Importance of riparian forest corridors for the ocelot in agricultural landscapes

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Worldwide, private lands have attracted increased attention from conservationists, not only because most of the globe is privately owned, but also because private lands can be an asset to the protected area conservation strategy. In Brazil, the riverine Areas of Permanent Protection (APPs) are a key instrument of the Forest Code to protect biodiversity on private lands, acting as wildlife corridors. We assessed this putative role of APPs by evaluating how ocelot (*Leopardus pardalis*) occurrence is influenced by covariates in 3 cerrado landscapes dominated by sugarcane and managed forests of eucalyptus and pine trees. We collected detection–nondetection data by camera trapping during 2 dry seasons (2013 and 2014) at 208 stations (6,606 camera-days). We estimated ocelot detection and mean relative abundance using a single-species, single-season occupancy model that accounts for heterogeneous detection probability induced by variation in abundance. Modeling results showed that percentage of native forest was the most important covariate to explain mean relative abundance of ocelots. This parameter was also affected positively by APPs, with ocelots being more abundant inside than outside APPs and, unexpectedly, by sugarcane. Given our study design, however, the positive effect of this crop likely reflects the contact zone between sugarcane and native forest. Our findings show that landscape composition affects ocelot abundance and highlight the importance of APPs and Legal Reserves in agricultural landscapes. We conclude that, in such landscapes, compliance to the Forest Code by private land owners is key to supporting ocelot occurrence.

As terras privadas vem atraindo cada vez mais a atenção dos conservacionistas mundialmente, não apenas porque ocupam a maior parte do globo, mas também como aliadas da estratégia de conservação de áreas protegidas. No Brasil, as Áreas de Preservação Permanente (APPs) ripárias são um instrumento fundamental do Código Florestal para proteger a biodiversidade em áreas privadas, pois agem como corredores biológicos. A fim de avaliar esse papel das APPs, nós analisamos como a ocorrência da jaguatirica (*Leopardus pardalis*) é influenciada pelas APPs e por outras covariáveis em 3 paisagens de cerrado dominadas por plantações de cana-de-açúcar e silvicultura de eucalipto e *Pinus* ssp.. Nós coletamos dados de detecção/não-detecção por meio de armadilhamento fotográfico durante 2 estações secas (2013 e 2014) em 208 pontos (6606 câmera-dias). Nós estimamos a detecção e a abundância média relativa da jaguatirica com um modelo de ocupação espécie-única/estação-única, o qual considera que a heterogeneidade existente na probabilidade de detecção é gerada por variações na abundância. Os resultados da modelagem mostraram que a porcentagem de vegetação nativa foi a covariável mais importante para explicar a abundância média relativa da jaguatirica. Esse parâmetro também foi positivamente influenciado pelas APPs, sendo que a abundância desse felino foi maior dentro do que fora de APPs, e, inesperadamente, pela cana-de-açúcar. Contudo, em função do nosso delineamento amostral, o efeito positivo dessa cultura agrícola provavelmente reflete a zona de contato entre a cana e a floresta nativa. Nossos resultados mostram que

a composição da paisagem é determinante para a abundância desse felino e ressaltam a importância das APPs e Reservas Legais em uma matriz agrosilvicultural. Nós concluímos que, em paisagens como essas, o cumprimento do Código Florestal é fundamental para a ocorrência da jaguatirica.

Key words: Areas of Permanent Protection, camera trap, cerrado, environmental law, *Leopardus pardalis*, occupancy, private lands

The ocelot (*Leopardus pardalis*) is a medium-sized feline that occurs from Texas in the United States, through Central America, to northern Argentina, southern Brazil, and Uruguay (Paviolo et al. 2015). Despite being widely distributed, ocelots show preference for forested habitats or areas of dense vegetation cover, and avoid open areas where they may be detected by predators and prey (Emmons et al. 1989; Murray and Gardner 1997; Sunquist and Sunquist 2002; Harveson et al. 2004). Preference of ocelots for forested or densely vegetated habitat has been found in several different biomes. For example, in the Amazon, continuous forest was an important environmental feature for this species (Michalski and Peres 2005). In the Brazilian cerrado (scrub savannah), ocelots occurred more frequently in the most heavily wooded physiognomy (cerradão—Lyra-Jorge et al. 2009).

Habitat loss and fragmentation are currently the main threats to populations of this cat, a sensitive species due to its natural low density and large home ranges (Murray and Gardner 1997; Crooks 2002; Goulart et al. 2009; Vetter et al. 2011; Oliveira et al. 2013). Therefore, the increasing conversion of native habitats to agroecosystems in recent decades has led to concern about ocelot conservation (Victor 1978; IBGE 2010). While changes in composition and function of native habitats may result in local extinctions of some species, other species can persist under ecologically friendly strategies of cultivation (Miranda and Miranda 2004), or even benefit from them (De Vivo et al. 2011; Verdade et al. 2012). Agroecosystems usually have low species richness but high abundance of small mammals, which may increase food resources for some generalist predators (Gheler-Costa et al. 2012; Verdade et al. 2012). Because the ocelot is a generalist mesopredator, but is also dependent on dense vegetation cover, it is crucial to assess the ocelot's occurrence in agricultural landscapes, which will likely increase even further in order to feed the growing human population (Godfray et al. 2010).

Although the ocelot is classified as "Least Concern" by the IUCN, its populations are decreasing rangewide (Paviolo et al. 2015). In Brazil, this cat is not threatened nationally (ICMBio 2014); nevertheless, it is on the red list of several states, particularly in the most densely populated states of south and southeastern Brazil (Beisiegel 2009; Oliveira et al. 2013). One important conservation strategy for the ocelot is to improve or maintain connectivity of the landscape through the creation and conservation of forest corridors (Murray and Gardner 1997; Haines et al. 2006b). The use of corridors by *L. pardalis* has been reported in gallery forests, strips of dense brush (5–100 m wide), and in drainage systems (Ludlow and Sunquist 1987; Laack 1991; Sunquist 1992). Thus, implementation of the riverine Areas of Permanent Protection (APPs), a requirement of the Forest Code, appears to be a potential conservation strategy

for this cat in Brazil, since the role of APPs as forest corridors has been suggested and recognized for several taxa (Galetti et al. 2010; Metzger 2010; IPAM 2014). According to the Native Vegetation Protection Law (Brazilian Forest Code—Law Nº 12 651/2012—Brasil 2012), APPs are protected areas in rural properties with the aim of preserving biodiversity and improving gene flow, besides other roles related to water and soil protection. In theory, at least, the effective preservation of APPs would help dispersal of carnivores, particularly those that are more dependent on dense vegetation cover, such as the ocelot (Lopes and Mantovani 2005). Furthermore, APPs can benefit the ocelot by increasing the amount of potential habitat in the landscape.

Another legal instrument of the Native Vegetation Protection Law is the delimitation of Legal Reserves (LRs), which are native or restored areas located on private lands that aim to ensure sustainable use of natural resources while also contributing to biodiversity conservation (Law Number 12 651/2012—Brasil 2012). Despite the importance of this law, changes in the previous Brazilian Forest Code, with the approval of Law Nº 12 651/2012, reduced legal enforcement of reforestation (Guidotti et al. 2017), diminished protection of remnants, and allowed exploration of environmentally fragile areas (Garcia et al. 2016). These legal environmental setbacks increased the need to understand the importance of APPs and LRs to biodiversity, especially in areas of intensive agriculture, notably because we need biologically based information to properly evaluate the impact of those changes (IPAM 2014).

Here, we used camera trapping to assess the efficacy of conservation strategies represented by riparian corridors (APPs) and forest patches (LRs) on private properties in Brazil, investigating specifically, the degree of dependence of the ocelot on these native forests, and the role of other habitat and landscape features in ocelot occurrence. Our study areas are located in the southern limit of the cerrado biogeographic region in northeastern São Paulo state, Brazil, where the rural landscape is strongly dominated by intensive agriculture and managed forests. Few cerrado fragments are still present in this region, which is the main producer of ethanol and sugar, both from sugarcane, in Brazil (UNICA 2015). Therefore, we expected that APPs would have a vital role for the ocelot in these landscapes, where extensive monocultures of sugarcane and, to a lesser degree, *Eucalyptus* plantations, predominate. Our general prediction is that ocelots would be more abundant inside riparian APPs than outside these areas, and that the relative role of APPs would be higher in poorly forested landscapes than in more preserved ones.

MATERIALS AND METHODS

Study area.—Our study area is composed of 3 landscapes in the northeast of the state of São Paulo, Brazil (Fig. 1). The first
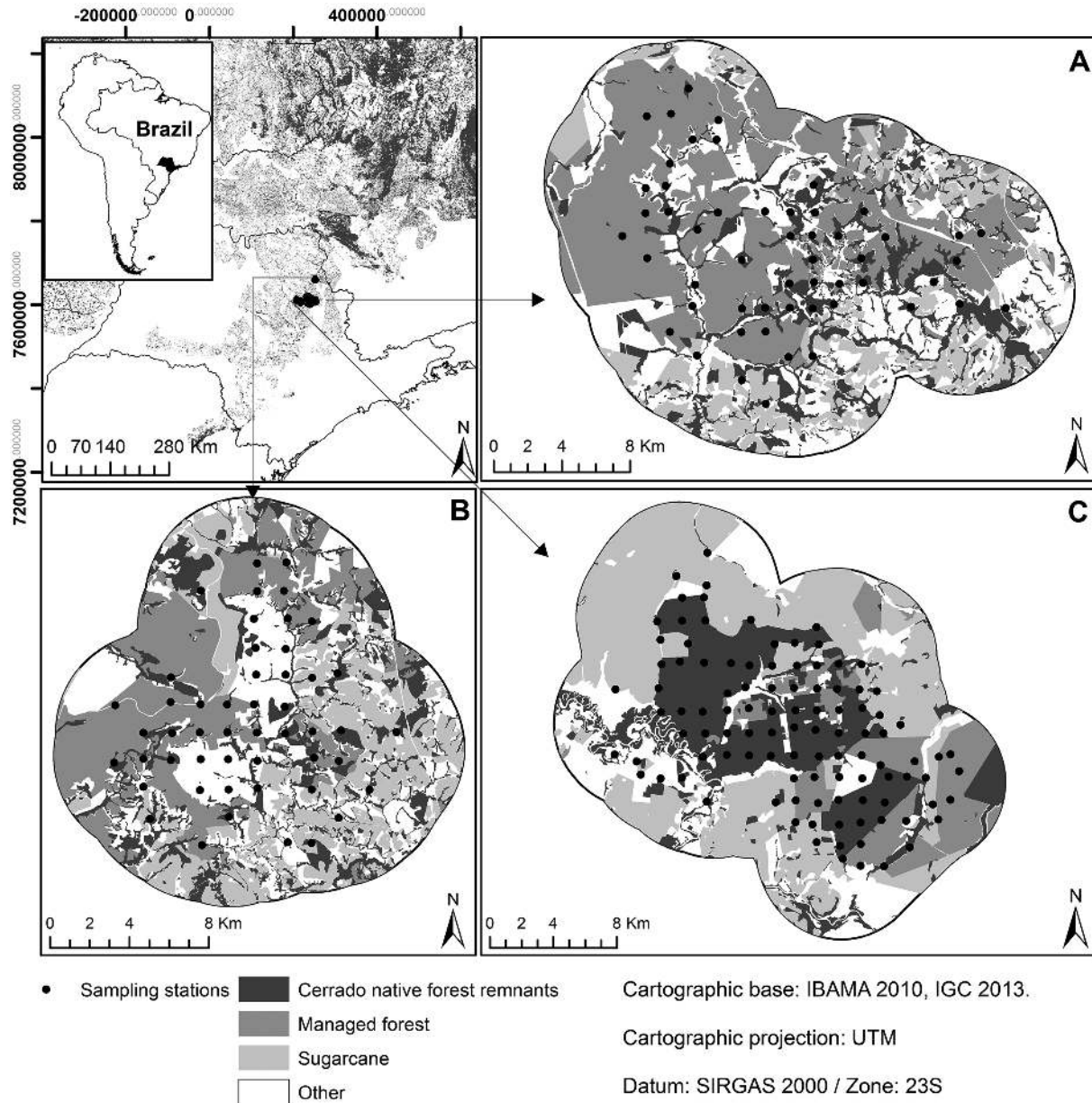
Fig. 1.—Study areas within the cerrado biogeographic region in the northeast of the state of São Paulo, Brazil, the configuration of the analyzed land-use types, and study design, showing the camera trap sampling stations (dots) distributed in a regular rectangular grid (200 ha). Landscape A: Cara Preta Farm (CPF) and surrounding area; Landscape B: Dois Córregos Farm (DCF), Cajuru State Forest (CSF), and surrounding area; Landscape C: Jataí Ecological Station (JES), Luis Antônio Experimental Station (LAES), and surrounding area.

landscape is composed of a protected area of integral protection (equivalent to category I of IUCN protected area categories— IUCN 2016) the Jataí Ecological Station (JES; 9,010 ha), as well as a protected area of sustainable use (equivalent to category VI of IUCN), the Luiz Antônio Experimental Station (LAES; 1,759 ha) and a 5-km-wide buffer surrounding the perimeter of these protected areas. This whole landscape (including the buffer) is mainly composed of sugarcane plantations (40.6%), native forests (27%; including cerradão, semideciduous, deciduous, and gallery forests), and managed forests (11%; including *Eucalyptus* spp. and *Pinus* spp. plantations). The second landscape, Cara Preta Farm (CPF) and its 5-km-wide buffer,

is 11 km from the first landscape and has 4,546 ha of native vegetation (mainly cerradão). *Eucalyptus* plantations are predominant (39.2%) in this landscape, followed by native forests (16.5%) and sugarcane (14%). The third landscape is located 54 km and 41 km from the first and second landscapes, respectively, and is composed of the Dois Córregos Farm (DCF; 2,017 ha), the Cajuru State Forest (CSF; 1,909 ha), a protected area of sustainable use (equivalent to IUCN category VI), and its 5-km-wide buffer. This landscape is covered by managed forests (24.9%), sugarcane (23.3%), and native forests (19.5%; mainly cerradão). Both CPF and DCF are private properties owned by the International Paper Company. APPs and LRs are

present in all study sites. All areas have a tropical humid climate, characterized by hot and wet summers and cold and dry winters. Mean annual rainfall and temperature are 1,684 mm and 22.7°C, respectively (Cianciaruso et al. 2006).

Study design and data collection.—We recorded the occurrence of ocelots with camera traps (Reconyx digital cameras, model HC 500; Reconyx, Holmen, Wisconsin) from April to September 2013 in the first study landscape and from April to September 2014 in the second and third landscapes. Sampling was restricted to only one season in each landscape in order to satisfy the closure assumption of occupancy models (no extinction or colonization of the study species at camera stations during the "sampling season"—Mackenzie et al. 2006).

We selected the locations to set camera traps (camera stations) by overlaying a grid of square cells (200 ha each or 1.4 × 1.4 km wide) over the study areas (Fig. 1). The center of each square was a potential point for sampling. Because the 5-km buffers are larger in extent than the area of the reserves, we sampled almost all potential points available within the perimeter of the reserves (some were discarded due to inaccessibility), but randomly selected an equivalent number of stations in the 5-km buffer area. A total of 208 camera stations were sampled, 105 in the first landscape (52 in the interior and 53 in the buffer), 53 in the second (26 in the interior and 27 in the buffer), and 50 in the third landscape (25 in the interior and 25 in the buffer).

If we were unable to access the exact location of the sampling point, we placed the camera station as close as possible to the originally selected site. Given logistical constraints (denial of entrance by some owners) and safety issues (exposure of equipment to damage and theft), all selected stations in sugarcane plantations or pasture were relocated to the nearest available native vegetation, where cameras were positioned to target the originally chosen land cover type (either sugarcane or pasture). The average distance between adjacent sampling points was 1,265.7 m (*SD* = 275.8 m) in the first landscape, 1,547.2 m (*SD* = 361.1 m) in the second landscape, and 1,460.2 m (*SD* = 335.8 m) in the third landscape.

Every month (April–September), 18 camera stations were established in the study area (and replaced in the next month). For each camera station, a single camera trap was fixed on a tree trunk 40–60 cm above the ground and programmed to operate continuously (24 h) during 30 consecutive days, recording date and time of each photograph. Due to some logistical problems (difficulty of access, rainfall, etc.), some cameras operated more or less than the programmed 30 days (minimum 17, maximum 40 days), but the average was 31.76 days/camera station. The total sampling effort was 6,606 trap-days.

Sampling stations within and outside APPs.—Camera stations were classified as located inside or outside an APP according to the legal definition present in the Brazilian Native Vegetation Protection Law (Law N° 12 651/2012). Thus, stations were considered inside an APP when located up to 30 m from small streams (up to 10 m wide); 50 m from small rivers (10–50 m wide); 100 m from larger rivers (50–200 m wide); 50 m from headsprings; 50 m from natural lakes (up to 20 ha of

surface area); 100 m from larger natural lakes (> 20 ha of surface), and within permanently flooded wetlands, which are part of a regular riverbed (Antunes 2013).

We classified the location of each camera station using predefined buffers over hydrologic maps of the state of São Paulo from Instituto Florestal with the geoprocessing software ArcMap 10.2.2 (ESRI 2002). In addition, using Google Earth, we analyzed stations that appeared to be closer to water during the fieldwork to confirm whether they were inside the legal limits for APPs.

Data analysis.—Because ocelots use the landscape differentially, preferring forested habitats or dense vegetation cover (Emmons et al. 1989; Murray and Gardner 1997; Sunquist and Sunquist 2002; Harveson et al. 2004), we believe that its abundance varies among sites. This variation in abundance causes differences in detection probabilities between sampling stations, being a source of heterogeneity in detection. Royle and Nichols (2003) developed a model of species occurrence that incorporates heterogeneous detection probabilities induced by variation in animal abundance that allows for extracting information about abundance from occupancy surveys (detection–nondetection data) without the need for marking individuals. We used the Royle and Nichols (2003) model (henceforth, "RN model") to analyze how APPs and other landscape covariates influence ocelot abundance. The RN model accommodates the effect of abundance on detection probability and allows the separation of variation in abundance among sampling stations from that in detection probabilities (equations 1 and 2 below).

The RN model has the following assumptions: 1) the population is closed during the sampling period (no births, deaths, colonization, extinction, or migration); 2) all individuals have the same probability of detection; and 3) the detection of an individual at a sampling station is independent of detection of other animals at that station. The method considers that the probability of detecting a species at a sampling station is conditional on abundance (N_i) (equation 1):

$$p_i = 1 - (1 - r_i)^{N_i} \qquad (1)$$

The parameter r_i is the individual-level probability of detection. That is, the probability that each individual is detected. According to equation 1, p increases with local (site) abundance and heterogeneity in site-level detection p_i can be modeled by assuming a parametric distribution for local abundance N_i. That is, we consider abundance as a random variable with probability distribution $\Pr(N = k) = f(N = k) = f_k$. A natural choice of abundance distribution f is the Poisson distribution, $N_i \sim$ Poisson (λ_i), which has probability mass function (PMF):

$$f_k = \frac{e^{-\lambda_i} \lambda_i^k}{k!} \qquad (2)$$

The parameter λ_i is the Poisson intensity parameter. Due to the relationship between p and N, f_k is also the density for a transformation of p_i. Hence, the model has 2 parameters to be estimated: r_i—intrinsic detection, and λ_i—the mean relative abundance per sampling station. The parameter lambda (λ_i) is

the mean of the Poisson distribution, and it can be regarded as the mean population size of individuals exposed to sampling by a camera trap. However, the effective sample area of a camera trap is unknown; therefore, it is not possible to interpret this parameter as absolute density (e.g., ocelots per ha).

Other sources of heterogeneity on detection probability can be modeled with the aid of explanatory covariates using link functions according to:

$$\text{logit}(r_i) = \beta_0 + \beta_{\text{covariate}} x_i \qquad (3)$$

$$\log(\lambda_i) = \sum_{j=1}^{p} x_{ij} \beta_j \qquad (4)$$

where β_0 is the intercept, $\beta_{\text{covariate}}$ is the effect of the covariate, and x_i is the value of the covariate at camera station i (Royle and Nichols 2003).

To analyze the influence of APPs and landscape features on ocelot detection and on their mean relative abundance, and to account for time and habitat variations, we modeled the effect of 12 site covariates on r_i (APP, degree of protection, native forest, sugarcane, managed forests of *Eucalyptus* spp. and *Pinus* spp., year, locale of the camera, distance from the nearest unpaved road, average temperature, total rainfall, average date, effort) and 5 site covariates on λ_i (APP, degree of protection, native forest, sugarcane, managed forests of *Eucalyptus* spp. and *Pinus* spp.), which are described in Table 1.

Correlation analyses (Spearman and Pearson) were performed to investigate collinearity between covariates in program R (R Development Core Team 2014). None of the covariates were highly correlated (correlation coefficients were < 0.6); therefore, we decided to keep all 12 covariates in the modeling.

Model selection was performed according to a 2-step process (Mackenzie et al. 2006). First, we modeled detection probability fixing λ at the global model (including all explanatory covariates as potential predictors of this parameter). We modeled the effect of each covariate for detection alone to choose the most explanatory variable and compared it to the null and the global model. Models were ranked using Akaike's Information Criterion (AIC—Burnham and Anderson 2002).

We then fixed the best model for detection and developed models for λ. All possible combinations of the 5 covariates for λ (additive effects) were included in the model set, up to a maximum of 5 explanatory covariates for λ per model. We also included pairwise interaction models between all pairs of covariates to investigate whether the effect of APPs and DP varied according to landscape composition, and if the effect of native forest, sugarcane, and managed forests depended upon the site being located inside or outside APPs and inside or outside protected areas. All of the models were fitted in program R with the package "unmarked" (Fiske and Chandler 2011).

We estimated the relative importance of each covariate by summing the Akaike weights (cumulative AIC_w) across all the models in the model set where each covariate occurred. The Akaike weight is the weight of evidence in favor of a given

Table 1.—Covariate name, description, range of values, and expected a priori relationships (positive or negative) with mean relative abundance (λ) and intrinsic detection (r) of ocelots (*Leopardus pardalis*) in cerrado landscapes, Brazil. Expected relationships were based on previous studies and on our own hypotheses. NA = covariate not evaluated for λ.

Covariates	Description	Range	Expected relationship with	
			λ	r
Area of Permanent Protection (APP)	Camera station outside APP (0) or inside APP (1)	0 or 1	+	+
Degree of protection (DP)	Camera station outside protected area (0) or inside protected area (1)	0 or 1	+	+
Native forest (NF)	Percentage (normalized) of native forest (semideciduous, deciduous, and gallery forest, and cerradão) in a 200-ha buffer around each camera station	−1.16 to 2.2	+	+
Sugarcane (C)	Percentage (normalized) of sugarcane in a 200-ha buffer around each camera station	−0.88 to 2.32	−	−
Managed forests of *Eucalyptus* spp. and *Pinus* spp. (EP)	Percentage (normalized) of managed forests (*Pinus* spp. and *Eucalyptus* spp. plantations) in a 200-ha buffer around each camera station	−0.59 to 5.15	−	−
Year	Year of sampling: 2013 (0), 2014 (1), to account for annual variation	0 or 1	NA	−
Locale	Locale of the camera: native forest (1), sugarcane (2), managed forests (3), others (4)	1 or 2 or 3 or 4	NA	1 (+); 2, 3, 4 (−)
Distance from the nearest unpaved road (DUR)	Distance (in meters, values normalized) of the camera station from the nearest unpaved road	−0.61 to 4.53	NA	−
Average temperature (Temp)	Average temperature (°C) during all the occasions of each camera station	−0.98 to 2.88	NA	−
Total rainfall (Rain)	Total rainfall (in millimeters, values normalized) during all the occasions of each camera station	−1.02 to 2.56	NA	−
Average date (Date)	Average Julian date for the sampling period of each sampling station beginning on our first sampling date of each year, to incorporate time variation	15.5 to 179.71	NA	+
Effort	Days of sampling of each sampling station, to account for differences in sampling effort	3 to 40	NA	+

model and is computed based on the ΔAIC of the given model in relation to the ΔAIC of all the models in the model set (Burnham and Anderson 2002).

To analyze whether APPs are being used differently by ocelots, we used λ estimates for each sampling station of the most explanatory model and compared values of the average mean relative abundance inside and outside APPs.

We used the parametric bootstrap approach based on 3 fit statistics: sum-of-squared errors, chi-square, and Freeman–Tukey, with 1,000 bootstrap resamples to evaluate the goodness-of-fit of the global model (the most parameterized model with all additive effects of covariates in λ and with the covariates of the best-ranked model for p) (Mackenzie and Bailey 2004; Fiske and Chandler 2011; Kéry and Royle 2016) in program R with the function *parboot* of the package "unmarked." The global model is considered an adequate description of the data, implying that there is no extra binomial variation (including, for example, spatial autocorrelation between sampling stations). If the P-values of the fit statistics are near 0, this suggests that the model does not adequately fit the data. We also estimated the overdispersion ratio (c-hat) that should be approximately 1 for a fitting model (Burnham and Anderson 2002). The P-values of the 3 estimated statistics were all distant from 0 and the c-hat of the global model was 0.62. Therefore, the goodness-of-fit analysis showed that the global model for λ adequately fit the data and may even suggest a slight overfitting (i.e., underdispersion).

RESULTS

We obtained 73 records of ocelots, which were located mostly in native forest (23 in cerradão, 12 in gallery forests, 7 in cerrado sensu stricto, and 6 in semideciduous forest), followed by regenerating areas (10), sugarcane (8), wetlands (4), and managed forests (3). The number of records in each land-use type did not occur proportionally to the extent of these types in the landscape (*G*-test with Williams correction = 44.24, *d.f.* = 12, $P < 0.0001$), indicating a preference for forested habitats.

Accordingly, percentage of native forest was by far the covariate with the highest relative importance in our models for

λ (cumulative AIC_w = 1.00), followed by percentage of sugarcane (0.79), location of sampled points in APPs (0.74), percentage of managed forest (0.34), and degree of protection (0.26).

The best-ranked model for mean relative abundance of ocelots (λ) was the one with the additive effects of percentage of native forest, APP, and percentage of sugarcane (Table 2; for the complete model ranks, see Supplementary Data SD1). As expected, both NF (Fig. 2A) and APP had a positive influence on λ (β_{NF} = 1.02, confidence interval [*CI*] = 0.65 to 1.39; β_{APP} = 0.73, *CI* = 0.05 to 1.4). The effect of percentage of sugarcane, on the other hand, was different from expected, also showing a positive influence on λ (β_C = 0.38, *CI* = 0.04 to 0.71; Fig. 2B).

Sampling-station-specific λ values of the best-ranked model showed that, on average, mean relative abundance of ocelots was higher inside APPs ($\lambda_{average\_APP}$ = 0.79 ± 0.16) than outside APPs ($\lambda_{average\_NAPP}$ = 0.47 ± 0.05).

The effect of managed forest of *Eucalyptus* spp. and *Pinus* spp. appeared in the 2nd best-ranked model together with the additive effects of NF, APP, and C, whereas the 3rd-ranked model included the additive effects of degree of protection, NF, APP, and C (Table 2). However, the influence of EP and DP on λ was weak and not conclusive, because the *CI*s of the beta coefficients overlapped zero (β_{EP} = 0.39, *CI* = −0.35 to 1.15; β_{DP} = −0.09, *CI* = −1.07 to 0.89).

The 2 best-ranked interaction models (Table 2) indicated that the effect of sugarcane and the effect of APP, respectively, on mean relative abundance of ocelots changed according to the amount of native forest in the landscape. However, interaction models did not explain mean relative abundance of ocelots well because, except for the interaction model between APP and EP, all of the other models ranked more poorly than the model with only the additive effect of the respective covariates (see Supplementary Data SD1).

The best-ranked model for r included the effect of distance from the nearest unpaved road (Table 3; for the complete model ranks, see Supplementary Data SD2). The estimated individual detection probability was r = 0.065. Ocelot detection probability was higher near unpaved roads, with higher sampling effort,

Table 2.—Model selection results for the best-ranked models (ΔAIC < 4) for mean relative abundance (λ) of ocelot (*Leopardus pardalis*). w_i = AIC weight; K = number of parameters. rDUR = the best-ranked model selected for ocelot individual sampling probability (r), which has the effect of the covariate distance from the nearest unpaved road (DUR). Covariates modeled for λ: APP = Area of Permanent Protection; C = quantity in hectares of sugarcane in a buffer of 200 ha; DP = degree of protection; EP = quantity in hectares of managed forests of *Eucalyptus* spp. and *Pinus* spp. in a buffer of 200 ha; NF = quantity in hectares of native forest in a buffer of 200 ha. λ(Gl) = global model, with the additive effect of all 5 covariates for λ.

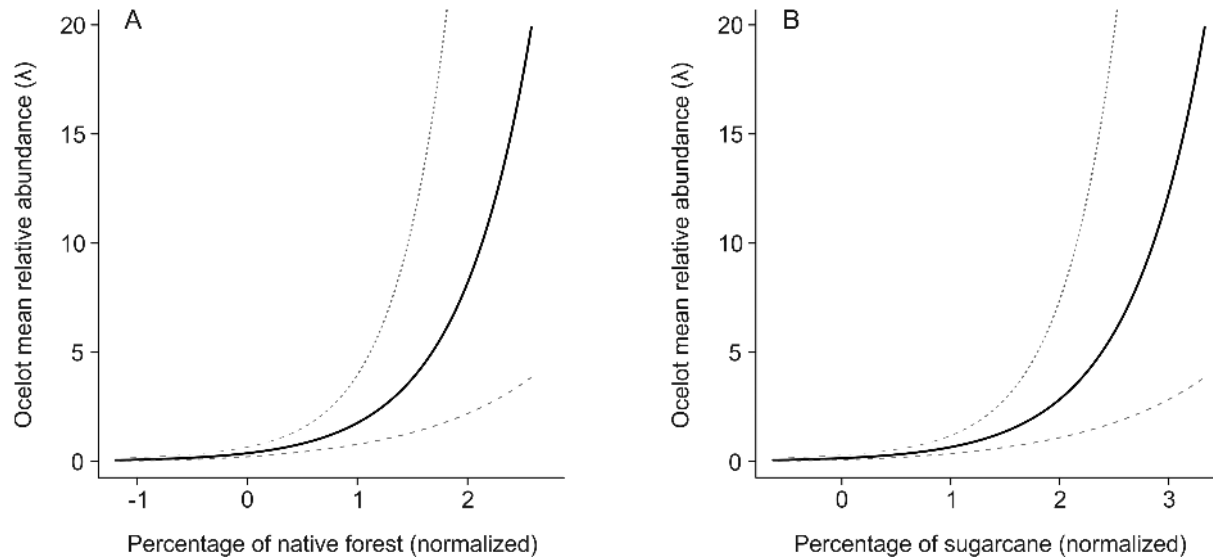| Model	ΔAIC	w_i	Cumulative weight	K	−Log likelihood
r(DUR), λ(NF + C + APP)	0.00	0.25	0.25	6	195.13
r(DUR), λ(NF + EP + C + APP)	0.87	0.16	0.41	7	194.57
r(DUR), λ(NF + C + DP + APP)	1.97	0.09	0.50	7	195.11
r(DUR), λ(NF + C)	2.14	0.09	0.59	5	197.20
r(DUR), λ(APP + NF)	2.72	0.06	0.65	5	197.49
r(DUR), λ(Gl)	2.87	0.06	0.71	8	194.56
r(DUR), λ(NF * C)	3.29	0.05	0.76	6	196.78
r(DUR), λ(NF + C + EP)	3.74	0.04	0.80	6	197.00
r(DUR), λ(APP * NF)	3.79	0.04	0.84	6	197.03
r(DUR), λ(NF + C + DP)	3.95	0.03	0.87	6	197.10

Fig. 2.—Effects of the covariates on mean relative abundance (λ) of ocelots (*Leopardus pardalis*) predicted by the best-ranked model, with the additive effects of native forest (A), sugarcane (B), and Area of Permanent Protection on λ (Table 2). Dashed lines indicate 95% *CI*s.

Table 3.—Model selection results for the best-ranked models (ΔAIC < 5) for individual sampling probability (*r*) of ocelots (*Leopardus pardalis*). w_i = AIC weight; *K* = number of parameters; Covariates analyzed for *r*: APP = Area of Permanent Protection; C = quantity in hectares of sugarcane in a buffer of 200 ha; Date = average Julian date for the sampling period; DP = degree of protection; DUR = distance from the nearest unpaved road; Effort = days of sampling; EP = quantity in hectares of managed forests of *Eucalyptus* spp. and *Pinus* spp. in a buffer of 200 ha; Local = local of the camera; NF = quantity in hectares of native forest in a buffer of 200 ha; Rain = total rainfall; Temp = mean temperature; Year = year of sampling. *r*(Gl) = global model, with the additive effect of all the 12 analyzed covariates for *r*. λ(Gl) is the global model for ocelot mean relative abundance, which has the additive effect of all the analyzed covariates for λ: APP, C, DP, EP, and NF.

Model	ΔAIC	w_i	Cumulative weight	K	−Log likelihood
r(DUR), λ(Gl)	0.00	0.88	0.88	8	194.56
r(Gl), λ(Gl)	4.09	0.11	1.00	21	183.61

at stations not located in managed forest of *Eucalyptus* spp. and *Pinus* spp., and in colder temperatures. The effects of APP, DP, NF, C, EP, year, rain, and date were not significant (see Supplementary Data SD3).

Discussion

Our results stress the fundamental importance of forested habitats for *L. pardalis*, not only because the percentage of native forest had a much stronger effect than all other covariates but also because this covariate influenced positively mean relative abundance of ocelots. The importance of forested habitats for this cat has been observed in other studies (Laack 1991; Emmons 1997; Murray and Gardner 1997; Sunquist and Sunquist 2002; Haines et al. 2006a; Lyra-Jorge et al. 2009). Ocelots need large areas of continuous forests or high-quality habitats (Di Bitteti et al. 2006; Massara et al. 2015; Nagy-Reis et al 2017), which are rare in fragmented landscapes such as ours.

Our modeling results also highlight the importance of APPs for ocelots, which may reflect, in part, the known preference of ocelots for gallery forests (Murray and Gardner 1997). In fact, gallery forests are known to be key areas for cerrado mammals in general, offering refuge, food resources, and acting as

corridors (Redford and Fonseca 1986). Indeed, the configuration and composition of our study landscapes may increase the importance of APPs as dispersal routes. According to Villard and Metzger (2014), corridors influence species more when the amount of habitat at the landscape scale is around 30%. If we pool all the most suitable land cover types for ocelots in our system (native forests, cerrado sensu stricto, regenerating areas, and wetlands), we get a similar figure, with native habitats covering about a third of the landscape (JES–LAES = 36.01%; CPF = 27.62%; DCF–CSF = 31.47%).

The presence of linear remnants such as APPs in fragmented landscapes increases connectivity and, consequently, increases gene flow between wild animal populations in general (Laurance and Laurance 1999; Lima and Gascon 1999; Galetti et al. 2010; Metzger 2010; IPAM 2014). Recent loss of habitat and increased isolation of ocelot populations in Texas seem to be the major proximate causes of the reduction in genetic variation (Janečka et al. 2014). In Brazil, Figueiredo et al. (2015) found evidence of a bottleneck in an ocelot population in the Interior Atlantic Forest resulting from isolation. These authors recommend conservation and restoration of riparian forests (APPs) and native woodland patches within private lands (LRs), as the most important management actions

to maintain the evolutionary potential of ocelots through persistence of gene flow, needed to ensure long-term conservation (Freeman and Herron 2009).

Whereas the positive effect of native forest and APP was expected, the positive influence of sugarcane on mean relative abundance of ocelots did not corroborate our initial hypothesis. Sugarcane may offer additional food resources for ocelots since some generalist rodents reach high abundance in plantations of this crop (Umetsu and Pardini 2007; Gheler-Costa et al. 2012). According to stable isotope analysis of ocelot hair, this cat is consuming prey that feed on crops such as sugarcane (M. Magioli, University of São Paulo, Piracicaba, pers. comm.). This finding stresses the need for more ecologically friendly agricultural techniques since the use of agrochemicals, fire, and machinery may injure or even kill ocelots that are using sugarcane as additional habitat.

The positive effect of sugarcane must be interpreted cautiously, however, because of a possible bias in our study design. To avoid damage or loss of camera traps, we could not install camera traps within sugarcane fields using, instead, the nearest contact zone between this plantation and native vegetation. Thus, all sampling stations located in sugarcane necessarily contained native forest in their 200-ha buffer. In addition, these contact zones invariably contained unpaved roads, which we used to position our cameras. (To facilitate agricultural practices, especially traffic of machinery, all contact zones between sugarcane and native forest were served by unpaved roads.) Ocelot detection probability was very high on unpaved roads, which carnivores are known to use for movement (Trolle and Kéry 2005; Di Bitetti et al. 2006; Srbek-Araujo and Chiarello 2013). We believe, therefore, that due to this restriction on placement of camera traps, the positive effect we detected for "sugarcane" might instead reflect the effect of the contact zone between this crop and native forests. Moreover, the positive influence of sugarcane on mean relative abundance of ocelots appeared in a model that has the additive effect of native forest and APP. This model represents a heterogeneous landscape with summed effects of native forest, APPs, and sugarcane plantations. If we look at the model where the sugarcane is the only covariate for occupancy, the effect of this covariate is weak (estimated beta coefficient with CI overlapping zero; see Supplementary Data SD3). Hence, we interpret this unexpected result as indicating that the ocelot might indeed occur in sugarcane, but only in the contact zone with native forest or when there is some native forest at the landscape level.

The degree of protection and managed forest had, in comparison with the other covariates, much weaker effects on the mean relative abundance of ocelots. These results might suggest that ocelots are not restricted to protected areas, which is understandable since this cat has large home ranges—up to 50 km² (Miranda et al. 2009) and 20 km² in our study area (Lopes and Mantovani 2005). Considering our results as a whole, the amount of native forest in the landscape (200-ha buffer scale) seems to be more important than whether this forest is a protected area or not. In other words, large governmental protected areas and small, privately protected areas such as LRs and APPs

are both important to ocelot occurrence. On the other hand, the weak effect of protected areas also suggests that protected areas might not differ from unprotected areas regarding either their effective protection against human conflicts or the abundance and diversity of prey species for ocelots. Although this is possible, this premise is not well-supported in the recent literature (Nagy-Reis et al 2017) and there is an absence of additional data on other aspects of ocelot ecology, particularly regarding population abundance, home range, and diet.

Notwithstanding the weak effect of managed forests, intrinsic detection (r) of ocelots was significantly lower in stations located in managed forests of *Eucalyptus* spp. and *Pinus* spp. than in native forest, as has been observed elsewhere (Lopes and Mantovani 2005; Di Bitetti et al. 2006; Haddad 2008; Lyra-Jorge et al. 2009; Dotta and Verdade 2011; but see Massara 2018 for a contrasting result). Lower detection in managed forests may be due to the absence of understory, or the presence of a drastically simplified understory, in our study managed forests. This important native vegetation layer increases structural complexity (Lindenmayer and Hobbs 2004), offers shelter and food (Oliveira 2002; Timo 2009), and decreases visibility. Hence, it is likely that the impact of managed forest on ocelots depends not only upon the adopted management practices, but also on landscape features (Massara et al. 2018).

Overall, our findings strengthen the relevance of considering the whole landscape, principally the amount of native vegetation and remnant connectivity, when planning conservation strategies. The existence of native forest located outside protected areas such as APPs and LRs is key for survival and movement of ocelots in landscapes with an agricultural matrix. Apart from wilderness areas such as the Amazon and Pantanal, existing protected areas in other main biomes of Brazil (Atlantic Forest and cerrado) have small ocelot populations (Massara et al. 2015). Hence, it is important to continue monitoring ocelot populations under the effective implementation of the Brazilian Native Vegetation Protection Law. The importance of this environmental law is evident because more than one-half (53%) of Brazilian native vegetation occurs on private properties (Soares-Filho et al. 2014).

Historically, the effective enforcement of Forest Code legislation has been weak. Almost half of the areas of APPs in Brazil are deforested (44 of 103 Mha—Sparovek et al. 2010). Moreover, the amount of protected area where restoration is mandatory was reduced, and intermittent springs and seasonally flooded areas are no longer protected with recent changes in this law (Law Nº 12 651/2012—Soares-Filho et al. 2014; Brancalion et al. 2016; Garcia et al. 2016). Considering the importance of APPs and LRs for biodiversity and ecological services (Metzger et al. 2010; Brancalion et al. 2016), these changes to the original Brazilian Native Vegetation Protection Law raise concern about future conservation and sustainable development. Studies such as ours present data-based arguments to help policy makers with their decisions. APPs and LRs can help to increase the total amount of habitat in the landscape and as such are crucial for conservation of the ocelot.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Model selection analysis for mean relative abundance (λ) ocelot (*Leopardus pardalis*). Model rank and the AIC, ΔAIC, AIC weight, cumulative weight, number of parameters, and −2 log likelihood of all models are presented.

Supplementary Data SD2.—Model selection analysis for individual sampling probability (*r*) ocelot (*Leopardus pardalis*). Model rank and the AIC, ΔAIC, AIC weight, cumulative weight, number of parameters, and −2 log likelihood of all models are presented.

Supplementary Data SD3.—Values of β for all covariates and their respective 95% confidence intervals estimated by model selection analysis for mean relative abundance (λ) and individual sampling probability (*r*) of ocelot (*Leopardus pardalis*).

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