

Use of Acoustic Tools to Reveal Otherwise Cryptic Responses of Forest Elephants to Oil Exploration

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Abstract: *Most evaluations of the effects of human activities on wild animals have focused on estimating changes in abundance and distribution of threatened species; however, ecosystem disturbances also affect aspects of animal behavior such as short-term movement, activity budgets, and reproduction. It may take a long time for changes in behavior to manifest as changes in abundance or distribution. Therefore, it is important to have methods with which to detect short-term behavioral responses to human activity. We used continuous acoustic and seismic monitoring to evaluate the short-term effects of seismic prospecting for oil on forest elephants (*Loxodonta cyclotis*) in Gabon, Central Africa. We monitored changes in elephant abundance and activity as a function of the frequency and intensity of acoustic and seismic signals from dynamite detonation and human activity. Elephants did not flee the area being explored; the relative number of elephants increased in a seasonal pattern typical of elsewhere in the ecosystem. In the exploration area, however, they became more nocturnal. Neither the intensity nor the frequency of dynamite blasts affected the frequency of calling or the daily pattern of elephant activity. Nevertheless, the shift of activity to nocturnal hours became more pronounced as human activity neared each monitored area of forest. This change in activity pattern and its likely causes would not have been detected through standard monitoring methods, which are not sensitive to behavioral changes over short time scales (e.g., dung transects, point counts) or cover a limited area (e.g., camera traps). Simultaneous acoustic monitoring of animal communication, human, and environmental sounds allows the documentation of short-term behavioral changes in response to human disturbance.*

Key words: acoustic monitoring, forest elephant, *Loxodonta cyclotis*, oil exploration

Utilización de Herramientas Acústicas para Revelar Respuestas Crípticas de Elefantes a la Exploración Petrolera

Resumen. *La mayoría de las evaluaciones de los efectos de actividades humanas sobre animales silvestres se han concentrado en la estimación de cambios en la abundancia y distribución de especies amenazadas; sin embargo, las perturbaciones del ecosistema también afectan aspectos del comportamiento animal como el movimiento de corto plazo, presupuestos de actividad y reproducción. Puede tomar mucho tiempo para que los cambios de comportamiento se manifiesten como cambios en la abundancia o distribución. Por lo tanto, es importante contar con métodos para la detección de respuestas conductuales de corto plazo a la actividad humana. Utilizamos monitoreo acústico y sísmico para evaluar los efectos de corto plazo de la prospección petrolera sísmica sobre elefantes (*Loxodonta cyclotis*) en Gabón, África Central. Monitoreamos cambios en la abundancia y actividad de elefantes como una función de la frecuencia e intensidad de las señales acústicas y sísmicas de la detonación de dinamita y la actividad humana. Los elefantes no huyeron del área en exploración; el número relativo de elefantes incrementó siguiendo un patrón estacional atípico en el ecosistema. Sin embargo, se volvieron más nocturnos en el de exploración. Ni la intensidad ni la frecuencia de las detonaciones de dinamita afectaron la frecuencia de llamados ni el patrón diario de actividad de*

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los elefantes. Sin embargo, el cambio de actividad a las horas nocturnas se volvió más pronunciado a medida que la actividad humana se acercaba a cada área de bosque monitoreada. Este cambio en el patrón de actividades y sus probables causas no hubieran sido detectadas por medio de métodos estándares de monitoreo, que no son sensibles a los cambios conductuales en escalas de tiempo cortas (e. g., transectos de excremento, conteos por puntos) o cubren un área limitada (e. g., trampas de cámara). El monitoreo acústico simultáneo de la comunicación animal y de sonidos humanos y ambientales permite la documentación de cambios conductuales de corto plazo como respuesta a la perturbación humana.

Palabras Clave: elefante, exploración petrolera, *Loxodonta cyclotis*, monitoreo acústico

Introduction

Pressure to extract natural resources from undeveloped lands continues to increase, particularly in the humid tropics, where human populations and economies are expected to grow dramatically (UN Population Division 2009). In some countries, there has been an increase in government commitment to protect natural resources, but the area required for effective conservation is nearly always much larger than the amount protected. Thus, conservation of wide-ranging species likely will require collaboration among conservation professionals and resource-extraction industries (Fagan et al. 2006; Clark et al. 2009).

The effectiveness of given conservation measures for a species of concern depends on the depth of understanding of the effects of particular human disturbances on the species. Common methods used to detect responses to disturbance (e.g., spot or transect surveys that count individuals, dung, nest sites, or other signs) measure changes in abundance or density of individuals. But other, less visible changes, for example in body condition, resistance to disease, and social interactions, may have substantial effects on fitness that in the short term do not manifest as changes in abundance or distribution. Acoustic monitoring of human activities and animal communication avoids biases introduced by the presence of an observer and can be used to collect data simultaneously at widely dispersed locations. In recent years this method has become a major tool in studies of animal behavior and distribution and of the effects of humans on animals in the marine environment (e.g., Croll et al. 2002; Moulton et al. 2005; Van Parijs & Clark 2006). In the terrestrial environment acoustic monitoring has been used to detect migrating birds (e.g., Larkin et al. 2002; Schrama et al. 2006; Farnsworth & Russell 2007) and the presence of bats (Ammerman et al. 2008; Kalko et al. 2008).

We used acoustic monitoring to evaluate whether oil exploration activities affect the movement and behavior of forest elephants (*Loxodonta cyclotis*) in Loango National Park, Gabon. Seismic prospecting for oil, which involves cutting transects through the forest and detonating dynamite, might disrupt the usual behavior of elephants because they communicate with low-frequency sound and are sensitive to seismic vibrations (e.g., Langbauer et al. 1991; McComb et al. 2000; O'Connell-Rodwell et al.

2006). Moreover, because forest elephants avoid roads and human activity (Wittemyer et al. 2007; Blake et al. 2008; Graham et al. 2009), elephants may move away from areas where exploration is being conducted.

Methods

Study Site

Loango National Park, on the coast of Gabon (2°S, 9°E; Fig. 1), is part of one of the most biologically diverse ecosystems in Central Africa (Alonso et al. 2006). The region has a dry season from mid May through mid October, and annual rainfall exceeds 1750 mm.

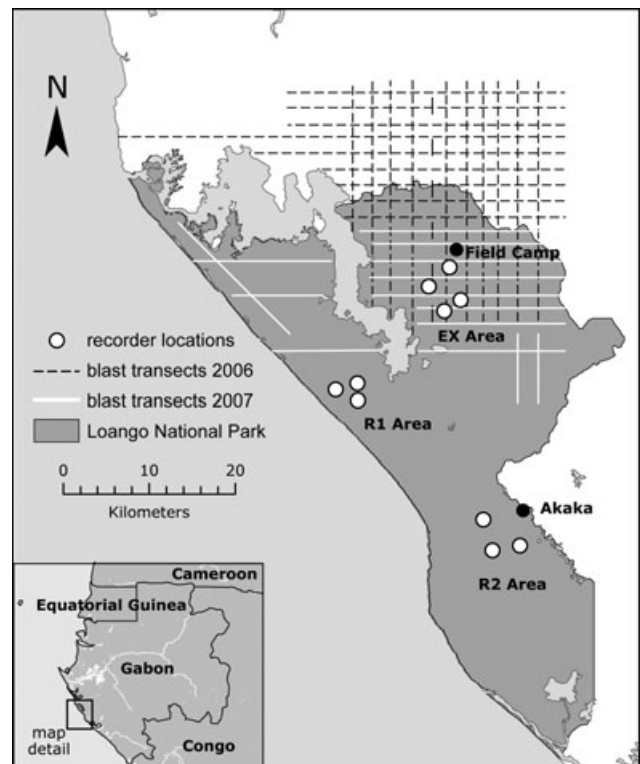


Figure 1. Loango National Park, Gabon, location of clusters of sound recorders and transects used for seismic oil exploration.

In 2006 the Gabonese government gave permission to an energy company for seismic prospecting for oil within and just outside the boundaries of Loango National Park. A series of north-south and east-west transect lines were demarcated. Transects were about 2 km apart and 2 m wide in the northeastern quadrant of the park (Fig. 1). Dynamite charges were detonated on most of these transects in 2006. A moratorium on all exploration activity was in effect from October 2006 to June 2007. Before activity resumed, the government and the energy company agreed to a set of relatively stringent protocols for further prospecting, including restrictions on the size of trees that could be cut and the width of new transects, a prohibition on driving vehicles at night or at any time on trails in the forest, a minimum depth for dynamite charges, and a prohibition on all hunting. An independent auditing team was commissioned to ensure compliance. The company provided data on the dates of blasting along each transect and GPS locations for all detonations within 1 km of our sound recording devices.

We divided the study period into four time blocks: before exploration activity resumed, preliminary activity (small road crew, no blasting), blasting, and after blasting. The “before” period, 15 March 2007 to 14 May 2007, ended with the onset of the dry season. During the “preliminary” period, 15 May to 31 July (dry season), a small road-clearing crew opened two existing dirt tracks running roughly north-south through the exploration area. The blasting period, 1 August 2007 to 31 October 2007 included construction and occupation of the field camp (Fig. 1) and all blasting activity. The “after” period, 20 December 2007 to 28 February 2008, was during a slightly drier part of the wet season and after all exploration activity had ceased.

During the “blasting” period anthropogenic activity involved transportation of workers and materials along two access roads, drilling of holes for dynamite charges, and detonation of dynamite charges along forest transects. The progression of activity was uniform from west to east along each transect beginning with the northernmost transect. On average it took 3–4 days to complete blasting along a transect, and it took about 9 weeks to complete all blasting activity. Activity near the field camp was nearly continuous; but elsewhere activity was concentrated in the forest along transect lines and the two roads.

Data Acquisition and Analyses

Autonomous recording units (ARUs) (Bioacoustics Research Program, Cornell University, Ithaca, New York) have microphone and geophone sensors that record acoustic and seismic signals, respectively. Both types of signal were sampled at 2000 samples/s, which is sufficient for recording elephant vocalizations (fundamental frequencies 10–35 Hz; Poole et al. 1988; Langbauer 2000;

Thompson 2009). Seismic signals were resampled in the ARU at 500 samples/s to reduce file size.

We placed 10 ARUs in the forest that were clustered to sample elephant activity in three areas (EX, R1, and R2) that differed in exposure to anthropogenic activity (Fig. 1). Each ARU was secured to a tree at a height of at least 7 m and at least 500 m from existing or proposed detonation transects. Geophones were buried in the ground 102–112 cm deep and 5–12 m away from the base of the tree. Within each sampling area, we spaced ARUs an average of 4.14 km apart (range 1.84–5.29 km, median 3.42 km) so that multiple units might record the same blast, but not the same elephant call. Four ARUs were embedded in the area of blasting activity, and each ARU was <1 km from a detonation transect. One unit was within 0.5 km of a patch of savannah where the energy company field camp was located, but all other units were in continuous forest. The R1 area (three ARUs) was within the study site of a primate research project, where six to eight researchers worked in the forest each day. Two ARUs in this cluster were close to extensive patches of savannah characteristic of this part of Loango National Park. The R2 area (three ARUs) was in continuous forest in the southern part of the park, where limited ecotourism occurred at distances >4 km from ARUs. When justified by our analytical methods, data from R1 and R2 were grouped as “research” areas. Each ARU records elephant calls from approximately 3.2 km² of forest (Thompson 2009). When all units were recording, the resulting sample areas were 12.8, 9.6, and 9.6 km² for the EX, R1, and R2 areas, respectively. Nevertheless, recording success varied among ARUs (mean = 113 days, range 25–180 days), so the total extent of forest monitored in each area was not consistent among sites.

Over 27,000 h of sound data were obtained from the 10 ARUs. We analyzed sound data recorded on the ARUs spectrographically with XBAT (Extensible Bioacoustics Tool; software available at <http://xbat.org>). Following Thompson et al. (2009b), we classified signals with a frequency of 10–50 Hz, a duration of at least 2 s, and that had some frequency modulation as elephant rumbles.

The calling rate of forest elephants is linearly related to elephant density (Thompson et al. 2009a, 2009b). The veracity of this relation was demonstrated by an independent acoustic study of an elephant population that estimated a total population size within the 95% confidence bounds of estimates determined from dung counts and DNA mark-recapture methods (Thompson et al. 2009a). Thus, the probability of recording an elephant call in a given time period is proportional to the number of elephants near the recorder.

Most recorded calls were probably produced by unit groups (one to four individuals; White et al. 1993; Turkalo & Fay 2001; Morgan & Lee 2007) moving through the forest while foraging. Clusters of calls, indicative of elephant groups interacting, were rare in recordings, and ARUs

were placed randomly with respect to concentrated resources (e.g., fruiting trees) that could be expected to attract elephants. Individual groups were unlikely to remain within the 3.2-km² detection area of one ARU for longer than a day because forest elephants in this region move 1–2 km/day and have home ranges of about 55 km² (Blake et al. 2008; Kolowski et al. 2010). Thus, variation in the probability of recording an elephant call (detection probability) may indicate either change in activity or change in local density, depending on the time scale used in the analysis. Assuming that resting or sleeping elephants call at low rates or not at all, a change in detection probability over hours generally would reflect a change in activity of the individuals still near a given recorder. But when detection probabilities are aggregated over days or weeks, a change in detection probability generally reflects a change in the number of individuals moving through the area of a given recorder.

We examined elephant activity (probability of a call being recorded) during the day and night because human activity occurred only during the day. Although there is no evidence that calling rates (M. Thompson, personal communication) or behavior (Wyatt & Eltringham 1974; Lewis 1986; Ruggiero 1992) differ between night and day for active elephants, any such differences would not affect our results because we examined relative changes in calling probability within and between the sampled areas of forest.

We used an automated template detector to identify likely elephant calls within more than 27,000 h of acoustic recordings. Template detectors use a set of example signals as patterns against which to evaluate novel signals. We determined detector efficiency by visually identifying all elephant calls in 48 representative days of recordings. The detector was 90% effective in identifying at least one elephant call per hour, given that one or more elephant calls were recorded during that hour. We visually examined all sound segments identified by the detector and retained those fitting the criteria of an elephant call. We used the probability of recording one or more elephant calls per hour of recording as a measure of elephant abundance in the vicinity of each ARU. We examined whether the probability of recording an elephant call increased or decreased as an immediate and direct response to the sound of detonations by modeling the likelihood of calling within each hour as a function of the measured intensity of blast signals at an ARU (measures included sum, mean, and maximum amplitude and number of blasts per hour).

Elephants are sensitive to seismic vibrations (O'Connell-Rodwell et al. 2006; Bouley et al. 2007) and may change calling behavior in response to explosions. Neither seismic nor acoustic signals from detonations were recorded on ARUs in R1 and R2, so data on detonation signals came only from the EX area. We logged all detectable blast signals recorded on

geophones and measured the amplitude of each blast. The ARUs differed markedly in the number of seismic signals detected, even when distance to the blast site was controlled. This variation was likely the result of heterogeneity of the soils and subsurface geology along the wave path from blast site to geophone. The greatest number of detonations ($n = 1513$) were recorded by the northernmost ARU in the EX area, so we included only data from this unit in our initial analysis of elephant response to the amplitude and frequency of seismic signals. The recorded amplitudes of seismic signals were large enough to be detected by forest elephants. Typical amplitudes were $0.2\text{--}1.8 \times 10^{-6}$ m/s rms (root mean square) ground vibration velocity, or up to nine times stronger than the signal amplitudes used in field experiments with wild elephants, and capable of eliciting a response (0.2×10^{-6} m/s rms; O'Connell-Rodwell et al. 2006).

Acoustic signals from detonations often were not detectable even when the seismic signal was detected because the objective of seismic exploration is to focus blast energy into the ground. We logged and measured the amplitude of all acoustic dynamite signals on the southernmost ARU in the EX area ($n = 656$) for preliminary analysis of elephant responses to such signals. We examined whether elephant activity was directly affected by detonations at a longer time scale by modeling elephants' day and night calling behavior within the period of human activity along a given transect. Overall human activity probably remained at roughly the same distance, day to day, from elephants in the exploration area during the 3–7 days of blasting along a given transect, but on some of those days no detonations occurred. We controlled for the distance between the ARU and each transect and compared elephant calling activity during days with and without detonations with general linear models (GLM).

Elephants in the forest near the two ARUs that were farthest south in the EX area were exposed to the longest period of gradually approaching disturbance, as human activity and detonations progressed south from transect to transect. We grouped days to reflect the duration of exploration activity along each transect and examined elephant activity patterns in this area compared with activity patterns near ARUs in the two research areas.

The acoustic signal from explosions was often of very high amplitude, but the duration of the signal was sufficiently short that it did not interfere with the detection of elephant calls in the sound files. Loud thunderstorm activity, however, did affect our ability to see elephant calls in the spectrograms. Exploratory analyses showed that when sound levels from thunder and heavy rain exceeded 80 dB for over 60% of an hour, elephant calls were significantly less likely to be detected ($p < 0.01$, $\chi^2 = 14.48$, $df = 1$, $n = 569$ h), either

because calls were masked by the thunder or because elephants call less during intense storms. Therefore, we omitted these hours from all analyses (9% of all hours of recording).

Statistical Analyses

Given a call-detection area around each ARU of about 3.2 km² and movement speeds of only 1–2 km/day (Blake et al. 2008), an individual elephant is likely to remain within recording range of a given ARU for longer than 1 h; therefore, the probability of recording a call is likely correlated from 1 h to the next.

We incorporated a repeated measures term and an auto-regressive correlation structure in models to control for this type of correlation. Except where specifically noted, all data from all ARUs were included in the analyses, with ARU identity entered in models as a repeated-measures term. We used GLMs with repeated measures to model the proportion of hours with calls as a function of environmental and human activity factors (e.g. season, blasting activity). We transformed proportions to the arcsine (Sokal & Rohlf 1995). We used logistic regression to model the probability of one or more elephant calls in an hour as a function of predictor variables. All statistical analyses were done in SAS (version 9.1), and type I error probabilities of 0.05 or less indicated significant effects. We used the Bonferroni method to adjust error probabilities for multiple comparisons of least squares means (LSM).

Results

Elephant abundance varied seasonally and geographically, with abundance increasing in all sampling areas through the dry season and peaking at the end of September. Average abundance varied significantly among the three areas (area by season interaction $F_{2,201} = 7.94$ $p < 0.01$; GLM) because elephant numbers were relatively low in the R1 area during the dry season (LSM comparisons: R1 versus EX, R1 versus R2, both $p < 0.01$, no other comparisons were significant). Seasonal variation in elephant abundance in the EX and R2 areas was similar, particularly during the preliminary and blasting exploration periods. Forest elephants tended to be more active at night than during the day in the rainy season, but during the dry season they were significantly more active during the day (Table 1). All main effects on elephant activity—season, area, and day-night period—were significant, as were all but one of the interaction terms. Data from the EX area after 1 August 2007 (the start of the blasting period) were omitted from this analysis because typical elephant activity could have been affected by the large increase in human activity.

Table 1. Forest elephant activity as a function of location (sampling area), season, and day-night period.^a

Effect	df num, denom	F	p
Area (R1, R2, EX) ^b	2,332	48.47	< 0.01
Season (dry vs. wet)	1,367	32.20	< 0.01
Day-night period	1,970	18.98	< 0.01
Area * season (interaction)	2,365	9.45	< 0.01
Area * day-night period (interaction)	2,970	8.49	0.44
Season * day-night period (interaction)	1,975	58.74	< 0.01
Area * season * day-night period (interaction)	2,975	6.42	< 0.01

^aOverall GLM model was significant ($\chi^2 = 325$, $p < 0.01$, 11 df). Repeated measures correlation structure was auto regressive and significant. The response variable was the proportion of hours during day and night periods with one or more elephant calls recorded.

^bSampling areas: two research areas (see Methods) (R1, R2) and the oil exploration area (EX).

In the EX area elephants significantly shifted their activity from day to night during the blasting period, whereas in the other areas they maintained typical dry-season patterns of activity (i.e., more active during the day) (Table 2; Fig. 2). This behavioral change could have been caused by the intense noise from detonations, human activity in the forest, or both. Noise from detonations (sum, mean, and maximum amplitude and number) did not significantly affect elephant calling behavior at the time of the disturbance (acoustic: $z = -0.45, -1.85, -1.25, -0.31$, $p = 0.66, 0.06, 0.21, 0.76$, sum, mean, maximum amplitude and number, respectively, $n = 547$ h; seismic: $z = -1.18, -0.50, -0.66, -1.26$, $p = 0.24, 0.62, 0.51, 0.21$, sum, mean, maximum amplitude and number, respectively, $n = 492$ h; repeated measures logistic regression). Over slightly longer time scales (24 h), elephants also did not change their behavior in response to whether or not detonations occurred on a particular day ($F_s = 0.51$, $p = 0.48$, $n = 126$ days; repeated measures GLM, controlling distance to detonation transect). Because there was no indication of a direct effect of the noise on elephant vocal behavior, we did not expand the analysis by logging equivalent data from other recorders.

As human activity in the forest progressed southward from transect to transect, forest elephant activity in the exploration area increased during the night and decreased during the day (Table 3; Fig. 3). In contrast, for at least 1 month after elephants in the exploration area became more active at night, the activity of elephants in the research areas changed little (Fig. 3).

Table 2. Factors affecting day–night activity of forest elephants in the presence of oil exploration activity.^a

Effect	df num, denom	F	p
Area (EX vs. R1, R2 combined) ^b	1,476	1.17	0.28
Activity period (before, preliminary, blasting, after) ^c	3,506	75.81	< 0.01
Day–night period	1,1118	0.56	0.46
Area * activity period (interaction)	3,506	9.16	< 0.01
Area * day–night period (interaction)	1,1118	19.87	< 0.01
Activity period * day–night period (interaction)	3,1122	21.44	< 0.01
Area * activity period * day–night period (interaction)	3,1122	12.51	< 0.01

^aOverall GLM model was significant ($\chi^2 = 420$, $p < 0.01$, 15 df). Repeated measures correlation structure was autoregressive and significant. The response variable was the proportion of hours during day and night periods with one or more elephant calls recorded.

^bSampling areas: two research areas (see Methods) (R1, R2) and the oil exploration area (EX).

^cTime periods relative to exploration activities (before, before exploration, March to 14 May; preliminary, small road-clearing crew, 15 May to July; blasting, major exploration activity including detonations, August–October; after, following all exploration activity, December 2007 to February 2008).

Discussion

Using acoustic tools, we detected and quantified an aversive behavioral response by forest elephants to activities associated with oil exploration in Loango National Park. Nevertheless, elephants did not move away from the exploration area altogether. Our acoustic data and data from dung counts conducted along transects in the exploration area (Rabanal et al. 2010) showed a gradual increase in elephant abundance over the period of oil exploration. In areas of the park with exploration activity, however, elephants became significantly more nocturnal at a time of year when they generally would have significantly higher diurnal activity. This increase in nocturnal activity is consistent with the observation that when poachers are active near forest elephants, the elephants reduce or curtail daytime activity at open forest clearings and appear in these areas only at night (A. Turkalo and N. Bout, personal communication). Similar shifts in behavior in response to human activity have been observed in savannah elephants (*L. africana*) (Lewis 1986; Ruggiero 1990; Graham et al. 2009) and in some North American mammals (George & Crooks 2006). We did not measure

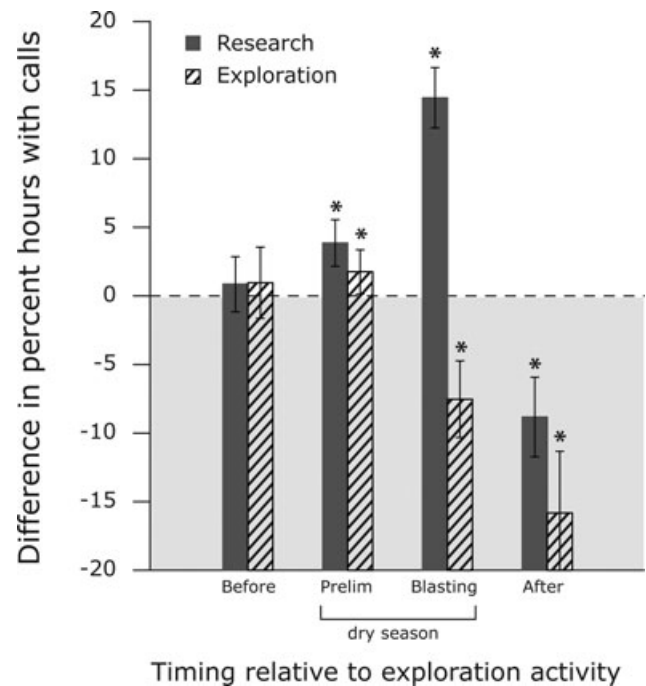


Figure 2. The effect of oil exploration activities on the day–night activity pattern of forest elephants (indicated by elephant calling rates). Research areas were far removed from exploration activity (no sounds of detonations were recorded), but elephants in the EX area were in the midst of human activity. Each bar (SE) represents the difference between daytime and nighttime activity (least-squares means calculated from coefficients in the model summarized in Table 2). Values less than zero indicate more nocturnal activity than diurnal activity. Asterisks indicate activity patterns that depart significantly from equal day and night activity (Bonferroni correction).

the effects on fitness associated with the elephants' shift in behavior, but we expect it to be relatively minor given that elephants did not leave the exploration area altogether. Nevertheless, reduced foraging time, potentially higher competition for high-quality food resources, and increased stress are likely consequences of compressing the activity budget into a smaller part of the daily cycle.

Our acoustic data suggest that forest elephants did not respond directly to the noise of dynamite detonations; rather, they responded to the activity of human workers moving through the forest and on the roads. Elephants did not respond directly to either acoustic or seismic signals although these signals were often of very high amplitude. Rabanal et al. (2010) assumed the blasting noise was responsible for changes in elephant distribution over small spatial scales. Nevertheless, the time scale of disturbance measures in their statistical models could not have

Table 3. The effect of human activity on the day–night activity of forest elephants over short periods of time.^a

Effect	df num, denom	F	p
Area (Ex vs. R1, R2 combined) ^b	1,83.4	1.98	0.16
Time block (inclusive days of human activity per transect)	1,83.4	17.35	< 0.01
Day–night period	1,238	14.37	< 0.01
Time block * day–night period (interaction)	1,237	11.84	< 0.01
Area * time block * day–night period (interaction)	2,122	4.00	0.02

^aOverall GLM model was significant ($\chi^2 = 99$, $p < 0.01$, 6 df). Repeated measures correlation structure was auto regressive and significant. The response variable was the proportion of hours during day and night periods with one or more elephant calls recorded.

^bSampling areas: two research areas (see Methods) (R1, R2) and the oil exploration area (EX).

distinguished between blasting and the presence of human teams conducting the blasting.

We did not expect elephants to remain in the forest tract where oil exploration activities were ongoing. Results of many studies show that forest elephants are more numerous far from human settlements and active roads (e.g., Laurance et al. 2006; Buij et al. 2007; Blake et al. 2008). The effects of the oil exploration in our study area may have been moderate because the duration of exploration activities was relatively short; activities were strictly regulated (e.g., vehicle use at night was prohibited); and blasting was concentrated in only a few parts of the forest at any one time and progressed in a regular manner through the exploration zone. This exploration regime apparently allowed elephants to avoid contact with humans and rendered the forest free of human activity at night. Our acoustic tools provided a method with which to simultaneously assess elephant density and activity at widely separated locations, continuously, and with equal sensitivity at all hours of the daily cycle. Although we focused on forest elephants, other species (e.g., great apes, many birds) could be monitored simultaneously, depending on recorder spacing, as could specific anthropogenic activities, such as vehicle traffic and hunting.

Acoustic monitoring of animals that communicate acoustically offers a powerful method with which to study behavior and estimate density (Thompson et al. 2009a), particularly in dense vegetation and for species that are elusive, wide ranging, or nocturnal. Our acoustic methods revealed changes in behavior that could be overlooked by more traditional, visually based methods.

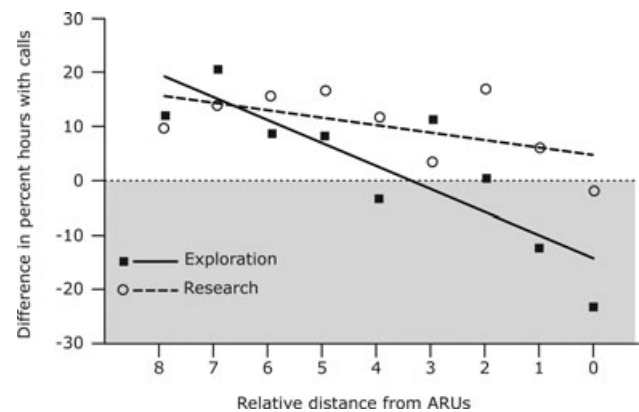


Figure 3. Correlation between elephant activity measured near specific ARUs (autonomous recording units) and approach of human activity to these locations. Research areas were far removed from exploration activity (no sounds of detonations were recorded) and therefore this line shows the normal seasonal pattern of elephant activity on the dates incorporated along the x-axis. Recording locations in the EX area were to the south and human activity approached these locations monotonically. Lines are the predicted relations from the model described in Table 3 (the different slopes reflect the significant 3-way interaction). Average variation is conveyed by the least-squares means at each distance interval (relative distance in the Table 3 model; categorical instead of ordinal). Values less than zero indicate more nocturnal activity than diurnal activity. Graph only includes data from the blasting time period.

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