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Density and activity patterns of ocelot populations in Yasuní National Park, Ecuador

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Abstract: Ocelots were historically hunted for their skins but habitat loss is now their most serious threat, causing rapid declines in populations throughout their range. Ocelot abundance has been estimated for various locations across the Neotropics, but we still lack this information from some countries, including Ecuador. Knowing whether ocelot abundance is increasing or decreasing is important to assess the conservation status of this species and the conditions of its habitats in the Ecuadorian Amazon and in the region. To determine whether ocelot abundance and its behavior are affected by human-related activities, camera-trap surveys were carried out in two localities of Yasuní National Park (YNP), one that has experienced hunting, oil extraction, and roads (Maxus Road) and one that is largely unaffected by these activities (Lorocachi). During the survey, 35 and 36 individual ocelots were photographed in Maxus Road and Lorocachi, respectively. Population density estimates were similar for both localities, ranging from 0.31 (SE±6) to 0.85 (SE±17) ocelots/km^2 in Maxus Road and 0.35 (SE±6) to 0.93 (SE±18) ocelots/km^2 in Lorocachi, when using the MMDM and the ½ MMDM to estimate the effective trapping area, respectively. Ocelots were more active during the night than during the day in both study sites, probably reflecting the activity patterns of their prey. Ocelot densities obtained in YNP are among the highest reported within the Neotropics. Yasuní's large tracts of suitable habitat can provide the resources necessary to support sufficiently large populations of ocelots and other species, and ensure their long-term survival.

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Introduction

The ocelot *Leopardus pardalis* (Linnaeus, 1758) is a spotted, medium-sized Neotropical cat with a broad geographic distribution, ranging from southern US (Texas) to northern Argentina. During the 1960s and 1970s, ocelots were heavily hunted for their fur, causing a significant reduction in populations across their range (Murray and Gardner 1997). Because of this direct threat, the Convention on International Trade in Endangered Species (CITES) listed *L. pardalis* in its Appendix I, and some ocelot populations started to recover (Murray and Gardner 1997, Sunquist and Sunquist 2002). However, ocelots are still hunted today, and more recent pressures, such as habitat loss and degradation, consequences of rapid development of human activities, continue to threaten the survival of ocelots (Nowell and Jackson 1996, Di Bitetti et al. 2008). Mesocarnivores, especially ocelots, are a significant component of Neotropical ecosystems mainly because of their capacity to indirectly affect plant communities. The main prey of ocelots, small and medium-sized rodents such as spiny rats, agoutis, and other members of the family Dasyproctidae, collect seeds from under parental plants, then the seeds are scattered over a large surface and buried in the topsoil of the forest (scatter-hoarding behavior) to be eaten when resources are scarce (Jansen et al. 2004, Roemer et al. 2009). These seed predators, whose abundance influences seed recruitment and seedling survival, can act as seed dispersers when buried seeds are not revisited if the rodents are preyed on by ocelots; thus, ocelots may promote indirect recruitment of those plants (DeMattia et al. 2004, Roemer et al. 2009).

Despite their significant ecological role in tropical forests, ocelots remain relatively understudied, likely because of their elusive nature and the remoteness of habitats they still occupy. However, the introduction of remote techniques such as camera traps has made it possible to study this species. Ocelots can be individually identified by their unique coat patterns (Karanth and Nichols 1998, Maffei et al. 2005, Espinosa 2012, Blake et al. 2013).

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Individual identifications can then be used in capture-recapture models to estimate population size (Karanth and Nichols 1998). Camera trapping has been previously used to estimate the size of ocelot populations in various locations across the Neotropics (Trolle and Kéry 2003, Maffei et al. 2005, Di Bitetti et al. 2006, Haines et al. 2006, Dillon and Kelly 2008, Kolowski and Alonso 2010), but we still lack this information from some countries, including Ecuador.

Current ecological knowledge of ocelots in Ecuador is limited to distribution records, with little data on abundance. Ocelots can potentially occur within an altitudinal range from sea level to about 1500 m, within Coastal, Andean foothills, and Amazonian regions of the country (Tirira 2007). They have disappeared from many parts of their original range, particularly in the Coastal region, where natural habitat has been severely degraded (Espinosa et al. 2011). We believe large and healthy populations of ocelots may be found in Ecuador's Amazon, where large tracts of their natural habitat are maintained within large protected areas and indigenous territories. Therefore, knowing the abundance of ocelots in this region is a priority for the conservation and management of the species.

The eastern Ecuadorian Amazon is a large and relatively continuous area, rich in biodiversity, with a mosaic of different habitats dominated by highly diverse terra firme moist tropical forest (Valencia et al. 2004, Bass et al. 2010). Within this region Yasuní National Park (YNP), with an extension of 10,000 km^2, is the largest protected area in mainland Ecuador. YNP is adjacent to the 8000 km^2 Waorani Ethnic Reserve, and together, they constitute the Yasuní Biosphere Reserve, considered as one of the most biologically diverse regions in the world (Bass et al. 2010). Additionally, in the south, YNP limits with other indigenous territories with very little disturbance. These lands form a continuous protected landscape that may become one of the last refuges for ocelots and other important species inhabiting the Ecuadorian Amazon. Despite their importance for conservation, both protected areas and indigenous territories are threatened by future development in the region, particularly associated with oil extraction and its associated impacts such as road development and colonization.

This is the first systematic study that uses camera trapping to assess the abundance of ocelots in Ecuador. We chose to conduct this study in Yasuní National Park because of its importance for the long-term conservation of ocelot populations. We compare two sites with different degrees of human intervention, one along a road and another far away from roads. We analyze ocelot abundance and activity patterns at each of these two sites.

Materials and methods

Study sites

The first site was located along the Maxus Road within YNP, and the second study site was located south of the Curaray River (southern border of YNP), close to the community of Lorocachi (Figure 1A). Yasuní is considered an aseasonal forest, annual rainfall is ~3200 mm, and temperature varies from ~22°C to ~34°C (Valencia et al. 2004, Bass et al. 2010). Both areas are covered by dense evergreen terra firme tropical forest. Topography is dominated by a succession of small hills and low areas that are temporarily flooded (Pitman et al. 2001, Valencia et al. 2004).

Although located within YNP, the Maxus Road site has been affected by more human-related activities than the Lorocachi site. This difference in level of anthropogenic disturbance is primarily due to the presence of several oil extraction platforms and a road network (150 km) (Figure 1A) that traverses the northern part of the Park (Zapata Rios et al. 2006). Construction of the Maxus Road within YNP (early 1990s) opened the area to colonization and commercial and subsistence hunting by indigenous groups, such as the Waorani and Kichwa that now live in permanent settlements along the road and river margins (Franzen 2006, Bass et al. 2010). In contrast to Maxus Road, Lorocachi is a remote area, no roads are present, and access is mainly achieved by aircraft. Activities are more focused on fishing, land cultivation, and subsistence hunting (personal observations). Our study site was located between 3 and 21 km from Lorocachi and was accessible only by foot.

Ocelot surveys

This study uses information obtained from a broader study designed to estimate the abundance of jaguar *Panthera onca* in the region (Espinosa 2012). We surveyed felids and other large and medium-sized mammals with conventional camera traps (LeafRiver C1-BU) equipped with a passive heat-and-motion sensor. To deploy camera traps, we created a trail system of 60 and 67 km in Maxus Road and Lorocachi, respectively. At each site, we set up a grid of 26 camera-trap stations (hereafter stations) that operated for 90 consecutive days (Figure 1B and C). Stations were 2–3 km apart and consisted of two camera traps facing each other and perpendicular to trails to cover a polygon of 104–110 km^2 in each site. Stations were placed at sites where we found evidence of wild cats such as tracks, scats, and scrapes (Karanth and Nichols 1998, Silver et al. 2004).

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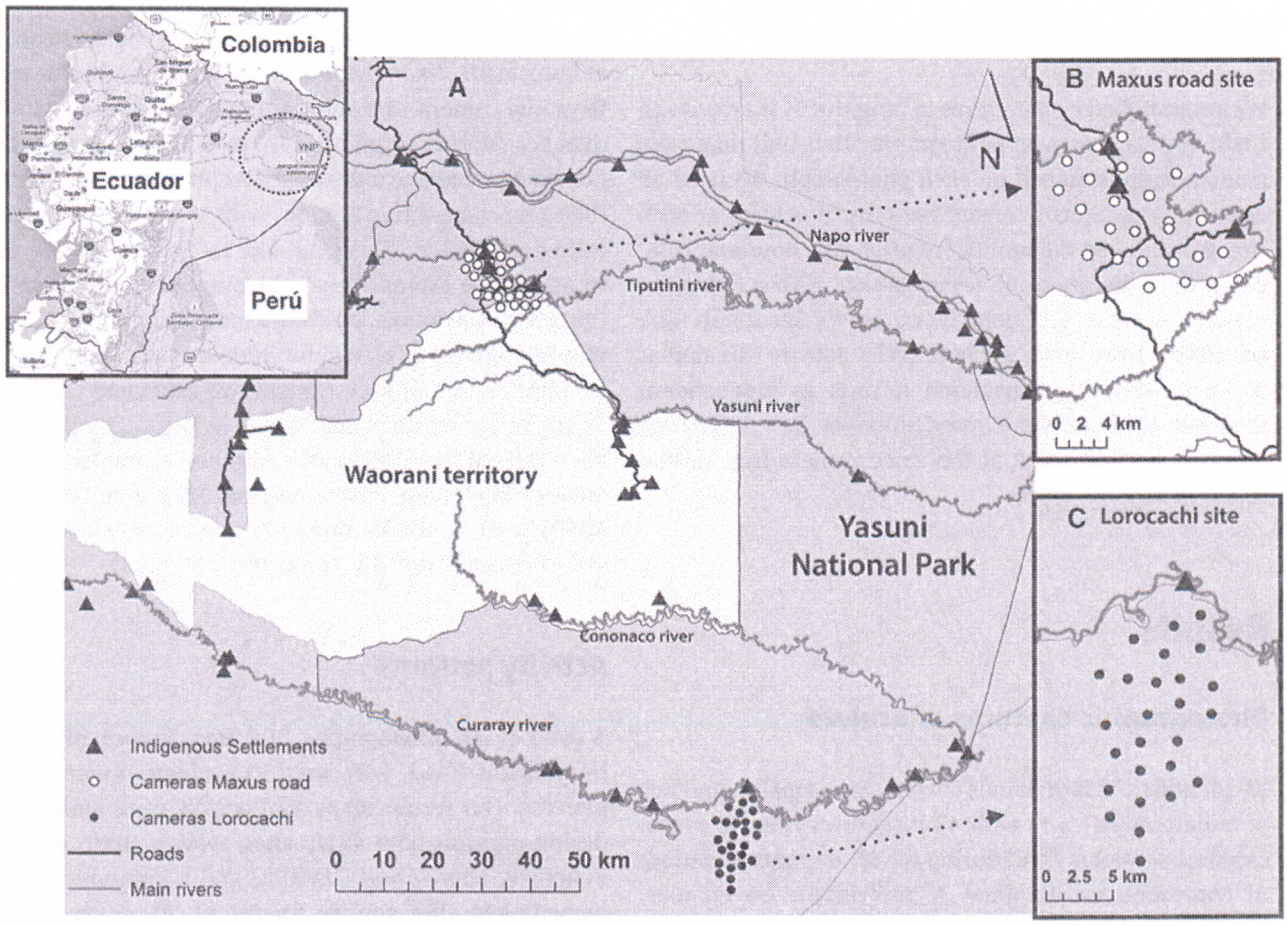


Figure 1: Study area showing the location of survey sites towards the north and south of Yasuní National Park (A), and the design of camera trap arrays to assess ocelot populations and activity patterns in Maxus Road (B) and Lorocachi (C).

Density estimation

We used distinctive pelage markings (e.g. spots, stripes, rosettes) to identify individuals and the presence or absence of testes to determine sex. Photographs that did not allow for unambiguous identification of individuals were discarded for this analysis. To estimate density, we first calculated population size using program CAPTURE (Rexstad and Burnham 1991). For this purpose, for each site, we created a capture matrix where the number of rows corresponded to the number of individuals captured, and columns to the number of trapping occasions. We considered a 24-h period as one trapping occasion. Matrices were filled by ones and zeros when an individual was captured or not in a given trapping occasion. We assumed demographic closure for our 90-day study period (Otis et al. 1978, Karanth and Nichols 1998). CAPTURE computes population estimates using models that differ in their assumed sources of variation in capture probability. We used CAPTURE's model selection algorithm to select the best-fit model (White 1982).

To estimate population density (individuals/100 km^2) in each study area, we divided the estimated abundance from program CAPTURE by the estimated effective trapping area (ETA) as described by Karanth and Nichols (1998). To calculate the ETA for each site, we added a buffer to each camera trap location, which was half the mean maximum distance moved "½ MMDM" of individual ocelots (Wilson and Anderson 1985, Karanth and Nichols 1998). We also used the full "MMDM" of ocelots, which provides a more conservative estimate (Parmenter et al. 2003; Trolle and Kéry 2005, Soisalo and Cavalcanti 2006, Dillon and Kelly 2008). To estimate MMDM at the Maxus Road, we included recapture distances of individual ocelots that were obtained from cameras that were placed every 500 m along 13 transects of 5 km each, during the same study (Espinosa 2012).

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Activity patterns

We programmed camera traps to be active 24 h a day, with 1 min of delay between photographs. Date and time were automatically stamped on each photograph. We used all ocelot photographs to create patterns of activity at each site. We summed the number of photos by hour and compared their distributions between sites with a Kolmogorov-Smirnov test. Additionally, we used a Spearman rank correlation to evaluate whether ocelot activity was similar between sites. We considered records as independent if 30 min or more had elapsed since the last occurrence of the same individual at the same camera trap station (Blake et al. 2012, 2013).

Results

Photographic captures of ocelots

We identified 35 individuals (19 females, 11 males, and five of undetermined sex) with 43 recaptures from 78 ocelot captures at Maxus Road during the 90-day survey period. At Lorocachi, we obtained 36 individuals (14 females, 17 males, and five undetermined) and 49 recaptures from 85 ocelot captures over the 90-day survey period. Total survey effort was 2340 trap-days at each site (90 days, 26 trap stations). The model selection algorithm of CAPTURE identified M_h (jackknife estimator) as the most appropriate model for both study areas. This model assumes heterogeneity among individual ocelots in their capture probabilities. Unique capture probabilities were expected because of individual variations in behavior (e.g. ocelot territoriality, unequal home range sizes, sex). Our estimated population sizes were 53 individuals (SE±9.8; 95% CI=42–83) in Maxus Road and 60 individuals (SE±10.7; 95% CI=47–92) in Lorocachi.

Few individuals were photographed at more than one camera location at either site, particularly in relation to the number of individuals captured (35 at Maxus Road, 36 at Lorocachi). Six individuals were photographed at more than one camera trap station in Maxus Road; maximum distance moved ranged from 370 m to 3140 m. However, in Lorocachi, only one individual was photographed at more than one camera trap station, with a maximum distance moved of 2550 m. Given the few recaptures among trap locations, we averaged the maximum distance moved of the seven individuals, yielding a mean maximum distance moved (MMDM) of 1770 m for both sites. Using ½ MMDM as a buffer around each camera, we estimated an ETA of 62 km² in Maxus Road and 64 km² in Lorocachi. When we used MMDM as a buffer distance, we estimated sample areas of 169 km² in Maxus road and 172 km² in Lorocachi. MMDM and ½ MMDM provided us a more or a less conservative ocelot density, respectively (Table 1).

Activity patterns

A total of 207 photographs, 108 from Lorocachi and 99 from Maxus Road, were used to evaluate ocelot activity patterns. Our results show that ocelots were more active during night at both study sites, with a sharp increase in activity after sunset (18:00 h) and a pronounced drop immediately after sunrise (06:00 h). As much as 87% of the total photographs (94/108) from Lorocachi and 89.9% (89/99) from Maxus Road were captured within the described time period. Activity patterns did not differ between sites (Smirnov test statistic=0.08, p=1) and were strongly correlated (r=0.71, p=0.0002) (Figure 2).

Discussion

Ocelot densities obtained in Yasuní National Park are among the highest reported (Table 2). YNP is one of the most biodiverse places on earth, and its vast and continuous pristine forest encompasses large tracts of suitable habitats for ocelots. This protected area can provide the

Table 1: Ocelot density obtained from estimated population size and the ETA for each site.

Site	Method used for buffer width calculations	N (M_h model)	Buffer (km)	ETA km²	Density n/100 km² (SE)
Maxus Road	½ MMDM	53 (SE±9.8)	0.885	62.70	84.5 (SE±17)
	MMDM	53 (SE±9.8)	1.77	169.24	31.3 (SE±6)
Lorocachi	¼ MMDM	60 (SE±10.7)	0.885	64.29	93.3 (SE±18)
	MMDM	60 (SE±10.7)	1.77	172.4	34.8 (SE±6)

Buffer values were derived from ½ MMDM and MMDM and used to calculate their respective ETAs.
MMDM, mean maximum distance moved; N, population size; ETA, effective trapping area.

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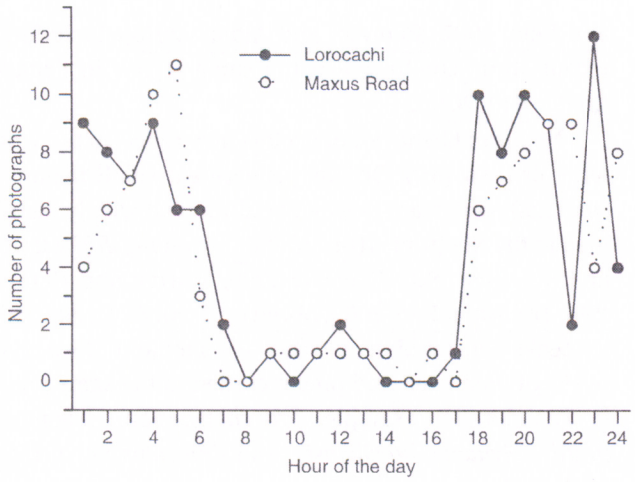


Figure 2: Daily activity patterns of ocelots at Maxus Road and Lorocachi sites in YNP.

Table 2: Ocelot density estimated from different locations within its range, with corresponding methods and buffer (½ MMDM and MMDM) used in camera-trapping studies.

Location and methods	Density (ocelots per 100 km²)	References
½ MMDM (camera trap)		
Argentina	19.99	Di Bitetti et al. 2006
Argentina	18.9	Di Bitetti et al. 2008
Belize	25.5–25.9	Dillon and Kelly 2007
Belize	25.88	Dillon and Kelly 2008
Bolivia	24.0–66.00	Maffei et al. 2005
Brazil	56.4	Trolle and Kéry 2003
Brazil	11.19	Trolle and Kéry 2005
Ecuador	85–93	This study
Peru	75–94.7	Kolowski and Alonso 2010
MMDM (camera trap)		
Argentina	12.84	Di Bitetti et al. 2006
Argentina	11.9	Di Bitetti et al. 2008
Belize	12.61	Dillon and Kelly 2008
Brazil	6.93	Trolle and Kéry 2005
Ecuador	31–35	This study
Peru	43.5–58.5	Kolowski and Alonso 2010
Radio telemetry		
Brazil	13.7	Crawshaw 1995
Peru	80.00	Emmons 1987
Texas	30.00	Haines et al. 2006
Venezuela	40.00	Ludlow and Sunquist 1987

necessary resources, such as prey and shelter, to allow the maintenance of high densities of ocelots. Other camera-trap studies have estimated ocelot densities that vary from 3 (Belizean pine forest) to 94 (northern Amazon of Peru) individuals per 100 km² (Dillon and Kelly 2007, Kolowski and Alonso 2010). However, it is still not clear what are the main factors that determine variation in ocelot densities among different regions. Some studies have proposed that prey abundance and other factors such as latitude and rainfall may be correlated with ocelot densities (Maffei et al. 2005, Di Bitetti et al. 2008). Di Bitetti et al. (2008) suggested that ocelots might be more abundant in areas close to the equator with high annual rainfall where primary productivity, and perhaps prey abundance, is higher than in other areas of the Neotropics. Consistently, our observations together with those obtained by Kolowski and Alonso (2010) in Peru show highest ocelot densities in the Western Amazon and near the equator, in the Napo Moist Forests terrestrial ecoregion (Bass et al. 2010). Yet, the status of ocelot populations is still unknown for much of this region.

Although human activities (hunting, oil exploitation, and access roads) are more pronounced in Maxus Road than in Lorocachi, the number of ocelots captured and their estimated population sizes did not differ between these two localities and, in fact, were surprisingly similar. These results can be explained by three main factors. First, Waorani living along Maxus Road do not hunt ocelots for subsistence or profit (Espinosa 2012). Second, ocelots and people are not competing for the same prey. For instance, ocelot diets mainly consist of small rodents (<1 kg), principally spiny rats (*Proechymis* sp.), opossums (*Didelphis marsupialis*), and medium-sized mammals (2–15 kg) such as agoutis (*Dasyprocta fuliginosa*), pacas (*Cuniculus paca*), armadillos (*Dasypus novemcinctus*), and anteaters (*Tamandua mexicana*), among others (Bisbal 1986, Emmons 1987, Ludlow and Sunquist 1987, Konecny 1989, Murray and Gardner 1997, Farrell et al. 2000, Abreu et al. 2008). In contrast, subsistence and commercial hunting by the Waorani are concentrated on large-bodied species (>15 kg) such as primates (*Ateles belzebuth*, *Lagothrix poeppigii*, and *Alouatta seniculus*) and ungulates (*Tayassu pecari* and *Pecari tajacu*, *Tapirus terrestris*, *Mazama americana*), which are not main prey for ocelots (Franzen 2006, Espinosa et al. 2014). Third, the area around Maxus Road is still a vast region of primary forest that provides refuge to many species including ocelots. Access to Maxus Road is strictly controlled by the oil company currently working there. People that do not reside in the area need a special permit to access the region. This control has prevented colonization by outsiders and maintained a small number of inhabitants within the park. Approximately 70 Waorani inhabitants are distributed in four communities in the study area along Maxus Road (Espinosa 2012). The economic system of the Waorani has been based on gathering, sharing forest products and horticulture, and hunting, which is a very important cultural aspect, especially for

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men who, at the time of our study, sold bushmeat in a local market (Rival 1996, Espinosa 2012). The vast area and the fact that land cultivation is still at a small scale around Maxus Road have possibly caused minimal impacts on ocelot habitats and populations. However, these activities are increasing every day in this area, and forest is being removed with higher frequency with little control by park rangers (personal observations).

Large protected areas, such as the Yasuní National Park, are biologically and ecologically important because they have the potential to support viable populations of ocelots. It is suggested that a population size of at least 50 or 100 individuals would be sufficient to maintain a viable population over the short term (i.e. five generations in the wild) and a population of 500 or 1000 individuals could avoid inbreeding depression and retain evolutionary potential for the long term (Franklin 1980, Frankham et al. 2014). Based on our conservative ocelot density estimates (average estimates of two sites using full MMDM: 33.05 ocelots/100 km^2), we would expect a population of at least 3300 ocelots in this protected area. This population number greatly exceeds the suggested size for long-term persistence. Our observations indicate that there is a high probability that ocelot populations will persist in YNP well into the future (i.e. >100 years).

Our extrapolation of expected ocelot population in YNP is based on the fact that most of the protected area (79.84% of the total area of YNP) is under low levels of human disturbance (Zapata Rios et al. 2006). In addition, YNP is adjacent to the 8000 km^2 Waorani Ethnic Reserve (constituting the Yasuní Biosphere Reserve), and toward the south, YNP limits with other indigenous territories with very little disturbance. These lands form a continuous landscape that has the potential to provide ocelots the necessary habitat extension, connectivity, and high-quality resources for their survival. However, the likelihood of ocelot persistence on this landscape will depend on future rates of habitat loss, degradation or fragmentation, and other human activities such as hunting that may affect the survival of this species within the park.

Activity patterns

Ocelots are mainly nocturnal in Yasuní National Park and elsewhere. Activity patterns were very similar at Maxus Road and Lorocahi, with higher peaks in activity after sunset and before sunrise at both localities. These results follow a general pattern that has been previously reported by other studies in the Neotropics (Emmons 1987, Gómez et al. 2005, Maffei et al. 2005, Di Bitetti et al. 2006, Dillon and Kelly 2007, Kolowski and Alonso 2010), including a recent study conducted in the same region in Ecuador (Blake et al. 2012).

Nocturnal behavior of ocelots may reflect activity patterns of their prey. Ocelots primary eat small mammals (rodents), which are mostly nocturnal and widely distributed in the Neotropics (Bisbal 1986, Emmons 1987, Ludlow and Sunquist 1987, Konecny 1989, Murray and Gardner 1997, Trolle and Kéry 2003, Abreu et al. 2008). Ocelot activity peaks registered in our study are similar to the activity peaks of their preferred prey recorded in the same region in Ecuador, for example, *Proechimys* spp., *Myoprocta pratti*, *Sylvilagus brasiliensis*, and *Cuniculus paca* (Blake et al. 2012).

The nocturnal habit of the ocelot also may be a strategy to avoid competition with other sympatric carnivores (Bisbal 1986, Emmons 1987, Konecny 1989, Sunquist et al. 1989, Gómez et al. 2005, Goulart et al. 2009). In YNP, ocelots coexist with jaguar, puma (*Puma concolor*), jaguarundi (*Puma yagouaroundi*), margay (*Leopardus wiedii*), and tayra (*Eira barbara*); however, there is ecological niche differentiation among them. Blake et al. (2012) found that in the same region, although jaguars are active throughout day and night, they were more active during daylight from 7:00 to 18:00 h and less active from 2:00 to 5:00 h. In contrast, we found that ocelots were more active from 18:00 to 6:00 h with peaks in activity within this range especially from 2:00 to 5:00 h when jaguars were less active. Thus, nocturnal behavior of ocelots can separate them from larger predators like the jaguar and puma to avoid competition or fatal encounters. Pumas also showed nocturnal and diurnal behavior near our study sites but were more active during night, similarly to ocelots (Blake et al. 2012). Some studies have highlighted resource partitioning between ocelots, pumas, and jaguars to allow the coexistence of these species in humid tropical forests (Gómez et al. 2005, Goulart et al. 2009). Other carnivores and potential competitors for the ocelot are the jaguarundi and tayra, but these species have mainly diurnal activity patterns. Although jaguarundi and tayra feed on small mammals and other vertebrates, as do ocelots, ocelots differ in prey preferences (Bisbal 1986, Emmons 1988, Konecny 1989, Sunquist et al. 1989). The margay, although also being nocturnal, has arboreal habits, whereas ocelots more often hunt on the ground (Konecny 1989).

Human disturbance (e.g. hunting and roads) may lead to changes in animal behavior, such as feeding behavior, to reduce the risk of being observed, trapped, or killed by hunters or other human-related activities (Lima and Dill 1990, Bonnot et al. 2013, Frid and Dill 2002). However,

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despite the differences in degree of human intervention, we did not observe differences in ocelot behavior nor density between our two sites. This suggests that current human interventions in YNP may not be affecting ocelot populations. Therefore, there is an opportunity to include management strategies for the conservation of this species in the face of future increases in economic development and extractive activities in this region.

Methodological considerations

Few individual ocelots were photographed at more than one camera location at either of our study sites. This may be primarily related to the fact that camera grids were designed to collect data on jaguar populations in YNP (Espinosa 2012), which explains the distances used to separate trap stations (2–3 km). These distances proved to be too large to precisely capture ocelot movements in this study. Other studies with ocelots have shown that placing cameras too far from each other may exceed the diameter of the ocelot home range, resulting in more recaptures of individual ocelots in only one trap station and a maximum distance movement of zero (Dillon and Kelly 2007, Maffei and Noss 2008). The maximum distance moved by an animal captured in more than one trap station is considered as an approximation of the diameter of its home range (Wilson and Anderson 1985). Knowing this, camera spacing applied in our study sites may have exceeded the diameter of ocelot home range and prevented us from recapturing individual ocelots in more than one trap station.

Trap station density at Lorocachi and Maxus Road was approximately one trap station per 2 to 3 km and each station covered an area of approximately 10 km^2. The fact that few individual ocelots were recaptured in more than one trap station suggests that ocelots may have small home ranges that generally do not exceed 10 km^2 in the studied localities in the YNP. Although this estimate is not accurate, it is a preliminary view on ocelot movements in the Ecuadorian Amazon and provides valuable information for future management and research in the region for this species. In addition, MMDM can be inflated when only few ocelots displaying long distance movement are captured in more than one station, this can potentially underestimate density (Dillon and Kelly 2007).

For future studies specifically on ocelots, we recommend using shorter distances to separate trap stations (0.5 km–1.5 km), in order to increase the likelihood of capturing individual ocelots in more than two trap stations and, thus, register movement more accurately.

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