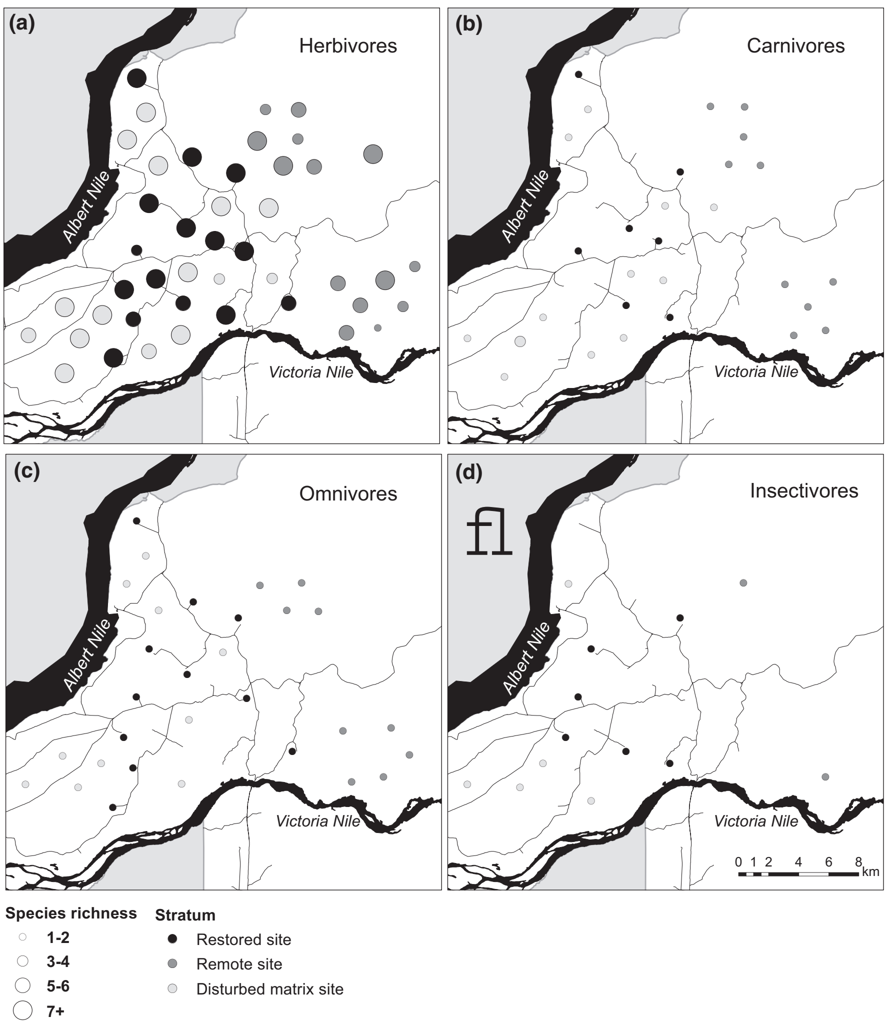

FIGURE 4 Mammal species richness at camera trap sites in Murchison Falls National Park, Uganda, in 2014 for (a) herbivores, (b) carnivores, (c) omnivores and (d) insectivores

associated with aardvark occupancy and positively associated with buffalo, hippopotamus and baboon occupancy (Table 2).

4 | DISCUSSION

Contrary to our expectations, we found little evidence to indicate that wildlife is avoiding areas with higher levels of human disturbance within MFCA. While a distance sampling study in 2011 found that several mammal species avoided areas up to 2 km around *active* drill pads in MFCA (Plumptre et al., 2015; Prinsloo et al., 2011), we did not detect avoidance of *restored* drill pads by any animals. In fact, giraffe indicated a positive association with higher restored drill pad densities. Furthermore, despite higher levels of disturbance, sites in the delta region of MFCA had greater herbivore species richness than remote sites (Figure 4a). During restoration, drill pad soils are scarified, replanted with native grasses and watered. The resulting disturbance and new vegetation growth associated with recently restored drill pads and access roads could attract grazing species to the delta area (Bischof et al., 2012; Merkle et al., 2016). A similar effect was seen in Colorado, where Webb et al. (2011) found that elk were attracted to drill pads due to reseeding and new growth on disturbed soils. Alternatively, the apparent attraction of some species to the more-disturbed delta area could be a function of differences in land cover/vegetation type not measured by our grassland/shrub categories, or even historical patterns of poaching. After years of conflict (and heavy poaching) in northern MFCA, the delta was the first area in MFCA that was reopened for tourism (Briggs, 2013). The delta is also an important watering ground for many species, and aerial surveys conducted prior to any oil activities found a higher species richness of large mammals in the delta region compared to other parts of MFCA, indicating that factors other than the presence of restored sites are likely attracting wildlife to the region (National Environment Management Authority, 2010).

We were able to run models for only one large carnivore species, spotted hyaena, and did not detect any impact of human disturbance covariates on hyaena occupancy. Since occupancy of most prey species was unaffected by disturbance covariates, it is likely that hyaena occupancy may be primarily driven by prey distribution. One species that did exhibit negative impacts of disturbance covariates was hippo, which was less likely to occupy sites with higher road densities, and more likely to be detected further from the park boundary. Hippos are the most commonly poached species in MFCA (Mudumba & Jingo, 2013) and may be more likely to avoid areas with higher human disturbance if humans pose a direct threat.

While many other studies have found that mammals avoid roads (Barnes, Barnes, Alers, & Blom, 1991; Basille et al., 2013; Kohn et al., 1999; Laurance et al., 2006; Leblond et al., 2011; Ngoprasert, Lynam, & Gale, 2007), we found that only hippos had lower occupancy in sites with high road density. Laurance et al. (2006) found that the negative effect of roads on mammal densities in Gabon was strong in a hunted area, but weak in an unhunted area. Roads in MFCA are mostly dirt tracks used primarily by tourists rather than hunters; therefore, wildlife may be less likely to avoid them as they are not currently associated with threats. Furthermore, studies assessing differences in densities are not directly comparable to our occupancy study as a site is considered occupied even if only one individual of a species used the site.

Top models for three species included a positive effect of noise levels (LEQ) on occupancy, but we suggest caution in interpreting these effects because LEQ was not significantly different among the three strata. If human disturbance was not the primary source of noise, areas with higher animal densities could potentially have higher noise levels due to increased animal communication, in which case occupancy could be positively related with higher noise levels. LEQ is a measure of ambient noise and it is possible that an analysis using measured transient noise events above a certain threshold may better isolate noise due to human disturbances (Pater et al., 2009).

An apparent source of confusion was wildlife responses to water. Whereas we would expect that certain water-dependent species such as buffalo and hippo would have higher occupancy rates at sites closer to water, our models failed to detect this relationship. However, all camera sites were located within 5 km of water, a distance that may be travelled by both hippo (Estes, 1991) and buffalo in one day (Mloszewski, 2010; Sinclair, 1977). Furthermore, findings by Ryan, Knechtel, and Getz (2006) suggest that in wetter environments such as ours (Diem, Ryan, Hartter, & Palace, 2014), available forage, rather than water, may be the primary determinant of buffalo distribution. Additionally, we measured only distance to streams, and while this study took place in the short dry season, there were other water sources such as seasonal pools and wallows present that we could not account for. A remotely sensed index such as the Modified Normalized Difference Water Index, which is useful for mapping water holes (Dzinotizei, Murwira, Zengeya, & Guerrini, 2017), might better represent water availability in this system, but was beyond the scope of this study.

Although our camera traps detected most mammals expected to occur in the MFCA, we focused on medium to large mammals, and our cameras were set too high to reliably detect smaller species. Therefore, we missed a few species of mesocarnivores: ratel, large-spotted genet, servaline genet and marsh mongoose, known to occur in the protected area. Of the 27 small to large mammal species detected, we had sufficient data to fit occupancy models for only 15, so inferences regarding disturbances on animal space use patterns are limited to these more common and widespread species. Further research is needed to determine impacts of oil exploration on rarer and more elusive species in MFCA.

5 | CONCLUSION

Results of this camera trap study indicate that wildlife may not avoid, and may even be attracted to, areas that were previously disturbed during the active drilling period in MFCA, suggesting that restoration of exploratory oil drill pads and access roads has been effective. This is an encouraging outcome, as the Nile Delta area, where oil activity is concentrated, is essential for tourism in MFCA, and tourists are largely attracted by the opportunity to view large mammals. There is a possibility for more energy development within Ugandan protected areas as an oil exploration block overlaps Queen Elizabeth National Park, another population tourist destination. Management of oil exploration within MFCA could offer lessons for other African parks considering development of oil reserves. Surface footprint was minimised through directional drilling and locating residential facilities for oil workers outside the park (MacKenzie, Fuda, Ryan, & Hartter, 2017). Furthermore, restoration of oil drill pads after the conclusion of the exploratory period further reduced surface footprint, albeit temporarily for some pads. However, our results may not translate to other systems; in more arid protected areas, wildlife may be more vulnerable to impacts if oil development affects access to limited water resources.

We were unable to assess impacts to several ecologically and economically important species in MFCA, including lions, leopards and elephants, due to poor model fit or inadequate sample sizes. Elusive and/or rare mammals may be those most vulnerable to human disturbance impacts; therefore, we recommend further research on space use of these species in relation to oil activities. Plumptre et al.(2015) found that radio-collared elephants avoided seismic activities and pads that were actively being drilled, with some individuals moving back following the cessation of exploratory activities. Mudumba and Jingo (2013) found that collared lions whose home ranges included drill pads spent more time further from the pads both during and after periods of active drilling. Furthermore, lions used densely vegetated areas more during and after drilling, which could potentially impact tourists' ability to view them (Mudumba & Jingo, 2013).

While our results suggest that restoration of drill pads has been effective at reducing impacts on some species in MFCA, production is scheduled to begin by 2020 and may continue for up to 20 years (Biryabarema, 2016; Nyanzi, 2012; Shepherd, 2013). During this phase, some pads will be reopened, and active pads may have a negative influence on wildlife occurrence, as was previously shown (Prinsloo et al., 2011). Plans for construction of a potential pipeline to transport oil from wells within the park to a processing facility also raise concern about further disturbance and the potential for spills (Ntujju et al., 2015).

Research focusing on oil impacts on wildlife in MFCA has thus far assessed avoidance (or lack thereof) by wildlife of areas currently or recently disturbed by oil activities. However, avoidance is a behavioural response, which may or may not have population-level consequences (Gill, Norris, & Sutherland, 2001). Moreover, animals may be unable to avoid anthropogenic disturbances when they directly coincide with large-scale gradients in habitat productivity; in MFCA, both oil and tourist activities are concentrated in the Nile Delta area, an important watering refuge for wildlife during the dry season. Further research is required to determine whether oil exploration has long-term and population-level impacts on wildlife in MFCA through prolonged and increased stress and consequently reduced survival rates or reproductive success. As the global need for energy drives further expansion in the oil industry, understanding the impacts of oil activities on African wildlife will become increasingly important.

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