Density and activity patterns of ocelots (*Leopardus pardalis*) in northern Peru and the impact of oil exploration activities

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ABSTRACT

The western Amazon is experiencing unprecedented levels of oil and gas exploration, a trend of particular concern given the high levels of biodiversity found in this relatively pristine and unstudied region. Despite the widespread use of seismic reflection technology for exploration, no studies have investigated the response of wildlife populations to this disturbance in the tropics. We conducted a trail camera survey inside a large oil concession (Block 39) in the Peruvian Amazon near the Ecuador border with ongoing 2D seismic explorations to investigate its effects on ocelot (*Leopardus pardalis*) activity and abundance. The estimated size of the ocelot population within our 22 km² study area was the same before (control period: 34 ± 6.9 ocelots) and during exploration operations (disturbance period; 34 ± 4.6 ocelots) and we detected no change in activity patterns between the two periods. Ocelot capture rate was unaffected by the presence of seismic crews, and distance to the nearest seismic line was not correlated with capture rate at individual stations. Our density estimates (ocelots/100 km²) from the control (75.2) and disturbance period (94.7) include the highest reported for the species, and represent the first ocelot density estimates from the northwest Amazon forest. These high values conform to recent research showing a positive association between ocelot density, annual rainfall, and proximity to the equator (this study: >2500 mm annual rainfall; <200 km from equator). We discuss the potential short- and long-term environmental impacts of seismic operations, particularly as they relate to large mammal populations.

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1. Introduction

The ever-increasing worldwide demand for energy has resulted in unprecedented levels of oil and gas exploration in the western Amazon, with some of the most intense activity occurring in Peru. As of 2008, 72% of the Peruvian Amazon was zoned by the government for oil and gas activities into 64 separate concessions or "blocks", 48 of which are currently active (Finer et al., 2008). Many of Peru's concessions are already, or will soon be subjected to active exploration, which includes the use of seismic reflection technology along a grid of "seismic lines". Along these straight-line transects, underground explosives are detonated to register reflected sound waves, which provide information about the presence and depth of potential oil and gas reserves. The frequency of use of seismic exploration in tropical rainforest ecosystems, combined with the fact that much of the western Amazon is relatively pristine and harbors some of the highest levels of biodiversity in the world (Ceballos and Ehrlich, 2006; Orme et al., 2005; Ter Steege et al., 2003), highlights the need to understand the impacts of these activities on the ecosystem, and exposes a remarkable gap in our understanding of the environmental impact of oil and gas industry presence in the Amazon.

Few studies have investigated the impact of terrestrial seismic exploration activities on mammal populations or any aspect of ecosystem function. The majority of the existing research has been conducted in Canada and the northern United States and has resulted in mixed conclusions regarding the extent to which these activities influence mammal populations. Based on radio-telemetry data, grizzly bears (*Ursus arctos*) in British Columbia showed no significant habitat displacement in response to seismic exploration activities (McLellan and Shackleton, 1989), whereas larger-scale landscape use modeling indicated that secondary effects of seismic lines on landscape structure influenced grizzly bear movements in Alberta, Canada (Linke et al., 2005). In the same region, GPS-monitored woodland caribou (*Rangifer tarandus caribou*) avoided areas within 250 m of seismic lines (Dyer et al., 2001), yet seismic lines, unlike roads, did not act as barriers to caribou movement (Dyer et al., 2002). Finally, although behavioral changes occurred in woodland caribou in response to noises simulating seismic exploration, no significant displacement occurred (Bradshaw et al., 1997). To our knowledge, no formal studies have investigated responses of wildlife to disturbances associated with seismic oil exploration in tropical systems.

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The ocelot (*Leopardus pardalis*) is the largest of the world's small spotted cats, exhibits an extensive range stretching from southern Texas to northern Argentina, and occurs in a wide variety of ecosystems, from thornscrub to tropical rainforest (Murray and Gardner, 1997). Due to the key role that large carnivores play in regulation of ecosystem function (Crooks and Soule, 1999; Ray et al., 2005; Ripple and Beschta, 2006; Terborgh et al., 1999), knowledge of how their populations respond to human disturbances is crucial to ecosystem conservation efforts. Unlike puma (*Puma concolor*) or jaguar (*Panthera onca*), ocelots do not exhibit the extensive home ranges that make population surveys problematic, and a relatively focal disturbance such as seismic exploration can influence numerous ocelot territories within a short time period, making ocelots a potentially more responsive indicator of disturbance impacts. Although their geographic range suggests a behaviorally flexible species, ocelots can be sensitive to habitat loss and fragmentation resulting from human development and habitat conversion (Haines et al., 2005; Tewes and Everett, 1986), and recent research also indicates that more subtle forms of anthropogenic disturbances (e.g. poaching and logging) in otherwise suitable habitat can significantly reduce local ocelot abundance (Di Bitetti et al., 2008).

A relatively new technique utilizing a combination of motion-triggered cameras and statistical methods associated with traditional mark-recapture techniques has allowed researchers to directly estimate the density and local abundance of spotted cat populations (Karanth, 1995; Karanth and Nichols, 1998) without the need for trapping and telemetry, or the problematic assumptions involved in track surveys (Karanth et al., 2003). Consequently, camera surveys have recently documented ocelot densities in various locations (e.g., Bolivia: Maffei et al., 2005, Argentina: Di Bitetti et al., 2006, Belize: Dillon and Kelly, 2007, Brazil: Trolle and Kery, 2003). However, densities have not been reported from a large portion of the western Amazon (Colombia, Ecuador and northern Peru). Ocelot densities are positively correlated to an area's rainfall, and negatively to its latitude (Di Bitetti et al., 2008); a suspected consequence of the connection between primary productivity and proximity to the equator. Due to its extremely high annual rainfall and proximity to the equator, this unstudied region of the western Amazon is therefore expected to support some of the highest ocelot densities throughout the species' range (Di Bitetti et al., 2008).

Our primary objective was to use a camera-trapping survey to assess the short-term impacts of seismic exploration on ocelot density, local abundance, and activity patterns by monitoring a single study area before and during the initiation and completion of a seismic exploration project. A secondary objective was to provide an important data point in the assessment of the continental correlates of ocelot abundance by estimating ocelot density at a location averaging more than 2500 mm of annual rainfall and located more than 700 km closer to the equator than any previous ocelot study site.

2. Methods

2.1. Study area

Our study was conducted within a large oil concession (Block 39; 1°35'12.3"S, 75°12'20"W) in the Peruvian Amazon in the department of Loreto near the Ecuador border. The concession covers approximately 8850 km^2 and is located 250 km NW of Iquitos (pop ~400,000), the closest center of commercial trading and residential development. The block includes the higher reaches of three notable rivers, the Curaray, which extends into Ecuador, the Arabela, and the Pucacuro. The watershed of the latter defines the Zona Reservada Pucacuro, an area set aside as pro-

tected by the government which is in the process of categorization. All rivers within the block drain into either the Tigre or Napo rivers which ultimately empty into the Amazon River near Iquitos. The block itself contains no roads and includes only a few small villages along its eastern edge. The largest of these, Buena Vista and Flor de Coco, are located along the Arabela River and each support less than 300 inhabitants (Vriesendorp et al., 2007).
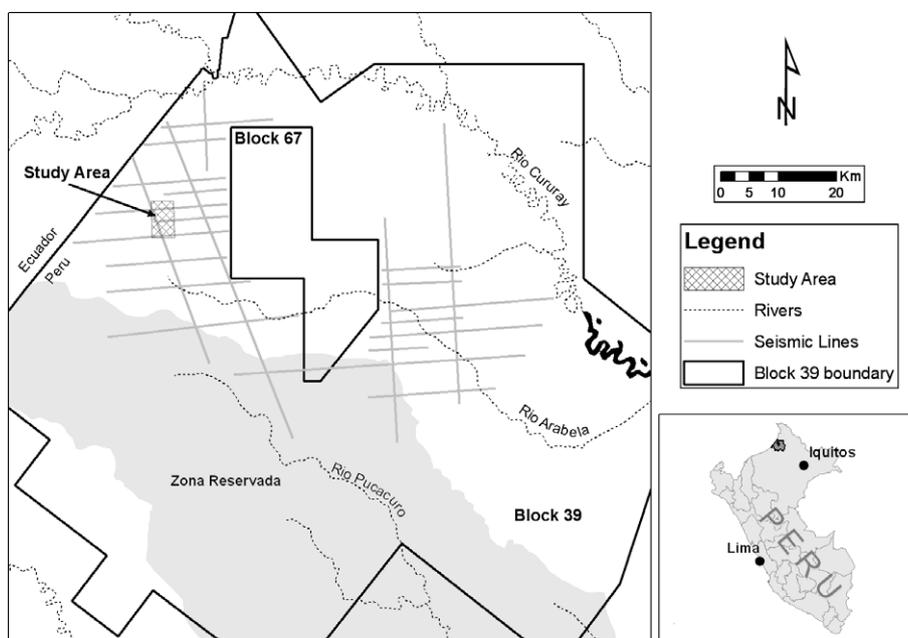
Due to its remote location and the resulting relative isolation from development and exploitation, the vast majority of Block 39 is composed of pristine lowland tropical rainforest. The block is characterized by rolling topography and is included in the Napo Moist Forest ecoregion (Olson et al., 2001). There is no distinct dry season in this region and annual rainfall averages 2500–3000 mm. During our study period from April through August 2008 monthly rainfall in Block 39 averaged 256 mm (range: 119–465 mm), and monthly daytime minimum and maximum temperatures averaged 20° and 32 °C, respectively, with little variation among months.

Seismic oil exploration activities in Block 39 began in early 2008 with Repsol, the operating company, planning for seismic drilling along 590 km of straight-line transects (Fig. 1). We began our study before the arrival of seismic work crews to our study site, and thus the seismic lines shown in Fig. 1 were not yet cleared.

Using a combination of SRTM digital elevation models (van Zyl, 2001), LANDSAT ETM + imagery, and the planned seismic routes, we selected our study site based on two primary factors: (1) did not include any major rivers or areas likely to be seasonally or permanently inundated, and (2) contained a high density of proposed seismic lines. This latter factor was critical to ensure that our study area was subject to the highest levels of disturbance associated with this seismic operation. We identified an optimal study area (~22 km^2) in the west of Block 39 (Fig. 1) with an elevation range of 205–279 m, and which ultimately contained a seismic line density of 680 m/km^2. This is the most remote portion of the concession; it is completely inaccessible by river, and no signs of human presence or hunting were encountered. To ensure that disturbances associated with our research camp (e.g. helicopter supply flights, generator noise) did not influence ocelots in our study, we established our camp approximately 1 km outside of the study area.

2.2. Seismic operations

Technological advances and adoption of more strict environmental practices have allowed companies to reduce the environmental damage previously associated with seismic operations (Rosenfeld et al., 2001), and use of an "offshore model", (no road construction, access only by boat or helicopter) is now standard. However, seismic exploration activities continue to involve an extensive influx of personnel, equipment and potential disturbance to the ecosystem. Seismic exploration in Block 39, as carried out by Repsol and their subcontractors, followed the offshore model and included three waves of activity; topography, drilling and registration. During topography, a relatively narrow (~1.2 m) straight-line trail is cleared using chainsaws and machetes, leaving all trees >20 cm dbh. Along these transects, holes of 15 m depth are drilled every 50 m and an explosive charge is buried. The final wave of activity includes the largest number of field personnel and involves laying recording devices and cables along seismic lines, detonation of the charges, and registration of the resulting seismic reflection waves. Within our study area topography, drilling and registration team activity lasted 14, 28, and 23 days, respectively, and never occurred simultaneously. Throughout the topography phase, camps of approximately 10 × 20 m are cleared approximately every 4 km along each transect and are always associated

Fig. 1. Location of study area inside Block 39 where camera trapping was conducted to estimate ocelot densities and assess impacts of seismic oil exploration. Note that the inset Block 67 is not managed by the same company as Block 39.

with helipads. When in use, these camps support from 8 to 60 workers and receive helicopter flights on average every 2–3 days. Helipads vary in size, but on average result in clearings of 30 × 40 m, within which all trees are felled. Much smaller "drop zones" (typically <50 m²) are cleared at more frequent intervals along seismic lines to allow equipment pick-up and drop-off, which occurs multiple times per day during registration. The above description refers to "2D" seismic operations as opposed to the more intensive "3D" operations which often follow successful 2D programs.
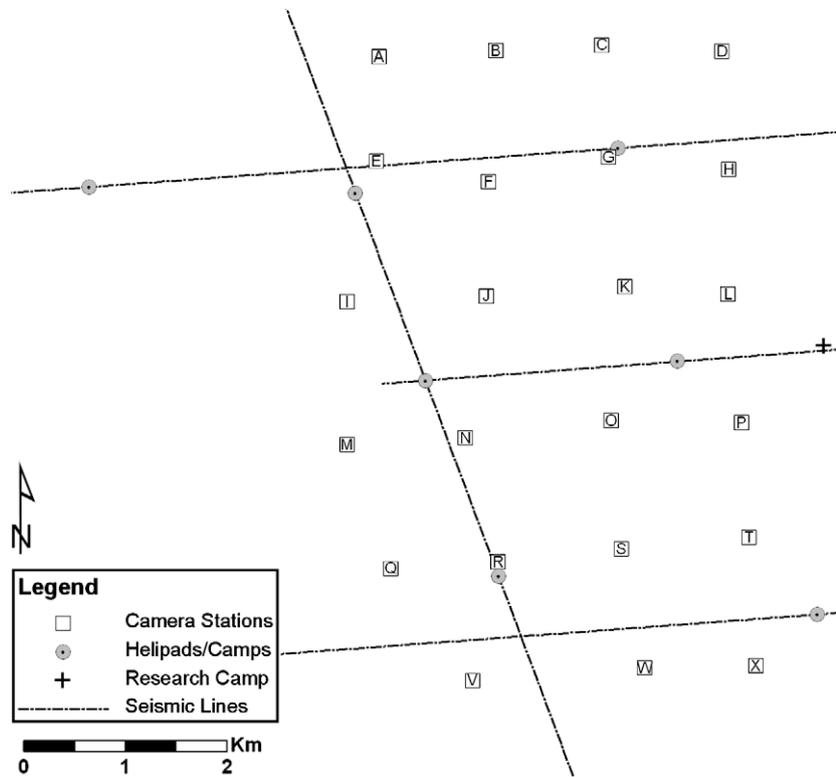
2.3. Camera trapping

We established a grid of camera stations specifically designed to characterize and monitor the local ocelot population. Due to the complete lack of roads and human-made trails, we used machete to open 35 km of trails, approximately 1 m in width, which were maintained vegetation-free throughout the study. Along these trails we established 23 camera stations, each with two Reconyx RC-55 digital infrared trail cameras (Reconyx Inc., Holmen, Wisconsin, USA) positioned on either side of the trail to obtain photos of both sides of the target animal. Camera stations were always placed either at the intersection or coincidence of our trail with an existing game trail. Cameras were placed 0.5–2.0 m off the trail at a height of approximately 25–45 cm. The stations formed a polygon of 22 km², and adjacent stations were separated by an average of 1122 m (range = 1022–1371 m, SD = 86 m; Fig. 2). The only home range data available for ocelots in Peru indicates that ocelots in the southeast of the country maintain home ranges as small as 1.62 km² (Emmons, 1988). Our short distances between cameras (trap density >1 trap/km²) were therefore necessary to ensure that no home range sized gaps occurred within our grid, and that all animals within the grid consequently had a capture probability >0. Cameras functioned 24 h/day and were typically checked every 10–14 days to monitor memory card space and battery power. We considered a single camera-night to be when at least one of the two cameras at a station functioned properly for an uninterrupted 24-h period.

2.4. Data analysis

To assess the influence of seismic exploration activities on ocelot abundance and activity patterns, we estimated these variables during two distinct periods. The first sampling period (control) extended from the establishment of the camera grid, to the day when initial seismic crews (topography) had begun to clear sections of all four local seismic lines. This period served as a baseline control period during which we were able to assess population size, density, and activity of ocelots in the absence of disturbance. A second sampling period (disturbance period) extended from the day when topography crews opened all seismic line sections in our study area (4 days after the end of the control period), to approximately 1 week after the conclusion of the seismic operation. This period included the full activities of all three phases of seismic work: topography, drilling, and registration.

2.4.1. Population size and density

We used mark-recapture statistical methods available in the program CAPTURE (Otis et al., 1978; White et al., 1982) to estimate population size of ocelots in our study area based on ocelot photographic capture events. Ocelots were identified using their unique spot patterns (Trolle and Kery, 2003) and sex was determined based on the presence of testes and overall body size and shape. Photos that did not allow for unambiguous identification of the individual (e.g. high movement blur, only head or tail in image) were discarded for this analysis but used for activity pattern analyses (see below). To achieve the recommended average individual capture probability of at least 0.10 (Otis et al., 1978), we considered a 4-day trapping period as a single trapping occasion and constructed capture histories for each individual accordingly. Of the seven models within the program CAPTURE available to model detection probabilities, we utilized the most appropriate model according to the model selection algorithm provided in the program. However, given a species like the ocelot, which is territorial and displays sex-biased home range sizes, use of the null model $M_{(o)}$, which assumes constant probability of capture for all individuals, is considered inappropriate (Karanth, 1995; White et al.,

Fig. 2. Grid of 23 camera stations used to estimate local density and activity patterns of ocelots and the response of these variables to seismic oil exploration activities conducted along the pictured seismic lines. The full array of seismic lines in this oil concession (Block 39) is pictured in Fig. 1.

1982). We therefore used the second-best model when $M_{(o)}$ was selected.

A primary assumption of the mark-recapture based population estimation used here is that the population is closed (i.e. no deaths, births, immigrations or emigrations) during the survey. Although a test for population closure is performed by CAPTURE (and we report the results below), it is generally agreed that an accurate statistical test for population closure based on capture–recapture data does not exist (White et al., 1982) and that closure should be judged on a biological basis (Otis et al., 1978). As in Karanth and Nichols (1998), we test for the presence of transient animals (animals simply passing through the study area), which results in a violation of the closure assumption, by testing for a behavioral response after initial capture ($M_{(b)}$). Significance or selection of this model would result from the presence of transient animals, which would appear as "trap-shy" individuals due to their lack of recaptures. However, as in most other studies, we assume that our population was closed given the short length of our trapping periods (44 and 96 days) relative to the lifespan of an ocelot. We report population sizes with standard errors and 95% confidence intervals (CIs) as reported in the program CAPTURE.

To calculate population density using abundance estimates, the effective area sampled by a camera survey must be identified to account for the fact that the area used by captured animals is larger than the area enclosed by the camera grid. To this end a buffer is typically added around each camera station (Silver et al., 2004) or the trapping grid polygon (Karanth and Nichols, 1998). The most commonly used buffer distance is half the mean of the maximum distance moved (½MMDM) by all individuals captured at more than one camera station (Di Bitetti et al., 2006; Maffei et al., 2005; Trolle and Kery, 2003). The MMDM is used to represent an approximation of the diameter of an average circular home range of the target animal (in the absence of home range information

from the study area) with ½MMDM representing the radius. We therefore buffered each camera location by a distance equal to ½MMDM, and dissolved buffer boundaries to calculate the total area sampled. Finally, we divided the estimated population size by the effective sampled area to calculate density values. Abundance, MMDM and density values were all calculated separately for the control and disturbance periods. Although recent research indicates that MMDM from camera surveys approximates actual average home range diameter of ocelots when survey areas are sufficiently large relative to the target animal's home range size (Maffei and Noss, 2008), other research suggests that at least under some conditions, density estimates are more accurate using a buffer size equal to the full MMDM (Dillon and Kelly, 2008; Parmenter et al., 2003; Soisalo and Cavalcanti, 2006). We therefore report densities using both the full and ½MMDM buffer to allow comparison with all published densities.

2.4.2. Capture rate and seismic disturbance

To further investigate the influence of seismic exploration activities on local ocelot abundance, we compared capture rate (# of ocelot photo events/100 camera-nights) at the 23 camera stations between the control and disturbance period, using the non-parametric repeated-measures Friedman test. For this analysis, three instances where a large juvenile was photographed with its mother were treated as single photo events to maintain independence of capture events. For visualization purposes, we present overall ocelot capture rate throughout the study, relative to the timing of each seismic activity, with the study period divided into 24, 6-day long time blocks. For both sampling periods we also calculated, using each camera station as a sample, the Spearman rank correlation coefficient (r_s) between the distance to the nearest seismic line and ocelot capture rate to investigate whether ocelot capture success was influenced by proximity to seismic lines.

2.4.3. Activity

Using time data collected with each ocelot photograph, we constructed activity patterns for both sampling periods with activity represented as the % of all ocelot photos collected in each hour of the 24-h cycle. Because of the cyclical nature of the temporal data, we used circular statistics, specifically the Kuiper's test (Batschelet, 1981), to compare the frequency distributions of capture times from the control and disturbance periods. To determine specifically whether ocelots reduced daytime activity during the presence of seismic activities, we compared the frequency of locations collected during daylight hours between the control and disturbance period using a Fisher exact test. All distance and area calculations were performed using ArcView 3.3 (ESRI, Redlands, CA, USA).

3. Results

3.1. Population size and density

Throughout the study, we were able to assign an individual identification to 97% of ocelot photos and were able to sex all but one adult ocelot. This unusually high success rate was undoubtedly due to our cameras' ability to take numerous photos of each ocelot (max = 79, mean = 8) as they approached and departed the camera station. Camera trapping during the control period (before seismic activities) extended for 44 days and 983 camera-nights. The closure test indicated a closed population ($z = 0.443$; $p = 0.671$) and there was no support for the behavioral response model of capture probability $M_{(b)}$. A total of 22 individual ocelots (11 M, 10 F, one unknown sex) were captured 42 times for a capture rate of 4.27 ocelot photo events/100 camera-nights (Table 1). Of the nine cats that were recaptured, 66% were only captured at a single camera station. Although the null model $M_{(o)}$ was selected as the most appropriate for population size estimation, we used the next most supported model $M_{(h)}$, which allows for capture probabilities to vary by individual, to estimate population size (goodness of fit test, $\chi^2 = 7.76$, $df = 10$, $p = 0.652$). Average probability of capture based on this model was 0.10. Population size was estimated at 34 individuals ±6.9 (95% CI = 26–55).

Camera trapping conducted during the disturbance period lasted for 96 days totaling 2085 camera-nights. As in the control period, the closure test indicated a closed population ($z = 0.139$; $p = 0.556$) and there was no support for the behavioral response model of capture probability $M_{(b)}$. A total of 27 different ocelots (12 M, 13 F, two large juveniles) were captured 86 times for a rate of 3.98 ocelot photo events/100 camera-nights (Table 1; juveniles with adults not counted as independent events). Of the 18 ocelots

that were captured more than once during this period, 50% were only captured at a single camera station. The $M_{(h)}$ model was selected by CAPTURE as the most appropriate ($\chi^2 = 21.12$, $df = 10$, $p = 0.575$) and calculated an average probability of capture of 0.09. Estimated population size was 34 ± 4.6 (95% CI = 30–49).

To estimate ocelot density we first calculated MMDM for both sampling periods (Table 2). Although estimated population size was the same for both sampling periods, estimated ocelot density, employing the most commonly used buffer of ½MMDM, was higher in the disturbance period (94.7 ocelots/100 km^2) than the control period (75.2 ocelots/100 km^2) due to differences in MMDM between periods (Table 2). Over the entire study period, the longest distance moved was 2.7 km for males and 1.4 km for females.

3.2. Capture rate and seismic disturbance

There was no relationship between the distance to the nearest seismic line and ocelot capture rate at the 23 camera stations during the control period ($r_s = -0.197$, $p > 0.35$; Fig. 3A), when seismic lines were not yet created. However, we also found no relationship between these two variables during the period ($r_s = -0.304$; $p > 0.15$; Fig. 3B) when seismic lines were open and active, indicating that ocelot capture rate at an individual camera station was unrelated to its proximity to a seismic line. In addition, although ocelot capture rate became more variable during seismic operations, there appeared to be no consistent effect of the presence of seismic crews on ocelot capture rate (Fig. 4). Ocelot capture rates at the 23 camera stations during the control period were not statistically different from capture rates during the disturbance period (Friedman repeated measures $\chi^2 = 0.0$, $p = 1.0$, $n = 23$).

3.3. Activity

Ocelots exhibited similar patterns of activity both before and during the presence of seismic exploration crews in our study area (Fig. 5; Kuiper's test with time of capture grouped into 72 intervals of 20 min each, each interval 5°; $K = 1.214$; $p > 0.20$). Ocelots were almost exclusively nocturnal regardless of the sampling period, and the proportion of photos taken during daytime hours (06:00–18:00 h) was equally low in both the control (8.9%) and disturbance period (8.4%; Fisher exact test, $p = 1.00$). Although peaks in activity during the night were not apparent, the primary nocturnal activity period was well defined, with ocelot activity beginning abruptly at sunset and ending at sunrise; in both sampling periods, we did not record a single ocelot photo in the 2 h preceding sunset (16:00–18:00 h) or the hour following sunrise (06:00–07:00 h).

4. Discussion

4.1. The influence of seismic exploration on ocelots

This study is the first to investigate the influence of seismic oil exploration activities on wildlife in a tropical rainforest. We predicted that if ocelots avoided areas subjected to seismic activities, even on a temporary basis, we should record a lower photo capture frequency and lower estimated local population size during the disturbance period compared to our control period. However, we found no evidence of spatial avoidance of our study area during seismic operations based on either capture frequencies or estimated local ocelot abundance.

Although there is evidence of wildlife avoidance of areas subjected to seismic exploration activities in Canada and the northern US (Dyer et al., 2001; Linke et al., 2005), Dyer et al. (2001) documented avoidance of seismic lines in caribou at only short dis-
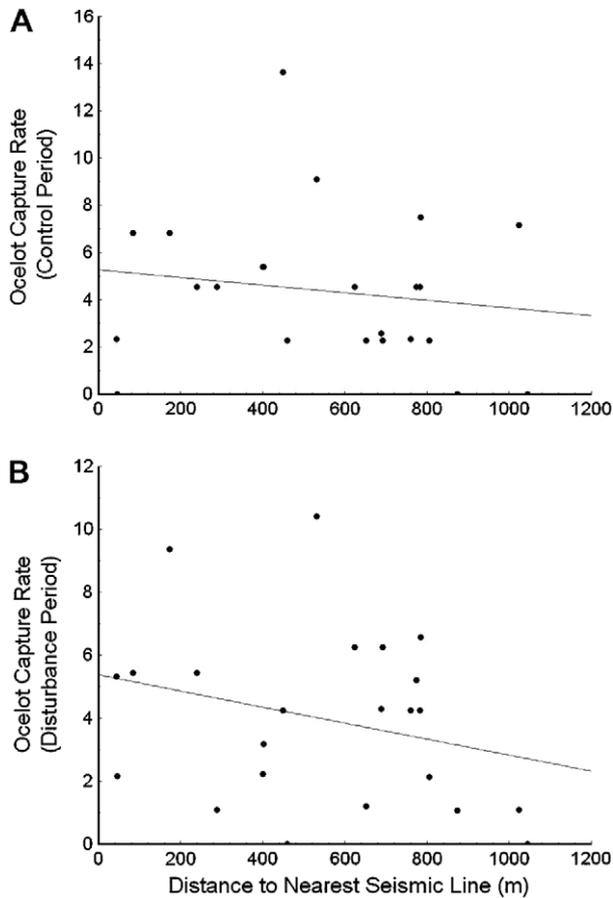
Table 1
Summary information for ocelot camera-trapping sampling periods before and during the activities of seismic exploration crews within the study area. One camera-night represents a single camera station functioning for a single 24-h period and a trapping occasion, for purposes of statistical modeling, was defined as a 4-day period.

	Control period	Disturbance period
Dates (2008)	April–May	June–September
Duration (days)	44	96
Trapping occasions	11	24
Camera-nights	983	2085
Ocelot photo captures	42	86
Capture rate (photos/ 100 camera-nights)	4.27	3.98
Total individuals	22	27
Males	11	12
Females	10	13
Unknown sex adults	1	0
Large juveniles	0	2

Table 2
Data used to calculate the density (D; #/100 km^2) of ocelots based on camera trapping before and during the activities of seismic exploration crews within the study area. The effective sampled area (area; km^2) was calculated by buffering all camera stations by two different buffer distances: MMDM and ½MMDM (buffer; m). The estimated population size (N) for each period was calculated using the program CAPTURE and is presented with a 95% confidence interval. We considered ½MMDM to be the more appropriate buffer (see discussion for more detail).

	Control period				Disturbance period			
	N	Buffer[a]	Area	D	N	Buffer[b]	Area	D
MMDM[c]	34 (26–55)	2214	78.1	43.5	34 (30–49)	1568	58.1	58.5
½MMDM	34 (26–55)	1107	45.2	75.2	34 (30–49)	784	35.9	94.7

[a] Based on 3 ocelots captured at more than one camera station.
[b] Based on 7 ocelots captured at more than one camera station.
[c] Buffer distance based on the mean maximum distance moved (MMDM) by ocelots captured at more than one station.

Fig. 3. Relationship between ocelot capture rate (photos/100 camera-nights) and distance from the camera station ($n = 23$) to the nearest seismic line: (A) before the line was opened and (B) during seismic operations.

tances (250 m) relative to caribou daily movements, and other research suggests wildlife tolerance of these activities (Bradshaw et al., 1997; McLellan and Shackleton, 1989).
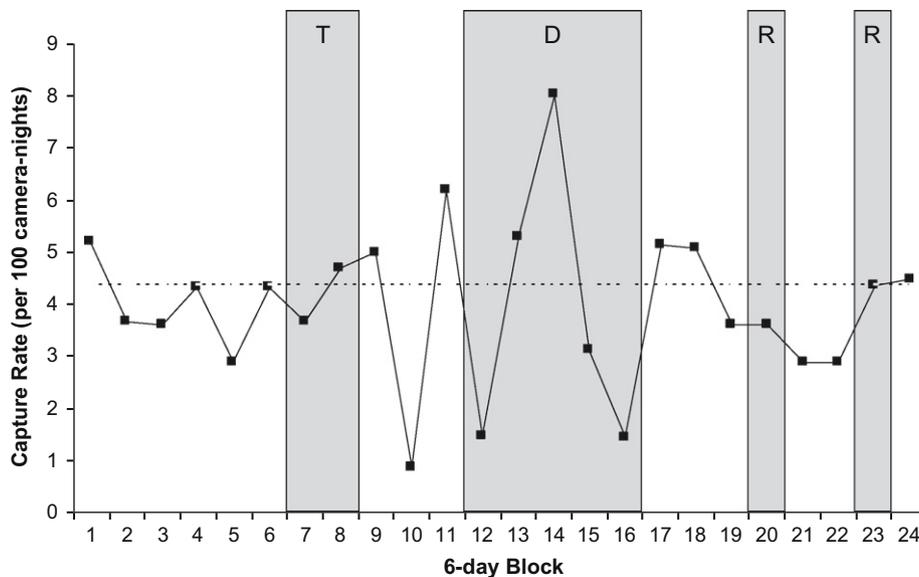
Responses of wildlife to other similar types of disturbance offer additional insight into potential responses to seismic exploration. For example, like seismic activities, military training, mining and selective logging operations, and certain recreational activities such as snowmobiling and high-volume tourism represent focal, relatively temporary, and strictly daytime disturbances characterized by both noise pollution and human presence. For example, mountain caribou (*R. tarandus caribou*) were found to avoid otherwise suitable habitat characterized by intense snowmobile use (Seip et al., 2007) and mining activity (Weir et al., 2007), and both coyotes (*Canis latrans*) and mule deer (*Odocoileus hemionus*) altered space use patterns to avoid areas subjected to intense military training activity (Gese et al., 1989; Stephenson et al., 1996). How-

ever, research has also discovered a capacity for tolerance in various large mammals to these types of disturbances. For example, black bears (*Ursus americanus*) did not avoid weapons-firing exercise areas on a military base in South Carolina (Telesco and Van Manen, 2006) and caribou (*R. tarandus granti*) responses to military jet overflights were generally mild and did not result in altered movement patterns (Lawler et al., 2005). Similarly, bighorn sheep (*Ovis canadensis*) and Dall's sheep (*O. dalli*) in the southwestern US are known to use active mining areas despite high levels of noise and vehicular traffic (e.g. Jansen et al., 2007, 2006).
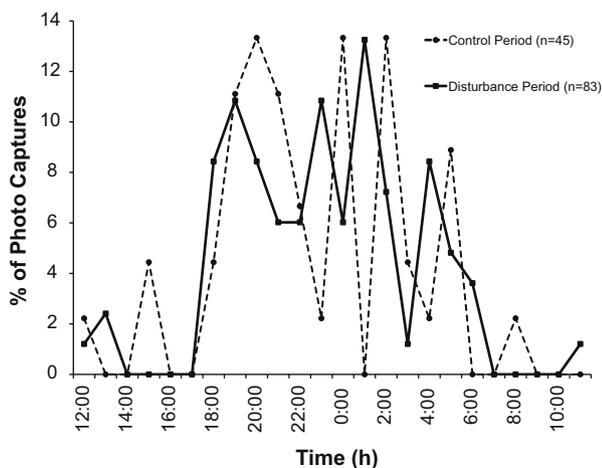
There is no doubt that even displacement on a small spatial scale can have serious consequences for wildlife, particularly if avoided areas are characterized by high-quality habitat or food resources, or if extra-territorial excursions result in higher potential for intraspecies aggression. However, even on a small scale we could not detect changes in movements of ocelots resulting from seismic exploration activities. For example, of the 18 suspected resident cats (i.e. more than one photo capture during the 144 days study) initially photographed in the control period, 14 were photographed at the same stations in the disturbance period, with four of these cats captured at an additional station. Of the four remaining suspected residents from the control period, only one was not photographed again in the disturbance period. Although telemetry would have provided a more detailed picture of ocelot movements in reaction to specific seismic activities, it would have been inappropriate for the study of this temporary, short-term disturbance, and our camera survey clearly showed continued use of the affected areas throughout the disturbance by a very dense local ocelot population.

Two critical assumptions relate to our ability to directly compare population estimates from our two sampling periods: (1) the control period was sufficiently long to accurately estimate population size, and (2) the disturbance period was sufficiently short to ensure population closure. The duration and sampling effort of both our control period (44 days, 983 camera-nights) and disturbance period (96 days, 2085 camera-nights) are typical for similar camera-trapping studies, which report survey durations ranging from roughly 1–3 months with numerous surveys of less than 45 days (e.g. Di Bitetti et al., 2008; Dillon and Kelly, 2007; Soisalo and Cavalcanti, 2006) and less than 1000 camera-nights (e.g. Karanth and Nichols, 1998; Maffei et al., 2005; Trolle and Kery, 2003). The fact that 20 of 23 camera stations recorded at least one ocelot photo during the control period (only one station less than in the much longer disturbance period), is further evidence that the duration of the control period was adequate to describe the local ocelot population. Although the 3-month duration of our disturbance period is at the high end of the range of published survey durations, closure tests and the lack of statistical support for the $M_{(b)}$ model indicated that assumptions of population closure were not violated.

Because the disturbances associated with seismic crew activities were almost entirely restricted to the daytime period (with the exception of noise from overnight camps) there was also the

Fig. 4. Ocelot capture rate (photos/100 camera-nights) across 24, 6-day time blocks throughout the course of the entire 144-day study (16 April–6 September 2008). The dotted line indicates the average capture rate during the control period before seismic exploration activities began in the study area. Shaded boxes indicate which 6-day blocks included activities within the study area of the different seismic crews (topography: T, drilling: D, or registration: R).

Fig. 5. Activity pattern of ocelots based on photo captures during sampling carried out before (control period) and during (disturbance period) seismic exploration activities in the study area. "12:00" represents the hour between 12:00 and 1:00 h. The control period includes two photo captures recorded before the formal camera grid was active. Sunset and sunrise occurred at approximately 18:00 h and 06:00 h, respectively throughout the study.

potential for ocelots to reduce exposure to these disturbances by reducing daytime activity. For example, grizzly bears in Alaska reduced daytime use of salmon streams exposed to high levels of use by tourists (Olson et al., 1998), and leopards (*Panthera pardus*) exhibited significantly lower diurnal activity in an active logging concession compared to an abandoned concession in Gabon (Henschel and Ray, 2003). We did not detect activity pattern differences in ocelots between our two sampling periods, indicating a lack of temporal avoidance of seismic disturbances. However, it should be noted that even undisturbed ocelots showed very low activity in daylight hours, leaving little potential for activity modification in response to daytime seismic exploration activities.

The activity pattern of ocelots is well-documented by both radio-telemetry (Crawshaw and Quigley, 1989; Emmons, 1988; Konecny, 1989; Ludlow and Sunquist, 1987) and trail camera methods (Di Bitetti et al., 2006; Dillon and Kelly, 2007; Maffei et al., 2005). The pattern described in this paper, showing the major-

ity of activity occurring in the night, is consistently reported by all these previous studies; an expected result given that the overwhelming majority of ocelot prey species are nocturnal (Konecny, 1989; Ludlow and Sunquist, 1987).

4.2. Ocelot density in the western Amazon

Based on a compilation of all available ocelot population surveys, Di Bitetti et al. (2008) showed that local density of ocelots is correlated to both rainfall and latitude, with the highest predicted densities occurring in areas close to the equator with very high annual rainfall; both characteristics of our study site. Reported ocelot densities vary widely throughout the range of the species with the lowest density reported at 3.1 ocelots/100 km^2 in the pine forests of Belize (Dillon and Kelly, 2007). The highest reported density from a camera trapping study is 59 ocelots/100 km^2 in the Transitional Chaco-Chiquitano dry forest ecoregion of Bolivia (Maffei et al., 2005); the highest from any study is from Manu National Park in southeastern Peru (80 ocelots/100 km^2) based on radio-telemetry (Emmons, 1988). Our estimated densities (ocelots/100 km^2) therefore include the highest density reported from any ocelot camera survey (75.2), and the highest density as yet reported in the literature (94.7), providing added support for the correlation between ocelot density, rainfall and distance to the equator.

The observed trend of increasing ocelot density with increasing annual rainfall and proximity to the equator was tentatively suggested to result from the general pattern of decreasing primary productivity with increasing degrees latitude (Di Bitetti et al., 2008). The authors also left open the possibility that a higher frequency of human impacts observed at study sites further from the equator could also have contributed to the trend (Di Bitetti et al., 2008). Ocelots in our study area, before the arrival of seismic crews, had been completely isolated from human activity, leaving open the possibility that this isolation played a part in the high observed densities. However, this factor cannot be separated from the potential effect of primary productivity, which is certainly high in this region given the extremely high annual rainfall, absence of a dry season, and proximity to the equator.

There is conflicting evidence regarding the utility of the ½MMDM distance as a proxy for average home range radius and

as a buffer for the estimation of the effective sampled area of camera surveys. While some studies, based on a combination of radio-telemetry and camera surveys, indicate that this methodology will typically overestimate density values (Dillon and Kelly, 2008; Soisalo and Cavalcanti, 2006), Maffei and Noss (2008) found that ½MMDM from a camera-trapping survey was a reliable estimate of the actual home range radius of tracked ocelots. Dillon and Kelly (2008) note that the local ranging behavior of a species may be the key determinant to the success of this method and, as was previously suggested (Williams et al., 2002), ½MMDM approaches will likely prove most useful when home range size is small relative to the sampling grid. The fact that the majority of our recaptured animals were not photographed at more than one station, given our relatively close camera spacing of 1.1 km, indicates that home ranges were indeed small in our study area relative to our sampled areas (35.9, 45.2 km^2 using ½MMDM buffer). Indeed, only two animals, both males, were captured at more than two camera stations throughout the entire study, despite all but one station recording ocelot photos. Therefore, although we report density values using both the ½MMDM and full MMDM buffer values, we maintain that the use of the more common ½MMDM buffer is the most appropriate here.

We further suggest that our density values, while among the highest reported, are actually conservative estimates due to our treatment of "zero-distance" cats in MMDM calculations. Some researchers have included animals recaptured at only a single camera station (zero-distance cats) in MMDM calculations, assigning them a MDM of zero (e.g., Dillon and Kelly, 2007; Silver et al., 2004), whereas most others include only individuals captured at least at two different stations (e.g. Di Bitetti et al., 2006; Maffei et al., 2005; Trolle and Kery, 2003) as we have done here. According to Dillon and Kelly (2007), when the majority of recaptures of individuals are at a single camera station (as occurred in this study), trap spacing may be too large, causing an overestimate of MMDM, and in these cases zero-distance animals should be used in MMDM calculations. However, there is little biological reason to assign a MDM of zero to what are likely resident animals and this practice can result in severely inflated density estimates; a particular concern since many of the animals surveyed by these methods are endangered or near-threatened at an international level (e.g., jaguar – *P. onca*, snow leopard – *Panthera uncia*, tiger – *Panthera tigris*). We note that incorporating the zero-distance ocelots in our own calculations would result in grossly inflated density estimates of 347.3 and 453.3 ocelots/100 km^2 (using the ½MMDM buffer) for the control and disturbance periods, respectively, due to extreme underestimation of average movement distances. However, it is likely that by ignoring these animals (the majority of our recaptures) we have overestimated average distances moved, and therefore underestimated ocelot density.

4.3. Conservation implications

It has been suggested that, relative to other activities in the full progression from exploration to production and transport of oil from Amazonian forests, seismic exploration is likely the least environmentally damaging (Thomsen et al., 2001). The fact that we detected no change in the local abundance and activity of ocelots in this concession during seismic exploration lends preliminary support to this suggestion. Potential impacts of seismic operations exist in both the short-term (e.g. resulting from noise disturbance, loss of understory vegetation, small-scale deforestation at camps and helipads, hunting by workers), and the long-term (e.g. increased access for local hunters and loggers along seismic lines, erosion along slopes of helipads and steep seismic lines). Whereas our research begins to address the short-term impacts, it cannot speak to the extent of potential long-term consequences.

Although hunting by oil personnel during operations was strictly prohibited, forest accessibility has been linked to population levels of large-bodied preferred game species (Peres and Lake, 2003), and increased access to previously remote and inaccessible forest by use of seismic lines is a concern regarding longer-term impacts of exploration activities (Thomsen et al., 2001). Indeed, research indicates that in heavily forested systems, hunting is a far more serious threat to the diversity and persistence of larger mammals than small scale vegetation disturbance (Naughton-Treves et al., 2003) and the potential for subsistence hunting to dramatically reduce large mammal populations in the Amazon is well-documented (Peres, 2000; Peres and Palacios, 2007). Due to the widespread use of seismic exploration in the Amazon, more research is needed into the use of seismic lines by bushmeat hunters and illegal logging operations.

The specific practices of the managing industrial company play a key role in determining the extent of damage and biodiversity loss resulting from their operations (Thomsen et al., 2001). In the case of the operations conducted during this study, relatively strict guidelines and procedures to minimize disturbance levels were implemented, including use of the roadless "off-shore" model, prohibition of hunting/fishing by personnel, complete refuse removal, and the minimization of vegetation disturbance along seismic lines mentioned above (Girton et al., 1991; IUCN, 1991; Repsol, 2006, 2007). We stress that the responses of wildlife to seismic operations are likely to vary widely depending on the specific ecological and operation-related conditions that are present, and we caution against the generalization of the results of individual, species-specific studies such as ours to other species, regions or operations.

Although our data indicate that seismic exploration as conducted in our study area is unlikely to have serious immediate negative impacts on ocelot populations, much more research is needed that investigates the response of other wildlife species and populations to not only 2D seismic exploration but also the subsequent phases of hydrocarbon exploration (including 3D seismic operations), production and transport in this fragile and important ecosystem. However, this study provides an important first step toward a broader understanding of the potential impacts of these operations, and we are currently analyzing additional camera survey data on other mammal species as well as line-transect data for primates to investigate the response of other mammal populations to these disturbances.

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