

Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*)

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Abstract: As top predators, wild cats play a key ecological role in tropical forests, but little is known about the factors that regulate their abundance. This study looked for correlates of ocelot (*Leopardus pardalis*) abundance at two spatial scales. First, camera-trap surveys conducted in the Atlantic Forest of Misiones, Argentina, were used to test the hypothesis that selective logging and poaching affect the local abundance of this cat. Second, published density estimates ($N = 21$) were used to test the hypothesis that rainfall and latitude are correlated with the abundance of ocelots across their continental range. In Misiones, ocelot densities ranged from 4.96 ± 1.33 individuals per 100 km^2 in the intensely logged and hunted areas to 17.6 ± 2.25 individuals per 100 km^2 in areas with low human impact. The frequency of records, number of individuals recorded per station, and density estimates were 2–3 times higher in areas with relatively low levels of logging and poaching. At a continental scale, ocelot densities decrease with latitude and increase with rainfall. Primary productivity seems to determine the abundance of wild cats across their range, but at a local scale their abundance may be affected by logging and poaching or by competition with other species.

Key Words: Atlantic Forest, density, felids, poaching, latitude, logging, neotropical cats, ocelot, rainfall, tropical forest

INTRODUCTION

Hunting of ocelots (*Leopardus pardalis* L.) for their pelts during the 1960s and 1970s reduced their populations (Murray & Gardner 1997, Nowell & Jackson 1996, Sunquist & Sunquist 2002). Since the decline of the fur trade in the early 1980s, some ocelot populations have rebounded, but habitat loss and degradation have become their major threat (Kitchener 1991, Sunquist & Sunquist 2002).

As a result of their top-down regulation effect wild cats play an important ecological role in tropical forests (Terborgh *et al.* 1999). Their local extirpation or their very low numbers (ecological extinction) may produce a cascade of effects through the entire ecosystem (Terborgh *et al.* 2001). Thus, it is important to understand what factors regulate their abundance. This is also important to develop predictive models that may aid in cat conservation planning (Carbone & Gittleman 2002, Nilsen *et al.* 2005). Particularly important are data from cat species

living in tropical forests since little is known about their ecology and behaviour, even when they constitute a large proportion of the living cats (Sunquist & Sunquist 2002).

At a regional scale, felids suffer from habitat fragmentation (Crooks 2002), particularly the large cats, as a result of human-predator conflicts (Crawshaw 2002, Woodroffe 2000, Woodroffe & Ginsberg 1998), or other human impacts, like vehicle collisions (Haines *et al.* 2005, 2006a). Across geographic ranges it would be expected that prey availability should set the carrying capacity of wild cat populations (Carbone & Gittleman 2002, Gros *et al.* 1996, Hetherington & Gorman 2007, Karanth & Nichols 1998, Stander 1991, Stander *et al.* 1997) and primary productivity was shown to predict home-range size in some felids (Herfindal *et al.* 2005, Nilsen *et al.* 2005).

The ocelot is a neotropical cat with a wide distribution, ranging from southern Texas to northern Argentina, and inhabiting a variety of different tropical and subtropical forests and scrubby habitats (Murray & Gardner 1997, Sunquist & Sunquist 2002). Several ocelot field studies conducted across the distribution of the species have provided information on ocelot densities, but it is still not clear what the main determinants of the variation in

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ocelot abundance observed across studies are. The ocelot may constitute a good model to understand what factors affect the abundance of neotropical cats. At a local scale the abundance of ocelots may be negatively affected by poaching or habitat degradation and at a continental scale prey abundance or some indirect measure of productivity (rainfall and latitude) may correlate with ocelot densities.

The Atlantic Forests of South America constitute a dramatic example of habitat loss and degradation (Di Bitetti *et al.* 2003, Galindo-Leal & de Gusmão Câmara 2003). Many mammals are confined to few, isolated and small forest fragments and affected by the effect of hunting (Chiarello 2000, Cullen *et al.* 2000, 2001). The Green Corridor of Misiones province of Argentina (Figure 1) contains the largest remnant of the Upper Paraná Atlantic Forest ecoregion (Di Bitetti *et al.* 2003). The Green Corridor suffers a high rate of forest conversion to cattle ranching, agriculture and monoculture plantations of pines, and the remaining forests are usually subjected to intense logging and poaching. Two main blocks of protected native forest are found in the Green Corridor: to the north, the Iguazú–Urugua-í complex of interconnected protected areas and in the south-east, the Yabotí Biosphere Reserve (Figure 1). The Yabotí Biosphere Reserve is located near the southern margin of the distribution of four neotropical cats: ocelot, jaguar (*Panthera onca* L.), margay (*Leopardus wiedii* Schinz) and oncilla (*Leopardus tigrinus* Schreber, Paviolo *et al.* 2006). Two wider-ranging cat species live in sympatry with these four species in the Green Corridor: puma (*Puma concolor* L.) and jaguarundi (*Puma yagouaroundi* É. Geoffroy Saint-Hilaire). Contrasting levels of disturbance (mainly as a result of poaching and logging) and law enforcement capacity (and consequently of the actual conservation status of the forests and protected areas) in Misiones (Bertonatti & Corcuera 2000, Cinto & Bertolini 2003, Giraudo *et al.* 2003) provide an excellent opportunity to evaluate how human impacts affect the local abundance of ocelots.

The objectives of this paper were twofold. First, we aimed at estimating ocelot densities in the Green Corridor of Misiones to test the hypothesis that the degree of habitat disturbance resulting from human activities, mainly timber logging and poaching, negatively affects the abundance of this cat. Second, using ocelot density estimates from published sources we tested the hypothesis that rainfall and latitude are correlated with the abundance of ocelots across their range. Since primary productivity (and indirectly prey densities) depends on water availability, temperature and the amount of photosynthetically active radiation (which are correlated with rainfall the first, and with latitude the last two), among other limiting resources, we predicted a positive correlation between ocelot population density and rainfall

and a negative correlation between ocelot density and latitude.

METHODS

The study of ocelot abundance at a local scale

We conducted camera-trap surveys at two different sites within the Green Corridor of Misiones, Argentina (see Di Bitetti *et al.* 2006a for details on previous surveys in the area): (1) Yabotí Biosphere Reserve (a reserve of 2742 km², from here on Yabotí) and (2) an area that comprised most of Iguazú National Park of Argentina (of 670 km²), a small portion of Iguazú National Park of Brazil (of 1750 km²) and the San Jorge Forest Reserve (of 174 km², Figure 1). We will refer to the second surveyed area as Iguazú. The two areas still contain the complete native assemblage of mammals (Galindo-Leal & de Gusmão Câmara 2003). Mean annual precipitation ranges between 1800 and 2200 mm and there is marked seasonality in day length, temperature and primary productivity (Crespo 1982, Di Bitetti 2001, Di Bitetti & Janson 2001, Placci *et al.* 1994). Hunting of wildlife is illegal in Misiones province (except for that practiced by Mbya-Guaraní indians) and thus, we will refer to this activity as poaching. The capacity for law enforcement varies among the protected areas of Misiones, with most of them undergoing significant poaching and illegal timber extraction and only a few where regulations are fully enforced.

The core area of Yabotí is represented by the 316-km² Esmeralda Provincial Park (Figure 1), a protected area that was logged until recently but is relatively inaccessible to poachers. Most of Yabotí lies within private properties. Despite efforts by the provincial government, there is still a relatively low capacity for law enforcement, thus poaching and illegal timber harvesting are common in the private properties of Yabotí (Cinto & Bertolini 2003, Giraudo *et al.* 2003). Although there is no available information on the amount of timber harvested and animals hunted in Yabotí, there is a clear contrast between an area with relatively higher protection (constituted by the northern portion of Esmeralda Provincial Park and an adjacent private property owned by Mr Miot, who does not allow poaching and abides by logging regulations), and the rest of Yabotí, composed of private properties the owners of which do not observe timber harvesting quotas and allow poaching. During the survey we found more poaching in the portion of Yabotí with lower protection and consequently a lower camera-trap recording rate of large ungulates. We will refer to these two sectors of Yabotí as the sub-areas with lower disturbance and higher disturbance respectively.

In clear contrast with Yabotí, the Iguazú National Park of Argentina has a well-trained and equipped team of park

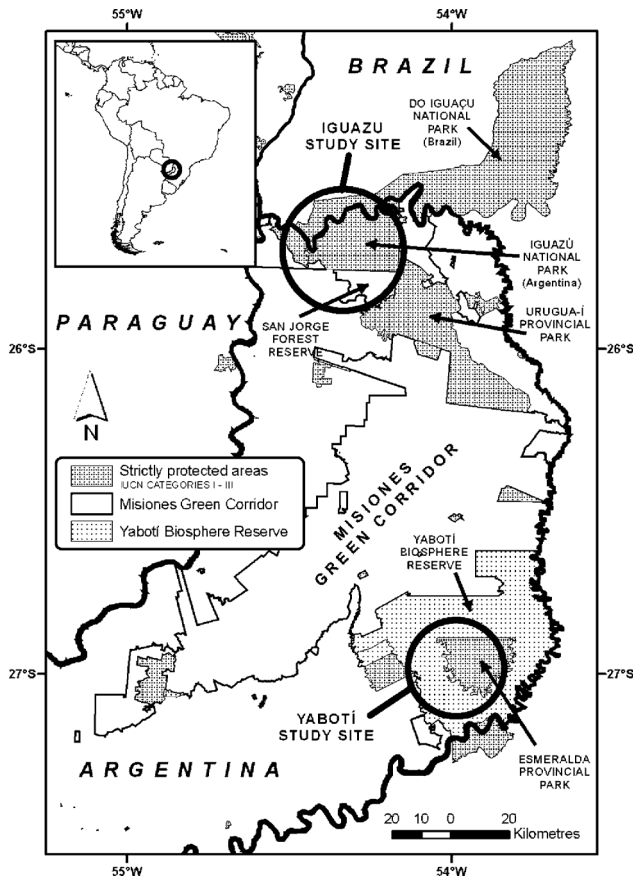


Figure 1. Location of the study sites in South America.

rangers and enough infrastructure and resources that provide a strong law enforcement capacity. This is the area best protected in the region (Bertonatti & Corcuera 2000, Cinto & Bertolini 2003, Giraudo *et al.* 2003). The Iguazú study site overlaps extensively with the area we previously surveyed in 2004 (Di Bitetti *et al.* 2006a) and with the area where Crawshaw (1995) conducted his ocelot study. The Brazilian portion of Iguazú study site suffers from moderate to high poaching, but only three sampling stations were located in this sector. The San Jorge Forest Reserve has been logged until recently and poaching is still present. Thus, there is variation in the degree of disturbance within the Iguazú study site, where Iguazú National Park of Argentina is considered a sub-area with lower relative disturbance than the San Jorge Forest Reserve. From now on we will refer to these two portions of Iguazú study site as the sectors with lower disturbance and higher disturbance respectively.

In this paper we use lower disturbance and higher disturbance as relative terms in between- and within-sites comparisons, but we have no quantification of the absolute number of animals or trees extracted from the areas. However, we have quantified all poaching evidence found in the study areas during the surveys (Paviolo

et al. in press) and the results are consistent with recent assessments of the level of protection and implementation of the protected areas of Misiones (Bertonatti & Corcuera 2000, Cinto & Bertolini 2003, Giraudo *et al.* 2003). Also, the camera-trap record of game animals suggests that the negative impact of poaching on the relative abundance of ungulates is strongest in the portion of Yabotí with higher disturbance and minimum or absent in the portion of Iguazú with lower disturbance, with intermediate values in the subarea of Yabotí lower disturbance protection and the sector of Iguazú with higher disturbance (Paviolo *et al.* in press).

To estimate ocelot densities we conducted camera-trap surveys, a methodology that has been used to estimate population densities of wild cats (e.g. tiger *Panthera tigris*, Carbone *et al.* 2001, Karanth 1995, Karanth & Nichols 1998, Karanth *et al.* 2006; jaguar, Maffei *et al.* 2004, Paviolo *et al.* in press, Silver *et al.* 2004, Soisalo & Cavalcanti 2006, Wallace *et al.* 2003; puma, Kelly *et al.* in press; ocelot, Di Bitetti *et al.* 2006a, Dillon 2005, Dillon & Kelly in press, Haines *et al.* 2006b, Jacob 2002, Maffei *et al.* 2005, Trolle & Kéry 2003, 2005; and Geoffroy's cat *Leopardus geoffroyi*, Cuellar *et al.* 2006).

At Yabotí we set 42 sampling stations along roads at regular intervals and with a mean (\pm SE) distance of 2.43 ± 0.81 km between nearest stations. At Iguazú we deployed 47 sampling stations with a mean distance to the nearest station of 2.58 ± 0.60 km. Mean distance between nearest stations at both sites was lower than the radius of the mean ocelot home range of this population (Crawshaw 1995), thus ensuring that most animals had more than one station within their home ranges. A sampling station consisted of two camera-traps operating independently and facing each other at both sides of unpaved roads or trails. The equipment consisted of a set of 50–60 passive infra-red-triggered scouting cameras of different models (Di Bitetti *et al.* 2006a). Camera traps were checked for film and batteries once every 3–12 d. Mean (\pm SD) sampling effort per station was 44.5 ± 3.56 d at Yabotí and 43.8 ± 8.60 d at Iguazú. Total sampling effort was 1871 trap-days at Yabotí and 2059 trap-days during the Iguazú survey. At Yabotí, 24 of the camera-trap stations were located in the sector with lower disturbance and 18 stations were located in the higher disturbance one. At Yabotí, all stations but one were located along unpaved roads. At Iguazú, 36 stations were located in the sub-area with lower disturbance and 11 in the portion with higher disturbance (San Jorge Forest Reserve); 33 of the stations were located on dirt roads and 14 along trails.

The surveys were conducted between 27 August and 30 November 2005 at Yabotí, and between 8 October 2006 and 11 January 2007 at Iguazú, totalling 96 consecutive days each. We subdivided the surveys into two periods, with about half of the stations operating during each one (Di Bitetti *et al.* 2006a).

Due to this sampling protocol we cannot assess the closure assumption with the test performed by program CAPTURE (Rexstad & Burnham 1991). However, the time frame of the surveys was short enough to ensure that few (if any) individuals could have disappeared or immigrated into the study areas during the surveys, as suggested by similar studies (Dillon & Kelly *in press*, Karanth & Nichols 1998).

We use the Kruskal–Wallis two-sample test to compare the frequency of ocelot records per station and the number of individuals recorded per station between the portions of the study sites with lower disturbance and those with higher disturbance. Ocelots rarely backtrack on their daily movements, but to reduce the chance that more than one record of the same individual or pair of individuals (mother–offspring) could be obtained in a short period of time, we used the criterion that more than 1 h had to pass for two consecutive ocelot photographs to be considered independent records.

To estimate the population size of ocelots in the study area we used the program CAPTURE (Rexstad & Burnham 1991). To make the ocelot capture probability per trapping occasion > 0.10 , as recommended by Otis *et al.* (1978) and White *et al.* (1982), the trapping history of each individual consisted of a string of 16 trapping occasions, where each trapping occasion consisted of six consecutive days. CAPTURE provides population estimates using different models (Otis *et al.* 1978, White *et al.* 1982) and compares all possible models among themselves and indicates which of the models best fits the data (models are ranked from 0 to 1, with 1 indicating best fit). Model M_h ranked among the best models in all the population estimates we performed with CAPTURE in this study, with values of ≥ 0.78 . M_h assumes heterogeneity among individuals in their capture probabilities and is adequate in most situations due to behavioural differences among individuals, their unequal access to stations and because it is robust to departures from the model (Karanth & Nichols 1998, 2002). Here we report the results of model M_h using the Jack-knife estimator.

To estimate ocelot densities we followed the methodology described by Maffei *et al.* (2005), Silver *et al.* (2004) and Soisalo & Cavalcanti (2006). CAPTURE provides an estimate of the population present in the area. To estimate the density of animals it is necessary to calculate the area effectively sampled. This is usually estimated by applying a buffer to each sampling station equivalent to half of the mean maximum distance of recaptures (MMDM) for the individuals recorded at two or more stations (Karanth & Nichols 1998, 2002; Maffei *et al.* 2004, 2005). However, Soisalo & Cavalcanti (2006) and Trolle & Kéry (2005) suggest that half of MMDM underestimates the actual buffer and suggest using MMDM instead. Where estimates of home-range size based on radio-telemetry studies are available they should be used as the buffer (Soisalo &

Cavalcanti 2006). We provide three density estimates for each study site or area corresponding to the three different buffers used to calculate the effectively sampled area: (1) 0.5 MMDM, (2) MMDM and (3) the radius of the mean home range of this ocelot population estimated with radio-telemetry by Crawshaw (1995). We used program ArcView 3.2 to build a GIS of the study sites and estimate MMDM and the effectively sampled areas.

The study of factors that affect ocelot densities at a continental scale

We obtained data on ocelot densities, latitude and mean annual rainfall across study sites from published sources and unpublished data requested from researchers (Appendix 1). When more than one study was conducted in the same ecoregion (Olson *et al.* 2001) or within the same conservation unit (but in different ecoregions, Figure 2), we used mean values per regional set of studies (the mean values were obtained for the Upper Paraná Atlantic Forest ecoregion, the Pantanal ecoregion, the Chiquibul Forest Reserve and National Park, Belize, and for the Kaa–Iya National Park, Bolivia) to test for a linear relationship between the \ln (ocelot densities) on rainfall and latitude (using simple and multiple least-squares regression). Since different studies used different methodologies to estimate ocelot densities, we also tested, with the whole data set, if there was an effect of sampling method (camera-traps vs. radio-telemetry studies) on the \ln (density), using latitude as a covariate in an ANCOVA model. We also used a similar ANCOVA to explore if study sites located in the northern hemisphere showed a different latitudinal effect on \ln (ocelot densities) from those located in the southern hemisphere.

We performed the statistical analyses with program JMP (3.2.2, SAS Institute). Densities and distances were transformed to their natural logarithms for statistical analyses. We used parametric (ANOVA, least-squares simple and multiple linear regression, Pearson's correlation and ANCOVA) or non-parametric (Kruskal–Wallis two-sample comparisons) statistical tests depending on whether the data comply with the assumptions required for the former (normal distribution and homoscedasticity of variances). We set a probability level to commit an alpha error to 0.05.

RESULTS

Patterns of abundance at a local scale

At Yabotí, there was a mean (\pm SD) of 2.89 ± 3.28 ocelot records per station during the survey (range 0–17) and a mean of 1.48 ± 1.27 individuals were recorded per station

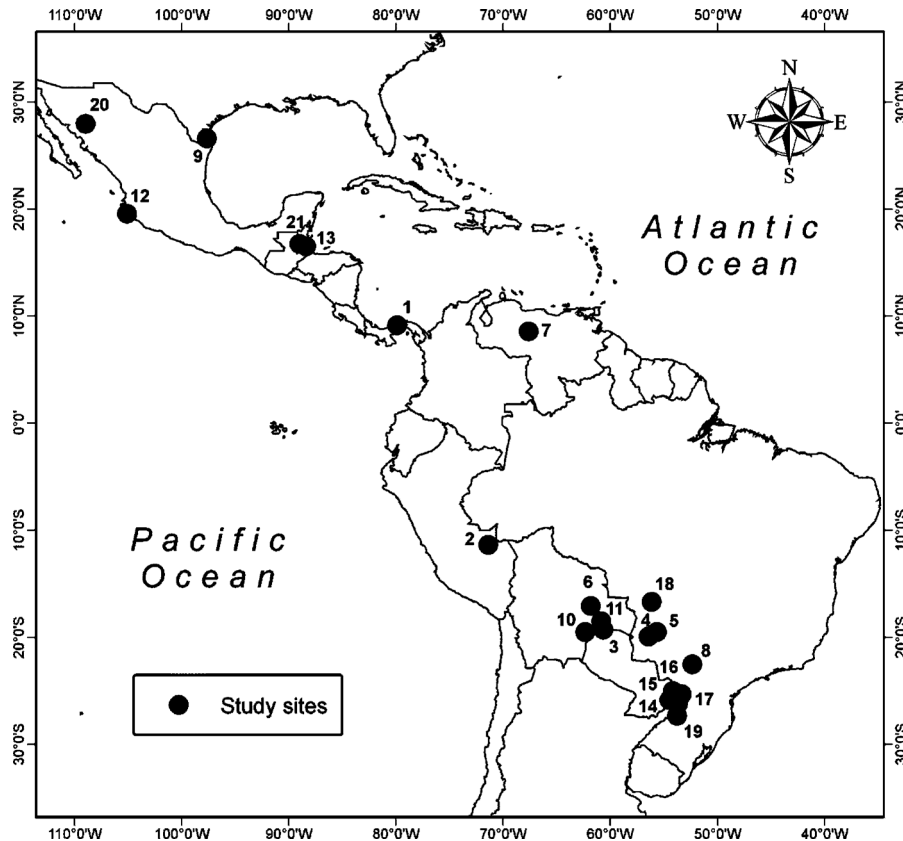


Figure 2. Location of the study sites for which ocelot density estimates have been reported in the literature. The numbers of the study sites correspond to those in Appendix 1.

(range 0–5, $N = 42$ stations). The frequency of records per station was three times higher in stations located in the sector of Yabotí with lower disturbance than in the portion with higher disturbance (Kruskal–Wallis two-sample test using the normal approximation, $Z = -3.03$, $P = 0.002$, Figure 3a). Similarly, the number of individuals recorded in stations located in the portion of the surveyed area with lower disturbance was more than twice as high than in the portion with higher disturbance (Kruskal–Wallis test, $Z = -3.09$, $P = 0.002$, Figure 3b).

At Iguazú, a mean of 4.15 ± 3.88 ocelot records was obtained per station (range 0–17) and a mean of 2.02 ± 1.48 individuals were recorded per station (range 0–5, $N = 47$). Stations located on trails had a lower frequency of ocelot records (mean \pm SD = 0.71 ± 0.99 , $N = 14$) than those located on roads (5.61 ± 3.73 , $N = 33$, Kruskal–Wallis test, $Z = -4.73$, $P < 0.0001$) and fewer individuals were recorded on trails (0.57 ± 0.85) than on roads (2.64 ± 1.25 , $Z = -4.57$, $P < 0.0001$). When excluding the stations located on trails, the frequency of records per station was more than three times as high in stations located in the sector of Iguazú with lower disturbance than in the portion with higher disturbance (Kruskal–Wallis test, $Z = -3.93$, $P < 0.001$, Figure 3c). Similarly, the number of individuals recorded

in stations located in the portion of Iguazú with lower disturbance was twice as high as those in stations located in the sector with higher disturbance (Kruskal–Wallis test, $Z = -3.36$, $P = 0.0008$, Figure 3d).

Density estimates using radio-telemetry data lay between those estimated using MMDM and 0.5 MMDM (Table 1). Density estimates (\pm SE) for the whole area surveyed at Yabotí ranged from 4.73 ± 0.53 ocelots per 100 km^2 to 8.64 ± 1.00 individuals per 100 km^2 (Table 1). The ocelot density estimates (\pm SE) for Iguazú were higher than those for Yabotí, ranging from 10.2 ± 1.21 individuals per 100 km^2 to 16.7 ± 2.12 individuals per 100 km^2 (Table 1). Both at Yabotí and at Iguazú density estimates were twice as high in the sub-areas with lower disturbance than in the portions with higher disturbance (Table 1).

Patterns of abundance at a continental scale

There was a positive linear relationship between mean rainfall and the $\ln(\text{mean ocelot density})$ ($R^2 = 0.32$, $F_{1,8} = 3.82$, $P = 0.043$, one-tailed test, Figure 4a). Ocelot density decreases with latitude ($R^2 = 0.50$, $F_{1,8} = 8.09$, $P = 0.011$, one-tailed test, Figure 4b). A multiple

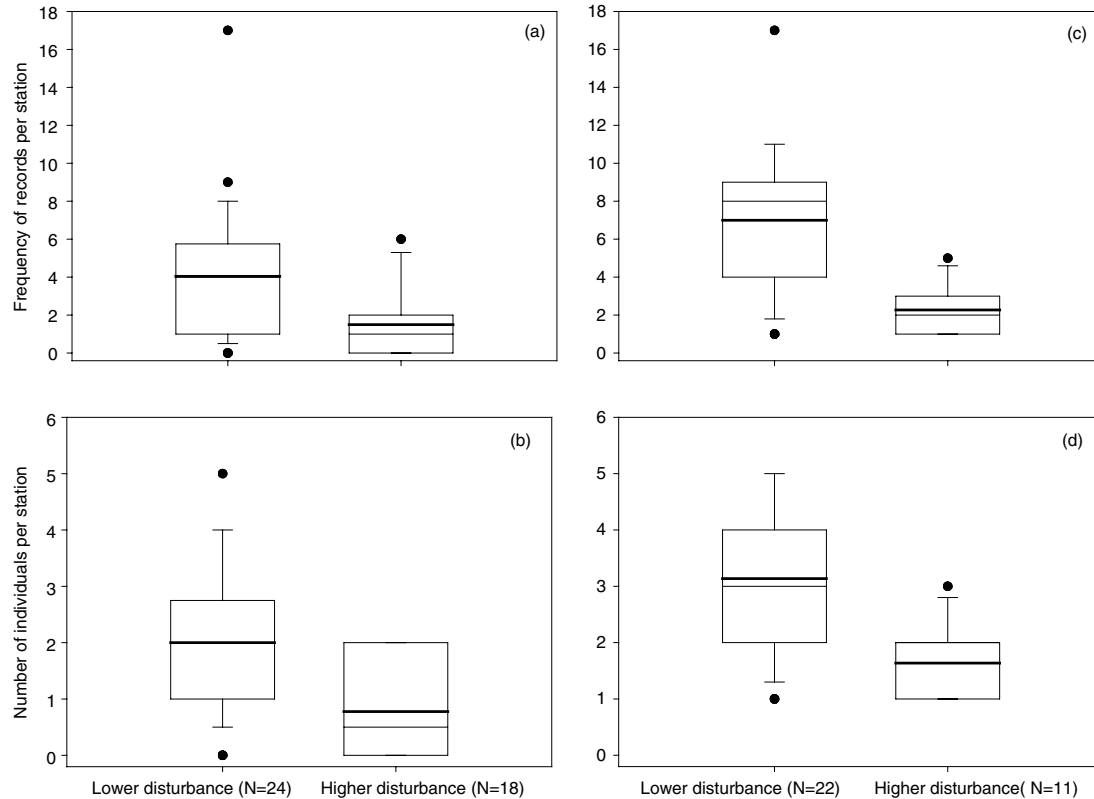


Figure 3. Box plots for: the frequency of records per station in the sector with lower relative disturbance and in the portion with higher relative disturbance of Yabotí Biosphere Reserve (a), the number of individuals recorded in stations located in the portion with lower disturbance and in the portion with higher disturbance of Yabotí Biosphere Reserve (b), the frequency of records in stations located in the sub-area with lower relative disturbance of Iguazú study site (excluding those located in trails opened with machete) and in stations located in the portion with higher relative disturbance (c) and the number of individuals recorded in stations located in the portion of Iguazú with lower disturbance and in the sector with higher disturbance (d). The ends of the box identify the 25% quartiles and the whiskers extend to the extreme values within 1.5 times the spread of the 25% quartile. The thin horizontal line within the box represents the median and the thicker one the mean. The dots outside the range of the whiskers represent outliers.

regression of the $\ln(\text{ocelot density})$ on rainfall and latitude shows no statistical effect of either variable and no interaction between them (whole model test: $R^2 = 0.54$, $F_{3,6} = 2.36$, $P = 0.171$; effect of latitude: $F_{1,6} = 0.13$, $P = 0.738$; effect of rainfall: $F_{1,6} = 0.47$, $P = 0.518$; interaction term: $F_{1,6} = 0.28$, $P = 0.614$), but this is no surprise given the strong collinearity between rainfall and latitude (Pearson's product-moment correlation coefficient $r = -0.665$, $df = 8$, $P < 0.05$, two-tailed test) and the few degrees of freedom available.

There was no effect of the methodology used to estimate density, whether tested alone (ANOVA, $R^2 = 0.07$, $F_{1,18} = 1.39$, $P = 0.254$) or with latitude as a covariate (whole model test: $R^2 = 0.24$, $F_{3,16} = 1.68$, $P = 0.212$; effect of latitude: $F_{1,16} = 2.96$, $P = 0.052$, effect of method: $F_{1,16} = 0.00$, $P = 0.984$; interaction term: $F_{1,16} = 0.04$, $P = 0.844$). There was no effect of the hemisphere where the study was conducted (north vs. south) on ocelot density, whether the effect was tested alone ($R^2 = 0.01$, $F_{1,19} = 0.27$, $P = 0.610$), or with latitude as a covariate (whole model test: $R^2 = 0.35$, $F_{3,17} = 3.08$,

$P = 0.055$; effect of latitude: $F_{1,17} = 8.89$, $P = 0.004$, effect of hemisphere: $F_{1,17} = 0.56$, $P = 0.464$; interaction term: $F_{1,17} = 0.14$, $P = 0.713$).

DISCUSSION

Patterns of abundance at a local scale

Ocelot density estimates for the Green Corridor of Misiones are at the lower end for the species, ranging from as low as 4.96 ± 1.33 individuals per 100 km^2 in the areas of Yabotí with higher relative disturbance to 17.6 ± 2.25 individuals per 100 km^2 in the Iguazú National Park (sub-area with lower relative disturbance). The ocelot density estimates for Yabotí, especially in the portions of the study site with higher disturbance, are similar to those observed in marginal areas, such as the scrublands and Sinaloan dry forests of Sonora in north-west Mexico (López González *et al.* 2003) and Belizean pine forests in Belize (Dillon 2005, Dillon & Kelly in press).

Table 1. Population and density estimates (mean \pm SE) for ocelots at Yabotí Biosphere Reserve and Iguazú National Park, Misiones, Argentina using three different buffers to estimate the effectively sampled area: (1) 0.5 MMDM (half of the mean maximum distance of recapture for individuals recorded at > 1 sampling stations), (2) MMDM (the mean maximum distance of recapture), and (3) the radius of a circle with an area equivalent to the mean home range based on Crawshaw's (1995) radio-telemetry study and using the minimum convex polygon method (radius = 2.63 ± 1.03 km, N = 14 adult individuals). The mean (\pm SD) MMDM at Yabotí was 4.34 ± 2.96 km (N = 22 individuals) and at Iguazú was 4.67 ± 4.06 km (N = 20 individuals).

Area and buffer	Relative intensity of logging and poaching	Number of individuals recorded	Population estimate from CAPTURE (model M_H)	95% confidence interval for population	Effectively sampled area (km ²)	Density (individuals per 100 km ²)
0.5 MMDM						
Yabotí (whole area)	High	33	39 \pm 4.3	35–54	451 \pm 17.1	8.6 \pm 1.0
Yabotí (lower disturbance)	Medium	24	26 \pm 3.2	25–42	241 \pm 12.5	10.8 \pm 1.4
Yabotí (higher disturbance)	Very high	10	12 \pm 3.2	11–27	206 \pm 11.6	5.8 \pm 1.6
Iguazú (whole area)	Low	65	86 \pm 9.0	75–111	513 \pm 36.5	16.8 \pm 2.1
Iguazú (lower disturbance)	Very low	54	72 \pm 8.8	61–98	381 \pm 19.5	18.9 \pm 2.5
Iguazú (higher disturbance)	Medium	11	12 \pm 2.8	12–29	122 \pm 23.2	9.8 \pm 3.0
MMDM						
Yabotí (whole area)	High	33	39 \pm 4.3	35–54	825 \pm 23.2	4.7 \pm 0.5
Yabotí (lower disturbance)	Medium	24	26 \pm 3.2	25–42	442 \pm 16.8	5.9 \pm 0.8
Yabotí (higher disturbance)	Very high	10	12 \pm 3.2	11–27	411 \pm 16.2	2.9 \pm 0.8
Iguazú (whole area)	Low	65	86 \pm 9.0	75–111	843 \pm 46.8	10.2 \pm 1.2
Iguazú (lower disturbance)	Very low	54	72 \pm 8.8	61–98	607 \pm 24.7	11.9 \pm 1.5
Iguazú (higher disturbance)	Medium	11	12 \pm 2.8	12–29	253 \pm 33.5	4.7 \pm 1.3
Radio-telemetry						
Yabotí (whole area)	High	33	39 \pm 4.3	35–54	549 \pm 18.7	7.1 \pm 0.8
Yabotí (lower disturbance)	Medium	24	26 \pm 3.2	25–42	289 \pm 13.6	9.0 \pm 1.2
Yabotí (higher disturbance)	Very high	10	12 \pm 3.2	11–27	242 \pm 12.4	5.0 \pm 1.3
Iguazú (whole area)	Low	65	86 \pm 9.0	75–111	566 \pm 19.0	15.2 \pm 1.7
Iguazú (lower disturbance)	Very low	54	72 \pm 8.8	61–98	409 \pm 16.1	17.6 \pm 2.3
Iguazú (higher disturbance)	Medium	11	12 \pm 2.8	12–29	158 \pm 10.0	7.6 \pm 1.9

Density estimates for the portion of Iguazú with lower disturbance are similar to those previously obtained by Crawshaw (1995) using radio-telemetry and our previous estimate for the same area (Di Bitetti *et al.* 2006a) and could be considered typical for the Upper Paraná Atlantic Forest in areas where anthropogenic effects are low.

At both study sites, the mean frequency of records per station, the mean number of individuals per station and the densities were two to three times higher in the portions of the study areas with lower relative disturbance, which indicates that ocelot abundance is negatively affected by anthropogenic effects. However, we cannot disentangle the effect of logging from that of poaching, and it is difficult

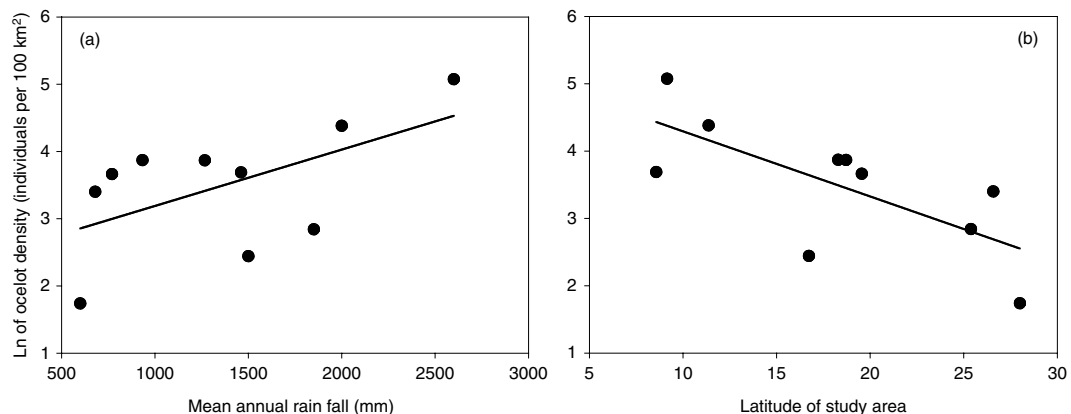


Figure 4. Relationship between the natural logarithm of mean ocelot density and mean annual rainfall (a) and mean latitude (b) for the main ecoregions or study areas where ocelot densities have been estimated. Regression equations for these linear relationships are: (a) $\ln(\text{density}) = 2.35 + 0.00084$ mean annual rainfall ($R^2 = 0.32$, $F_{1,8} = 3.82$, $P = 0.043$, one-tailed test), (b) $\ln(\text{density}) = 5.26 - 0.097$ latitude ($R^2 = 0.50$, $F_{1,8} = 8.09$, $P = 0.011$, one-tailed test).

to assess the direct and the indirect effects that these factors may have on ocelots. Several lines of evidence suggest that changes in the structure of the forests associated with logging activities and partial habitat replacement, independently of poaching, negatively affect the abundance of ocelots. First, at the Urugua-í study site in Misiones, ocelot relative abundance was higher in areas with relatively high poaching but no recent logging than in areas of relatively low poaching pressure but where the native forest was partially converted into pine plantations (Di Bitetti *et al.* 2006a). Similarly, the relative abundance of ocelots in the three stations located in the Brazilian side of Iguazú National Park was similar to that observed in the Argentinean portion of Iguazú National Park (with lower relative disturbance) and higher than in San Jorge Forest Reserve (also an area of higher relative disturbance), despite the high poaching pressure in Brazil but the absence of logging in the area. These patterns suggest that habitat disturbance in the form of intense logging or partial habitat conversion may have a stronger effect on ocelot abundance than poaching. In South-East Asian forests, some felids seem to be negatively affected by logging, but evidence on the contrary also exists (Meijaard *et al.* 2005), which suggest that we are not yet in a condition to generalize and extrapolate our results to other cat species. However, poaching may also affect ocelot densities directly, because hunters may occasionally kill this cat, or indirectly, because they may deplete their prey base, since ocelots are known to occasionally include in their diets peccaries, brocket deer, pacas and agoutis (Sunquist & Sunquist 2002), species that are locally hunted. Poaching with the aid of dogs, a practice very common in the area, may particularly affect ocelots, since the escape response of this cat to the chasing dogs is to climb to a tree where it is easily shot by hunters. Thus, both logging and poaching may be contributing to the patterns of ocelot abundance observed, but their relative contribution still needs to be assessed. Ocelot abundance in the Green Corridor co-varies with that of jaguars and pumas (Di Bitetti *et al.* unpubl. data), which suggests that predation by or competition with them has no strong effect on this ocelot population but rather, that they are being affected by similar factors.

Patterns of abundance at a continental scale

Reported ocelot densities across the distribution of the species range from as low as 3 individuals per 100 km² in the tropical pine forests of Belize to 160 individuals per 100 km² in Barro Colorado Island (Appendix 1). Several authors have noted that ocelots occupy a wide diversity of habitat types, ranging from scrublands to tropical rain forests. What all these habitats have in common is a well-structured vegetation cover (Emmons 1988, Emmons *et al.* 1989, Sunquist & Sunquist 2002).

Ocelot densities have been estimated under a relatively wide range of environmental conditions, with an annual rainfall range of 500–2600 mm y⁻¹, and spanning 54.5 degrees of latitude on both sides of the Equator (Appendix 1, Figure 2). Primary production should set the limit to the abundance of prey and thus to the carrying capacity and abundance of most wild cat populations (Carbone & Gittleman 2002, Karanth & Nichols 2002). Nilsen *et al.* (2005) found a negative relationship between primary productivity and territory size in a range of carnivore species and Herfindal *et al.* (2005) found a similar pattern in the Eurasian lynx (*Lynx lynx*). These authors explain these relationships as a result of increased prey densities with increased productivity. In fact, Hetherington & Gorman (2007) have recently shown that prey density directly determines the density of the Eurasian lynx.

Thus, we expect to find a positive relationship between primary productivity and ocelot density across its distributional range. Rainfall and latitude are in general correlated (positively the former and negatively the latter) with productivity (Sandell 1989). The relationship with rainfall is due to the fact that water is usually a limiting factor for plants in most terrestrial ecosystems. Similarly, the total availability of photosynthetically active radiation, usually a limiting factor for plants, and the mean temperature of a site, which affects plant physiology, are usually positively correlated with primary productivity and decrease with latitude (Prince & Goward 1995). However, temperature also increases evapotranspiration and may create a water deficit for plants and thus, its relationship with productivity is not so simple. Maffei *et al.* (2005) first suggested that ocelot densities are positively correlated with mean annual rainfall, but the few data points available did not render a statistically significant result. We found that ocelot densities increase with rainfall and decrease with the latitude of the study site. Some authors have suggested that latitude is not a good predictor of productivity and should not be able to predict territory size of wild cats (Herfindal *et al.* 2005, Nilsen *et al.* 2005). However, given the wide distribution of the ocelot across both sides of the equator we tentatively suggest that the relationship observed is due to the general pattern of decreasing primary productivity with latitude, a relationship that seems to be similar in both hemispheres. However, it remains possible that higher frequency of human impacts occurring in study sites located at higher latitudes may have contributed to this trend. To test this possibility we need a standardized, ideally quantitative, measure of human impacts across study sites.

Patterns of abundance in other neotropical wild cats

Jaguar and puma have extremely low densities in Misiones, mostly as a result of habitat conversion, poaching and the systematic elimination of 'problem'

animals (Di Bitetti *et al.* 2006b, Kelly *et al.* in press, Paviolo *et al.* in press). The co-variation of their abundance with that of the ocelot in the Green Corridor of Misiones (Paviolo *et al.* in press) suggests that they may be affected by similar factors, but this cannot be extrapolated to the smaller cats and other carnivores.

Interspecific interactions among cat species, mainly in the form of food competition (Caro & Stoner 2003, Dayan & Simberloff 2005) and intra-guild killing (Donadio & Buskirk 2006), may also affect the abundance of some species. It is possible that at a local scale the population densities of the smaller cats and other small carnivores are mostly affected by those of the larger cats, something that has been amply documented in Palaearctic and Palaeotropical carnivore communities (Caro & Stoner 2003, Crooks & Soulé 1999, Palomares *et al.* 1995, Rogers & Caro 1998). The ocelot is suspected to exert a strong negative effect on the smaller cat species living in sympatry (Oliveira *et al.* in press) through intra-guild killing (Donadio & Buskirk 2006). If this is the case, we predict a negative correlation between the abundance of the smaller cats with that of the ocelot. The ocelot may thus play a key ecological role as a top-down regulating force in the neotropical forests. Changes in its abundance may affect the populations of the smaller wild cats and produce a cascade of ecological effects that still need to be studied.

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Appendix 1. Study sites where ocelot studies have been conducted ordered by decreasing density. The numbers of the study sites correspond to those depicted in Figure 2. Ecoregions are classified following Olson *et al.* (2001).

Study site	Ecoregion	Rainfall (mm y ⁻¹)	Latitude	Density (individuals per 100 km ²)	Source
1 Barro Colorado Island, Panamá	Isthmian-Atlantic moist forests	2600	9° 09' N	160	Ricardo Moreno (pers. comm., 2006)
2 Manú National Park, Perú	Southwest Amazon moist forests	2000	11° 22' S	80	Emmons (1988)
3 Miranda Ranch, Mato Grosso do Sul, Brazil	Pantanal	1213	19° 57' S	76	Crawshaw (1995)
4 Ravelo, Kaa-Iya del Gran Chaco National Park, Bolivia	Transitional Chaco-Chiquitano dry forests	800	19° 17' S	59	Maffei <i>et al.</i> (2005)
5 Research and Conservation Reserve, UNIDERP, Brazil	Pantanal	1213	19° 30' S	56.4	Trolle & Kéry (2003)
6 San Miguelito, Kaa-Iya del Gran Chaco National Park, Bolivia	Transitional Chaco-Chiquitano dry forests	1200	17° 05' S	56	Maffei <i>et al.</i> (2005)
7 Hato Masaguaral and Hato Flores Moradas, Venezuela	Llanos	1461	8° 34' N	40	Ludlow & Sunquist (1987); Sunquist <i>et al.</i> (1989)
8 Morro do Diabo State Park, Brazil	Upper Paraná Atlantic Forest	1347	22° 22' S	31	Jacob (2002)
9 Yturria Ranch, Willacy County, Texas	Western Gulf coastal grasslands	680	26° 35' N	30	Haines <i>et al.</i> (2006b)
10 Cerro Cortado, Kaa-Iya National Park, Bolivia	Chaco dry forest	500	19° 31' S	29.5	Maffei <i>et al.</i> (2005)
11 Tucavaca, Kaa-Iya National Park, Bolivia	Transitional Chaco-Chiquitano dry forests	800	18° 31' S	29	Maffei <i>et al.</i> (2005)
12 Chamela-Cuixmala, Jalisco, México	Central American dry forest	770	19° 33' N	39	Fernandez (2002, pers. comm.)
13 Chiquibul Forest Reserve and National Park, Belize	Petén-Veracruz moist forests	1500	16° 44' N	25.9	Dillon (2005), Dillon & Kelly (in press)
14 Iguazú National Park, Argentina	Upper Paraná Atlantic Forest	1919	25° 40' S	19.9	Di Bitetti <i>et al.</i> (2006a)
15 Iguazú National Parks of Argentina and Brazil and San Jorge Forest Reserve	Upper Paraná Atlantic Forest	1919	25° 45' S	16.8	This study
16 Iguazú National Parks, Brazil and Argentina	Upper Paraná Atlantic Forest	1919	25° 38' S	13.7	Crawshaw (1995)
17 Urugua-i, Argentina	Upper Paraná Atlantic Forest	1900	25° 58' S	12.9	Di Bitetti <i>et al.</i> (2006a)
18 Estância Ecológica SESC Pantanal, Brazil	Pantanal Flooded Savannas	1375	16° 42' S	11.2	Trolle & Kéry (2005)
19 Yabotí Biosphere Reserve, Argentina	Upper Paraná Atlantic Forest	2100	26° 55' S	8.6	This study
20 Sonora, México	Sinaloan dry forests	600	Approx. 28° N	5.7	López González <i>et al.</i> (2003)
21 Chiquibul Forest Reserve and National Park, Belize	Belizean pine forest	1500	16° 44' N	3.1	Dillon (2005), Dillon & Kelly (in press)