



Oil prospecting and its impact on large rainforest mammals in Loango National Park, Gabon

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ABSTRACT

Resource extraction is increasingly affecting protected areas worldwide. However, aside from studies on logging, limited information is available about the effect this has on wildlife, which may be of great consequence, especially when endangered species could be affected. Specifically, the effect of intense human-induced noise during oil exploration on wildlife is poorly understood. We explore the effect of seismic oil exploration on large mammal distribution in an 80 km² area of Loango National Park, Gabon. Following the ecological theory of habitat disturbance, we predicted that changes in habitat use in response to noise disturbance would scale with the body/home range size of each species examined. Our study was conducted over six months before, during and after low-impact seismic operations. We recorded counts along transects of indirect signs of elephants (*Loxodonta africana cyclotis*), chimpanzees (*Pan troglodytes troglodytes*), gorillas (*Gorilla gorilla gorilla*), duikers (*Cephalophus* spp.), and the vocalizations of five monkey species (*Cercocebus torquatus*, *Cercopithecus cephus*, *C. nictitans*, *C. pogonias* and *Lophocebus albigena*) and modeled seismic impact over different spatial scales (small, intermediate and large). We found that elephants avoided seismic activity on all three spatial scales, apes avoided on the intermediate and small scales, and there was no effect for duikers and monkeys. We conclude that low-impact seismic operations can cause considerable temporary habitat loss for species with large ranges and suggest that the impact on those endangered species can be minimized by adequately spacing seismic lines and activity in space and time to enable species to move away from the progressive noise disruption.

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1. Introduction

Global economic development has led to an increase in the extraction of natural resources such as wood, oil and minerals in developing countries. As a consequence the pressure on protected areas has intensified worldwide. Many of these projects involve high noise production, such as chain saw noise for logging and dynamite explosions during seismic activities for oil prospecting and the extraction of certain minerals. The impact of intense human-produced noise has been the subject of several studies on a variety of marine and terrestrial dwelling species, but in general the effects are poorly understood (Larkin et al., 1996; Brown, 2001). First, activities that create loud noise and the studies that concern their impact are generally not conducted simultaneously. Second, not all species respond to noise disturbance in the same manner.

The most common behavioral change exhibited by wildlife to intense human-produced noise is active avoidance. Examples of this phenomenon in response to seismic sound are reported for several whale species, e.g. blue whales (*Balaenoptera musculus*;

McDonald et al., 1995) and humpback whales (*Megaptera novaeangliae*; McCauley et al., 2000). For some terrestrial large mammals, such as grizzly bears (*Ursus arctos*; McLellan and Shackleton, 1988) and caribou (*Rangifer tarandus*; Dyer et al., 2002), between 8.7% and 48% of their available habitat may be lost through active avoidance.

Seismic activities can also produce physiological responses in large mammals, for example a significant increase in heart rate in grizzly bears (Reynolds et al., 1986). More extreme cases reveal that weddell seals (*Leptonychotes weddellii*; Bohne et al., 1985) and humpback whales (Ketten et al., 1993) can suffer temporary or persistent damage to their auditory systems. In the long term, species may even be adversely affected by a decrease in survival probability (caribou; Harrington and Veitch, 1992).

In contrast, studies deemphasizing the impact of noise on wildlife include reports on moose (*Alces alces*) which seem to be less sensitive than other wildlife, and do not show intense reactions to aircraft flying overhead (Klein, 1973). Consequently, generalizations across species are of limited use (Larkin et al., 1996), and currently no coherent framework exists that would help to understand differences in species' responses to noise disturbance.

Evidently wildlife responses to noise disturbance depend on a variety of factors pertaining to the species such as the auditory

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system, inherent physiological responses, ranging patterns and many other factors related to species ecology. Yet species' reactions will also vary with sound properties such as noise level, frequency distribution, duration, number of events, and level of ambient noise (Brown, 2001). In contrast to the multifaceted analysis that such a complex issue would require, many of the existing noise disturbance studies have been rather anecdotal and do not quantitatively measure the behavioral response related to the noise impact. Very often noise disturbance is evaluated as a case study with a single species only, and predictive models relating quantifiable behavioral or physiological responses to disturbance dosage are only rarely applied. A potential solution to this problem would be to study a specific type of response on a number of species simultaneously, and make predictions of the response following the ecological theory of habitat disturbance and the species' biological characteristics. Studies of the effect of habitat disturbance, in particular habitat fragmentation, have revealed that species' body size is a key factor in understanding species' responses (Johns and Skorupa, 1987).

We therefore evaluated the impact of loud noise only, resulting from seismic exploration, on the spatial distribution of several large rainforest mammals. Although the effects of oil exploration include chemical pollution of water and soil that has the potential to impact on a broad range of species, we focused on large fauna, which are a main concern given their low survival ability as compared to smaller species following habitat disturbance (Johns and Skorupa, 1987). The longer maturation period and slow reproduction of large species render them particularly vulnerable and their population densities are also associated with hunting pressure (Peres and Palacios, 2007). Furthermore, our study examined the case of a petroleum company conducting seismic exploration inside Loango National Park, Gabon (Fig. 1a), an area which, like other protected areas in the Congo Basin, acts a stronghold for populations of endangered large mammals, such as elephants (*Loxodonta africana*), chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*). To date, most of the available information regarding how these species are affected by such economic development projects comes from studies on the impacts of logging (Tutin and Fernandez, 1984; White and Tutin, 1996; Arnhem et al., 2008). Here we therefore expand on this knowledge by presenting the first results on the impact of oil exploration.

In 2006 seismic operations were undertaken in Loango National Park in the absence of clear environmental regulations. We were unable to conduct any research during this time due to the speed at which the seismic operations were initiated. Following this first

period of oil exploration, an ecological and sociological impact assessment study was instigated by the Gabonese Ministry of the Environment. As a result, prior to the second phase of exploration which began in June 2007, several requirements were established to limit the impact of the seismic operation on the flora and fauna of the park. An auditing team headed by the Wildlife Conservation Society (WCS) and the World Wide Fund for Nature (WWF) was commissioned by the Gabonese Ministry of Environment to monitor the implementation of the following guidelines: (1) no chainsaws were to be used; (2) trees larger than 10 cm diameter could not be cut; (3) transects could be no wider than 120 cm; (4) all transects had to be walked by foot and not by using mechanized vehicles; (5) all rubbish and materials (e.g. cables) had to be removed from the forest; (6) dynamite explosives had to be placed at least 6 m deep; (7) no poaching was permitted; (8) only one access road for vehicles was made; (9) the bridge that gave access to the park would be destroyed after the end of the operations. In summary, these guidelines and the monitoring program lead to this being considered a relatively low-impact seismic operation.

For a period of six months before, during and after the 2007 seismic survey we monitored the spatial distribution of elephants, chimpanzees, gorillas, duikers (*Cephalophus* spp.) and monkeys (*Cercocebus torquatus*, *C.cephus*, *C.nictitans*, *C.pogonias*, *Lophocebus albigena*) using counts of signs along transects to obtain encounter rates. Specifically, we investigated if: (i) species would respond to the loud noise produced by the dynamite explosions from these seismic activities by avoiding areas of high-impact and (ii) a discernible pattern of inter-species differences existed in these responses. Due to the variation in home range size of the above species, we predicted a spatial response on a larger scale in the following large-bodied species using larger ranges: elephants, chimpanzees and gorillas. On the contrary, given the smaller home range sizes for monkeys we predicted that they would be less impacted by the exploration activities than the large-bodied mammals. In summary, we expected that the seismic impact on a species' spatial distribution would scale with home range/body size.

2. Methods

2.1. Study site and seismic exploration

The oil exploration site was located in the northeastern part of the 1550 km² Loango National Park, Gabon. The park contains a

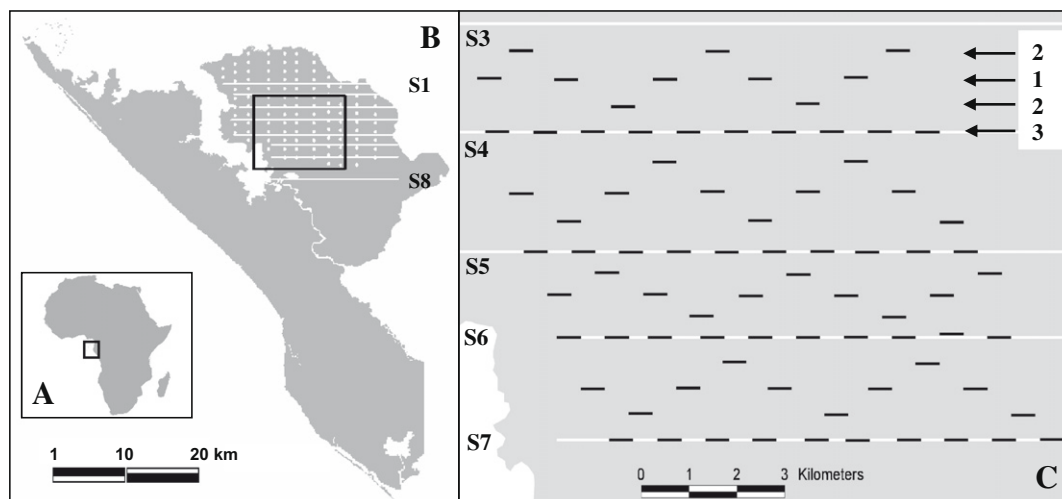


Fig. 1. Location of Loango National Park, Gabon (A), seismic transects explored in 2006 (broken lines) and seismic lines explored in 2007 (solid lines) in the northeast sector of Loango National Park (B), and study area (black square). The seismic impact monitoring design is shown in (C), transect length was 0.5 km. The impact of the dynamite explosions for each line of transects is indicated from 1 to 3 (3 being the highest), with the highest impact directly on seismic lines decreasing with increasing distance from the line.

mosaic of moist tropical lowland forest, permanently and seasonally inundated swamp forest, coastal forest, lagoon and savannah. The terrain is mainly flat with little variation in topography. In 2005 the Chinese petroleum company, Sinopec, was granted a concession for oil exploration in the 'Lotus bloc' within Loango National Park, Gabon. They planned to use 2D seismic methodology which uses one line of geophones positioned on the surface alongside underground dynamite charges to record the seismic waves from explosions. Data from these seismic waves can indicate which subsurface rock formations may contain large quantities of oil (Severson-Baker, 2004). Seismic operations began in the northeast section of the park in 2006. A network of transects was cut for the placement of the seismic lines, half of these were orientated north-south and the other half east-west. Dynamite explosions were conducted exclusively on the north-south lines in 2006 (Fig. 1B).

In June 2007 the second period of seismic activities began on the eight east-west seismic lines. These lines had a mean length of 20.6 km (range 17–23.7 km) and a mean separation distance of 2 km (range 1.5–3.2 km). Dynamite charges were spaced on average 50 m apart along seismic lines. Attempts were made to minimize surface damage from the explosions, for example, holes created had to be filled in after explosions to avoid potential problems for wildlife. Dynamite explosions took place during 25th August–6th October 2007; they started at the western limit of the northernmost seismic line and continued east until the entire line had been exploded. Seismic activity then gradually worked southwards, completing one line at a time from west to east, with each line in turn receiving explosions for 2–7 days. Based on our field observations, we estimated an average interval of 0.5 min between dynamite explosions. The sound level pressure of this type of seismic oil exploration reaches usually up to 210 dB next to the explosion site. This is about 10,000 times louder than a jet aircraft flying by at 300 m altitude.

2.2. Field methods

We measured the presence of the following large mammals in 80 km² out of 332 km² of the Sinopec activity in the northeastern zone of the park: elephants, gorillas, chimpanzees, monkeys and duikers with approximate home range sizes of 75 km² (mean value for Loango; Blake et al., 2008), 38 km² (mean value for Goulougo NP; Sanz, 2004), 18 km² (mean value for Dzangha-Sanga NP; Cipolletta, 2004), 0.5–1 km² (Kingdon, 2003), and 0.12 km² (Estes, 1992) respectively. We systematically placed a total of 80 line transects of 0.5 km length across the study zone orientated east-west (Fig. 1C), with 40 of them located on the seismic lines and 40 placed 0.4–1 km away from seismic lines between lines. Transects were walked a total of six times, each transect once per month (Appendix A) in the same order at a speed of 0.5 km/h and each survey took on average 16 days to complete. During the first passage, we recorded counts of all indirect signs of elephants and duikers (faeces), apes (nest groups), and monkey vocalizations. Standard categories of fresh, recent and old were used to age indirect signs (Tutin and Fernandez, 1984; White and Edwards, 2000). We marked each sign with flagging tape, indicating the date of observation. During all other passages, we only recorded counts of those indirect signs which appeared since the last visit and continued to mark them with the date encountered.

2.3. Analytical methods

We modeled the impact of seismic activity on wildlife distribution considering three different spatial scales. The first approach ('large-scale-impact') assumed a more or less evenly distributed impact of the dynamite explosions on the entire study area. Seismic activities started in the north and progressed southwards,

and thus possibly lead to higher densities of animals in the south of the study area briefly after the dynamite explosions ended, subsequently turning into a more even distribution again as time passed. To model and test these presumed effects we included latitude, date and the squared date of the transect survey (see below) as well as the interactions between latitude and date and latitude and squared date into the model. Including the squared date and its interaction with latitude allowed us to model a north-south gradient being particularly pronounced in the middle of the study period (i.e. soon after the seismic exploration ended). We assumed this model to be particularly suitable in explaining distribution of wide ranging animals, like elephants, which potentially could leave the impacted area. Throughout, 'date' refers to and was measured in days elapsed since the beginning of the study. 'Latitude' was based on UTM coordinates and indicated in meters.

The second approach ('small-scale-impact') assumed the impact to be high on the seismic transects and then decline rapidly with increasing distance from them. Additionally, this approach assumed that the impact was greatest immediately after the dynamite explosions and then decreased with an increasing time lag between the date of the dynamite explosions and each survey. Hence we categorized the impact by defining it as 3 on seismic lines (highest impact), 1 on transects in the middle between two seismic lines (lowest impact), 2 on transects placed half-way between a seismic line and transects categorized as impact 1, and 0 before the dynamite explosions began (Fig. 1c). In addition to this small-scale-impact variable ('SSI'), we included date and squared date of transect survey as well as the interactions between date and SSI and squared date and SSI into the model. Again, including the squared date allowed us to model the impact as being particularly strong soon after the seismic exploration ended. We predicted that this model would explain responses to the seismic impact for all species included into our study.

The third approach ('intermediate scale impact') represented a mixture between the other two approaches, by including two new variables aiming at measuring the temporal impact of the dynamite explosions more directly (rather than by just using the date as a proxy as in the previous models) and measuring the spatial impact of the dynamite explosions more precisely (rather than just at an integer scale from 1 to 3). We calculated a temporal impact variable ('TI') by dividing the duration of the dynamite explosions on a line (or, in cases when a transect survey occurred simultaneously with the seismic explosions, the duration since the beginning of the dynamite explosions) by the number of days elapsed between the beginning of the dynamite explosions and the date when a transect survey was walked. We incorporated the duration of the impact into this variable because some transects were walked while the impact was still going on and total duration of the impact varied between impacted transect lines. Hence, we deemed it was required to account for differences in the number of days the impact actually took or had taken place when the transect was walked. Note though, that these differences in durations influence the impact variable mainly during and shortly after the impact since later the weight by the time elapsed prevails this measure. This variable was calculated for each individual combination of transect-ID and replicate (i.e. each individual survey of the transect) and generally was zero before the dynamite explosions began, largest right after it started and then declined asymptotically with increasing time lag between the dynamite explosions and date of a transect survey (Fig. 2, left column). In addition, we calculated a spatial impact variable ('SI') by dividing the duration of the dynamite explosions on a line (or, in case a transect survey took place while the dynamite explosions were going on, the duration since the beginning of the dynamite explosions) by the distance (in kilometers) between a transect line and a seismic line plus one. The reason for incorporating duration of the explosions into this variable was the same as for the temporal impact variable. This variable

was calculated for each individual combination of transect-ID and replicate, generally was zero before the dynamite explosions began and reached a maximum after the dynamite explosions were completed at which it stayed until the end of the survey (Fig. 2, right column). We also included the interaction between these two variables into the model. We assumed this model to be effective in explaining large as well as small-scale movements of animals (but not the potential large-scale movement directed southwards).

To summarize, the large-scale impact model is built to detect a large-scale movement (through incorporation of latitude) towards the south (and its interaction with date) but does not account for the specific locations and times of the impact. The small-scale impact model is built to detect small-scale movements away from the directly impacted transect lines to those which are in between them but does not account for the specific times of the impact. The

intermediate scale model, finally, aims in detecting movements on both scales. It has the advantage of measuring the magnitude of both aspects of the impact (temporal and spatial) more directly and specifically, but the disadvantage that these measures are to some extent arbitrary. We used these three different models since we wanted to detect movements at different spatial scales (since we investigated animals with presumably very different movement patterns and home range sizes) and since we are not aware of a single model allowing to incorporate all these aspects of the impact and its consequences without leading to problems such as over fitting and co linearity.

In addition to the (scale specific) impact variables, we included a set of environmental covariates considered to be useful in explaining heterogeneity in wildlife distribution as control variables in all models: distance to road (hunting impact, square

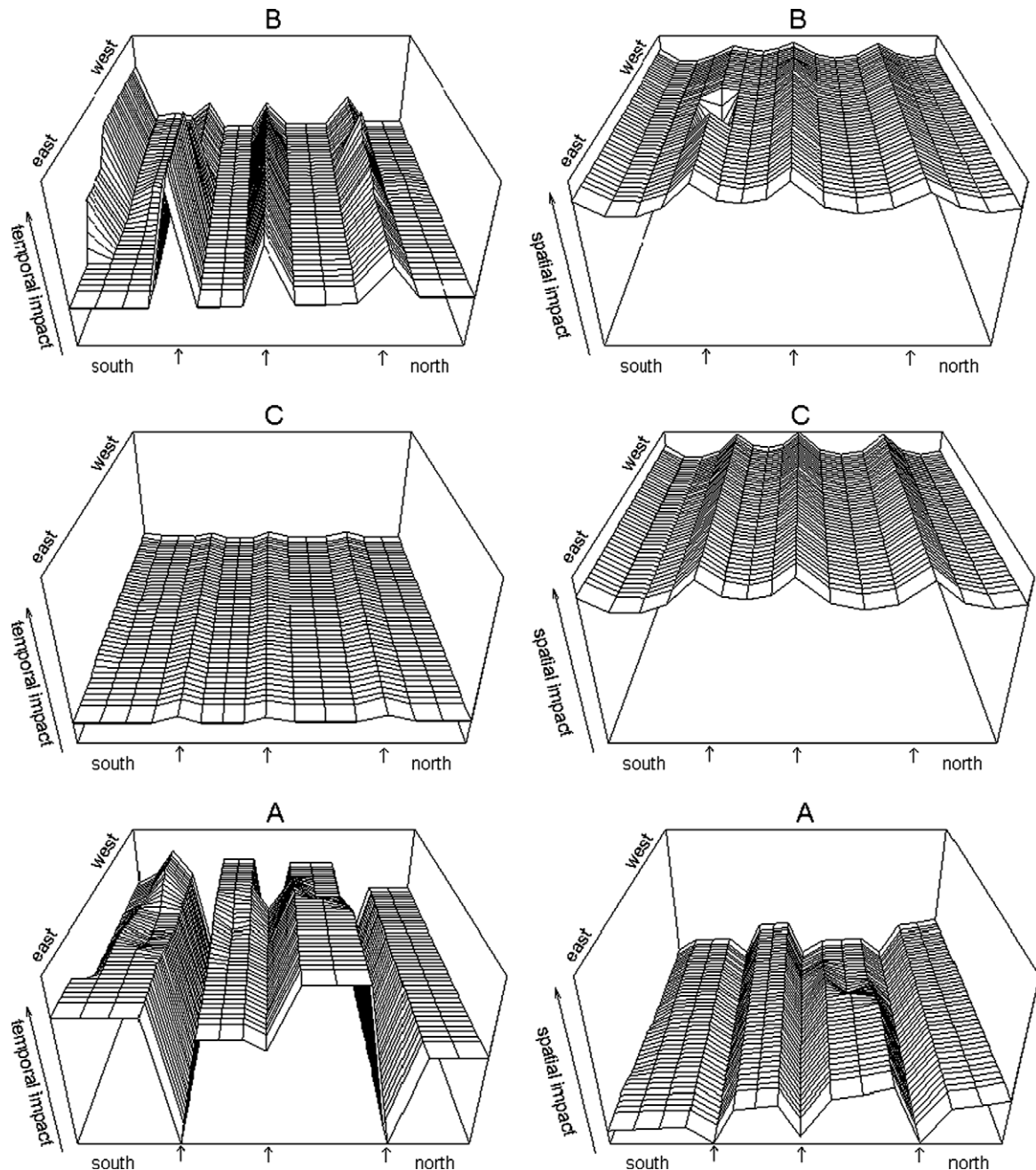


Fig. 2. 3D visualization of the explanatory variables created to represent the intermediate scale temporal (left) and spatial impact (right) (A) during, (B) one month after and (C) two months after the seismic operations. Prior to the beginning of the seismic operations both impact variables were zero throughout.

root-transformed), compound topographic index (CTI also referred to as the Wetness Index is a function of the upstream contributing area and the slope of the landscape, it therefore gives a measure of how swampy or flooded an area is, log-transformed) and forest type (liana forest, rivers, secondary forest, temporarily inundated forest and tree falls) which was measured by noting in meters all changes in forest type per transect during the first passage and subsequently calculating the proportion of each forest type that was present in each transect.

We estimated the impact of the dynamite explosions separately for each of the three impact scenarios and group of species, using Generalized Linear Models (GLM) with Poisson distributed error and log-link function (Dobson, 2002). All environmental covariates as well as all impact variables (and date) were z-transformed (i.e. standardized to a mean equaling zero and a standard deviation equaling one) prior to their inclusion into the model. We z-transformed these variables to achieve valid estimation for variables being involved in interactions or occurring also squared and to obtain comparable estimates. Interaction terms were calculated as products of z-transformed variables, and squared terms were also calculated based on z-transformed variables.

To account for survey effort, we also included lengths of transect lines and time interval between two surveys on a given transect (for ape nests and elephant faeces see below) or length of the transect line (for duiker faeces) as well as duration of a given survey (for monkey vocalizations) as 'offset' variables into the models. Including time between surveys as an offset controls for differences in time spans between two successive walks on the same transect which is likely to result in different numbers of ape nests and elephant faeces accumulated over time. Similarly, including length of the transect line or duration of a given survey controls for differences in effort taken to detect duiker faeces and monkey vocalizations, respectively. For the very first survey on a given transect the time interval elapsed since the 'previous survey' was set equal to that between the first and the second survey. In addition, whenever possible only fresh or recent signs were included into the counts for the first survey. When this was not possible, we reduced the number of signs counted during the first survey to that counted at the second survey (in case the first survey count exceeded that of the second survey count). Note that this approach is conservative with regard to our estimation of the impact since it may lead to an underestimation of the number of observations prior to the impact.

To account for potential spatial autocorrelation we first calculated a model with all the respective (environmental and impact) covariates included, calculated the residuals from the derived model and then used these to get an additional covariate, the autocorrelation term ('AC-term'). The AC-term for a given transect and day equalled the weighted average of residuals of all other combinations of transect and day, with the weight equaling $1/(\text{distance in kilometers between the two transects} + 1)$. Then we calculated the model again, this time with the AC-term included. Including this autocorrelation term aims in leading to (spatially) uncorrelated residuals, a crucial assumption of the statistical method we applied. In essence it models clustering of signs not accounted for by any of the environmental covariates and impact variables in the model.

We derived significance by comparing full (saturated) models with reduced models using likelihood ratio tests (Faraway, 2006). To test for the impact of the dynamite explosions, we first tested the overall effect of all impact variables (main effects and interactions), for example, taking the intermediate scale model; elephant dung count $\sim SI + TI + SI * TI$. If these revealed significance, we then tested the interactions terms being part of the impact covariates (using likelihood ratio tests). If these appeared insignificant ($P > 0.1$), we removed them from the model and ran it again, this time including only the main effects of the respective dynamite explosions impact model, for example, elephant dung count $\sim SI + TI$. In satu-

rated models the AC-term and all environmental covariates were generally included. However, when the AC-term of a given model appeared not at all significant ($P > 0.2$) we removed it from the saturated model. We compared the explanatory value of the three different impact models using AIC (Burnham and Anderson, 2002).

We checked for model validity by visual inspection of plots of residuals against predicted values. If these suggested one or few outliers or influential cases, we removed them from the data and repeated the analysis. The results never differed considerably between models for data with and without such potential outliers. None of the plots of residuals against predicted values suggested over-dispersion or strong deviations from homogeneous errors or over-dispersion.

3. Results

The scale over which we detected species' responses to the seismic activity clearly differed between the four groups of animals. Elephant dung encounter rate was influenced by the seismic impact on all three spatial scales (Table 1). Ape nest encounter rate was related to the impact on the small and intermediate scale, but not on the large-scale. No pattern of disturbance was evident on the spatial distribution of the smaller, territorial species (e.g. duikers and monkeys). Duiker dung encounter rate tended to be influenced only on the intermediate scale, and none of the models showed an obvious effect on the number of monkey vocalizations.

Comparing the different impact models by AIC revealed that the small-scale impact scenario best explained heterogeneity in elephant distribution, whereas ape nest distribution was similarly well explained by the small and intermediate scale impact (Table 1). For ape nests and elephant dung the small-scale impact model showed that these signs were less abundant in areas with large spatial impacts, i.e. impact three transects and this effect increased with the duration of the study (Fig. 3a, b). Regarding the intermediate scale impact, ape nests were predominantly concentrated on transects with small impacts, and this was particularly the case during and shortly after the seismic exploration. For elephants both the intermediate and the large-scale impact model indicated a seasonal increase in their general abundance (Fig. 3c).

4. Discussion

To our knowledge, our study is the first to quantitatively measure considerable disturbance of large rainforest-dwelling mammals caused by seismic activities. We emphasize that we were assessing the case of a relatively low-impact study, given that the presence of an auditing team during the 2007 oil prospection led to the implementation of rigorous environmental guidelines. In addition, seismic transects in this survey were only 1.2 m wide, given that new GPS technology has reduced the requirements of large, open-canopy transects cut with chain saws to facilitate the placement of straight lines (Gibson and Rice, 2003). Yet despite these measures a clear disturbance signal was still observed for large endangered mammals.

Our results provide a greater understanding of how different species respond to noise impact and revealed two important findings. First, as predicted, we found that seismic activity had a negative impact on certain large rainforest-dwelling mammals through substantial temporary habitat avoidance. Specifically we demonstrated that apes and elephants avoided the seismic lines in the four months after the dynamite explosions had finished. We did not observe this effect for duikers and monkeys. These behavioral changes shown by elephants and great apes in response to intensive human noise confirm reports from previous research on terrestrial (Kuck et al., 1985; McLellan and Shackleton, 1988;

Table 1 Results of the three different spatial scale models to measure the effect of seismic operations on large mammals in Loango National Park, Gabon.

Species	Spatial scale model	χ^2	df	P	AIC	Lat	Impact variables ^a									
							SSI	Date	Date ²	TI	SI	Date ² /SSI	TI/SI	Lat/Date Lat/Date ²		
Elephant	Small	226.1	5	<0.001	1570.0		-0.3892 ^c	0.4602 ^c	-0.1276							
	Intermediate ^b	169.9	2	<0.001	1597.6						0.8421 ^c	-0.1031				
	Large ^b	167.4	3	<0.001	1602.9	0.0684	0.6115 ^c	-0.2858 ^c	-0.2009 ^c	0.8421 ^c				-0.0865		-0.0334
Apes	Small ^b	22.5	3	<0.001	388.6		-0.7997 ^c	0.7412 ^c	0.0405							
	Intermediate	19.5	3	<0.001	389.6						-0.4618 ^d	-0.8428 ^c				0.0874
	Large ^b	6.7	5	0.243	406.7	-0.2606	0.2672	-0.0138	0.0405					0.1091		
Duikers	Small	8.2	5	0.148	82.3		-0.2768	0.8806	0.2550							
	Intermediate ^b	5.8	2	0.054	80.2						1.0990 ^d	-0.8509				-0.0829
	Large	7.5	5	0.189	83.0	0.2287	0.7200	0.3690	-1.1161	1.0990 ^d				-0.0775		
Monkeys	Small	6.1	5	0.293	292.0		-0.2503	0.0285	0.2310							
	Intermediate	3.6	3	0.314	290.6						-0.2199	-0.0991				
	Large	5.6	5	0.344	292.5	0.1702	-0.1369	-0.2298	0.2310	-0.2199				-0.0148		-0.1980

^a Abbreviations: χ^2 , df, P: statistics of likelihood ratio tests comparing full models with respective reduced models; AIC: Akaike's Information criterion; Lat: latitude; SSI: small-scale impact; Date: date at which the survey was conducted (measured in days elapsed since the beginning of the study); TI: temporal impact at intermediate scale; SI: spatial impact at intermediate scale; the last five pairs of variables are interactions.
^b Interaction(s) removed because of non-significance ($P > 0.2$); estimates of main effects are from models without interaction(s).
^c $P \leq 0.05$.
^d $0.05 < P \leq 0.1$.

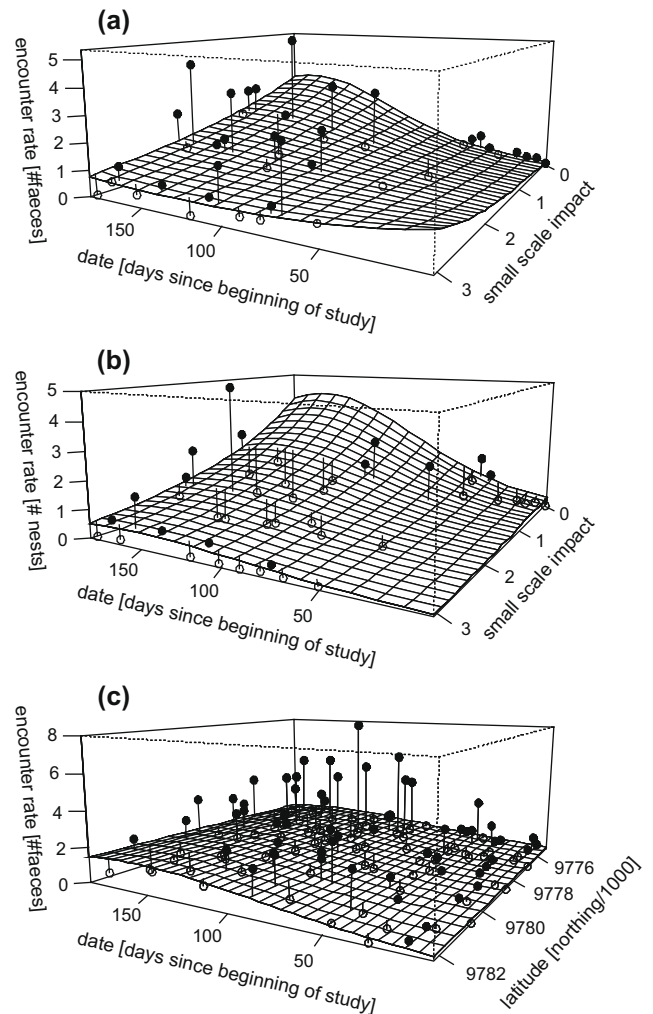


Fig. 3. Observed (circles) and predicted (surfaces) encounter rates of elephant dung (a and c) ape nests (b). Predictions are based on the small-scale impact model in (a) and (b) and on large-scale impact model in (c). Observed encounter rates depict number of signs per transect and survey, averaged per combination of binned impact and date or latitude. Observed encounter rates larger than the respective predicted value are indicated as filled circles, those lower than the predicted value are indicated as open circles.

Weir, 2007) and marine species (McCauley et al., 2000; McDonald et al., 1995).

Second, we found a size-specific relationship between each of the four groups of mammals and the impact of seismic activity on three spatial scales. The results reflect the biology and limitations of movement and ranging patterns of the species. Seismic operations had a greater effect for large mammals (e.g. elephants and apes) which have the possibility to move elsewhere, i.e. further away from the dynamite explosions, due to their large home ranges, than for smaller territorial mammals (e.g. duikers and monkeys) whose movements are more restricted. In particular, we highlight that the incorporation of a variety of response scenarios is crucial when studying multiple species in noise disruption and habitat disturbance studies in general. Given the extremely high sound level pressure of dynamite explosions (a maximum of over 200 dB), we can safely exclude the possibility that species' differences in sound perception have led to the observed pattern in our study.

Elephants' sensitivity to noise disturbance is demonstrated by the negative effects of road and forest operations on elephant abundance (Griffiths and van Schaik, 1993; Barnes et al., 1997; Theuerkauf et al., 2001), although in some areas with no hunting elephants can be attracted to human presence (Laurance et al.,

2006). The results of our small-scale impact analysis agree with the notion that elephants are susceptible to intense human-induced noise, otherwise we would not have expected to see decreased encounter rates of elephant sign on impact 3 transects after explosions. However the fact that these encounter rates tended to increase throughout the study period requires further attention as it raises the issue of whether or not elephant movements were influenced by other factors aside from the seismic operations. There is limited information on the seasonal movements of elephants in Loango National Park, but a large mammal census in the Gamba complex suggests that elephant movements in our study area are more localized as they did not find evidence of seasonal migrations (Thibault et al., 2001). Without further investigation, it is not possible to draw firm conclusions and we stress that our results underscore the urgency to obtain data on the seasonal movements of such wide ranging species in order to better understand the effects of anthropogenic disturbance.

Guidelines for minimizing habitat loss due to seismic exploration should therefore include a precise knowledge of the animal species living in that area. Furthermore, large-bodied mammals need a refuge area, where no dynamite explosions will take place. Thereafter, an adequate temporal spacing between seismic lines should be planned, so as to enable large mammals to move away from the progressively closer explosions. We reiterate the concern for large-bodied species as the risk of extinction is often higher following forest disturbance because they are typically slow breeders, require large home ranges to accommodate their resource demands and are more vulnerable to hunting (Isaac and Cowlishaw, 2004).

The issue of within-species conflict could be especially relevant to oil prospection in forested areas harbouring high densities of chimpanzees and gorillas. The present study demonstrated a small and intermediate scale effect on the spatio-temporal movement of apes in which they avoided areas highly impacted by seismic activity. However, it is important to note that in our study, we did not find a large-scale impact for the apes nor a decrease in encounter rates for the whole study site. Thus, when low-impact seismic operations are implemented, apes are unlikely to be forced into neighboring territories, as was proposed to account for a decline in chimpanzee densities following logging in some areas of the Lopé forest, Gabon (White and Tutin, 1996). Chimpanzees are highly territorial, with males frequently engaging in patrolling behavior to defend their territories (Boesch and Boesch-Achermann, 2000; Goodall, 1986) and there are several documented cases of aggression between con-specific intruders leading to death (Boesch et al., 2007, 2008; Goodall, 1986; Watts et al., 2006). Therefore, if chimpanzees are forced into neighboring territories, even temporarily, we might expect to see an increase in mortality and decline in density. In cases of high-impact seismic operations, it may be that chimpanzee densities could decline, as has been observed to be the case for animal species subject to higher levels of logging (Johns and Skorupa, 1987).

The absence of a large-scale impact on the spatial distribution of apes should be interpreted with caution. Given that our study was limited to changes in habitat use that resulted from seismic impact, the fact that a range of other behaviors might be affected must be addressed. Our results may also suggest that the apes were even more disturbed by the explosions if they were unable to move larger distances and hence we stress the need for other methods of examining the seismic impact such as hormone and physiological measures. This also applies to certain species whose movements are restricted by their ranging patterns (e.g. duikers) where stronger responses may be exhibited through physiological mechanisms such as increased stress levels and/or reduced reproductive output. Alternatively, shifts in activity patterns could also be a response to loud noise disturbance, a phenomenon reported for elephants in Loango National Park, who shifted their daily activity pattern signif-

icantly into nocturnal hours as a response to the general increase in human activity within the forest during seismic operations (Wrege, unpublished data). During our study, we explicitly measured the impact of loud noise only, but additional human disturbance most likely resulted from human traffic, primarily when people were working on the seismic lines prior to the explosions. Wildlife responses to oil exploration are complex, and future studies should therefore attempt to incorporate additional elements of response behaviors and evaluate other types of human disturbance in order to improve our understanding of the negative and potentially diverse effects of seismic exploration on wildlife.

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Appendix A

The dates between which each large mammal survey took place (total of six surveys, each transect walked one per month) are listed on the left hand column with the corresponding survey replicate number in the middle column. The right hand column lists

Table A1

The dates that large mammal surveys were conducted together with the corresponding explosions on seismic lines.

Survey dates	Survey replicate	Coinciding explosions on seismic lines ^a
19/07/07–25/07/07	1	No explosions
28/07/07–17/08/07	1	No explosions
22/08/07–27/08/07	2	S1
31/08/07–08/09/07	2	S2 and S3
30/09/07–08/10/07	3	S7 and S8
13/10/07–23/10/07	3	No explosions
02/11/07–07/11/07	4	No explosions
11/11/07–20/11/07	4	No explosions
03/12/07–08/12/07	5	No explosions
14/12/07–20/12/07	5	No explosions
03/01/08–08/01/08	6	No explosions
12/01/08–23/01/08	6	No explosions

^a Explosions on seismic lines 4–6 took place between 08/09/07 and 26/09/07 where access to the study zone was prohibited due to safety regulations.

which seismic lines were exploded during the survey dates and these are shown in bold (see Table A1).

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