EFFECTS OF HUNTING AND HUMAN DISTURBANCE ON WILDLIFE

NEAR VILLAGES IN NORTHEASTERN GABON

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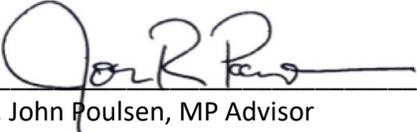Dr. John Poulsen, MP Advisor

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EXECUTIVE SUMMARY

Bushmeat from wild animals is the primary source of protein and income for many rural communities in northeastern Gabon, but mammals also provide valuable ecosystem services that may be jeopardized by unsustainable hunting practices and human disturbance. In this study, we deployed nearly 200 camera traps over two years to investigate whether hunting and other forms of human disturbance resulting from resource extraction activities, such as logging, alter mammal communities in tropical forests. The results of our study indicate that hunting and human disturbance reduces large mammal abundance close to roads and in more populated areas. In particular, chimpanzees and mandrills occurred far from roads, possibly reflecting more intense hunting of these species either for meat or in retaliation for crop raiding. Low relative abundances may be partially offset by in-migration from source populations in remote forests, but the further expansion of logging roads could disrupt this buffering mechanism. Although we did not find any significant effects for medium mammals as a group, Peter's duikers and white-bellied duikers responded negatively to hunting intensity and were more numerous farther from villages and Makokou. By contrast, small mammals, such as rats and brush-tailed porcupines, responded positively to the density of logging roads, suggesting that low abundances of medium and large mammals release them from predation and competition for resourcesor that disturbed forest provides a more favorable habitat for small mammals than primary forest. Our results indicate that anthropogenic factors strongly influence the abundances and distributions of species in our study and forecast wildlife communities dominated by small mammals in human disturbed areas.

To ensure a sustainable supply of animal protein for rural people, rural communities must actively manage their forests for wildlife. Wildlife management systems near villages should include a quota system that allows year-round hunting of small mammals, but limits hunting of large mammals to specific months, seasons, and areas. Government- or NGO-funded compensation for crop damage could ease the antipathy towards animals and conservation, and funding of community-led wildlife monitoring could raise awareness of the effects of hunting and the ecological and livelihood benefits of large mammals. Likewise, forestry operations should prohibit hunting in their concessions, and actively enforce regulations against hunting and use of logging roads.

Approved:

_____   __April 27, 2018___
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INTRODUCTION

Mammals are undergoing unprecedented declines in both geographic range and population size across much of the world (Ceballos, Ehrlich, & Dirzo, 2017). Defaunation, the loss of animals from ecological communities, is driven directly by hunting, either for subsistence or commercial purposes, and indirectly by habitat destruction and extraction of non-animal products like timber, fruits, and nuts (Brodie et al., 2014). In the tropics, large forest mammals (i.e., greater than 20 kg) are especially vulnerable to hunting and human disturbance because of their relatively low population densities, slow reproductive rates, and hunter preference for their meat (Cardillo et al., 2005). Effects of hunting and human disturbance on mammal communities are often most pronounced in 'hunting halos,' the wilderness areas closest to human populations, but may extend far into remote forest due to rapid road expansion in the area, (Abrahams, Peres, & Costa, 2017; Koerner, Poulsen, Blanchard, Okouyi & Clark, 2016).

The loss of wildlife in these areas is worrisome because wild animals are a major source of protein and income for many rural populations in the tropics (Abernethy et al., 2013; Coad et al., 2010; Poulsen, Clark, Mavah, & Elkan, 2009; Redford, 1992), especially in Central Africa where at least 1 to 3.4 million metric tons of wild meat, and possibly as much as 4.5 million metric tons, is harvested annually (Van Vliet, Fa, & Nasi, 2015; Milner-Gulland & Bennett, 2003; Fa, Peres, & Meeuwig, 2002; Fa & Peres, 2001; Wilkie & Carpenter, 1999). Among Central African countries, Gabon has the second highest bushmeat consumption per capita (Wilkie & Carpenter, 1999) with most rural households consuming bushmeat at least once every two weeks and consumption increasing with household wealth (Foerster et al., 2011). Additionally, households with members that hunt are significantly wealthier than households in which no one hunts, possibly because the availability of bushmeat offsets household food costs (Coad et al., 2010). Thus, declines in abundances of large mammals, particularly in the principal hunting areas, could affect the nutritional health and livelihoods of rural people.

In tropical forests, hunting typically occurs on foot; thus, killing the first prey encountered would minimize labor costs and effort. But game harvest profiles from Neotropical forests indicate that hunters bypass small-bodied vertebrates for large-bodied prey, especially in areas where larger species are known to exist (Jerozolimski & Peres, 2003). Previous studies of the effects of humans on wildlife communities indicate hunting and resource extraction are most intense near villages and reduce populations of large mammals in those areas (Abrahams, et al., 2017; Morrison, Sechrest, Dinerstein, Wilcove, & Lamoreux, 2007). In response, small mammals (i.e., less than 3 kg) may increase in abundance if they are released from resource competition with larger mammals (Koerner et al., 2016; Harrison, 2011). If these patterns hold true throughout the tropics, we would expect: (1) anthropogenic variables to have stronger effects on animal populations than environmental variables, (2) the relative abundance of large animals to increase in areas under less intense hunting and disturbance pressure (i.e., far away from roads and populated areas), and (3) the relative abundance of small animals to decrease with distance from villages.

Measuring the distribution and abundance of forest mammals is challenging because of the difficulty of observing cryptic, rare, or small-bodied animals in dense forest. To overcome these challenges, camera traps (i.e., motion-sensitive cameras) are increasingly being used to monitor forest mammal populations, as advances in technology have made them just as effective as traditional methods like line transects (Rovero, Zimmerman, Berzi, & Meek, 2013; Silveira, Jácomo, & Diniz-Filho, 2003). Camera traps have been used to create faunal checklists (Tobler, Carrillo-Percastegui, Leite Pitman, Mares, & Powell, 2008), detect endangered species (Head, Robbins, Mundry, Makaga, & Boesch, 2016), estimate relative abundance (Rovero et al., 2017), and model species occupancy (Tobler, Zúñiga Hartley, Carrillo-Percastegui, & Powell, 2015; Ahumada et al., 2011). Because camera traps operate non-stop and are nearly silent, they can

record nocturnal and diurnal species, as well as rare and elusive species that other methods fail to observe (Rovero et al., 2017; Ahumada et al., 2011; Tobler et al., 2008; Rovero, Jones, & Sanderson, 2005; O'Brien, Kinnaird, & Wibisono, 2003). Camera traps recently captured conclusive evidence that lions still roam the forests of Plateaux Bateke National Park in Gabon, despite being listed as locally extinct because of the lack of from other field methods (Hedwig et al., 2017; Bauer, Packer, Funston, Henschel, & Nowell, 2017).

In this study, we examine the effects of hunting and human disturbance on mammal communities in northeastern Gabon. Specifically, we test the hypothesis that hunting and human disturbance alter forest mammal community composition within village 'hunting halos' through the removal of large mammals. To do so, we employed 191 camera traps across 60 sites within 8 km of 10 villages for two years. Here we use the distances from village, nearest road, and the regional capital, Makokou, as indicators of hunting intensity. Separately, we consider logging road density and village population as indicators of disturbance intensity. To test whether human activity influences species abundances more than environmental factors, we include forest type and distance from nearest river as indicators of habitat and dry and wet seasons as indicators of climate. Based on these metrics, we examine the effects of hunting and human disturbance on forest mammal populations and identify fine-scale gradients in community composition and structure.

METHODS

Study area

We studied wildlife communities in the Ogooué-Ivindo Province near the regional capital of Makokou in northeastern Gabon (Figure 1). The study area covers approximately 8,000 km^2 and is characterized by continuous broadleaf tropical forest that gives way to a mosaic of cropland and herbaceous vegetation cover near human settlements. Elevation across the region is relatively flat, ranging between 450 and 600 m above sea level. Mean annual precipitation is approximately 1700 mm with most precipitation occurring during two wet seasons (September-December and April-May) interspersed between two relatively dry periods (January-March and June-August). The mean annual temperature near Makokou is 23.9 °C with higher temperatures (mean high temperature = 30.6 °C) between March and April and lower temperatures in July (mean high temperature = 26.7 °C). The study area is intersected by three main roads and includes approximately 60 small villages (ranging in population from 22-335) and two active forest concessions under sustainable management agreements (Koerner et al. 2016). Before the study, we visited all villages within 10–60 km of Makokou to explain the goals of the study and to assess their interest in participating. We then randomly selected 10 villages out of the 27 villages that agreed to participate, maintaining an equal representation of small, medium, and large villages (Table 1).
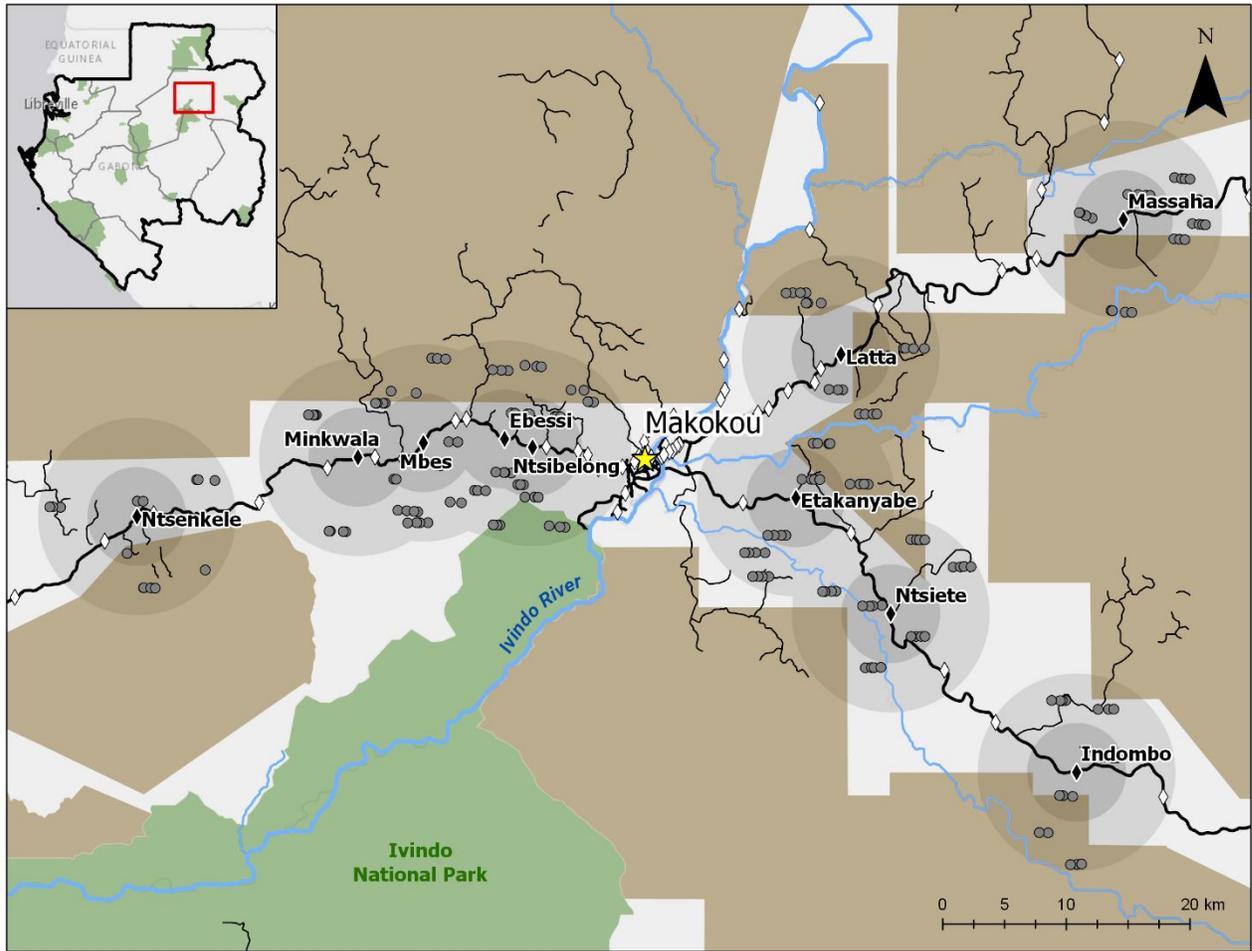
Figure 1. Map of forest concessions (brown), national parks (green), major roads (thick black lines), logging roads (thin black lines), waterways (blue lines), cities (yellow star), study villages (black diamonds), villages (white diamonds), and camera traps (dark gray circles) in the study area. Camera traps were deployed along six transects at each study village. We situated the transects at random distances and directions to study villages, locating two transects within 4 km (near) of villages and four transects between 4-8 km (far) from villages as depicted by the buffers around the villages. We chose 8 km as the maximum distance because it is roughly the distance a hunter travels in a single day, based on interviews with villagers and previous studies.

Table 1. Study village characteristics, including location, population size, distance from Makokou, number of camera traps operational for at least one day, species richness (observed and rarefied), and number of camera trapping days completed at each village. Latitude and longitude values are given in decimal degrees east of the prime meridian and north of the equator.

Village	Longitude	Latitude	Pop.	Dist. from Makokou (km)	Species Richness Observed	Species Richness Rarefied	No. of Cameras	Camera Days
Ebessi	12.74583	0.57943	36	11.5	25	21	20	611
Etakanyabe	12.95756	0.53645	256	12.6	21	16	27	565
Indombo	13.16159	0.33546	189	43.2	21	15	23	589
Latta	12.99024	0.64161	31	17.9	21	16	25	494
Massaha	13.19547	0.74036	303	43.2	19	16	21	455
Mbes	12.68680	0.57658	123	18	15	15	13	255
Minkwala	12.63930	0.56603	79	23.2	21	19	14	368
Ntsengkelle	12.47872	0.52261	149	41.4	20	19	15	358
Ntsibelong	12.76611	0.57335	87	9.1	22	18	18	511
Ntsiete	13.02649	0.45159	305	23.6	16	14	15	477

Data collection

Between January 15, 2015 and January 16, 2017, we collected wildlife data using Bushnell Trophy Cam camera traps set to record 60-second videos within one second of detecting animal movement. These camera traps have a maximum detection range of 30 m in ideal conditions and use an array of infrared LEDs to capture videos at night. We employed this camera trap model because of its high-quality videos, fast trigger speed, relatively low cost, and extensive use in other camera trap studies (Howe, Buckland, Després-Einspenner, & Kühl, 2017; Arroyo-Arce, Thomson, Fernández & Salom-Pérez, 2017; Rovero et al., 2013).

We established two 2-km transects within 4 km and four 2-km transects within 4–8 km of each village to test the effect of distance from villages on species richness and relative abundance (Figure 1). We limited the study to an 8-km radius from villages because conversations with villagers and previous studies suggest that most hunting and foraging occurs within 8–10 km from villages, although trips farther into the forest do occur (Abrahams et al., 2017; Koerner et al., 2016; Abernethy et al., 2013). Along the transects, we deployed four camera traps, placed 500 m apart. We recruited 20 para-ecologists from the study villages and trained them to operate and deploy the camera traps. To ensure that methods were consistently applied across villages (see below), each para-ecologist received three days of classroom training and practiced setting up camera traps under supervision of an expert ecologist at least twice before deploying camera traps in the field.

Para-ecologists deployed camera traps near signs of animal activity (e.g., game trails, footprints, scratch marks, scat) or fruiting trees along each transect for roughly 30 days at a time, returning every two weeks to ensure that the equipment remained operational. Camera traps were fixed to trees approximately 50 cm above the ground and no bait was used to attract animals to the observation points. After each month of data collection, the para-ecologists collected the camera traps, replaced the batteries and redeployed the camera traps along a different transect. We took precautions to limit camera trap malfunctions by storing them in cool, dry places and fully recharging batteries between deployments. Despite these precautions, high humidity, frequent rainfall, and heavy use caused several camera traps to malfunction.

To obtain data on forest types around villages, para-ecologists also recorded the dominant forest type (i.e., closed canopy, transformed, inundated) every 50 m along the transects. We considered bamboo, liana, Marantaceae, mixed, and monodominant forests as closed canopy forests. Transformed forests included plantations, logging paths, abandoned roads, and active roads. Lastly, inundated forests were characterized by the presence of standing water and included swamps, marshes, rivers, and seasonally flooded forests.

Data processing

At Duke University, six trained research technicians viewed each video and photo and electronically sorted them into directories based on the species name, number of individuals, and camera trap location, using animal guides to assist with species identification. After sorting all videos and photos, we used an automated script to extract the village, phase, transect, camera trap, species name, number of individuals, and date and time of each observation to a comma-separated values file based on the directory structure and file metadata. Using a standardized method for organizing and extracting the data helped minimize typographic errors during data entry.

Anthropogenic and environmental covariates

Both anthropogenic and environmental variables likely influence the spatial distributions of animal species. Therefore, we developed indices of the intensity of hunting and human disturbance as well as environmental indices related to habitat preferences. We calculated the Euclidean distance between each camera trap and the closest village, road, and Makokou as measures of hunting intensity with increasing distance representing a reduction in hunting intensity. To test the effects of human disturbance not necessarily related to hunting pressure, we calculated logging road density (i.e., length of logging roads) and population within the 8-km buffer (i.e., walking distance) of each camera trap with the intensity of human disturbance increasing with logging road density and population. To assess habitat preferences, we projected the information on forest type collected by para-ecologists onto each transect and assigned the nearest forest type to each camera trap and calculated the Euclidean distance between each camera trap and the nearest river. We extracted all spatial variables using ArcGIS Pro 2.0.1 (ESRI 2017).

Data analysis

We quantified sampling effort as the number of days that a camera trap operated at a single location (i.e., camera days). To avoid repeated counting of an individual animal, we defined independent species events as photo or video events separated by more than 30 minutes (Abrahams et al., 2017). In addition to excluding duplicate events from the analysis, we excluded camera trap locations with less than one day of sampling effort, assuming they were not active long enough to adequately sample the animal community. We also excluded camera trap locations if the equipment malfunctioned or did not record accurate date and time information. After filtering the data, we visually assessed sampling completeness for each village by building species accumulation curves using the "vegan" package (Figure 2; Oksanen et al., 2011).

To uncover community-level trends, we assessed species richness with three different metrics. First, to identify the most common species in the study area, we calculated the Relative Abundance Index (RAI), defined as the number of independent species events divided by the total number of events for each species (Table 2). Second, we calculated naïve occupancy to determine the spatial distribution of each species in our study site by dividing the number of camera trap sites where a species was recorded by the total number of camera trap sites (n = 191). Third, we calculated rarefied species richness, which accounts

for variation in sampling effort, by using a rarefaction function to estimate species richness around each village (Hurlbert, 1971).
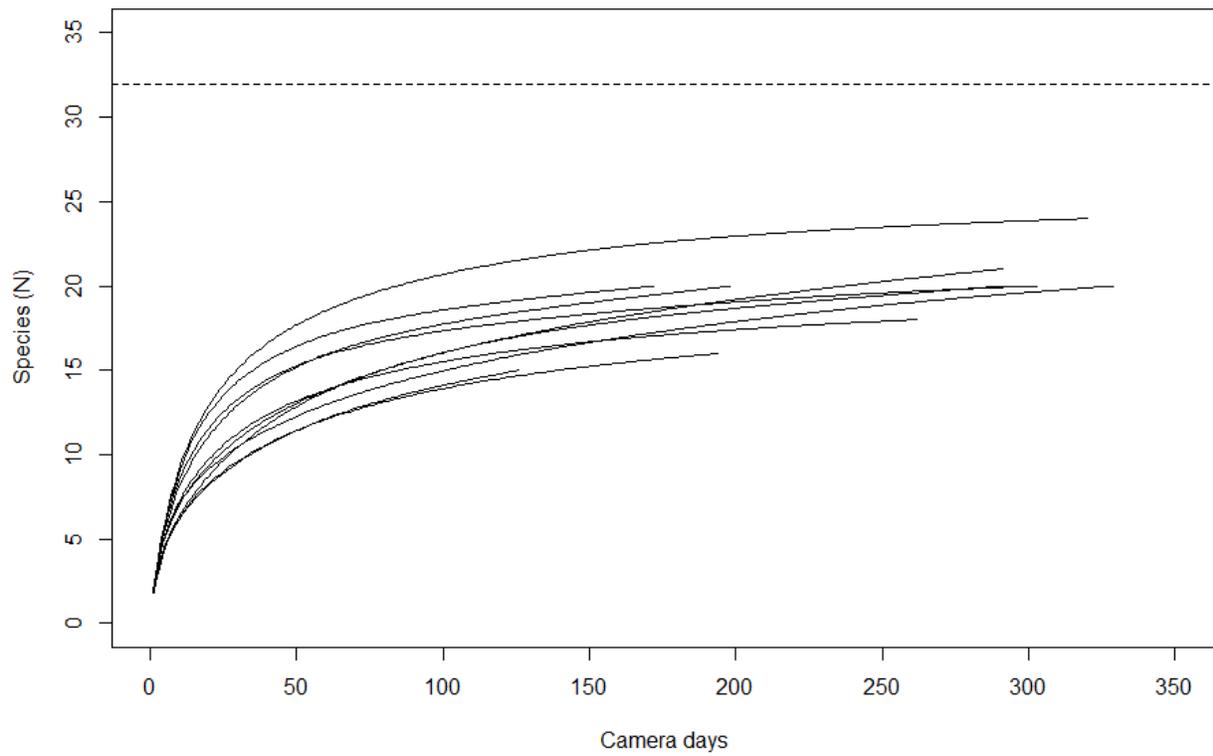

Figure 2. Species accumulation curves demonstrating sampling completeness for each village. Solid lines indicate the number of species observed at each village. The dashed line shows the total number of species observed across the entire study area.

Table 2. Mammals detected by camera trapping in northeastern Gabon, including IUCN status, mass (kg), species group (Small, Medium, Large), number of independent events (i.e., separated by at least 30 minutes), Relative Abundance Index (RAI; i.e., number of independent events for each species divided by the total number of events), and naïve occupancy (i.e., number of sites occupied by species divided by total number of sites in the study area).

Common Name	Scientific Name	Status	Mass (kg)	Species Group	No. of Events	RAI	Naïve Occupancy
Aardvark	*Orycteropus afer*	LC	61	Large	4	0.09	0.02
Civet	*Civet sp.*	-	8.5	Medium	5	0.12	0.03
Bat	*Bat sp.*	-	0.2	Small	7	0.17	0.03
Bay Duiker	*Cephalophus dorsalis*	NT	20.5	Large	62	1.46	0.21
Black-fronted Duiker	*Cephalophus nigrifrons*	LC	16	Medium	36	0.85	0.07
Blue Duiker	*Philantomba monticola*	LC	5	Medium	997	23.55	0.75
Brush-tailed Porcupine	*Atherurus africanus*	LC	2.5	Small	89	2.10	0.15
Chimpanzee	*Pan troglodytes*	EN	48	Large	47	1.11	0.18
Common Cusimanse	*Crossarchus obscurus*	LC	0.7	Small	272	6.43	0.35
De Brazza's Guenon	*Cercopithecus neglectus*	LC	5.5	Medium	8	0.19	0.01
African Forest Elephant	*Loxodonta cyclotis*	VU	2700	Elephant	216	5.10	0.44
Gabon Squirrel Galago	*Sciurocheirus gabonensis*	LC	0.3	Small	1	0.02	0.01
Genet	*Genet sp.*	-	2	Small	93	2.20	0.30
African Golden Cat	*Caracal aurata*	VU	10.8	Medium	16	0.38	0.07
Western Lowland Gorilla	*Gorilla gorilla*	CR	180	Large	5	0.12	0.03
Gray-cheeked Mangabey	*Lophocebus albigena*	LC	7.5	Medium	1	0.02	0.01
Red River Hog	*Potamochoerus porcus*	LC	88	Large	46	1.09	0.18
Honey Badger	*Mellivora capensis*	LC	10	Medium	4	0.09	0.02
Leopard	*Panthera pardus*	VU	41	Large	13	0.31	0.06
Mandrill	*Mandrillus sphinx*	VU	32.8	Large	100	2.36	0.25
Mongoose	*Mongoose sp.*	-	2.7	Small	96	2.27	0.32
Northern Talapoin	*Miopithecus ogouensis*	LC	1.3	Small	17	0.40	0.02
Pangolin	*Pangolin sp.*	-	5.5	Medium	50	1.18	0.15
Peter's Duiker	*Cephalophus callipygus*	LC	20	Medium	311	7.35	0.55
Potto	*Potto sp.*	LC	0.8	Small	4	0.09	0.02
Rat	*Rat sp.*	-	3	Small	895	21.14	0.65
Sitatunga	*Tragelaphus spekii*	LC	87.5	Large	2	0.05	0.01
Squirrel	*Squirrel sp.*	-	0.5	Small	682	16.11	0.68
Water Chevrotain	*Hyemoschus aquaticus*	LC	11.0	Medium	22	0.52	0.04
White-bellied Duiker	*Cephalophus leucogaster*	NT	15	Medium	68	1.61	0.19
White-nosed Guenon	*Cercopithecus nictitans*	LC	5.4	Medium	3	0.07	0.01
Yellow-backed Duiker	*Cephalophus silvicultor*	NT	70	Large	61	1.44	0.24

We assessed the relative effects of the anthropogenic and environmental covariates at the community-, body size, and species-level. For the community-level analysis, we examined variation in rarefied species richness across village areas using a generalized linear model (GLM) with quasi-Poisson to account for overdispersion. For the body size groups, we assigned species to small (n = 10), medium (n = 12), and large (n = 9) categories. We used a 3-kg threshold for small mammals because previous studies observed a sharp increase in extinction risk above that weight (Cardillo et al., 2005) and a 20-kg cutoff for large mammals because of differences in dietary preferences between medium and large mammals of that size (Morrison et al., 2007; Carbone, Mace, Roberts, & Macdonald, 1999). We did not include elephants in this analysis due to their extreme size and unique life history traits. For the species-level analysis, we only included species with more than 10 observations. In addition, for some species (e.g. rats, squirrels, pangolins) we assessed as species groups because we were unable to distinguish between similar species from camera trap videos and photos.

For the body size group and species-level analyses, we used generalized linear mixed models (GLMMs) to quantify the effects of anthropogenic and environmental variables on the number of observations of similar sized animals and species. GLMMs handle count data and random effects that are typical of ecological data (Bolker et al., 2009). We modeled distance from villages, distance from roads, distance from Makokou, logging road density, village population, forest type, distance from rivers, and dry/wet season as fixed effects, with month and transects nested in villages as random effects. Before building models, we screened independent variables for multicollinearity, excluding variables with a correlation coefficient greater than 0.7. We applied an offset equal to the number of camera days to account for sampling effort and used a negative binomial distribution to account for high overdispersion in the data. We used a backwards model selection process to find the best-fitting model based on minimizing AIC (Rovero et al., 2017). We used the "glmmTMB" package (Brooks et al., 2017) for all GLMMs and conducted all analyses in the R statistical software, version 3.4.2.

RESULTS

Camera traps captured 4,233 independent records of 32 mammal species over 4,726 camera trap days. Sampling effort varied between 126 and 329 camera trap days per village, primarily due to differences in rates of camera trap failure at each site. Out of 191 deployment events, 165 worked reliably (i.e., operated longer than one week)—a failure rate of 13.6%—similar to other studies in the tropics (Rovero et al., 2017).

Species richness

Blue duikers, rats, squirrels, Peter's duikers, common cusimanses, and elephants had the highest RAI and naïve occupancies. Altogether, the 15 most-detected species made up over 90% of all detections. In contrast, the Gabon squirrel galago, gray-cheeked mangabey, sitatunga, and white-nosed guenon had the lowest RAI and naïve occupancies and were only observed during one camera trap deployment each.

Observed species richness varied greatly among villages (15-25 species), likely reflecting variation in both the distribution of species and sampling effort. No village recorded all mammal species in the study area, as indicated by non-saturating species accumulation curves for each village (Figure 2). Rarefied species richness ranged from 15 species near Mbes to 21 species near Ebessi (Table 1). Although the final GLM model included village population (*p = 0.17*), distance from Makokou (*p = 0.55*), and distance from rivers (*p = 0.70*), none of the anthropogenic or ecological variables significantly predicted rarefied species richness (i.e., their effects on rarefied species richness were not significantly different from 0).

Effects of covariates on animal abundances

None of the independent variables explained significant variation in observations of the small and medium mammal groups (Figure 3; Table 3). In contrast to small and medium mammals, we observed a significant, positive effect of distance from roads ($p < 0.01$) and a significant, negative effect of population on the relative abundance of large mammals ($p = 0.01$).

Although our analysis of species grouped by body size demonstrated few effects of anthropogenic and environmental variables, our analysis of individual species was more informative and tended to follow similar trends. The relative abundances of small mammals generally increased in human dominated landscapes: for example, rats demonstrated a significant, positive response to the density of logging roads ($p = 0.01$). Brush-tailed porcupines were also found more often in areas with a high density of logging roads ($p = 0.04$) as well as close to roads ($p = 0.04$). Genets, however, tended to be found farther away from Makokou ($p = 0.02$).

In contrast, the relative abundances of medium and large mammals were generally lower in areas where humans are present. Observations of Peter's duikers increased with distance from villages ($p < 0.01$), while the relative abundance of white-bellied duikers increased with distance away from Makokou ($p < 0.01$). Population had significant, negative effects on the relative abundance of bay duikers ($p = 0.03$) and the relative abundance of golden cats ($p = 0.05$). For chimpanzees, we found significant, positive effects of distance from villages ($p = 0.01$) and distance from roads ($p = 0.03$). Mandrills were significantly more likely to be found away from roads ($p = 0.01$) and in less populated areas ($p < 0.01$).
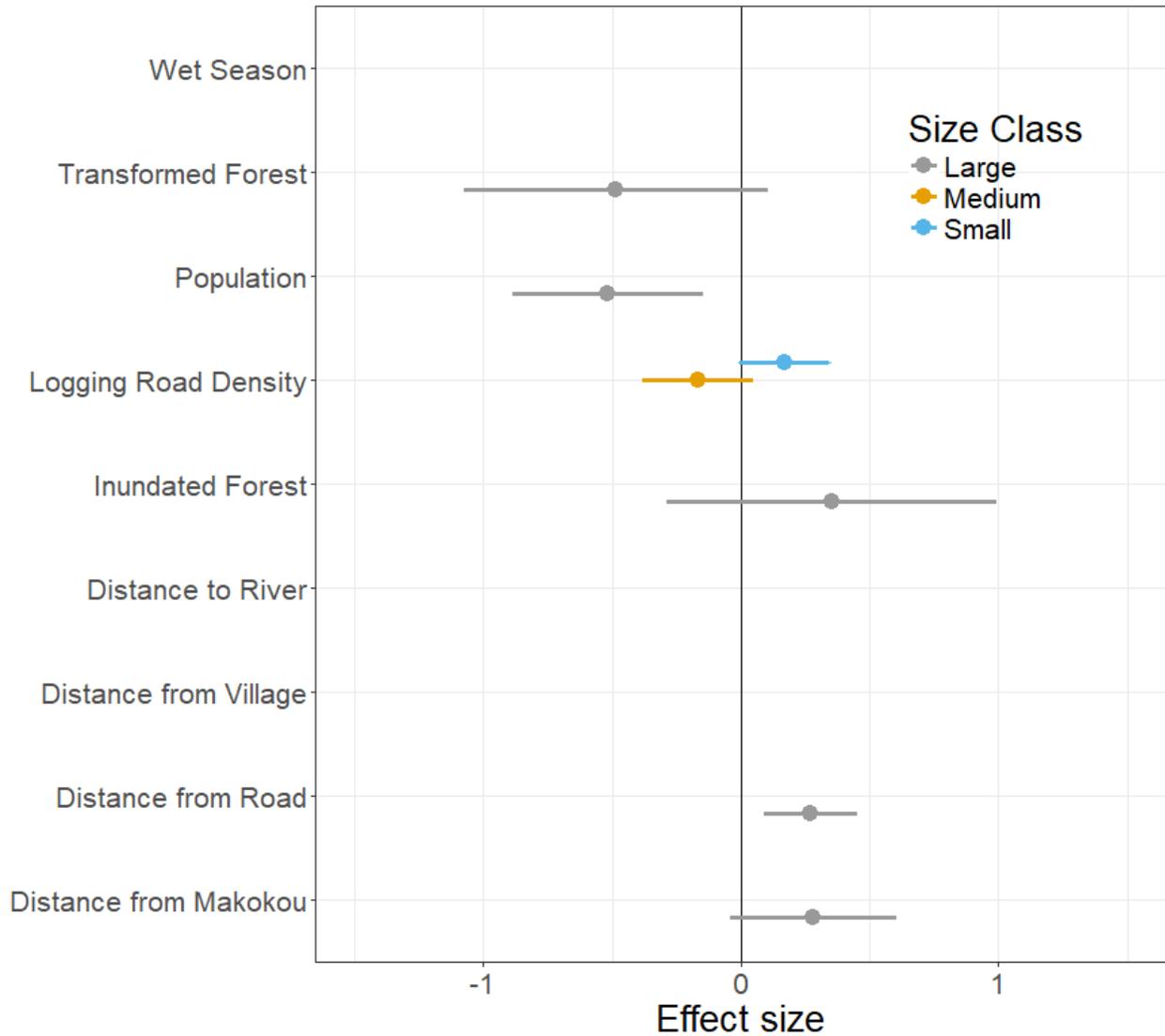
Figure 3. Relative effects and 95% confidence intervals for anthropogenic and environmental variables used in GLMMs. Large mammals (> 20 kg) are represented in gray, medium mammals (3-20 kg) are shown in orange, and small mammals (< 3 kg) are shown in blue.

Table 3. Model coefficients from GLMMs for individual species and size groups from the best-fitting model for each. Significant effects are highlighted in bold. We did not include the effects of season because seasonal differences in climate did not accurately predict relative abundances for any of the species in the study. Elephants were modeled separately from the size groups due to their extreme size and unique life history traits.

Species	Anthropogenic Factors					Environmental Factors		
	Hunting Intensity			Disturbance Intensity		Habitat		
	Distance from Villages (km)	Distance from Roads (km)	Distance from Makokou (km)	Logging Road Density (km)	Population	Transformed Forest	Inundated Forest	Distance from River (km)
Small mammals				0.169 (0.05)				
Rat				**0.288 (0.01)**				
Genet			**0.370 (0.03)**					
Squirrel	-0.143 (0.23)							
Brush-tailed porcupine		**-1.520 (0.04)**	-1.000 (0.14)	**0.794 (0.04)**		-1.826 (0.10)	1.622 (0.10)	
Common cusimanse				0.316 (0.16)		**1.101 (0.02)**	**-2.694 (0.04)**	**0.430 (0.04)**
Mongoose				0.173 (0.15)				
Medium mammals				-0.167 (0.13)				
Blue duiker				-0.194 (0.19)				
White-bellied duiker			**1.153 (< 0.01)**		-0.536 (0.12)			
Peter's duiker	**0.453 (< 0.01)**							
African golden cat		0.519 (0.09)			-0.992 (0.08)			
Pangolin	-0.380 (0.14)							
Black-fronted duiker	-1.279 (0.07)							**1.223 (0.05)**
Water Chevrotain					-1.954 (0.08)			
Large mammals		**0.270 (< 0.01)**	0.280 (0.09)		**-0.516 (0.01)**	-0.486 (0.11)	0.351 (0.28)	
Bay duiker	-0.470 (0.14)				**-0.693 (0.04)**	0.189 (0.76)	**1.262 (0.02)**	
Chimpanzee	**0.592 (0.01)**	**0.348 (0.03)**			-0.350 (0.05)	-0.895 (0.07)	0.556 (0.27)	-0.374 (0.06)
Mandrill		**0.662 (0.01)**			**-1.190 (< 0.01)**			
Red river hog	0.298 (0.13)							
Yellow-backed duiker	0.285 (0.19)							
Leopard			0.411 (0.24)					0.408 (0.28)
Elephant				0.293 (0.07)				

DISCUSSION

Human activity, even at relatively low population densities, strongly influences the abundances and distributions of terrestrial mammals in close proximity to villages in northeastern Gabon, with responses varying by species and body size. In general, large mammals exhibited negative responses to indicators of hunting and human disturbance, whereas the relative abundances of small mammals were either not affected or positively affected by human activities in disturbed areas. Medium mammals generally were not affected by anthropogenic factors, except for Peter's duikers and white-bellied duikers, which were found in higher abundances away from villages and Makokou, respectively. These results suggest that current management efforts, to the extent that they exist, are not sufficient to conserve large-bodied species within the village 'hunting halo' because they are vulnerable to overexploitation. Community wildlife monitoring programs that encourage sustainable hunting of species may be one solution to the overharvesting of large mammals.

Species richness

Despite the relatively modest sampling effort for some villages, rarefied species richness estimates obtained in this study are comparable to other camera trap studies conducted in African tropical forests (Rovero et al., 2017). Although large villages tended to support fewer species than small villages, we found no significant relationship between rarefied species richness and any of the covariates in our study. Population had the strongest negative effect on rarefied species richness and might reflect high hunting pressure or disturbance intensity. Other studies have shown similarly weak negative effects of human population density on species richness (Newbold et al., 2015). Because the analysis was conducted at the village level, our sample of 10 villages may not have provided enough statistical power to determine among-village drivers of species richness.

Effects of covariates on animal abundances

Our results suggest that body size is one component of sensitivity to hunting and human disturbance, but other factors like species-specific habitat preferences and hunter preferences likely also play roles. We found that large-bodied mammals, as a group, were negatively affected by human activities. By contrast, we did not detect significant effects of human or environmental variables on small- and medium-sized groups of mammals. There are several possible explanations for the lack of consistent drivers of abundances of small and medium mammal groups: 1) small sample sizes for some of the species within body size groups may have obfuscated overarching trends when species are grouped by body size; 2) body size groups may incorporate multiple trophic guilds (omnivores, herbivores, carnivores) that respond differently to the environment and human activities, and therefore body size alone may be a poor descriptor of animal groups; or, 3) small and medium mammals may not be affected by human activities, either because they are less frequently hunted than large mammals, or can reproduce rapidly to replenish their populations in hunted areas.

When assessed at the species-level, the relative abundance of small species generally increased in response to hunting and human disturbance. Relative abundances of rats and brush-tailed porcupines both increased in areas with higher densities of logging roads, supporting other studies that show a similar relationship between rodent abundance and logging roads (Malcolm & Ray, 2000). We also observed brush-tailed porcupines more frequently near roads, where we assume hunting activity is more intense. These results are similar to findings in southern Gabon that found a positive effect of hunting intensity on rodent abundance and suggest that hunting intensity can be approximated by distance from nearest road (Effiom, Nunez-Iturri, Smith, Ottosson, & Olsson, 2013; Laurance et al., 2008). Because mandrills and other

large mammals, which prey upon brush-tailed porcupines and other small mammals, are found in lower abundances close to roads, hunting pressure on large mammals may release small mammals from predation or competition for resources, allowing small mammals to increase in abundance (Fa & Brown, 2009; Lahm, 1986). Alternatively, degraded secondary vegetation (i.e., transformed forests) created by road construction, agriculture, or logging and resource extraction could account for the patterns of abundance we observed, regardless of hunting pressure (Djagoun et al., 2018; Muchaal & Ngandjui, 1999). However, this alternative explanation is only supported for the common cusimanse as it is the only small mammal species that showed a significant, positive association with transformed forests and other habitat variables. Therefore, because hunters also use logging roads as forest entry points, increased rodent abundances close to roads and in areas with high densities of logging roads suggest that hunting and human disturbance may be reducing large mammal populations in these areas.

Although the relative abundances of some species (i.e., white-bellied duikers and Peter's duikers) increased in response to decreasing hunting pressure (i.e., greater distance from villages or major cities), we found no evidence that medium mammals, as a group, are influenced by any of the anthropogenic variables in this study. The lack of significant effects of hunting and human disturbance on medium mammals could suggest that hunting has depressed the abundance of this group throughout the 8-km radius, but this cannot be the case for all medium species as blue duikers are among the most abundant species observed and the most hunted in the region. Alternatively, several species may have been too rare to detect frequently enough and model accurately. Five of the 12 medium mammal species had fewer than 10 observations.

Interestingly, Peter's duikers and white-bellied duikers, two of the largest species included in the medium mammal group demonstrated significant, negative responses to human activity, indicating they may be less resilient than other frequently hunted medium mammals like the blue duiker, which can tolerate a range of human-modified landscapes and persist in small patches (Hart & Kingdon, 2013). White-bellied duikers generally occur at lower densities than other medium duikers and are rarely recorded outside of primary forests (Newing, 2001; Hart, 2013). Peter's duikers are widespread in primary forests and logged forests with dense undergrowth, but population levels tend to be low where hunting pressure is high (East, 1999). In Gabon, Peter's duikers are also more likely to be sold than other species, which may account for our observation of localized depletions near Makokou, where demand is higher (Van Vliet & Nasi, 2008). The combination of habitat degradation and hunter preference for these larger species may make them more susceptible to anthropogenic factors and suggests that they face threats similar to species in the large mammal group.

Of the three size classes, large mammals were the most sensitive to our indicators of hunting and human disturbance indicators. Large mammals generally avoided roads and populated areas, but responses varied by species. For example, the relative abundance of mandrills was higher with distance from roads and in less populated areas. These patterns may reflect elevated hunting intensity near villages and roads because they are frequently used by hunters as entry points into the forest (Laporte, Stabach, Grosch, Lin, & Goetz, 2007). Retaliation for crop-raiding, which is more likely to occur in highly populated rural areas, may also be responsible for lower abundances in these areas (Oates & Butynski, 2008). Alternatively, mandrills may avoid these areas because they are sensitive to human noise and activity. Like mandrills, chimpanzees were especially sensitive to our measures of hunting pressure (i.e., distance from roads and villages), which again could reflect real population declines or human avoidance behavior. More research is needed to decouple these possible explanations.

Study limitations

Camera traps enabled the monitoring of nocturnal and rare animals like pangolins and porcupines that are rarely surveyed in census of tropical mammals (Koerner et al., 2016; Poulsen, Clark, & Bolker, 2011). But, despite these advantages, we only sampled a subset of the wildlife community in this study. Camera traps consistently capture ground-dwelling mammals, but the same threats of hunting and human disturbance affect many arboreal species as well, including monkeys like the De Brazza's guenon and the gray-cheeked mangabey (Oates, Groves, & Ehardt, 2008; Struhsaker, Oates, & Butynski, 2008). Sampling designs for arboreal camera traps are being tested across the tropics and could be used to augment existing ground-based designs to capture a wider range of the mammalian community in the future (Whitworth, Braunholtz, Huarcaya, MacLeod, & Beirne, 2016; Bowler, Tobler, Endress, Gilmore, & Anderson, 2016). Similarly, more than half of the camera trap deployments we sampled operated for less than 30 days, which may not be sufficient to adequately sample rare species or species with large home ranges (Rovero et al. 2013; Hammel et al. 2013). Deployment of all camera traps for at least 30 days would increase the chances of capturing rare species and species of conservation concern, such as gorillas, leopards, and golden cats, for which we had few observations. Animal attacks, high humidity and precipitation caused camera trap failures that prematurely ended several deployments and reduced our ability to draw inferences from the data. Future studies should maintain extra camera traps to replace faulty equipment. Using desiccants or purchasing camera traps with better weather-sealing or weatherproof housings might reduce camera trap failures from humidity and frequent rainfall (TEAM Network 2011).

Capture-recapture methods for estimating animal densities from camera trap data exist but rely on individual recognition of members of the study population that is typically not feasible for community-wide studies (Foster & Harmsen 2012). Rowcliffe et al. (2008) proposed a random encounter model for estimating animal density from camera traps without the need for individual recognition based on the ideal gas model. This model requires the estimation of several detection parameters (i.e., detection distance, field of view, and angle of animal approach) for each camera trap as well as estimates of animal movement speed and average group size, which would also be extremely difficult to obtain in species diverse communities like tropical forests. Methods for estimating species occupancy using camera trap data are popular because they allow for the calculation of detection probabilities and offer better estimates for species with sparse data (Tobler et al. 2015). However, modeling species distributions in the occupancy framework depends on the assumption that populations are closed between surveys (i.e., no births, deaths, immigration, or emigration), which is not realistic. Violations of this assumption lead to overestimates of occurrence for species (Rota et al. 2009).

Conservation and management

Our findings largely support previous research and reinforce the theory that large mammals face multiple threats that make them highly susceptible to extinction (Abrahams et al., 2017; Benitez-Lopez et al., 2017; Koerner et al., 2016; Cardillo et al., 2005). Declines in the abundance of large species may be partially offset by in-migration from source populations in more remote forests, but continued road expansion in logging concessions allows hunters easy access to frontier forest and threatens to disrupt this buffering mechanism (Clark, Poulsen, Malonga, & Elkan, 2009; Laporte et al., 2007, Hanski, 1998). Most of the roads in the study area are logging roads; thus, regulating access to those areas and making firearms, snares, and bushmeat hunting forbidden inside concessions would likely reduce hunting pressure, as suggested elsewhere (Clark et al., 2009).

Although hunting and human disturbance negatively affect large mammal species, several small mammal species had higher relative abundances in areas of high human disturbance relative to areas of low human disturbance. Because small mammals are typically more abundant in the forests surrounding villages, forest managers should consider allowing hunting of small mammals year-round while limiting hunting of larger mammals to certain months, seasons, or areas. Currently, Gabonese hunting laws restrict hunting of all species to a six-month hunting season. This type of management system might permit too high of an intensity of hunting on slow-reproducing large species, while also leaving rural communities without a source of protein for half of the year. We also propose only allowing hunting within the 8-10 kilometer radius around villages, as our study demonstrated that most species existed within that distance from villages.

Our study also demonstrates that local communities can actively engage in wildlife monitoring. Incorporating rural people in forest monitoring, including the organization/processing of camera trap photos, could help raise awareness of threats facing forest mammals as well as the threat to human livelihoods resulting from the extirpation of large mammals close to villages. Management of wildlife in human-dominated areas will require investment and engagement by local people, but could also be the key to the maintenance of biodiversity and the future sustainable supply of animal protein in rural Africa.

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